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Assessing extinction risk from geographic distribution data in Neotropical freshwater fishes

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The IUCN Red List (RL) provides high-quality conservation assessments for individual species, yet the rate and scale of environmental deterioration globally challenges the conservation community to develop expedited methods for risk assessment. Here we compare threat assessments for 3,001 species of Neotropical freshwater fishes (NFF) in the IUCN–RL using readily accessible data types as proxies for extinction risk: geographic range, elevation, and species publication date. Furthermore, using geographic and taxonomic data alone, we generated preliminary conservation assessments for 2,334 NFF species currently awaiting IUCN assessment, identifying an additional 671 NFF species as potentially threatened. This number of potentially threatened species represents an increase of 59% over the number of species currently assigned to threat categories by the IUCN–RL. These results substantially expand the number of threatened NFF species from 422 currently on the IUCN RL to 1,093 species as threatened or potentially threatened, representing about 18% of all NFF species. Extinction risk is greater in species with smaller geographic ranges, which inhabit upland rivers, and which were described more recently. We propose the Central and Southern Andes, and Eastern Guiana Shield as priorities in the upcoming IUCN RL assessment of NFF species conservation risk.

Keywords: Biodiversity, Conservation status, Extent of Occurrence, IUCN Red List.

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A Lista Vermelha (IUCN) fornece avaliações precisas sobre status de conservação das espécies, porém a taxa e escala de deterioração ambiental desafia a comunidade conservacionista a desenvolver métodos rápidos para avaliações de riscos de extinção. Aqui, comparamos as avaliações da IUCN para 3.001 espécies de peixes dulcícolas neotropicais com dados facilmente acessíveis de risco de extinção: extensão de ocorrências, altitude e data de publicação das espécies. Além disso, usando apenas dados geográficos e taxonômicos, geramos avaliações preliminares de conservação para 2.334 espécies de peixes neotropicais aguardando avaliação da IUCN, e identificamos 671 espécies adicionais como potencialmente ameaçadas. Este número de espécies potencialmente ameaçadas representa um aumento de 59% em relação aquelas classificadas nas categorias de ameaça pela IUCN. Estes resultados expandem o número de espécies ameaçadas segundo a IUCN de 422 para 1.093 espécies ameaçadas ou potencialmente ameaçadas, representando cerca de 18% das espécies de peixes neotropicais. O risco de extinção é maior para espécies com distribuições geográficas restritas, que habitam rios de terras altas e que foram descritas mais recentemente. Sugerimos a região Central e Meridional do Andes e o Escudo das Guianas Orientais como prioridades para as próximas avaliações da IUCN sobre a conservação das espécies de peixes dulcícolas neotropicais.

Palavras-chave: Biodiversidade, Conservação, Extensão de Ocorrência, Lista Vermelha (IUCN).

INTRODUCTION

Continental freshwaters are home to vertebrate species density higher than most other ecosystems on Earth. Almost half of the world's fish species (about 14,750 of 35,700) are restricted to continental freshwater environments, including rivers, streams, springs, lakes, ponds, swamps, and wetlands, in a habitat volume that comprises less than 0.001% of the Earth's total water supply. Freshwaters are a renewable, yet a finite natural resource, being essential to maintain hydro-climatic regimes and almost all economic human activities (Dudgeon *et al*., 2006; Hoekstra, Mekonnen, 2012). Freshwater ecosystems are increasingly threatened worldwide, especially by the expansion of energy production (Finer, Jenkins, 2012), mining (Ferreira *et al*., 2014), aquaculture (Valladão *et al*., 2018), agriculture (Rosa *et al*., 2020) and urban landscapes (McKinney, 2006). Besides, freshwater environments are being depleted more quickly than their terrestrial counterparts (Albert *et al*., 2020a), and biodiversity losses are proportionately greater in freshwater than in terrestrial ecosystems (Turak *et al*., 2017). Fishes and amphibians are among the most threatened of all vertebrates, and their species richness and abundances are declining rapidly at regional and continental scales (Reid *et al*., 2019).

Freshwater ecosystems are unequally distributed across the Earth's surface, with c. 30% of the global river discharge flowing through Neotropical river basins. Neotropical freshwaters comprise continental waters of South America, Middle America, and the

Caribbean islands (Berra, 2007; Nelson *et al*., 2016). This vast realm encompasses a variety of aquatic environments, with distinct faunas adapted to torrential mountain rapids and cascades, upland rainforest rivers and streams, karstic and phreatic caverns, lowland floodplains, oxbow lakes, deep (to 100 m) river channels, and coastal rivers and estuaries (Albert *et al*., 2011a; Crampton, 2011). Those environments are distributed throughout the northern, central, and southern portions of the Andean cordilleras, Central America and the Greater Antilles, the upland Guiana and Brazilian shields, and the lowland Amazon, Orinoco and La Plata River basins. Each of those regions displays a heterogeneous combination of aquatic ecosystems, and a unique composition of fish species and local communities (*e.g*., Albert *et al*., 2020a).

Neotropical freshwater fishes (NFF) constitute the most species-rich vertebrate fauna on Earth (Fig. 1). With over 6,200 valid species (Albert *et al*., 2020b), the NFF species represent c. 30% of the world's continental fishes, or about 10% of all living vertebrates (Nelson *et al*., 2016). Dozens of new species are described each year (Fricke *et al*., 2020), such that total NFF species richness has been projected to exceed 9,000 species (Reis *et al*., 2016). As with most ichthyofauna, the remarkable NFF species diversity is unevenly distributed among higher taxa, with approximately 70% of the species concentrated within the two most species-rich of the 40 NFF taxonomic orders, and 95% in just the top five orders: Siluriformes (catfishes), Characiformes (tetras, piranhas and allies), Cyprinodontiformes (killifishes, rivulids, and allies), Cichliformes (cichlids), and Gymnotiformes (Neotropical electric fishes). Species richness is also unevenly distributed within taxonomic orders, with 60% of the species in the top five of the 97 NFF taxonomic families (van der Sleen, Albert, 2017; Dagosta, de Pinna, 2019). The phylogenetic diversity represented by these diverse NFF taxa is accompanied by an enormous diversity of functional traits, ecophysiological specializations for feeding and habitat utilization, reproductive modes, and life history strategies (Albert, Reis, 2011; Crampton, 2011; Toussaint *et al*., 2016).

The mega-diverse Neotropical ichthyofauna also has an uneven distribution of geographic range sizes in which most species have small ranges, and a few species have exceptionally widespread geographic ranges across multiple ecoregions (Albert *et al*., 2011b). In the Amazon, the largest hydrographic basin in the world, most fish species are not exclusive to a single drainage (Dagosta, de Pinna, 2019), corroborating the hypothesis that the NFF's biogeographical history is complex and that basins are historically composite (Dagosta, de Pinna, 2017). Range-restricted NFF species are usually limited to rugged upland regions with high topographic relief located towards the continental periphery (*e.g*., Andes, shields), while the more geographically widespread species occur mostly on low-relief (*i.e*., flat) lowland river basins at the continental core (Albert *et al*., 2011b; Dagosta, de Pinna, 2019). Consequently, upland drainages generally exhibit relatively lower local species richness (*i.e*., lower alpha diversity) but a relatively greater change in species composition across neighboring watersheds (*i.e*., higher geographic beta diversity) as compared with lowlands (Albert *et al*., 2017). Even though lowland rivers at the continental core are centers of species richness, upland rivers and coastal drainages at the continental periphery have higher species endemism (Albert *et al*., 2018).

Neotropical waterways, as with other tropical freshwater systems worldwide, are experiencing accelerating conservation threats because of myriad anthropogenic

activities (Dagosta *et al*., 2020). Worldwide, an average of 30% of freshwater fishes are classified under threat categories by the International Union for Conservation of Nature (IUCN) Red List (RL) assessments (IUCN, 2020). Extinction risk in much of the Neotropics is generally lower than in other continents, where about 10% of all continental Brazilian fishes are currently assigned to threatened categories (Reis *et al*., 2016; ICMBio, 2018). Despite commendable efforts, approximately half of all NFF currently await IUCN assessment, an expensive, laborious and time-consuming process, and many Latin American countries do not have reliable conservation information on potentially threatened species.

