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Freshwater fish diversity hotspots for conservation priorities in the Amazon Basin

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Abstract: Conserving freshwater habitats and their biodiversity in the Amazon Basin is a growing challenge in the face of rapid anthropogenic changes. We used the most comprehensive fish-occurrence database available (2355 valid species; 21,248 sampling points) and 3 ecological criteria (irreplaceability, representativeness, and vulnerability) to identify biodiversity hotspots based on 6 conservation templates (3 proactive, 1 reactive, 1 representative, and 1 balanced) to provide a set of alternative planning solutions for freshwater fish protection in the Amazon Basin. We identified empirically for each template the 17% of sub-basins that should be conserved and performed a prioritization analysis by identifying current and future (2050) threats (i.e., degree of deforestation and habitat fragmentation by dams). Two of our 3 proactive templates had around 65% of their surface covered by protected areas; high levels of irreplaceability (60% of endemics) and representativeness (71% of the Amazonian fish fauna); and low current and future vulnerability. These 2 templates, then, seemed more robust for conservation prioritization. The future of the selected sub-basins in these 2 proactive templates is not immediately threatened by human activities, and these sub-basins host the largest part of Amazonian biodiversity. They could easily be conserved if no additional threats occur between now and 2050.

Keywords: conservation scenarios, freshwater biodiversity, neotropics, spatial prioritization

Puntos Calientes de Diversidad de Peces de Agua Dulce para las Prioridades de Conservación en la Cuenca del Amazonas

Resumen: Cada día, la conservación de los hábitats de agua dulce y su biodiversidad en la cuenca del Amazonas es un reto creciente de cara a los rápidos cambios antropogénicos. Usamos la base de datos de presencia de peces más completa que existe (2,355 especies válidas; 21,248 puntos de muestreo) y tres criterios ecológicos (carácter irremplazable, representatividad y vulnerabilidad) para identificar los puntos calientes de biodiversidad

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con base en seis patrones de conservación (tres proactivos, uno reactivo, uno representativo y uno balanceado) y así proporcionar un conjunto de soluciones alternativas para la planeación de la protección de peces de agua dulce en la cuenca del Amazonas. Identificamos para cada patrón de manera empírica el 17% de las subcuencas que deberían conservarse y realizamos un análisis de priorización identificando amenazas actuales y a futuro (2050) (es decir, grado de deforestación y fragmentación del hábitat causado por presas). Dos de nuestros tres patrones proactivos tuvieron alrededor del 65% de su superficie cubierta por áreas protegidas; niveles altos de carácter irremplazable (60% de especies endémicas) y de representatividad (71% de la fauna ictiológica del Amazonas); y una vulnerabilidad baja actual y a futuro. Entonces, estos dos patrones parecen estar más completos para la priorización de la conservación. El futuro de las subcuencas en estos dos patrones proactivos no está amenazado por las actividades humanas a corto plazo. Además, estas subcuencas albergan la mayor parte de la biodiversidad amazónica. Se podrían conservar fácilmente si ninguna amenaza adicional sucede entre ahora y el 2050.

Introduction

The Amazon Basin is the largest river basin on Earth (total hydrographical area >6 million km^2) and contributes approximately 16% of the planet's freshwater flow (Venticinque et al. 2016; Latrubesse et al. 2017). The basin also supports the greatest freshwater biodiversity on Earth (Tisseuil et al. 2013). For example, >2200 strictly freshwater species have been described (Oberdorff et al. 2019), and these species represent around 15% of all freshwater fishes worldwide (Tedesco et al. 2017). This diversity is probably greatly underestimated given the large number of new species described every year (Antonelli et al. 2018; Machado et al. 2018). Compared with most other riverine ecosystems, the Amazon Basin and its fish fauna are still relatively well preserved (Reis et al. 2016) but could be affected soon by substantial increases in anthropogenic threats, such as habitat fragmentation by dams, deforestation, urban and agricultural pollutants, species introductions, and overfishing (Castello & Macedo 2016). Climate change may exacerbate these threats and potentially endanger some Amazonian fishes in the near future (Oberdorff et al. 2015). The Amazon Basin currently has a relatively high level of protection (i.e., 52% of the catchment is in protected areas [PAs] or on indigenous lands [ILs]), notwithstanding that the current PA network is potentially subject to shifts in national legislation that could erode protections (Ferreira et al. 2014; Begotti & Peres 2019; Golden Kroner et al. 2019). However, the capacity of this network to protect freshwater biodiversity remains unclear (Fagundes et al. 2016; Frederico et al. 2018; Azevedo-Santos et al. 2019) because ILs are by definition only designed to protect people, not to preserve ecosystems (Peres 2006), and PAs are generally assessed using terrestrial biodiversity metrics that do not encompass freshwater ecosystems and their hydrological connectivity (Abell et al. 2007; Leitão et al. 2018). However, PAs and ILs still provide some protection to freshwaters and their biodiversity because they control riparian deforestation, pollution, and overharvest of natural resources (Soares-Filho et al. 2010; Penha et al. 2014; Keppeler et al. 2017).

