Freshwater fish diversity hotspots for conservation priorities in the Amazon basin

Abstract

Conserving the freshwater habitats and their biodiversity in the Amazon basin is a growing challenge in face of the rapid anthropogenic changes currently occurring. Here, making use of the most comprehensive fish occurrence database currently available (~21,000 sampling points, 97 sub-basins, 2,355 valid species) and relying on three major ecological criteria, namely irreplaceability, representativeness and vulnerability, we define biodiversity hotspots under six conservation strategy templates to provide a set of alternative scenarios. The comparison of these different templates, regarding fish diversity encapsulated and current and future (2050) threats, brings elements on the overall prioritization outcomes and may guide defining priorities and initiating conservation actions for freshwater fishes in the Amazon basin. Templates integrating high levels of fish diversity (irreplaceability and/or representativeness) in addition to low vulnerability (low degree of anthropogenic threats) seem more robust approaches for planning conservation prioritization in the basin.

Introduction

The Amazon basin is the largest river basin on Earth with a total hydrographical area greater than 6 million km^2 and contributes ~16% of the planet's freshwater flow (Venticinque et al. 2016; Latrubesse et al. 2017). The Amazon River also supports the highest freshwater biodiversity on earth (Tisseuil et al. 2013), with, for example, > 2,200 strictly freshwater species already described (Oberdorff et al. 2019), representing around 15% of all freshwater fish worldwide (Tedesco et al. 2017). This freshwater fish diversity is probably greatly underestimated given the high number of new species described every year (Winemiller and Willis 2011; Reis et al. 2016; Antonelli et al. 2018, Machado et al. 2018). Compared to most other riverine ecosystems, the Amazon basin and its fish fauna are still relatively preserved (Reis et al. 2016), but could be impacted in the near future due to the substantial increase in anthropogenic threats such as habitat fragmentation and flow modification by dams, deforestation, urban and/or agricultural pollutions, species introductions and overfishing (Castello et al. 2013; Castello & Macedo 2016). Climate change may exacerbate these threats, potentially endangering some Amazonian fish species in the near future (Oberdorff et al. 2015). The Amazon basin currently benefits from a relatively high level of protection (*i.e.* 52% of its catchment area under protective measures either under the form of Protected Areas (PAs) or of Indigenous Lands (ILs)), even if this current network is potentially subjected to any shifts in national legislation toward eroding protections (Ferreira et al. 2014; Oliveira et al. 2017; Begotti & Peres 2019; Golden Kroner et al. 2019; Ferrante & Fearnside 2019). The capacity of this network in protecting freshwater biodiversity remains however unclear (Nogueira et al. 2010; Fagundes et al. 2016; Azevedo-Santos et al. 2018; Frederico et al. 2018) as (i) ILs are by definition only designed to protect people, not to preserve ecosystems (Peres 2006) and (ii) PAs are generally assessed using terrestrial biodiversity metrics, with little regard to freshwater ecosystems and their hydrological connectivity (Fagan 2002; Abell et al. 2007; Leal et al. 2018; Carvajal-Quintero et al. 2019). However, even if not perfect, PAs and ILs still provide some protection to freshwaters and their biodiversity by controlling for riparian deforestation, pollution and overharvesting (Soares-Filho et al. 2010; Penha et al. 2014; Keppeler et al. 2017). Different approaches have been developed within the past 30 years to identify Biodiversity Conservation Priority areas (Brooks 2006). The best known, the Biodiversity Hotspot concept, 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 upon three ecological criteria, namely irreplaceability, representativeness and vulnerability (Brooks 2006). Irreplaceability refers to the biodiversity uniqueness (or rarity) of an area. Representativeness refers to areas representing the full variability of habitat types, species assemblages and, presumably, ecological processes (Margules et al. 2000). Vulnerability refers to the likelihood that the biodiversity within an area will be endangered or lost by current or future processes. Despite some criticisms (e.g. focusing on species rich areas only gives a partial response for conservation by ignoring transition ecosystems, Marchese 2015), the hotspot concept is widely used to develop cost-effective strategies for biodiversity conservation (Myers 2003; Orme et al. 2005).