The urgency to prioritize species conservation has encouraged the development of alternative tools for performing preliminary conservation assessments based on geographic and taxonomic information alone (Bachman *et al*., 2011; Dauby *et al*., 2017; Zizka *et al*., 2020). Recently, efforts have been made in combining IUCN RL assessments with species' traits to assign preliminary extinction risks to not-evaluated or data-deficient species (Bland *et al*., 2015; Pelletier *et al*., 2018; Gonzalez-del-Pliego *et al*., 2019; Lughadha *et al*., 2019). Although body size and functional traits are widely known to be correlated with extinction risk in fish faunas (Poff *et al*., 2012; Kalinkat *et al*., 2017), the relationships among those variables have only recently been studied in NFFs (Castro, Polaz, 2020; Tagliacollo *et al*., 2020). Estimates based on recent rates of species discovery suggest that almost 3,000 species of NFF species have yet to be formally described by taxonomists (Reis *et al*., 2016), and hundreds of fish species with small adult body size and restricted geographic ranges are already known to be threatened with extinction (Castro, Polaz, 2020; Tagliacollo *et al*., 2020).

Here we investigate the use of geographic and taxonomic data as a proxy to rapidly assess potential conservation threats for species of the NFF species. Specifically, we explore whether species geographic ranges, topographic elevation data, and publication date are associated with extinction risk using a dataset of 3,001 NFF species with threat categories assigned by the IUCN–RL. Furthermore, we use geographic coordinates data to generate a preliminary extinction risk assessment for 2,334 NFF currently awaiting formal IUCN assessment. We identify data types correlated with extinction risk, illustrate geographic distributions of NFF threatened species, predict distributions of potentially threatened species, and suggest possible priority areas for upcoming conservation assessments. Given the runaway rate of habitat destruction and the disproportionately limited resources available for such studies, we provide an important tool for urgently-needed conservation of neotropical freshwater fishes.

MATERIAL AND METHODS

Spatial database. Estimating species ranges for conservation assessment requires compiling, organizing, and proofing a comprehensive database with thousands of geographic coordinates. We compiled a database of NFF species based on geographic information of preserved specimens from the taxonomic literature and museum collections, the latter accessible through metadata repositories (*e.g*., GBIF, FishBase, SpeciesLink). After combining specimen occurrences from multiple sources, we applied an automated cleaning pipeline (Robertson *et al*., 2016) to remove duplicates and

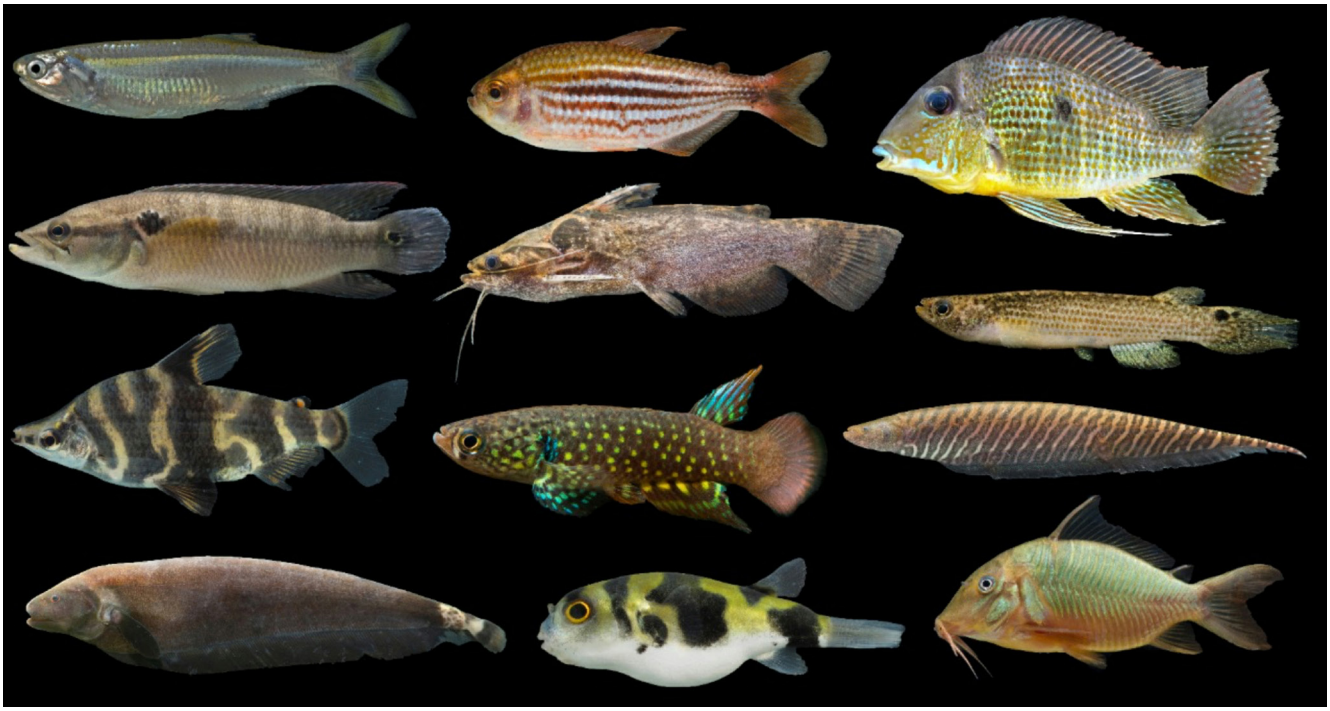

FIGURE 1 | Sample of the phenotypic diversity of Neotropical freshwater fishes. Upper left to lower right: *Lycengraulis grossidens* (Spix & Agassiz, 1829); *Hyphessobrycon hexastichos* Bertaco & Carvalho, 2005; *Geophagus neambi* Lucinda, Lucena & Assis, 2010; *Crenicichla lepidota* Heckel, 1840; *Trachelyopterus galeatus* (Linnaeus, 1766); *Anablepsoides xinguensis* (Costa, 2010); *Abramites hypselonotus* (Günther 1868); *Pituna xinguensis* Costa & Nielsen, 2007; *Gymnotus cuia* Craig, Malabarba, Crampton & Albert, 2018; *Apteronotus caudimaculosus* de Santana, 2003; *Colomesus tocantinensis* Amaral, Brito, Silva & Carvalho, 2013; *Corydoras britskii* (Nijssen & Isbrücker, 1983). Species not shown in scale.

geographic records with apparent geo-referenced mistakes. This procedure excluded incongruent occurrences, such as those placed in the ocean or outside the Neotropics, those without precise locality or country names, coordinates along the whole degree latitude or longitude (*i.e.*, latitude or longitude exactly zero) or collected on coarse-scale grid lines without decimal precision. We validated the NFF species distributions by plotting maps of individual species and comparing them with those published in the primary taxonomic literature. For many taxa, in particular those without range maps in the specialized literature, we solicited expert opinions by taxonomists who provided additional data points to improve species distributions and suggestions to exclude unreliable occurrences. In the absence of published maps or expert opinions, we kept only the coordinates of the holotype and paratypes.

IUCN threat categories. We compiled a list of 3,001 NFF species and their respective extinction risks based on assessments using the IUCN criteria and categories (IUCN, 2019). This list contains information about species extinction risks from the IUCN Red List database (IUCN, 2020), Brazilian Ministry of Environment Red List of endangered species (ICMBio, 2018), and Colombian Red List Book (Mojica *et al.*, 2012). Those extinction risk assessments list recognized species as Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), and Data Deficient (DD). We changed the threat classification scheme by

combining the categories Least Concern (LC) and Near Threatened (NT) into a single category considered "non-threatened" to match the classification scheme exported by the R package ConR (Dauby *et al*., 2017).

Variables. We investigated the utility of three variables as proxies for extinction risk categorizations recognized by the IUCN–RL. We compiled a list of NFF species from William Eschmeyer's Catalog of Fishes (Fricke *et al*., 2020), including all 6,226 valid NFF species names, publication dates, and synonyms. We replaced all junior synonyms in the spatial database with valid names. We sub-sampled this list of publication dates to include 5,335 valid species having geographic coordinates in the spatial database, including 3,001 NFF species with IUCN–RL extinction risk assessments, and additionally 2,334 awaiting IUCN assessment. We discretized the species publication dates for the dataset of 3,001 NFF species into 15 intervals, each with approximately equal frequency values, including around 200 data points per interval.