The best known approach to identify areas of conservation priority is the biodiversity hotspot approach, which was originally used by Myers (1988) to identify areas facing exceptional degrees of threat and supporting exceptional concentrations of species with high levels of endemism (Myers et al. 2000). This concept is built on 3 ecological criteria: irreplaceability, representativeness, and vulnerability (Brooks 2006). *Irreplaceability* refers to the level of biodiversity uniqueness (or rarity) of an area. *Representativeness* refers to the variability of habitat types, species assemblages, and ecological processes in an area (Margules & Pressey 2000). *Vulnerability* refers to the likelihood of biodiversity in an area is currently endangered or will be endangered in the future. Despite some criticisms (Marchese 2015), the hotspot concept is widely used to develop cost-effective strategies for biodiversity conservation (Myers 2003; Orme et al. 2005).

We applied the hotspot concept to freshwater fish diversity at a sub-basin level in the Amazon Basin. We used irreplaceability, representativeness, and vulnerability in 6 general conservation-strategy templates to provide a set of alternative conservation-prioritization scenarios. Five of these templates (3 proactive, 1 reactive, and 1 representative) were proposed by Brooks (2006). We developed a sixth, what we call, balanced template that combines irreplaceability, representativeness, and vulnerability criteria. Using the most comprehensive fish-occurrence database available (2355 valid species; 21,248 sampling points) (AmazonFish database; https://www.amazon-fish.com/) (Jézéquel et al. 2019), we sought to identify empirically for each template the 17% of sub-basins that should be conserved (threshold recommended by Aichi Biodiversity Target 11 [CBD 2010]). We aimed to quantify the level of freshwater biodiversity in each of the 6 templates in order to suggest priorities for conservation actions. We also performed a prioritization analysis with the selected sub-basins by identifying current and future (2050) threats (degree of deforestation and habitat fragmentation by dams).

Methods

Species Distribution Data

Species distribution data at the site grain (sampling point) were extracted from the AmazonFish database (Jézéquel et al. 2019). The database contains information from peer-reviewed journals, books, online databases, unpublished data from fishing campaigns, and collections from museums and universities. The database follows the nomenclature in the California Academy of Science's *Catalog of Fishes* (Fricke et al. 2019) and FishBase (Froese & Pauly 2019) and was subjected to a cleaning process to exclude invalid or unlikely occurrences, resulting in a total of 21,248 sampling points and 234,204 occurrences (Supporting Information). The database shows that there are 56 families, 514 genera, and 2355 native freshwater species in the Amazon Basin. Among species, 1351 are endemic to the Amazon Basin.

To equalize sampling effort, we worked at the sub-basin grain. We used the HydroBASINS framework (levels 5–6), a subset of the HydroSHEDS database (Lehner & Grill 2013), to delineate hydrological sub-basins of $>20,000$ km^2. Some adjacent sub-basins were further grouped to optimize sampling effort (i.e., number of sampling sites in each sub-basin). The sub-basins in the river mainstem were delineated based on the distance between 2 main tributaries entering the mainstem. This resulted in 97 sub-basins covering the entire Amazon system (Oberdorff et al. 2019) (Supporting Information).

Survey Completeness

We evaluated survey completeness and sampling effort of the database with 3 approaches (Troia & McManamay 2016). For each sub-basin, we applied the Chao2 nonparametric richness estimator in the fossil from R (Vavrek 2011; R Core Team 2019) to calculate a sub-basin completeness ratio (i.e., observed species richness divided by estimated richness). A sub-basin with completeness ratio >0.6 is considered well surveyed (Troia & McManamay 2016). The second approach characterizes the right end of the slope of the species accumulation curve (SAC) (specaccum, method random, in vegan from R) (Oksanen et al. 2019; R Core Team 2019). High completeness is characterized by a slope ≤ 0.15, meaning that richness has reached an asymptote with the number of occurrence records (Yang et al. 2013; Troia & McManamay 2016). We used the density of occurrences recorded for each sub-basin as a measure of sampling effort and applied logistic models (binomial glm in stats from R [Core Team 2019)] to verify that better sampled sub-basins were equally likely to be selected as less well-sampled sub-basins.

Sub-Basin Selection Criteria

We used irreplaceability, representativeness, and vulnerability to describe the sub-basins in each template (Schmitt 2011). Irreplaceability was measured using the corrected weighted endemicity index (Crisp et al. 2001). This index indicated the proportion of restricted-range species in a sub-basin (range 0–1). A sub-basin with 100% of endemic species would have a maximum value of 1.

Total species richness in each sub-basin indicated representativeness (Fleishman et al. 2006; Carrara et al. 2017). A posteriori we checked that the selected sub-basins also represented at the template scale the full variability and proportional representation of floodplains and small and large rivers. We used data from Nardi et al. (2019) to delineate floodplains and from Shen et al. (2017) to define small (Strahler order 1 to 3) and large (order 4 to 9) rivers.