Here we apply this approach to the Amazon basin, focusing on freshwater fish diversity at a sub-basin grain. We retained the three classical criteria (*i.e.* irreplaceability, representativeness and vulnerability, Brooks 2006) under six general conservation strategy templates to provide a set of alternative scenarios. Five of these templates namely the pro-active (further split into three alternative scenarios), reactive and representative were proposed by Brooks (2006). We developed a sixth "balanced" strategy template, combining the irreplaceability, representativeness and vulnerability criteria (see Methods for templates description). Using the most comprehensive fish occurrence database currently available (*i.e.* 2,355 valid species, 21,248 sampling points in 97 sub-basins) (https://www.amazon-fish.com/, Jézéquel et al. 2019), we empirically identified for each template the 17% most relevant sub-basins that should be effectively conserved, following the threshold recommended by the Aichi Biodiversity Target 11 of the Convention on Biological Diversity (CBD 2010). We quantified the level of freshwater biodiversity encapsulated within each of the six conservation strategy templates and further performed a prioritization analysis by identifying current and future (2050) threats (*i.e.* degree of deforestation and habitat fragmentation by dams) to the selected sub-basins in order to suggest priorities for conservation actions.

Material and Methods

Species Distribution data

Species distribution data were extracted from the AmazonFish database (Jézéquel et al. 2019, version 4, 06/19, https://www.amazon-fish.com/) that contains the most complete and up-to-date information currently available on freshwater fish species distribution at the site grain (sampling point) for the entire Amazon drainage basin. AmazonFish integrates information published in peer-reviewed journals, books, grey literature, online databases, unpublished data from recent fishing campaigns and collections from museums and/or universities. The database follows the nomenclature provided by the California Academy of Science's Catalog of Fishes (Fricke et al. 2018) and FishBase (Froese & Pauly 2018), and has beneficiated from a cleaning process to exclude invalid or unlikely occurrences, resulting in a total of 21,248 sampling points and 234,204 occurrences (Figure S1). The AmazonFish database highlights impressive levels of diversity for the Amazon basin, including 56 families, 514 genera and 2,355 native freshwater species, virtually half of the *circa* 4,760 species described for the whole Neotropical biogeographic region (Leroy et al. 2019). Among these 2,355 species 1,351 are endemics (*i.e.* species present only in the Amazon basin and nowhere else in the world).

To harmonize 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 units with a constraint area > 20,000 km^2. Some adjacent sub-basins were further grouped in order to optimize the sampling effort (*i.e.* the number of sampling sites in each sub-basin). The sub-basins located in the river mainstem were delineated based on the distance between two main tributaries entering the mainstem. This resulted in 97 sub-basins covering the entire Amazon system (Oberdorff et al. 2019) (Figure 1 and Table S1).

Survey completeness analysis

We evaluated the survey completeness and sampling effort of the AmazonFish database using three analytical approaches proposed by Troia & McManamay 2016. An “expected” richness was estimated for each sub-basin using the Chao2 non-parametric richness estimator (‘Chao2’, in the *fossil* Package from R ;Vavrek 2011; R Core Team 2019) in order to calculate a sub-basin completeness ratio (*i.e.* observed species richness divided by estimated richness). A sub-basin achieving a completeness ratio higher than 0.6 can be 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 the *vegan* Package from R; Oksanen et al. 2019; R Core Team 2019). High completeness is characterized by a slope approaching zero (slope ≤ 0.15), meaning that the richness has reached an asymptote with the currently available number of occurrence records (Yang et al. 2013; Troia & McManamay 2016). Finally, we used the density of occurrences recorded for each sub-basin as a measure of sampling effort.

We finally applied logistic models (binomial ‘glm’, in the *stats* Package from R Core Team 2019) to verify that these completeness values did not influence sub-basins probability to be selected within each template (*i.e.* we verified that better sampled sub-basins had equal chances to be selected as less sampled ones).