We measured the Extent of Occurrence (EOO) as a proxy for species geographic distribution. The intent of the EOO estimates is to measure the degree of extinction risks from threatening factors across the taxon's geographical distribution (IUCN, 2019). We measured species EOO using coordinates plotted on geographic maps projected in the WGS84 coordinate reference system. We calculated the EOO for each species in the database as the area in square kilometers of the minimum convex polygon encompassing all localities of the species. To avoid overestimating geographic ranges, we removed projected regions extending beyond the Neotropical boundaries into the oceans. For species with less than three geographic coordinates, we calculated the Area of Occupancy (AOO) on a 2 x 2 km grid line (*i.e*., 4 km^2 per coordinate). We discretized the species EOOs for the dataset of 3,001 NFF species into 15 range-size intervals, each including approximately equal frequency values, including around 200 data points per interval.

We assessed differences in elevation of geographic coordinates as a proxy for species topographic elevation ranges. For each specimen of every species in the spatial database, we gathered elevation estimates using NASA's Shuttle Radar Topography Mission (SRTM) dataset in a Digital Elevation Model (DEM) (Farr *et al*., 2007). We gathered these elevation estimates on geographic maps projected in the WGS84 coordinate reference system. As before, we discretized species altitude ranges into 15 elevation intervals, each including approximately equal frequency values, including around 5,930 data points per interval.

Preliminary assessments. We used the R package ConR (Dauby *et al*., 2017) to provide a preliminary conservation assessment for 2,334 NFF species for which extinction risks have not been assigned by the IUCN–RL. We used the ConR package to assign threat categories to the unclassified species assuming only criterion B, specifically sub-criterion B1 (*i.e*., EOO). This sub-criterion is one of the necessary conditions used by the IUCN–RL for classifying species into threat categories. It must also apply other conditions when assigning extinction risks properly; *e.g*., number of locations or population fragmentation, continuing decline of species distributions or habitat quality, population extreme fluctuations through time (IUCN, 2019). However, these conditions are too complex for automated conservation assignments,

because they depend on detailed knowledge of species ecology and behavior, habitat utilization, and existing actual threats to part or all of the species' geographic range. Preliminary conservation assessments by ConR classified species into Non-threatened (Least Concern or Near Threatened), and three threat categories: Vulnerable (VU), Endangered (EN), and Critically Endangered (CR). Species with fewer than three geographic coordinates received the status of Data Deficient (DD).

RESULTS

Species occurrences. After verification and validation steps we obtained a database of 125,685 unique geographic coordinates for 5,335 species or 83% of the entire Neotropical ichthyofauna. Of those, 4,154 species were represented by three or more coordinates, with a median of 11 occurrences per species with interquartile range (*i.e.*, Q3–Q1) of 26. By taxonomic order, the database included 60,374 (48.0%) occurrences for 1,758 characiform species, 32,407 (25.8%) occurrences for 1,964 siluriform species, 12,262 (9.7%) occurrences for 465 cichliform species, 6,495 (5.2%) occurrences for 596 cyprinodontiform species, 6,811 (5.4%) occurrences for 258 gymnotiform species, and 7,336 (5.8%) for 294 species in the other taxonomic orders. The geographic coordinates were heterogeneously distributed throughout most of the Neotropical region, with geographic gaps in the Argentinean pampas, a region with a few rivers and comparatively lower species density.

IUCN–RL: conservation assessments. We evaluated the extinction risks for 3,001 NFF species with existing IUCN assessments, including 1,068 Characiformes, 1,106 Siluriformes, 302 Cyprinodontiformes, 259 Cichliformes, 146 Gymnotiformes, and 120 species in other taxonomic orders. We identified that about 14% (or 422 out 3,001 species) of NFF species are under extinction risk, including 176 as VU, 147 as EN, and 99 as CR. Partitioned by taxonomic order, NFF species are classified by the IUCN-RL in threat categories in the following proportions: (i) Characiformes: 8.2% (88 out 1068 species), including 43 as VU, 36 as EN, and nine as CR; (ii) Siluriformes: 10.8% (119 out 1106 species), including 41 as VU, 47 as EN, and 31 as CR; (iii) Cyprinodontiformes: 48.0% (or 145 out 302 species), including 61 as VU, 40 as EN, and 44 as CR; (iv) Cichliformes: 10.0% (26 out 259 species), including 14 as VU, 10 as EN, and two as CR; (v) Gymnotiformes: 14.9% (21 out 146 species), including 11 as VU, five as EN, and five as CR, and (vi) species in other clades: 19.2% (23 out 120 species); including six as VU, nine as EN, and eight as CR (Tab. 1; Fig. 2).

Taxonomic and spatial variables. We obtained information on publication dates, EOOs, and elevation for 3,001 NFF species with IUCN–RL extinction risks. This dataset comprises NFF species published from 1758 to 2016. The Fig. 3 shows general trends of relationships among these three variables and extinction risks in NFF species.

We identified about 33.5% (or 1,007 of 3,001 species) NFF species described in a time-interval of 20 years, between 1996 to 2016. Approximately 18.7% (or 188 of 1,007 species) of these recently described NFF species are classified by the IUCN–RL as either VU, EN or CR (Tab. 2). Partitioned by taxonomic order, we verified that

TABLE 1 | Summary of the IUCN–RL data for 3,001 Neotropical freshwater fish (NFF) species. Threatened = number of threatened NFF species.

Order	NFF	Threatened	%
Characiformes	1068	88	8.2
Siluriformes	1106	119	10.8
Cyprinodontiformes	302	145	48.0
Cichliformes	259	26	10.0
Gymnotiformes	146	21	14.4
Other orders	120	23	19.2
TOTAL	**3,001**	**422**	**14.1**

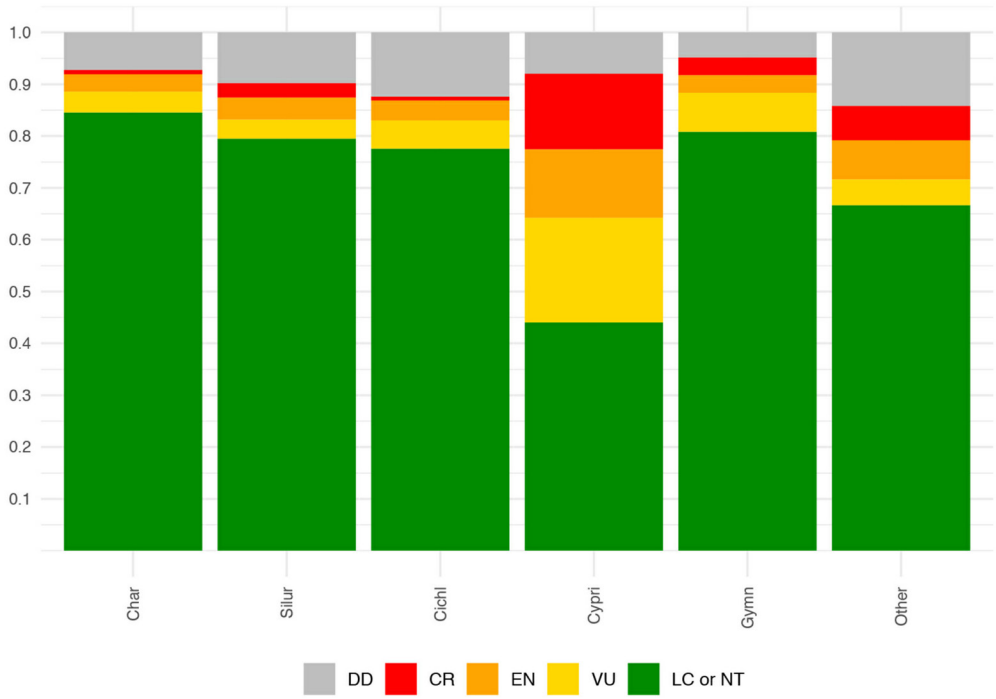

FIGURE 2 | Extinction risks in 3,001 Neotropical freshwater fishes (NFF). On average, 14% (422 of 3,001) NFF species are classified by the IUCN Red List (RL) as Vulnerable (VU), Endangered (EN) or Critically Endangered (CR). Extinction risks are relatively similar among the orders Characiformes (8.2%), Siluriformes (10.8%), Cichliformes (10.0%), and Gymnotiformes (14.9%). An exception is the clade Cyprinodontiformes, where about 48% of species are classified as either VU, EN, or CR. LC or NT: Least Concern or Near Threatened; DD: Data Deficient.