We used sub-basin degree of deforestation and fragmentation by dams to quantify vulnerability. These 2 descriptors alter freshwater ecosystems and their biodiversity (Vörösmarty et al. 2010; Dias et al. 2017). We used an empirical model of Amazon deforestation (SimAmazonia 1) (Soares-Filho et al. 2006) that produces simulated deforestation trends under different scenarios of road paving, deforestation rates, and human population density and thus indirectly integrates other anthropogenic threats to freshwater ecosystems (e.g., agriculture and urbanization [Castello & Macedo 2016]). We used the business-as-usual (BAU) scenario for 2018 to quantify the current degree of deforestation for each sub-basin. The threat posed by habitat fragmentation by dams is linked to spatial connectivity for fish dispersal (Winemiller et al. 2016; Carvajal-Quintero et al. 2017). The density of dams currently operational or under construction in a sub-basin was estimated based on data in Winemiller et al. (2016), ANA (2018), and Anderson et al. (2018). Degree of deforestation and habitat fragmentation by dams were standardized using the Box–Cox power family (vegan in R) (Oksanen et al. 2019; R Core Team 2019) and later averaged to obtain a single vulnerability value for each sub-basin.

Because sub-basin size affects species richness in our dataset (Oberdorff et al. 2019), we standardized the metrics corrected weighted endemicity and total species richness by calculating the residuals of the linear regressions between values of the 2 metrics and the log-transformed area of sub-basins (Brooks 2006; Lamoreux et al. 2006). Standardized irreplaceability, representativeness, and vulnerability were further used to select hotspots in each template.

Templates

We compared 6 conservation-strategy templates: 3 proactive, 1 reactive, 1 representative (Schmitt 2011), and 1 balanced (Supporting Information). Proactive approaches prioritize areas of low vulnerability that harbor a large portion of undisturbed ecosystems and help identify conservation activities before disturbance occurs (Sanderson et al. 2002; Brooks 2006). Three proactive templates coexist. The first uses the low vulnerability criterion alone, the second adds irreplaceability to the low vulnerability criterion, and the third adds representativeness. Reactive approaches prioritize areas of high vulnerability and high irreplaceability (Eken et al. 2004; Brooks 2006) because conservation is thought most crucial in highly threatened areas that support a large number of rare species. Representative approaches select areas considered important for conserving a representative part of biodiversity (both richness and endemism); vulnerability is not considered. These areas have high degrees of irreplaceability and to a lesser extent representativeness. The balanced approach gives the same weight to the 3 criteria and thus identifies areas with high degrees of irreplaceability, representativeness, and vulnerability.

For each template, we selected 16 of the 97 sub-basins based on 17% protection of terrestrial and inland waters (CBD 2010). The 17% protection threshold is arbitrary and criticized from an ecological perspective (Carwardine et al. 2009), but it remains an important political target for guiding international conservation (Schmitt 2011). We used a ranking procedure to select sub-basins under each template. The criteria were ranked independently from 1 (low value) to 97 (high value) (inverse rank for low vulnerability). For the proactive templates (low vulnerability main criterion), we excluded sub-basins with the lowest rank (i.e., 50% highest values of vulnerability). The low vulnerability criterion alone (proactive 1) was further summed with the irreplaceability (proactive 2) or representativeness criteria (proactive 3) to identify the 16 sub-basins with the highest ranks. For the reactive template, we summed the vulnerability and irreplaceability criteria without prioritizing one over the other. For the representative template (high irreplaceability main criterion), we excluded sub-basins with the lowest rank (i.e., 50% lowest values of irreplaceability) and summed the irreplaceability and representativeness criteria. For the balanced template, we summed the 3 criteria.

We quantified the total fish biodiversity in each template (i.e., number of families, genera, and species). The number of threatened species was estimated using 2 red lists (ICMBio 2019; IUCN 2019) (500 and 1000 species assessed, respectively). Because the 2 previous lists were established using the same basic methodology, we combined them to obtain the conservation status for 66% of the total fish species recorded in the Amazon Basin. Only vulnerable, endangered, and critically endangered species were considered threatened (43 species).

Biodiversity recorded in PAs (i.e., protected biodiversity) was quantified for each template by combining records from PAs and ILs (RAISG 2019 & Supporting Information). Unprotected biodiversity (not recorded in the Amazon Basin's PA and IL networks) was also estimated for each template.

Finally, we evaluated the relevance of 17% protection (16 sub-basins) by comparing the fish diversity in each template with 11% and 23% protection (10 and 22 sub-basins, respectively).