<u>*Criteria to select sub-basins for each template*</u>

Three ecological criteria were used to describe the sub-basins in each template, namely (1) irreplaceability, (2) representativeness and (3) vulnerability (Zachos & Habel 2011).

(1) Irreplaceability was measured using the “corrected weighted endemicity” index defined by Crisp et al. (2001). This index was calculated as the sum of each species present in a sub-basin weighted by the inverse of the number of sub-basins where the species occurs and divided by the total species richness of the sub-basin. This index measures the ‘proportion’ of restricted-

range species in a sub-basin and ranges from 0 to 1, a sub-basin having 100% of species present only in this sub-basin (and nowhere else) reaching a maximum value of 1.

(2) Representativeness was measured using the total species richness in each sub-basin (Fleishman et al. 2006; Carrara et al. 2017). We further ensured *a posteriori* that the selected sub-basins also represented, at the template scale, the full variability of habitat types existing in the whole Amazon basin (*i.e.* floodplains, small streams and large rivers).

(3) Vulnerability was quantified by measuring the degree of human impact in each sub-basin based on two descriptors, *i.e.* sub-basins degree of deforestation and fragmentation by dams. These two descriptors are known to alter freshwater ecosystems and their biodiversity (Vörösmarty et al. 2010; Castello & Macedo 2016; Dias et al. 2017). We first used an empirical and policy-sensitive model of Amazon deforestation (SimAmazonia 1, Soares-Filho et al. 2006). This model produces simulated deforestation trends under different scenarios of road paving, deforestation rates and density of human population, thus indirectly integrating other important anthropogenic threats acting on Amazonian freshwater ecosystems such as agriculture, mining or urbanization (Castello and Macedo 2016). We used the 'business-as-usual' (BAU) scenario for 2018 to quantify the current degree of deforestation for each of our sub-basins. We added a second essential threat linked to the importance of spatial connectivity for fish dispersal processes (Fagan 2002), *i.e.* habitat fragmentation by dams (Winemiller et al. 2016; Carvajal-Quintero et al. 2017). The density of dams currently operational or under construction within a sub-basin was estimated using three datasets available at the Amazon basin scale (Winemiller et al. 2016; ANA 2017; Anderson et al. 2018). The two descriptors (*i.e.* degree of deforestation and habitat fragmentation by dams) were standardized using the Box-Cox power family (*vegan* Package from R; Oksanen et al. 2019; R Core Team 2019) and later averaged to obtain a single vulnerability value.

As sub-basin size affected species richness in our dataset (Oberdorff et al. 2019), we standardized our two ecological criteria (*i.e.* “corrected weighted endemicity” and total species richness) by taking the residuals of the linear regressions between values of the two criteria and the log-transformed area of sub-basins (Brooks 2006; Lamoreux et al. 2006).

The three standardized criteria (*i.e.* the “corrected weighted endemicity” for irreplaceability, the total species richness for representativeness and the level of threat for vulnerability) were further used to select the sub-basins within each template (*i.e.* the hotspots). It should be noted here that we assessed fish diversity in our sub-basins and conservation strategy templates using only criteria based on taxonomic richness, setting aside more recent indicators such as functional or genetic diversity (Vane-Wright et al. 1991; Desalle & Amato 2004; Stuart-Smith et al. 2013). However, the applicability of these indicators for Amazonian fishes remains difficult due to data deficiency on species functional traits and/or phylogenetic characteristics (Antonelli et al. 2018) and may not necessarily improve the results (Winter et al. 2013; Rapacciuolo et al. 2018).

Conservation strategy templates

We compared six conservation strategy templates: (1) pro-active 1, (2) pro-active 2, (3) pro-active 3, (4) reactive, (5) representative (Zachos & Habel 2011) and (6) balanced (Figure 2).