NFF species described in this 20-year interval are classified by the IUCN–RL in threat categories in the following proportions: (i) Characiformes: 11.6% (34 of 294 species), including 16 as VU, 12 as EN, and six as CR; (ii) Siluriformes: 15.1% (59 of 390 species), including 19 as VU, 26 as EN, and 14 as CR; (iii) Cyprinodontiformes: 44.1% (67 of 152 species), including 34 as VU, 13 as EN, and 20 as CR; (iv) Cichliformes: 11.3% (seven of 62 species), including five as VU, and two as EN; (v) Gymnotiformes: 21.8% (19 of 87 species), including 10 as VU, four as EN and five as CR; and (vi) species in other clades: 9.1% (two of 22 species), including two as EN (Tab. 2).

TABLE 2 | Summary of the IUCN–RL data for 1,007 NFF species described in a 20–year interval, from 1996 to 2016.

	Publ. dates: 1996–2016		
Order	**NFF**	**Threatened**	**%**
Characiformes	294	34	11.6
Siluriformes	390	59	15.1
Cyprinodontiformes	152	67	44.1
Cichliformes	62	7	11.3
Gymnotiformes	87	19	21.8
Other orders	22	2	9.1
TOTAL	**1,007**	**188**	**18.7**

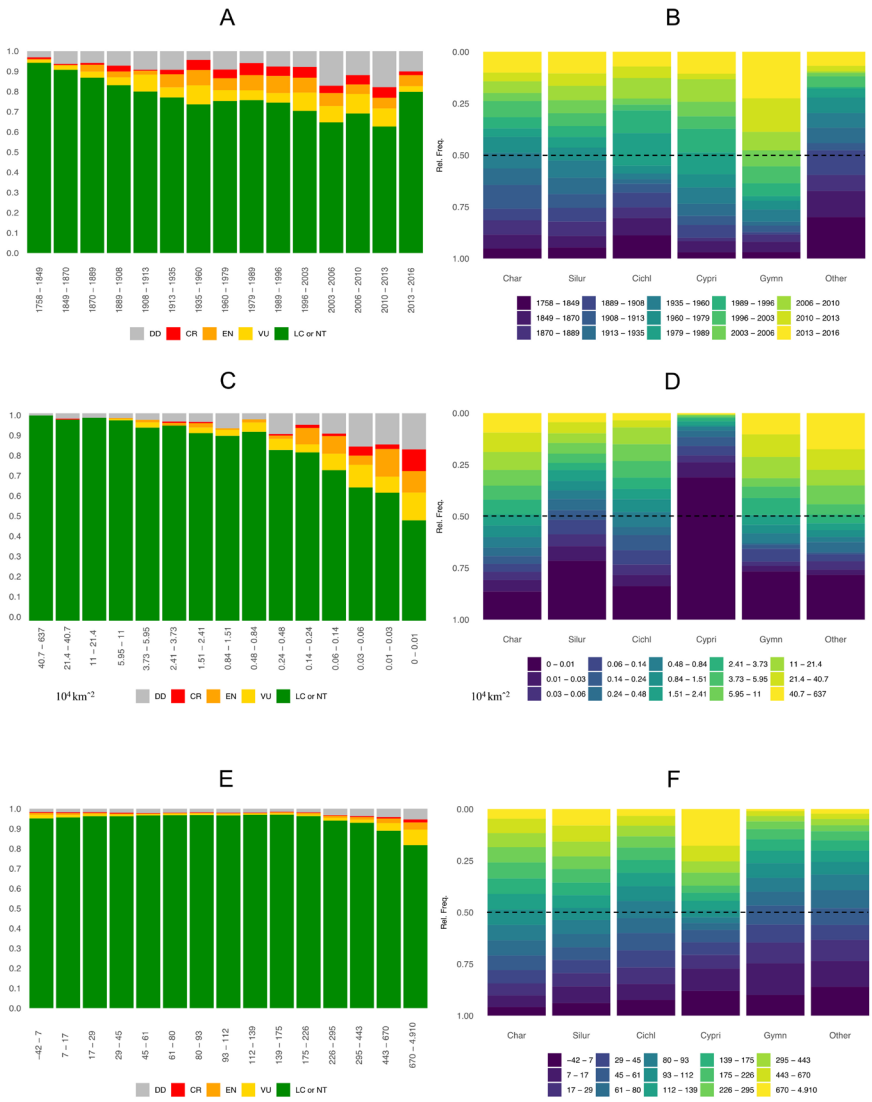

FIGURE 3 | Association among three variables and extinction risks in 3,001 Neotropical freshwater fishes (NFF). **A.** IUCN-Red List (RL) threat categories by species description dates. **B.** Species description dates by taxonomic orders. **C.** IUCN-RL categories by geographic ranges. **D.** Geographic ranges by taxonomic orders. **E.** IUCN-RL categories by elevation ranges. **F.** Elevational ranges by taxonomic orders. Threatened status are usually higher for recently described NFF species, those inhabiting narrow geographic ranges, and those confined to upland river drainages. CR: Critically Endangered; EN: Endangered; VU: Vulnerable; DD: Data Deficient.

We estimate 44.5% (1,337 of 3,001 species) of NFF species have an EOO under 20,000 km². Approximately 27.9% (373 of 1,337 species) of these NFF species with EOOs under 20,000 km² are classified by the IUCN–RL as either VU, EN or CR (Tab. 3). Partitioned by taxonomic order, NFF species with EOO estimates of less than 20,000 km² are classified by the IUCN–RL in threat categories in the following proportions: (i) Characiformes: 21.8% (70 of 321 species), including 33 as VU, 29 as EN and eight as CR; (ii) Siluriformes: 18.6% (106 of 570 species), including 34 as VU, 44 as EN and 28 as CR; (iii) Cyprinodontiformes: 52.7% (138 of 262 species), including 55 as VU, 39 as EN and 44 as CR; (iv) Cichliformes: 22.1% (21 of 95 species), including 13 as VU, seven as EN and one as CR; (v) Gymnotiformes: 37.2% (19 of 51 species), including 10 as VU, four as EN and five as CR; and (vi) species in other clades: 50% (19 of 38 species), including three as VU, nine as EN and seven as CR (Tab. 3).

We obtained elevation data from 88,977 geographic coordinates, ranging from -42 to 4,910 meters elevation. Dividing this elevation range by interquartile, we showed that species in upland river systems above 253.00 meters are more often classified by the IUCN–RL in threat categories (Tab. 4). Approximately 23.6% (217 of 918 species) of the NFF species with median altitudes ranging between 253.0–4911.0 m (Q4) are classified by the IUCN–RL as either VU, EN or CR (Tab. 4). Partitioned by taxonomic order, NFF species with median altitudes ranging between 253.0 - 4911.0 meters (Q4) are classified by the IUCN–RL in threat categories in the following proportions: (i) Characiformes: 14.9% (47 of 316 species), including 24 as VU, 17 as EN and 6 as CR; (ii) Siluriformes: 17.8% (73 of 409 species), including 27 as VU, 26 as EN and 20 as CR; (iii) Cyprinodontiformes: 60% (73 of 121 species), including 36 as VU, 24 as EN and 13 as CR; (iv) Cichliformes: 17.5% (seven of 40 species), including 40 as VU and three as CR; (v) Gymnotiformes: 41.2% (six of 17 species), including one as VU, four as EN and one as CR; and (vi) species in other clades: 73.3% (11 of 15 species), including two as VU, four as EN and five as CR (Tab. 4).

TABLE 3 | Summary of the IUCN–RL data for 1,337 NFF species with geographic range estimates less than 20,000 km². EOO = Extent of Occurrence.

Geographic ranges: EOO < 20,000 km²			
Order	**NFF**	**Threatened**	**%**
Characiformes	321	70	21.8
Siluriformes	570	106	18.6
Cyprinodontiformes	262	138	52.7
Cichliformes	95	21	22.1
Gymnotiformes	51	19	37.2
Other orders	38	19	50.0
TOTAL	**1,337**	**373**	**27.8**

ConR: preliminary conservation assessments. The R package ConR generated preliminary conservation assessments for 2,334 NFF species awaiting IUCN assessments, including 858 Siluriformes, 690 Characiformes, 294 Cyprinodontiformes, 206 Cichliformes, 112 Gymnotiformes, and 174 species in other orders. We verified in this preliminary survey that about 28.7% (671 of 2,334) species were considered under potential extinction risk, including 301 as VU, 346 as EN, and 24 as CR (Tab. 5). Partitioned by taxonomic order, we verified that NFF species are assigned by the ConR package in threat categories in the following proportions: (i) Characiformes 30.4% (210 of 690 species), including 97 as VU, 106 as EN, and seven as CR; (ii) Siluriformes: 29.2% (251 of 858 species), including 109 as VU, 130 as EN, and 12 as CR; (iii) Cyprinodontiformes 30.9% (91 of 294 spp.), including 40 spp. as VU, 49 spp. as EN, and two spp. as CR; (iv) Cichliformes: 26.2% (54 of 206 spp.), including 25 spp. as VU, 27 spp. as EN, and two spp. as CR; (v) Gymnotiformes 32.1% (36 of 112 spp.), including 14 spp. as VU, 21 spp. as EN, and one as CR; and (vi) species in other clades: 16.6% (29 of 174 spp.), including 16 spp. as VU, and 13 spp. as EN (Tab. 5).