Prioritization

The characterization of the land cost and initial conditions is usually an important prerequisite to identify the best strategy to optimally allocate resources for regions identified as priorities for conservation (Wilson et al. 2006, 2007; Bottrill et al. 2008). Instead of quantifying land cost, we characterized sub-basin initial conditions (degree of deforestation, habitat fragmentation by dams, and PAs) and identified sub-basins that could face increased threats in 2050. To do this, we used the SimAmazonia 1 model of deforestation (BAU scenario) for 2050 (Soares-Filho et al. 2006) and the projected future density of dams in the Amazon Basin (119 projected large dams and 78 existing dams) (Winemiller et al. 2016; ANA 2018; Anderson et al. 2018). Degree of deforestation and density of dams were standardized following the same method as that implemented for the vulnerability criterion, after grouping current and future data to ensure a common distribution of values ($n = 97$ sub-basins $\times$ 2). We averaged the 2 standardized descriptors into a single descriptor to obtain current and future vulnerability values. The sub-basins (in current and future states) with the top 25% highest values ($n = 49$) of vulnerability (17 sub-basins currently plus 32 sub-basins in 2050 [Supporting Information]) were considered threatened, and their unique fish biodiversity quantified for each conservation strategy template (species recorded only in the selected sub-basins). Due to methodological constraints, we could not include the potential effects of future climate change on biodiversity (details are given in Supporting Information).

Results

Survey Completeness

The completeness descriptors generally confirmed the quality of our database. Seventy percent of the sub-basins had at least 1 metric (Fig. 1) over the threshold for being well surveyed. The sampling effort was, on average, higher in the Amazon mainstream than in other parts of the basin (Fig. 1). Apart from our 3 proactive templates, survey completeness and sampling effort seemed to influence sub-basins selection for the reactive, representative, and balanced templates, which weakened their robustness (Supporting Information).

Templates

Corrected weighted endemicity for irreplaceability, total species richness for representativeness, and level of threat for vulnerability had different geographical patterns (Fig. 2). The sub-basins with the highest levels

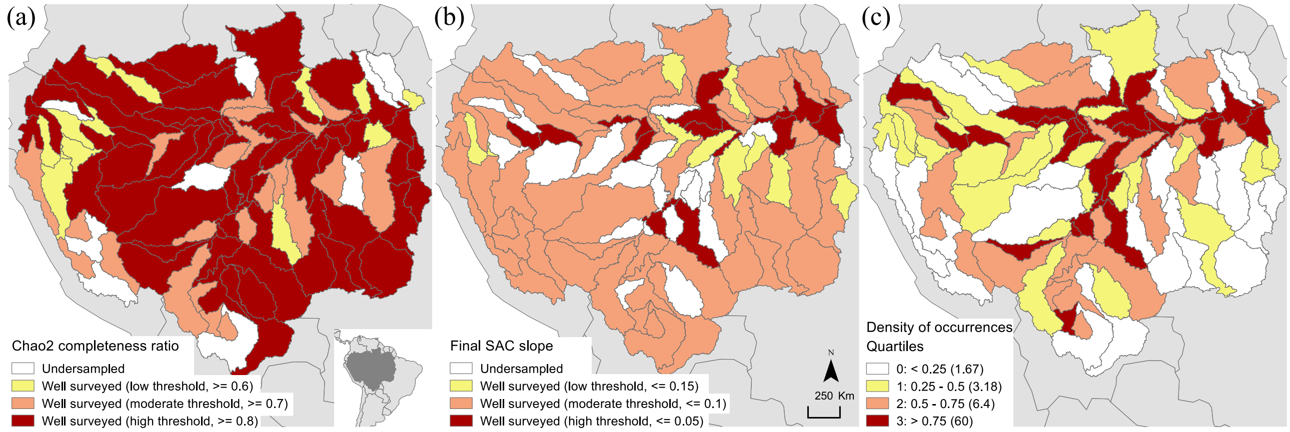

Figure 1. Distribution of well-surveyed and undersampled sub-basins based on (a) Chao2 completeness ratio, (b) right end of the slope of SAC, and (c) density of occurrences. The classification is based on Troia and McManamay (2016) (low, liberal thresholds used to define well-surveyed sub-basins; high, conservative thresholds used to define well-surveyed sub-basins).