Pro-active approaches prioritize areas of low vulnerability that still harbor a large portion of undisturbed ecosystems, recommending conservation activities before disturbance reaches these areas (Sanderson et al. 2002; Brooks 2006). Three pro-active templates coexist: the first one uses the low vulnerability criterion alone, the second one adds irreplaceability to the low vulnerability criterion while the third one adds to it representativeness. Reactive approaches, for their part, prioritize areas of high vulnerability and high irreplaceability (Eken et al. 2004; Brooks 2006). The underlying principle is that conservation measures are most crucial in areas under immediate threat of destruction supporting a high number of rare species. Representative approaches highlight areas considered important for conserving a representative part of the biodiversity (both richness and endemism). These areas are selected for their high degree of irreplaceability and to a lesser extent representativeness, without considering vulnerability. Finally, we proposed the balanced approach which gives the same weight to the three criteria and thus identifies areas with high degrees of irreplaceability, representativeness and vulnerability.

For each template we selected 16 out of our 97 sub-basins, based on the 17% protection of terrestrial and inland water threshold recommended by the Convention on Biological Diversity, Aichi Biodiversity Target 11 (CBD 2010). While this 17% protection threshold is arbitrary and subject to criticism from an ecological point of view (Carwardine et al. 2009), it remains an important political target for guiding international conservation commitment (Zachos & Habel 2011). We selected sub-basins under each conservation strategy template described above using a rank procedure (*i.e.* the different criteria, irreplaceability, representativeness and vulnerability were ranked independently from 1, low values, to 97, high values, with an inverse rank for the low vulnerability criterion).

For the three pro-active templates, low vulnerability being the first criterion, we excluded the sub-basins having the highest values of vulnerability (using the second quartile, > 50%). The low vulnerability criterion, used alone for the pro-active 1 template, was summed with the irreplaceability (pro-active 2 template) or representativeness criteria (pro-active 3 template) to finally identify the 16 sub-basins having the highest ranks. For the reactive template, we summed both the vulnerability and irreplaceability criteria. For the representative template, high irreplaceability being the first criterion, we first excluded sub-basins having the lowest values of irreplaceability (using the second quartile, < 50%) and summed the irreplaceability and representativeness criteria. For the balanced template, we summed the three criteria to identify the 16 sub-basins having the highest ranks.

We further verified that the selected sub-basins within each conservation strategy template were proportionally representative of the main habitat types occurring in the whole Amazon basin (*i.e.* floodplains using data gathered from Nardi et al. 2019, small streams (Strahler order 1 to 3) and large rivers (Strahler order 4 to 9) using data from Shen et al. 2017).

We quantified the total fish diversity encapsulated in each conservation strategy template (*i.e.* number of families, genera and species; number of Amazonian endemic species; number of threatened species). The number of threatened species was estimated using the IUCN and ICMBio 2018 Red Lists (*i.e.* 500 and 1000 species assessed, respectively). As the two previous lists were established using the same basic methodology (note that the ICMBio assessment was done at the national level, such that only species endemic to Brazil would be expected to correspond directly to those assessments made for the IUCN Global Red List), we combined them to obtain the conservation status for 66% of the total fish species recorded in the Amazon basin. Only species having the status Vulnerable, Endangered and Critically Endangered were considered threatened (*i.e.* a total of 43 species).

The biodiversity "protected" (*i.e.* species recorded within protected areas) was quantified for each template using the existing protected areas network (combining PAs and ILs, RAISG 2019, Figure S3). The biodiversity "unprotected" (*i.e.* not benefiting from any protection measure at the Amazon basin scale) was also estimated for each template.

Finally, we run a simple sensitivity analysis to evaluate the relevance of the 17% protection threshold (*i.e.* 16 selected sub-basins) by comparing the fish diversity encapsulated within each template when applying a lower or higher threshold (10 or 22 sub-basins selected, respectively 11% or 23%).