TABLE 4 | Summary of the IUCN–RL data for 3,001 NFF species, with estimates of median elevation within interquartile ranges. Thr = Threatened species.

	Q1			Q2			Q3			Q4		
	-42.0 : 42.0 m			42 : 105.0 m			105.0 : 253.0 m			253.0 : 4910.0 m		
Order	NFF	Thr	%	NFF	Thr	%	NFF	Thr	%	NFF	Thr	%
Characiformes	112	11	9.8	358	10	2.8	282	20	7.1	316	47	14.9
Siluriformes	179	15	8.4	277	17	6.1	241	14	5.8	409	73	17.8
Cyprinodontiformes	89	43	48.3	40	14	35.0	52	15	28.8	121	73	60.3
Cichliformes	60	5	8.3	94	10	10.6	65	4	6.2	40	7	17.5
Gymnotiformes	57	6	10.5	50	6	12.0	22	3	13.6	17	6	35.3
Other orders	46	5	10.9	47	5	10.6	12	2	16.7	15	11	73.3
TOTAL	543	85	**15.7**	866	62	**7.2**	674	58	**8.6**	918	217	**23.6**

TABLE 5 | Summary of the ConR preliminary conservation assignments for 2,334 NFF species.

Order	NFF	Threatened	%
Characiformes	690	210	30.4
Siluriformes	858	251	29.3
Cyprinodontiformes	294	91	31.0
Cichliformes	206	54	26.2
Gymnotiformes	112	36	32.1
Other orders	174	29	16.7
TOTAL	**2,334**	**671**	**28.7**

DISCUSSION

Threat status in NFF species. The Neotropical ichthyofauna is among the most diverse on Earth, with published estimates of more than 9,000 species or about 14% of all vertebrate species. This diversity of NFF species is dominated by three orders of ostariophysan fishes (Characiformes, Siluriformes, and Gymnotiformes) and two orders of acanthomorph fishes (*i.e.*, Cichliformes, Cyprinodontiformes). This study suggests that ca. 14%, or about one species in seven, of all NFF species are under some level of extinction risk (Fig. 2). The estimated 14% of threatened NFF species is lower than corresponding figures for the freshwater ichthyofauna in other continents; *e.g.*, about 37% in Europe (Freyhof, Brooks, 2011), 27% in North America (IUCN, 2020), and 22% in Africa (Snoeks *et al*., 2011). However, absolute numbers are alarming with 422 species at extinction risk (Tab. 1) and it will certainly increase because nearly half of all NFF species are still awaiting IUCN assessment. The extinction risk is similar among ostariophysans and cichliform species, with an average of 11.0% of species assigned to threat categories, but cyprinodontiform killifishes are at much greater risk, with nearly 48% of species in threat categories (Tab. 1). Cyprinodontiformes include a high proportion of small-bodied species living in seasonal pools and other ephemeral aquatic habitats, with narrow geographic distributions within hydrologically isolated upland and coastal river basins (Fig. 3D), often in areas of the Brazilian shield with high human impact (Costa, 2019). These features place killifishes among the most vulnerable vertebrates in the Neotropical region (Costa, 2016; Costa, 2019).

Predictor variables of extinction risks. To evaluate species' extinction risks, the IUCN-RL uses a standardized protocol with a widely-accepted set of criteria (IUCN, 2019). This assessment is a laborious and time-consuming process based on experts' opinions and data that are not readily available for many taxonomic groups. The urgency to prioritize species conservation of threatened ecosystems has motivated the use of alternatives for speeding conservation assessments, by identifying geographic regions and species traits linked to higher extinction risks (Bland *et al*., 2015; Gonzalez-del-Pliego *et al*., 2019). Our findings support the longstanding view that geographic range size is a predictor of extinction risk (Purvis *et al*., 2000; Poff *et al*., 2012), and also more recently hypothesis that threatened status is, to some degree, associated with elevation gradients (Reis *et al*., 2016) and species' publication date (Tagliacollo *et al*., 2020) (Fig. 3).

Biodiversity patterns seen here for NFF resembles those of most biotas on Earth, in being characterized by a highly-skewed frequency distribution of organisms among species, in which most individuals are members of just a few highly abundant species (>80% measured as numbers of individuals). Some argue that conservation efforts should prioritize ecologically dominant species that are purported to perform most of the current ecosystem functions (*e.g.*, Gaston, Fuller, 2008; Winfree *et al*., 2015). This is a shortsighted strategy from both ecological and evolutionary perspectives. Some less abundant species (*e.g.*, top predators, ecosystem engineers) contribute disproportionately to the functional structure of species assemblages (Leitão *et al*., 2016; Jousset *et al*., 2017). Other species are spatially structured so that they are only less abundant locally, despite being geographically widespread (Violle *et al*., 2017).

In general, less abundant species often buffer ecosystem resilience to disturbance by providing stabilizing functional redundancy (Lyons *et al*., 2005; Mouillot *et al*., 2013; Dee *et al*., 2019). Although the functional diversity of NFFs is still poorly documented, preliminary studies show it is greater than other freshwater faunas (Su *et al*., 2019).

This study estimates that 44.5% (1,337 of 3,001 species) of NFF species have an EOO smaller than 20,000 km^2, which is an area equivalent to a square land parcel just 213 km on each side (Tab. 1; Fig. 3D). Like all species, freshwater fishes have particular habitat requirements (*e.g*., large river channels, floodplain lakes, rainforest streams, etc.) with specialized ecological and physiological traits, and therefore most NFF species occupy only a fraction of the theoretical maximum amount of aquatic habitat, with many species occupying a tiny spatial footprint of less than 100 km^2 of aquatic habitat, equivalent to a parcel less than 10 km on a side.

The effect of geographic range size on extinction risk varies both by region and among taxa. Fish diversity is often correlated with forest cover at a regional scale, although this pattern is more heterogeneous at more local scales (Lo *et al*., 2020). Both paleontological and macroecological studies have shown that geographic range is often the most important predictor of long-term evolutionary survival (Harnik *et al*., 2012; Toledo *et al*., 2014; Foote *et al*., 2016; Longrich *et al*., 2016). These conclusions suggest that current reductions in geographic range size will lead to pronounced increases in long-term extinction risk even if local populations are relatively large and stable at present. Such a pattern is even more critical for groups whose distributions are already naturally restricted, as seen in Cyprinodontiformes (Tab. 3; Fig. 3D).

The diverse NFF resembles that of other continents in exhibiting pronounced elevation biodiversity gradients, with greatest species richness in the lowlands below about 250 meters (Oberdorff *et al*., 2011; Costa *et al*., 2018; Albert *et al*., 2020b). This elevation-diversity gradient is part of a larger core-periphery biodiversity pattern observed in South American freshwater fishes, with higher species richness and lower percent endemism in lowland basins of the continental core (*i.e*., Amazon-Orinoco lowlands) and lower species richness and higher percent endemism in upland basins of the continental periphery (*e.g*., Shields and Andes) (Albert *et al*., 2011b; Dagosta, de Pinna, 2019; Oberdorff *et al*., 2019). Similar core-periphery patterns of species richness and percent endemism are also observed in many groups of South American plants (Ramírez-Barahona *et al*., 2011; Antonelli *et al*., 2018), frogs (Vasconcelos *et al*., 2019), and snakes (Azevedo *et al*., 2020).