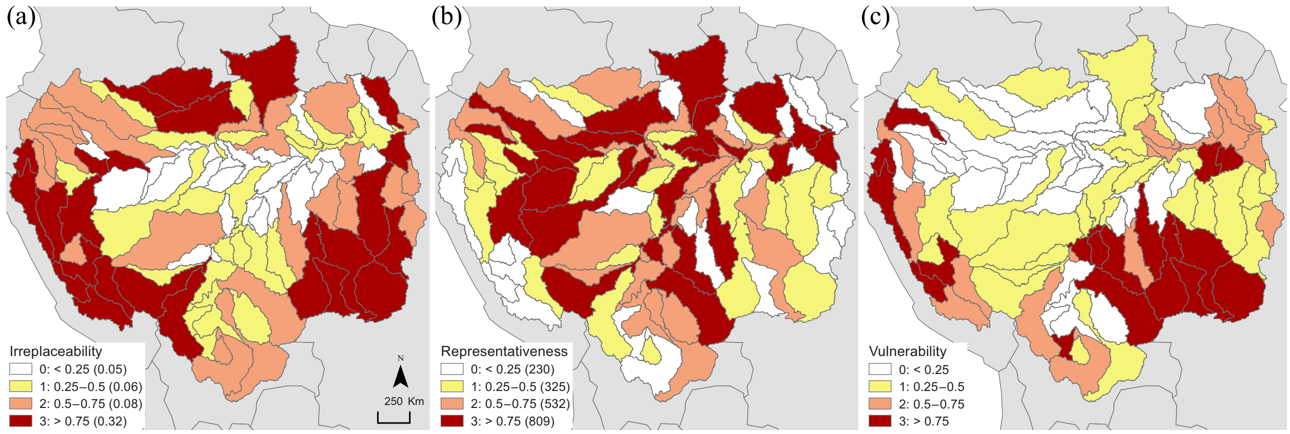

Figure 2. Distribution of (a) irreplaceability (corrected weighted endemicity), (b) representativeness (total species richness), and (c) vulnerability (level of threat based on degree of deforestation and habitat fragmentation by dams) of sub-basins based on the quartiles discretization (relative values in parentheses).

of irreplaceability were in upstream parts of the basin, whereas the lowest values were in the Amazon mainstream and its main lowland tributaries. The sub-basins with the highest levels of representativeness (>500 species) were in lowland Amazon and its 2 main tributaries, Negro and Madeira Rivers. The sub-basins with the highest levels of vulnerability were mostly located in the Andean and southeastern parts of the basin (Marañon, Ucayali, Madeira, and Tapajós Rivers) (Fig. 2).

Our 6 conservation-strategy templates identified sub-basins in different parts of the basin (Fig. 3). The 3 proactive templates mainly identified sub-basins in the center of the Basin and had a high number of sub-basins in common (7–10 [Supporting Information]). The reactive template highlighted sub-basins in the upper western and southeastern Amazon Basin (Fig. 3), whereas the representative and balanced templates selected sub-basins showed no clear geographical pattern (10 sub-basins in common) (Fig. 3 & Supporting Information).

The templates were mostly equivalent in terms of area selected (15–19% of the Amazon Basin) and were representative in terms of currently PA (15–31% of PAs and 23–46% of ILs; respectively, 26% and 30% at the Amazon Basin grain) (Supporting Information). The 3 proactive templates contained the highest proportions of PA (28–31% of PAs and 39–46% of ILs), whereas the reactive template contained the lowest ones (15% of PAs and 23% of ILs). All templates were representative of floodplains (8–22% relative to 16% at the Amazon Basin level), small rivers (85–87% relative to 86%), and large rivers (13–15% relative to 14%) (Supporting Information).

The representative template contained the highest level of fish diversity (82% of Amazonian species and 74% of Amazonian endemic species). The balanced,