Prioritization

The characterization of the land cost and initial conditions (area of land currently deforested, converted or protected) 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). We did not quantify the land cost but characterized the initial conditions at the sub-basin scale (degree of deforestation, habitat fragmentation by dams, protected areas) and identified sub-basins that could face an increase in deforestation and dams building in the future (2050). To do this, we used the SimAmazonia 1 model of deforestation (under the 'business-as-usual' BAU scenario) for 2050 (Soares-Filho et al. 2006) and the projected future density of dams in the basin (*i.e.* 119 projected large dams in addition to the 78 already existing ones) (Winemiller et al. 2016; ANA 2017; Anderson et al. 2018). The two descriptors (degree of deforestation and density of dams) were standardized following the same method as the one implemented for the vulnerability criterion (Box-Cox power family), after grouping current and future data to ensure a common distribution of values. We averaged the two standardized descriptors in a single one to obtain current and future vulnerability values. The sub-basins of the third quartile (25% of the sub-basins with the highest values of vulnerability) were considered threatened. The biodiversity currently threatened and potentially threatened in 2050 was quantified for each conservation strategy template (*i.e.* number of families, genera, total and endemic species recorded only in the sub-basins considered threatened).

We could not evaluate here the potential effects of climate change on selected sub-basins due to methodological constraints. Indeed, the use of Species Distribution Models (SDMs) to simulate changes in species distribution and ultimately future sub-basins richness requires at least 10 occurrence points by species. This was unfortunately possible for only 60% of the fauna, excluding most of endemic species that constitute the core of the irreplaceability criterion

(Oberdorff et al. 2019). Nevertheless, climate change could impact Amazonian fish communities by changing water temperatures, water availability and discharge (Knouft & Ficklin 2017). These changes may generate shifts in the distribution of species following their habitat preferences and could lead in fine to local or regional population extinctions in case of total loss of suitable habitats (Comte & Olden 2017). However, considering the Amazon basin as a whole, only moderate water temperature increases (< 1.0°C on average) and moderate changes in the timing and magnitude of seasonal streamflow are predicted for 2050, whatever the scenario considered (Van Vliet et al. 2013, 2016; Eisner et al. 2017). These projections thus minimize the strength of the future impact of these drivers on our sub-basins biodiversity even if some modelling studies suggest that the combination of climate change and deforestation could increase regional drying and consequent extinction processes due to freshwater habitat shrinking in the south eastern part of the basin (Davidson et al. 2012; Leadley et al. 2014).

Results and Discussion

Survey completeness analysis

The two survey completeness descriptors generally confirm the quality of our database, with 70% of the sub-basins being considered at least once well-surveyed (68 over 97 sub-basins, Chao2 completeness ratio and SAC slope, Figure 3). The sampling effort (density of occurrence) is more important in the Amazon mainstream (Figure 3). However, apart from our three proactive templates, survey completeness and sampling effort seems to influence sub-basins selection for the reactive (*i.e.* SAC slope), representative (*i.e.* SAC slope and density of occurrences) and balanced (*i.e.* Chao2 completeness ratio and density of occurrences) templates, currently weakening their robustness (see Supplementary materials, Table S2).

Geographical patterns of ecological criteria

The three criteria used to select our different sub-basins (*i.e.* the “corrected weighted endemicity” for irreplaceability, the total species richness for representativeness and the level of threat for vulnerability), show different geographical patterns (Figure 4). The sub-basins with the highest levels of irreplaceability are located in upstream (western) parts of the Amazon basin whereas the lowest values are found in the Amazon mainstream and its main lowland tributaries, with the notable exception of the most south eastern part of the basin (*i.e.* Tapajós and Xingu Rivers) also showing high levels of endemism. The sub-basins with the highest levels of representativeness (*i.e.* those hosting more than 500 species) are located in the lowland Amazon and its two main tributaries, the Negro and Madeira Rivers. According to the vulnerability criterion, 17 sub-basins can be considered threatened (third quartile of vulnerability, > 75%) with a mean deforestation of 34% and a mean density of dams of 0.29 (see Supplementary materials, Figure S2). These sub-basins are mostly located in the Andean and south eastern parts of the basin (e.g. Marañon, Ucayali, Madeira and Tapajós Rivers, Figure 4).