Our results suggest that extinction risks for NFF species are higher in upland rivers at the continental periphery (Fig. 3E; Fig. 4). About 23.6% of species at an elevation above 253.0 meters are recognized as threatened species by the IUCN-RL (Tab. 4). As noted above, many cyprinodontiform species are at higher extinction risk in uplands areas at the continental periphery, including regional species flocks in the Altiplano (*e.g*., Orestias; Guerrero-Jiménez *et al*., 2017), Central America (*e.g*., Goodeidae; Foster, Piller, 2018), and Mata Atlântica (*e.g*., *Nematolebias*; Costa *et al*., 2014). Although phenotypic specialization is often thought to promote adaptive diversification (Petren *et al*., 2005; Seehausen, 2006; Pinto *et al*., 2008), the specializations of many NFF species to specific habitat types in upland rivers (*e.g*., waterfalls, torrential hill streams) potentially constrain their elevational and geographic distributions. Therefore the same traits that may contribute to higher local species richness may be disadvantageous

for survival in environments affected by humans (Ceretta *et al*., 2020). Although the aggregated effects of ecological and physiological constraints on elevation distributions in NFF species are poorly understood, it is likely that restricted geographic ranges, habitat availability, and habitat connectivity all strongly contribute to the threatened status of NFF species in upland rivers (Lanés *et al*., 2014; Silva *et al*., 2015).

We found that the dates of NFF species' publications are associated with extinction risks, in which more recently described species are assigned to higher threat categories by the IUCN–RL (Fig. 3). This association is most apparent in Cyprinodontiformes, with about 44% of species described in a 20–year interval from 1996 to 2016 (Tab. 2; Fig. 3). As in other taxonomic groups (*e.g*., birds, mammals), NFF species with widespread geographic distributions and/or high local abundances are often described earlier in

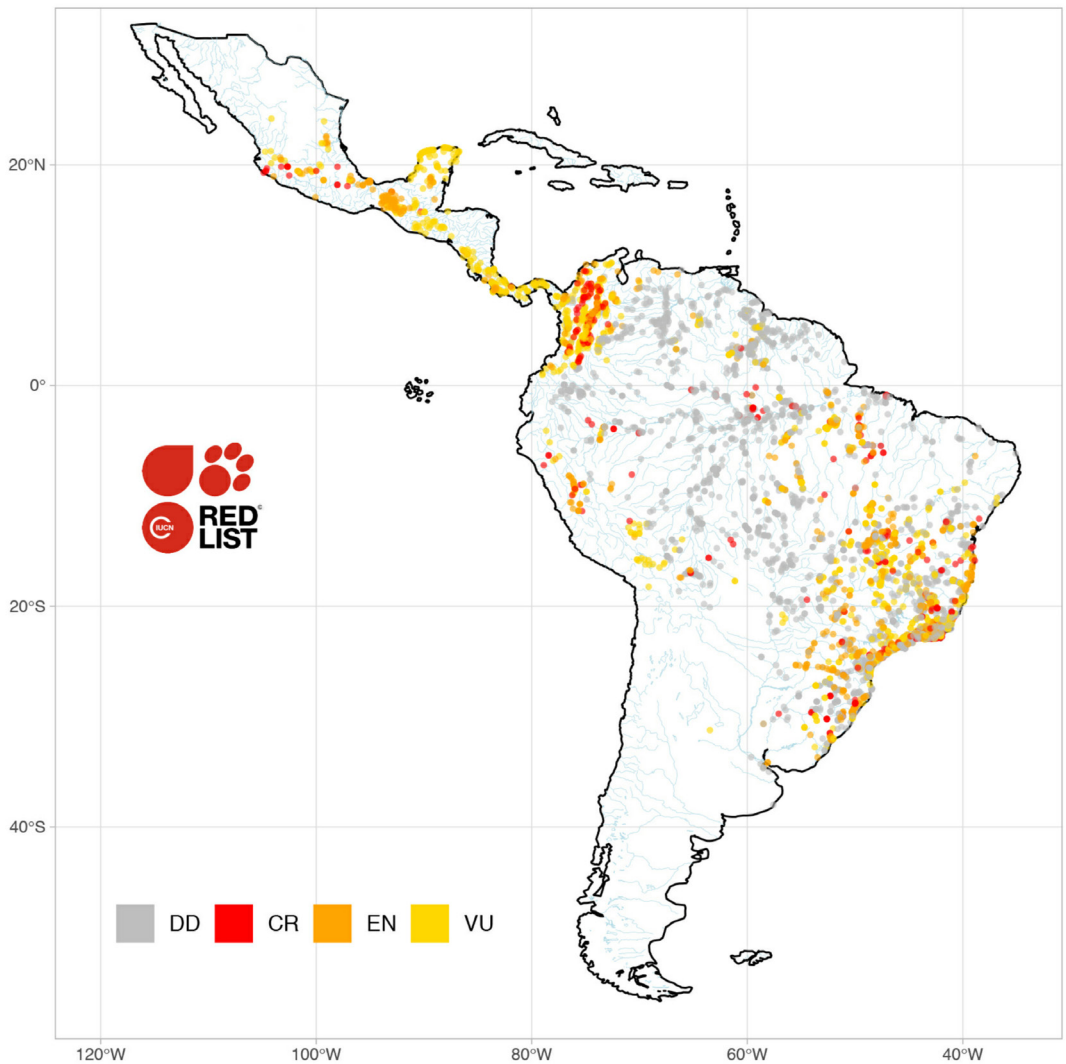

FIGURE 4 | Collection points for 442 threatened Neotropical freshwater fishes (NFF). Threatened NFF species classified by the IUCN Red List (RL) are often distributed in the upland rivers of the Brazilian Shield and the Colombian Andes, and coastal Atlantic and Caribbean drainages. CR: Critically Endangered; EN: Endangered; VU: Vulnerable; DD: Data Deficient. Data for 4,412 localities with geographic coordinates.

the discovery process, and these species therefore also suffer lower extinction risk. In contrast, range-restricted species, often located in remote areas or unusual habitats of South America, are only recently being collected and described by ichthyologists (*e.g.*, *Akawaio penak* Maldonado-Ocampo, López-Fernández, Taphorn, Bernard, Crampton & Lovejoy, 2014, and *Tarumania walkerae* de Pinna, Zuanon, Rapp Py-Daniel & Petry, 2017), and we generally have much less knowledge about their actual geographic and ecological ranges.

Using recent rates of species discovery and description, studies have forecast that about *ca*. 3,000 NFF species remain to be described (Reis *et al*., 2016, and reference therein). Results from this study indicate that most of these "yet-to-be-described" NFF species will be range-restricted, potentially threatened, and possibly data deficient on arrival. This is obviously a large and alarming number, which potentially exceeds the total number of (breeding) Neotropical birds (*ca*. 2,250 species; Rahbek *et al*., 2007), or the total number of obligate freshwater fish species in North America and Europe combined (*ca*. 1,460 species). The highly endemic spatial structure of Neotropical fishes means this fauna is vulnerable to mass extinction due to anthropogenic activities (Pelicice *et al*., 2017; Bezerra *et al*., 2019; Grasel *et al*., 2019).

Distribution range sizes of threatened NFFs species. Threatened NFF species are often distributed in upland rivers at the continental periphery (Fig. 4). In general, such species include those described decades ago with range-restricted distributions in the Brazilian Shield and the Colombian Andes, and coastal Atlantic and Caribbean drainages (Fig. 5). Higher concentration of threatened species in Colombia and Brazil, and a few species in other Latin American countries, is explained by the efforts of those two countries in generating national lists of threatened species in accordance with IUCN protocols (Mojica *et al*., 2012; ICMBio, 2018). NFF species in those aquatic environments are under higher extinction risks due to increasing threats caused by, among other things, expansion of agriculture (Rosa *et al*., 2020), implementation of hydropower plants (Finer, Jenkins, 2012), and urbanization (McKinney, 2006).

The amount of land surface area converted to agricultural activities varies substantially by region, but across the Neotropics natural vegetation cover is being removed to support human demands for commodities like soy, corn, palm oil, among others (Pütz *et al*., 2014). The conversion of natural lands to agriculture fields has been increasing in recent years with tropical forests, savannas and temperate forest being the most affected areas (Poorter *et al*., 2016). Agriculture activities can have a significant impact on freshwater ecosystems due to the flowing of fertilizers, herbicides and pesticides into rivers affecting the ecology of aquatic organisms and imposing threat on fish populations already under extinction risk (Albert *et al*., 2020a).

Hydroelectric dams impose other threats to NFF species, by transforming rivers into reservoirs leading to the extirpation of rheophilic species and collapse of migratory fish populations (Winemiller *et al*., 2016; Hrbek *et al*., 2018). Besides changes in environmental landscapes, hydropower plants modify the hydrological regime downstream, disturbing seasonal reproductive, feeding cycles, and migratory routes (Helfman, 2007). Small capacity dams have proliferated across the South America continent blocking headwater streams in upland regions (Grill *et al*., 2019). Brazil alone has built close to 500 small dams and many other projects are pending licensing

by the national agency of energy production (ANEEL, 2015). As a consequence, the connectivity of fish populations in headwater river systems have been fragmented, preventing faunal movements and the expansion of geographic ranges.