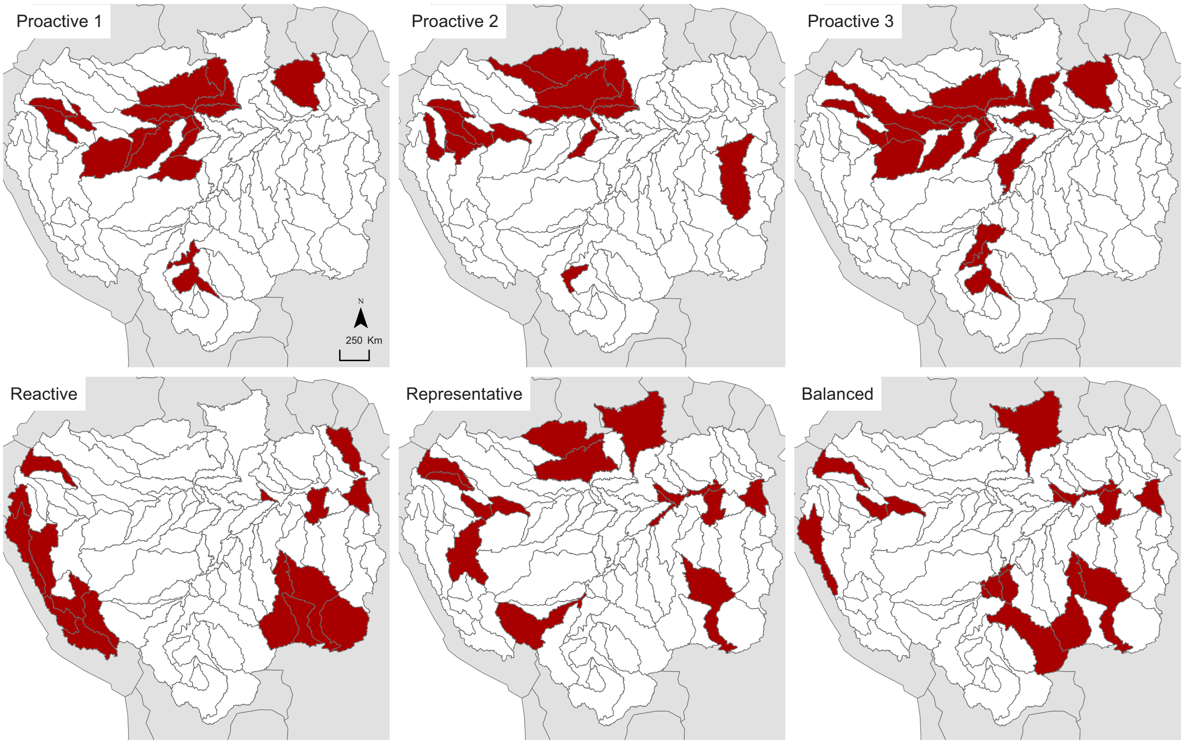

Figure 3. The 16 sub-basins selected (shaded) in each conservation-strategy template (proactive 1, 2, 3; reactive; representative; and balanced). Strategies defined in the text.

Table 1. Amazonian freshwater fishes included in the 6 conservation-strategy templates examined.

	Biodiversity[a]					Biodiversity protected[b]		Biodiversity unprotected[c]		
Template	families (%)	genera (%)	total species (%)	Amazonian endemic species (%)	threatened species	total species	Amazonian endemic species	genera	total species	Amazonian endemic species
Proactive 1	53 (95)	428 (83)	1487 (63)	676 (50)	3	1222	524	9	61	48
Proactive 2	53 (95)	456 (89)	1676 (71)	804 (60)	20	1408	618	12	108	95
Proactive 3	54 (96)	442 (86)	1682 (71)	810 (60)	7	1380	619	12	120	97
Reactive	55 (98)	442 (86)	1552 (66)	770 (57)	41	1061	485	19	136	116
Representative	54 (96)	478 (93)	1935 (82)	998 (74)	33	1562	721	15	172	137
Balanced	55 (98)	465 (90)	1830 (78)	949 (70)	30	1414	654	15	171	142
Amazon Basin	56	514	2355	1351	43	1990	1043	34	365	308

[a]*Number of families, genera, species, endemic species, and threatened species.*
[b]*Number of species and endemic species in template PAs and ILs.*
[c]*Number of genera, species, and endemic species of the template not recorded in the Amazon Basin's PA and IL networks.*

proactive 2, and proactive 3 templates presented an intermediate state with, respectively, 78%, 71%, and 71% of Amazonian species and 70%, 60%, and 60% of Amazonian endemic species (Table 1). The reactive and proactive 1 templates had the lowest levels of species and endemic species richness (respectively, 66–63% and 57–50%). The number of threatened species was, as expected, highly dependent on the vulnerability criterion: very low in the proactive templates (<10 species in proactive 1–3) and very high in the reactive template (41 of the 43 species on red lists) (Table 1).

At the Amazon Basin grain, 1990 species and 1043 endemic species were recorded inside PAs and ILs, representing 84% of Amazonian species and 77% of Amazonian endemics (Table 1). This apparently high level of protected biodiversity must be put into perspective because the configuration of PA and IL networks excludes freshwater ecosystems and their hydrological connectivity. However, 34 genera, 365 species, and 308 endemic species were not included in the basin's PA and IL networks (Table 1). The representative and balanced templates included approximately 40% of unprotected