Biodiversity concerned under our conservation strategy templates

Our six conservation strategy templates, according to their criteria, highlight sub-basins in various parts of the Amazon basin (Figure 5). The three pro-active templates mainly identify sub-basins in the central part of the Amazon basin, with a high number of sub-basins in common (*i.e.* from 7 to 10, see Supplementary materials, Table S3). The reactive template highlights sub-basins in the upper western or southeastern parts of the basin (Figure 5). The representative and balanced templates select sub-basins displaying no obvious geographical pattern (10 sub-basins in common, see Supplementary materials, Figure 5 and Table S3).

The different conservation strategy templates are mostly equivalent in terms of surface area selected (15-19% of the Amazon basin area) and are representative in terms of surface area already under protection measures (15-31% of PAs and 23-46% of ILs, against respectively 26% and 30% at the Amazon basin scale) (Table 1). The three pro-actives templates contain the highest proportion of surface area already under protection measures (28-31% of PAs, 39-46% of ILs) whereas the reactive template contains the lowest proportions (15% of PAs, 23% of ILs, Table 1). All templates are representative of the three main freshwater habitats considered at the Amazon basin grain, *i.e.* floodplains (8-22% against 16%), small rivers (85-87% against 86%) and large rivers (13-15% against 14%) (Table 1).

The template containing the highest level of fish diversity, with 82% of Amazonian species and 74% of Amazonian endemic species is the representative one. The balanced, pro-active 2 and pro-active 3 templates present an intermediate state with respectively 78-71-71% of Amazonian species and 70-60-60% of the Amazonian endemic species represented (Table 2). The reactive and pro-active 1 templates have the lowest levels of species and endemics richness (respectively 66-63% and 57-50%). The number of threatened species (43 species in the IUCN and ICMBio 2018 red lists) is, as expected, highly dependent of the vulnerability criterion, being very low in the pro-active templates (less than 10 species in the pro-active 1-3, and 20 species in the pro-active 2 templates), high in the representative and balanced templates (respectively 33 and 30 species) and very high in the reactive template (41 of the 43 Amazon basin threatened species) (Table 2).

On the one hand, at the Amazon basin grain, 1,990 species and 1,043 endemics are currently recorded inside PAs and ILs, representing 84% of Amazonian species and 77% of Amazonian endemics (Table 2). This apparently high level of protected biodiversity must be put into perspective as the actual configuration of the protected areas (PAs and ILs) network ignores freshwater ecosystems and their hydrological connectivity. On the other hand, 34 genus, 365 species and 308 endemics do not currently benefit from any protection measure at Amazon basin scale (Table 2). The representative and balanced templates offer an important benefit in terms of protection, with ~ 40% of the unprotected biodiversity (overall species and endemics) included in these templates, followed by the reactive and pro-actives 2-3 templates that also encapsulate ~30% of this biodiversity (Table 2).

Our sensitivity analysis evaluating the 17% threshold area to be protected recommended by the Aichi Biodiversity Target 11 of the Convention on Biological Diversity (CBD 2010) shows a 11% mean decrease in the total number of endemics species when applying a 11% threshold (10 sub-basins selected) compared to the 17% one, and an increase of only 5% when applying a threshold of 23% (22 sub-basins selected) (see Supplementary materials, Table S4). In view of the substantial increase in surface area under the 23% threshold (27-41% of the template area) for relatively little gains in terms of protected species, the selection of 16 sub-basins, guided by the 17% threshold recommended, appears to be a good compromise.

Current and future fish biodiversity preserved under our conservation strategy templates

We evaluated for each template the evolution of threats for 2050 (*i.e.* degree of deforestation and habitat fragmentation by dams) in their selected sub-basins (Figure 6). The sub-basins selected by the three pro-active templates will remain mostly unaffected by the predicted change in these threats, except for a few of them that may suffer from increasing deforestation (Figure 6 and Supplementary materials, Table S5). In contrast, the majority of the sub-basins identified by the reactive template are currently threatened and predicted to be further threatened by 2050 (with 57% of the template area predicted to be deforested in 2050 and an important projected increase of the density of dams, see Table 3 and Table S5). The representative template, which by definition does not consider the vulnerability criterion, presents a more contrasted situation, with sub-basins remaining relatively preserved and others facing an increase in threats (Table 3, Figure 6). The balanced template presents a majority of sub-basins currently threatened and, for most of them, predicted to be further threatened in 2050 (Table 3, Figure 6).