Worldwide about 1.7 billion people live in cities that draw water from freshwater ecoregions of high biodiversity value (Abell *et al*., 2019). Some of the largest Brazilian metropolitan areas lie at the headwaters of large tropical river basins. For example, the São Paulo greater metropolitan area (*ca*. 23.4 million people) strides the headwaters of the Tietê River, Brasília (*ca*. 4.3 million people) the headwaters of the Tocantins, São Francisco and Paraná Rivers, Belo Horizonte (*ca*. 2.7 million people) at headwaters of the das Velhas River (largest tributary of the São Francisco River), Curitiba (*ca*. 1.9 million people) at headwaters of the Iguaçu River, and Cuiabá (*ca*. 600,000 people) at headwaters of the Cuiabá River (major tributary of the Paraguay River). Outside of Brazil, there are examples of the same pattern in Colombia: metropolitan areas of Medellín (*ca*. 3.7 million people) and Cali (*ca*. 2.3 million people) at the headwaters of the Cauca-Magdalena River, and Barranquilla (*ca*. 2 million people) at its mouth. These large cities significantly reduce both the quality and quantity of water flowing downstream, from the combined effects of water withdrawals that lower the regional water table, and water pollution from urban and agricultural runoff, as well as industrial and residential sewage effluents. Finally, human footprint on aquatic resources from these and other cities throughout Latin America is expected to rise dramatically in coming years, with projected increases both in absolute numbers of people and per capita consumption of water, energy, food and other resources (Hoekstra, Mekonnen, 2012; Mekonnen, Gerbens-Leenes, 2020).

Additional impacts are projected in Atlantic coastal drainages, as more seashore and coastal estuaries are converted to urban and agricultural landscapes, affecting the quantity and quality of freshwater habitats in these areas with high local fish endemism (Camelier, Zanata, 2014; Bertaco *et al*., 2016; Hughes *et al*., 2020; Silva *et al*., 2020). Urbanization has distinct patterns in the Neotropics, with remote regions in, *e.g*., the Western Amazon, Guianas and Altiplano having the lowest fraction of land converted to urban or agricultural purposes, at least to date. However, the southeast Atlantic, Maracaibo-Caribbean and Eastern Atlantic regions have suffered the highest degree of urbanization (Gwynne, 2017), pressuring biotas with the highest concentration of threatened species in the Neotropics.

Distribution range sizes of potentially threatened NFF species. This study generated preliminary conservation assessments using EOO for 2,334 NFF species currently awaiting IUCN assessment, identifying an additional 671 NFF species as potentially threatened. This number represents 29% of NFF species currently lacking IUCN assessment. With 422 species currently on the IUCN RL, and the addition of 671 species suggested by the ConR package, the total number of threatened or potentially threatened Neotropical freshwater fish species has risen to 1,093 species, or about 18% of all species in the fauna.

Geographic range is widely regarded as an important predictor of extinction risk in freshwater taxa (Olden *et al*., 2010; Collen *et al*., 2014). The ConR package integrates information on species geographic data to calculate EOOs and compute IUCN threatened categories without explicit locations (*sensu* IUCN, 2019) that may affect

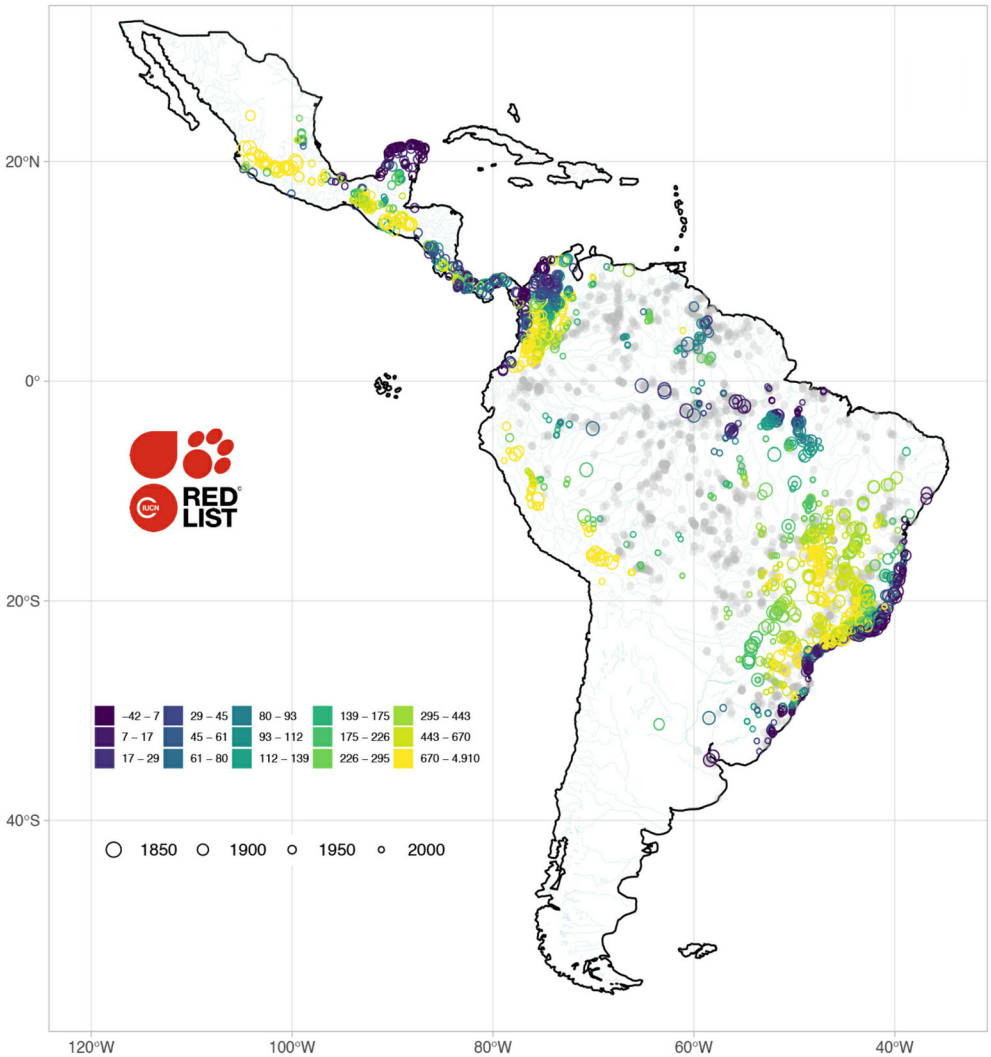

FIGURE 5 | Collection points for 442 threatened Neotropical freshwater fishes (NFF) colored by elevation and sized by species' description year. Threatened NFF species are often those described decades ago, with range-restricted distributions in the upland rivers of the Brazilian Shield and the Colombian Andes, and coastal Atlantic and Caribbean drainages. CR: Critically Endangered; EN: Endangered; VU: Vulnerable; DD: Data Deficient (gray). Data for 4,412 localities with geographic coordinates.

species' spatial ranges. A location is defined by the IUCN guidelines as a geographically or ecologically distinct area in which a single threatening event can rapidly affect all individuals of the taxon. Thus, the ConR provides a preliminary solution to estimate species conservation threat status without detailed information (*e.g.*, locations) required to achieve complete IUCN–RL status. We applied ConR to generate a data-driven baseline to identify potentially threatened species and their geographic ranges in the Neotropical region. We stress the ConR package is not at all intended to replace the IUCN Red Listing assessments; rather, it aims to assist and facilitate this process by red-flagging potentially threatened species and geographic areas. ConR estimates of threat status must be determined carefully, and the flagged species must be understood

as potentially threatened which may be endangered in the presence of environmental threats.