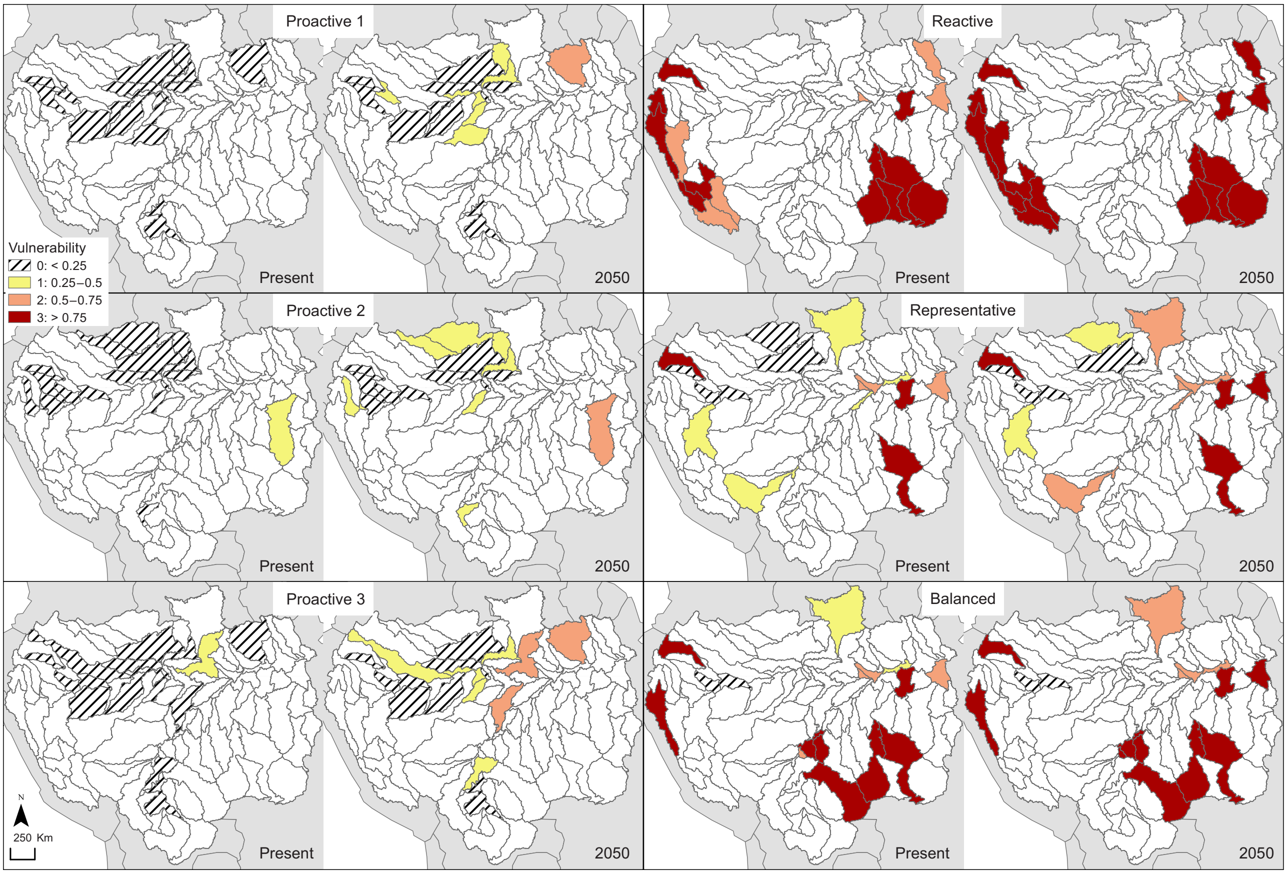

Figure 4. Sub-basin vulnerability to deforestation and habitat fragmentation by dams based on quartiles discretization of the 16 sub-basins selected by each conservation-strategy template (proactive 1, 2, and 3; reactive, representative; and balanced) currently and in 2050.

biodiversity. Reactive and proactives 2 and 3 templates contained approximately 30% of unprotected biodiversity (Table 1).

Our sensitivity analysis showed a 10% mean decrease in total number of species and endemic species with an 11% protection threshold (10 sub-basins) relative to the 17% threshold and a mean increase of 4% with a 23% threshold (22 sub-basins) (Supporting Information). In view of the substantial increase in area under the 23% threshold (27–41% of template area) for relatively little gains in terms of protected species, the selection of 16 sub-basins, guided by the 17% threshold recommended, appeared a good compromise.

Prioritization

The sub-basins selected by the 3 proactive templates remained mostly unaffected by the predicted change in these threats, except for a few that had increased deforestation (Fig. 4 & Supporting Information). In contrast, the majority of sub-basins identified by the reactive template were currently threatened and predicted to be further threatened by 2050 (Fig. 4). Some sub-basins selected with the representative template remained relatively preserved, whereas others faced threat increases (Fig. 4). The balanced template presented a majority of sub-basins currently threatened and, for most of them, predicted to be further threatened in 2050 (Fig. 4 & Supporting Information).

Each template highlighted different situations for biodiversity threatened currently and in the future. For unthreatened biodiversity, the representative template seemed the best compromise. It currently contained 77% of the Amazonian species and 66% of the Amazonian endemic species. Proactive 2 and 3 contained 71% and 60% of these species, respectively, and proactive 1 contained 63% and 50%, respectively (Table 2). The balanced and reactive templates had 8 and 10 threatened sub-basins and contained fewer Amazonian fishes (respectively, 62% and 46% of species and 48% and 33% of endemic species) (Table 2).

For future threats in 2050, ranking was overall the same but had lower percentages of unthreatened biodiversity. The representative template contained 72% of the species and 60% of the endemic species. Proactive 2 and 3 contained 71% and 60% of these species, respectively, and proactive 1 had 63% and 50%, respectively (Table 2). The balanced and reactive templates, which

Table 2. Number of Amazonian freshwater fishes included in each conservation-strategy template currently and in 2050 that occur only in threatened sub-basins.

	Current					*2050*				
Template[*]	*number of sub-basins*	*families*	*genera*	*total species*	*Amazonian endemic species*	*number of sub-basins*	*families*	*genera*	*total species*	*Amazonian endemic species*
Proactive 1	0	0	0	0	0	0	0	0	0	0
Proactive 2	0	0	0	0	0	0	0	0	0	0
Proactive 3	0	0	0	0	0	0	0	0	0	0
Reactive	10	3	64	463	327	15	8	197	1021	627
Representative	3	0	9	122	102	4	0	34	233	181
Balanced	8	3	39	370	301	10	3	69	535	414

[*]*By definition, the 3 proactive templates include no threatened sub-basin.*

should face an increase in threat levels, contained even lower percentages of species and endemic species (balanced 55% and 40%, respectively; reactive 23% and 11%, respectively) (Table 2).

Discussion

The comparison of the different conservation-strategy templates based on vulnerability, irreplaceability, and representativeness under current and future scenarios is usually absent in conservation-planning studies. Our analysis allows the discussion of advantages and constrains of each template and, even though our results are case specific, could help generate general principles for prioritization of conservation strategies.

Based on our results, we suggest that to protect Amazonian fish biodiversity at large, the representative template and its selected sub-basins seems, at first glance, a good option to prioritize for conservation. The future of these sub-basins, not immediately threatened by human activities and hosting the largest part of the Amazonian biodiversity, could be secured easily if no additional threats occur between now and 2050. However, this template's sub-basins were influenced by low survey completeness, which weakened slightly its robustness. Undersampled areas still exist (Wallacean shortfall [Antonelli et al. 2018]). The AmazonFish project has already started to fill these gaps by supporting the numeric digitalization of the national freshwater fish collections in Peru (Ortega & Hidalgo 2008; Quezada-Garcia et al. 2017) and by initiating sampling in undersampled areas in Colombia, Peru, and Brazil (DoNascimiento et al. 2017).

The proactive 2 and 3 templates, not influenced by low survey completeness and, respectively, integrating high levels of irreplaceability and representativeness in addition to low vulnerability, seemed more robust for conservation prioritization. Sub-basins within these templates currently had no habitat fragmentation and very low degrees of deforestation (<4%) and should remain mostly undisturbed in the near future (generally <16% of expected deforestation in 2050 and only 1 new dam per template [Supporting Information]). Hence, these templates selected functionally intact sub-basins that are, therefore, more valuable for conservation (Wilson et al. 2006, 2007; Bottrill et al. 2008). Given that around 65% of the area in these 2 templates is covered by PAs and ILs, the expanded PA should be minimal if PAs and ILs operate effectively. Human pressure on many PAs has increased, suggesting a gap in their management with regard to halting habitat loss and intensified human use (Adams et al. 2019).

By contrast, templates based on high vulnerability (i.e., reactive and balanced) do not seem robust relative to costs to protect these areas. For instance, the number of large dams that would need mitigation to maintain connectivity of the fluvial system and dam projects that would need relocation to protect current and future fish diversity is substantial (Supporting Information). Protection measures would be needed to limit the large expected increase in deforestation in these 2 templates (>40% of the area affected for the reactive template in 2050, up to 57% affected for the balanced template [Supporting Information]). The compromises required to protect fish biodiversity in these 2 templates appear thus extremely difficult to achieve, provided that any protection measures could really be considered due to political priorities of developing small and large hydroelectric dams (Latrubesse et al. 2017; Anderson et al. 2018), increasing deforestation for economic growth (Seymour & Harris 2019), and shifting PA policy (Golden Kroner et al. 2019). A template focusing only on pristine areas (e.g., proactive 1 template) is clearly not a good option for ecosystem protection because it provides, at least in our case, limited biodiversity benefits and thus little conservation value.

Independently of the conservation strategy template selected, it is worth mentioning that hydrological connectivity among sub-basins should be a priority as dispersal is a key process to maintain viable fish populations (e.g., Carvajal-Quintero et al. 2019).

As a next step, we envision the application of the key biodiversity areas (KBAs) approach to identify important biodiversity areas within the priority sub-basins we identified. These KBAs, delineated within sub-basins, are defined as “sites contributing significantly to the global persistence of biodiversity” (http://www.keybiodiversityareas.org/home). The KBAs can support the strategic expansion of PA networks by governments and civil society working toward achievement of the Aichi Biodiversity Targets (in particular Target 11 and 12).

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Supporting Information

Distribution of sampled sites in the AmazonFish database (Appendix S1), delimitation and codes of the 97 sub-basins (Appendix S2), list of sub-basin units, number of sites, occurrences, taxonomic units, and endemic species in sub-basins (Appendix S3), schematic representation of the 6 conservation strategy templates and the 3 criteria (Appendix S4), PAs and ILs networks (Appendix S5), distribution of the vulnerability criterion (Appendix S6), methods used to determine potential effect of future climate change (Appendix S7), *p* values from the logistic binary models (Appendix S8), number of common sub-basins among all templates (Appendix S9), coverage of protected areas, floodplains, and small and large rivers in each template (Appendix S10), biodiversity values in each template after selection of sub-basins (Appendix S11), and 16 sub-basins selected (Appendix S12).The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. The complete biological database (version 4), including raw data on species names and occurrences by sub-drainage basin, is available on request from C.J.

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