ConR reveals that potentially threatened NFF species are often restricted to single river basins located outside protected areas at high altitudes of the northern, central and southern Andes, and Eastern Guiana Shield (Fig. 6). These highland regions in the Neotropics are relatively species-poor, comprising less than 30.6% of the Neotropical ichthyofauna inhabiting river drainages above 253.0 meters (Tab. 4). The low diversity contrasts with the high endemism in both the Andean Cordillera (Schaefer, 2011) and Eastern Guiana Shield (Lujan, Armbruster, 2011), which encompasses an ichthyofauna comprised of relictual lineages with specialized phenotypes. Potentially threatened species along the Andean Cordilleras includes emblematic species in the Chilean ichthyofauna (*e.g.*, the catfishes *Diplomystes* and *Nematogenys* (Guichenot, 1848)), climbing catfishes (*Astroblepus*) in Peru, Ecuador and Colombia, and Altiplano killifishes (*Orestias*) in Lake Titicaca, to mention a few. The isolated Brazilian coastal drainages and the Guiana Shield also harbor a disproportionate number of low-diversity fish clades (*i.e.*, with few species), but which represent long phylogenetic branches (*i.e.*, relatively early-branching) within all the major taxonomic orders; *e.g.*, *Conorhynchus conirostris* (Valenciennes, 1840), *Delturus*, *Lithogenes*, *Trichogenes* and *Wertheimeria maculata* Steindachner, 1877 (Siluriformes), *Hollandichthys*, *Lignobrycon myersi* (Miranda Ribeiro 1956), *Mimagoniates*, *Nematocharax*, and *Spintherobolus* (Characiformes), *Akawaio penak* and *Japigny kirschbaum* Meunier, Jégu & Keith, 2011 (Gymnotiformes), *Guianacara* and *Mazarunia* (Cichliformes), and *Nematolebias* (Cyprinodontiformes). Peripheral basins in the Guiana Shield have been proposed as museums of diversity where lineages have resisted extinction for many millions of years (Albert *et al.*, 2011b). The unique ichthyofaunas of the South American uplands are centers of taxonomic and phylogenetic diversity (Faith, 1992; Magurran, 2013), and important biodiversity measures should be considered by policy makers when developing conservation actions (Strecker *et al.*, 2011; Li *et al.*, 2020).

The upland reaches of large Amazonian tributaries draining the central Brazilian Shield are also important centers of threatened freshwater fish species; *e.g.*, the upper Aripuanã, Juruena, Teles Pires, and Iriri Rivers. That region concentrates species highlighted by the ConR package as potentially Critically Endangered (CR) including highly specialized rheophilic lineages; *e.g.*, *Gymnotus Lamontianus* (Gymnotiformes), *Baryancistrus longipinnis* (Kindle 1895), *Scobinancistrus* (Siluriformes), *Rhinopetitia*, *Leporinus tristriatus* Birindelli & Britski, 2013, *Sartor*, *Ossubtus*, *Utiaritichthys* (Characiformes), *Retroculus*, *Teleocichla* (Cichliformes). That portion of the northern Brazilian Shield is a high conservation priority for freshwater fishes, as a region of high endemism, few protected areas and numerous planned or existing hydropower dams (Winemiller *et al.*, 2016; Dagosta *et al.*, 2020). This region is also the focus of intense deforestation along the expanding agricultural frontier of the Brazilian uplands (Spera *et al.*, 2016). The analysis also highlights the occurrence of some potentially threatened species in drainages near the South American Atlantic margin, with emphasis on the Iguaçu River (Daga *et al.*, 2016) and Uruguay River (Bertaco *et al.*, 2016). The latter two basins belong to the most threatened Brazilian biome, the Mata Atlântica, and are located close to large urban centers.

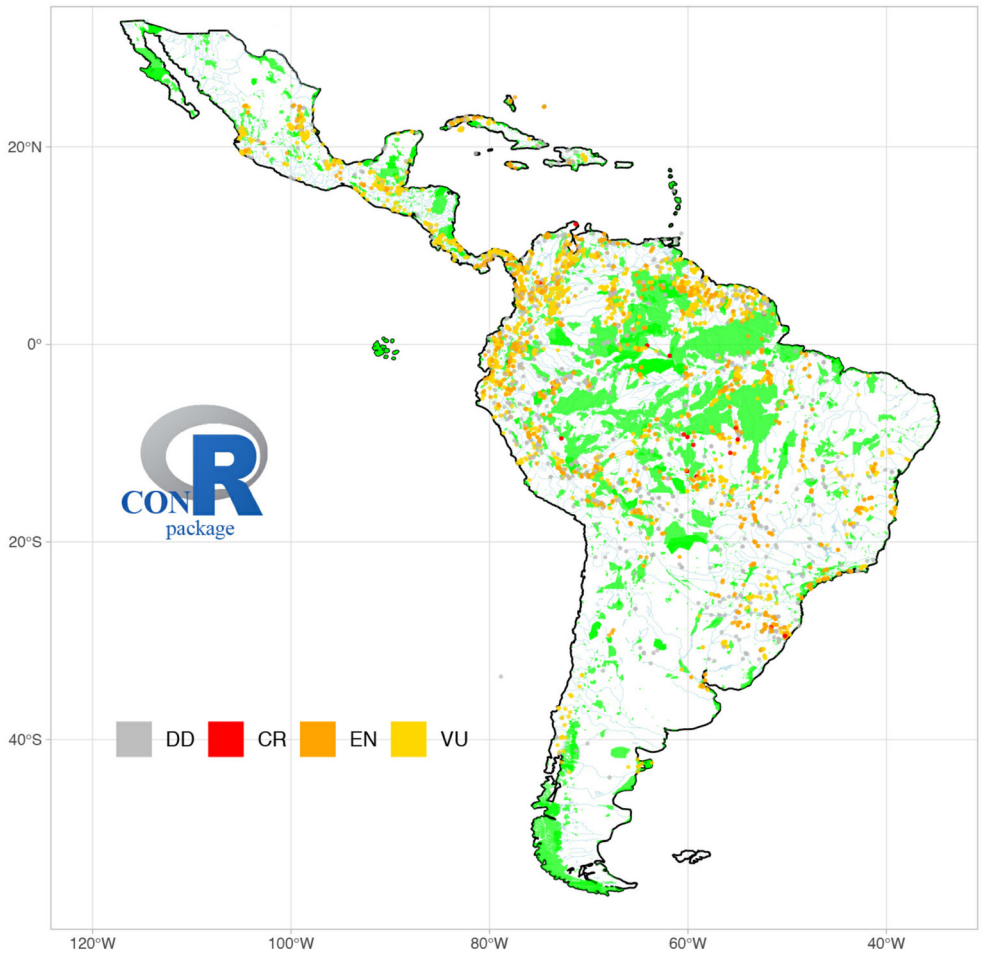

FIGURE 6 | Collection points for 671 potentially threatened Neotropical Freshwater Fishes (NFF). Potentially threatened NFF species predicted by the ConR package using EOO estimates are usually distributed outside protected areas (*e.g.*, national parks, indigenous lands: green) and more often located in the upland rivers of the northern, central and southern Andes, and Eastern Guiana Shield. CR: Critically Endangered; EN: Endangered; VU: Vulnerable; LC or NT: Least Concern or Near Threatened; DD: Data Deficient. Data for 4,412 localities with geographic coordinates. Protected areas (green) from: https://www.protectedplanet.net.

Concluding remarks. Continental freshwaters support diverse but fragile ecosystems that are widely imperiled by human activities. The conservation status of many freshwater fishes will benefit by prioritizing geographic areas with the largest number of coexisting and threatened species (Jézéquel *et al.*, 2020; Leal *et al.*, 2020). Hundreds of fishes with smaller adult body sizes and restricted geographic ranges are known to be threatened with extinction (Castro, Polaz, 2020). This study verifies that often threatened NFF species were recently described, are range-restricted, and are confined to certain upland portions of the Brazilian Shield and Northern Andes and to lowland portions of the Brazilian and Caribbean coastal drainages. Based on the ConR preliminary assignment estimates for NFF species, we estimate that about 29% of the species awaiting extinction risk assessments are potentially threatened. These potentially threatened NFF species are more commonly located outside formally protected

areas (Azevedo-Santos *et al*., 2019; Dagosta *et al*., 2020) in the Central and Southern Andes and Eastern Guiana Shield. Our results expand the number and geographic distribution of threatened NFF species from 422 species currently on the IUCN RL to 1,093 threatened or potentially threatened, representing about 18% of all described NFF species. Therefore, conservation efforts directed towards Neotropical aquatic biodiversity must prioritize habitats in uplands and coastal lowlands, particularly in the Andean Cordilleras, South American shields, and Brazilian and Caribbean coastal drainages. Rivers of the Central and Southern Andes, and Eastern Guiana Shield should be prioritized in the upcoming IUCN RL assessments for NFF species conservation efforts.

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The authors declare no competing interests.

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