Each template highlights different situations regarding the current and future threatened biodiversity. Considering the unthreatened biodiversity, the representative template seems the best compromise, currently containing 77% of the Amazonian species and 66% of the Amazonian endemic species, followed by the pro-active 2 and 3 (containing 71% of the Amazonian species and 60% of the Amazonian endemic species) and pro-active 1 (63-50%) templates (Table 3). The balanced and reactive templates, with a high number of sub-basins considered threatened, contain a lower level of Amazonian fish fauna (respectively, 62-46% of the Amazonian species and 48-33% of the Amazonian endemic species) (Table 3).

Considering now the projected future threats in 2050, the ranking obtained is overall the same but with lower percentages of unthreatened biodiversity, with the representative template still containing 72% of the Amazonian species and 60% of the Amazonian endemic species, followed by the pro-active 2 and 3 (containing 71% of the Amazonian species and 60% of the Amazonian endemics) and pro-active 1 (63-50%) templates (Table 3). The balanced and reactive templates should face an increase in threat levels and contain an even lower proportion of the fish fauna (55-40% for the balanced template and 23% of the Amazonian species, 11% of the Amazonian endemic species for the reactive template, Table 3).

Synthesis

The comparison of different conservation strategy templates (*i.e.* pro-active 1-2-3, reactive, representative and balanced templates), using three criteria (vulnerability, irreplaceability and representativeness) under current and future scenarios, is an exercise most often absent in conservation planning studies. This exercise allows us to discuss advantages and constrains linked to each template and, even if our results are obviously case specific, could help generating some general principles for prioritization of conservation strategies. On the one hand, we can suggest from the above that to protect the 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 insofar as no additional threats occur between now and our projected trends for 2050. However, the sub-basins selected within this template are unfortunately influenced by the survey completeness, weakening slightly its robustness. Even if the AmazonFish database is the most complete and up-to-date information currently available on freshwater fish species distribution at the sub-basin grain for the entire Amazon drainage (Jézéquel et al. 2019; Oberdorff et al. 2019), under sampled areas obviously still exist *(i.e.* the Wallacean shortfall, Antonelli et al. 2018). The AmazonFish project has already started to fill in 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 campaigns in under-sampled areas in Colombia, Peru and Brazil (DoNascimiento et al. 2017).

On the other hand, the proactive 2 and 3 templates, not influenced by survey completeness and also respectively integrating high levels of irreplaceability and representativeness in addition to low vulnerability, seem more robust approaches for planning conservation prioritization. Sub-basins within these templates currently suffer from no habitat fragmentation and very low degree of deforestation (less than 4%) and should remain mostly undisturbed in the near future (generally less than 16% of expected deforestation in 2050 and only one new dam by template expected in 2050, see Table S5). Hence these templates select sub-basins that are still functionally intact and, therefore, more valuable from a conservation perspective (Wilson et al. 2006, 2007; Bottrill et al. 2008). Further, given that around 65% of the area encapsulated in these two templates is already covered by PAs and ILs, the expanded protected area should be minimal, as far as PAs and ILs operate effectively. Indeed, many protected areas have experienced increases in human pressure since declaration, suggesting a real gap in the management of protected areas with regards to halting habitat loss and intensified human use (Adams et al. 2019).

By contrast, templates integrating high vulnerability as one of the criteria to define areas for the protection of biodiversity (*i.e.* the reactive and balanced templates) seem little credible in front of the costs of achieving this goal. For instance, in our specific case, the number of large dams that would need technical solutions to maintain the fluvial system connectivity (*i.e.* essential to ensure dispersion processes of aquatic organisms Carvajal-Quintero et al. 2019) and dam projects revisited (e.g. optimizing dam placement to more effectively balance conflicting energy and biodiversity interests), to protect current and future fish diversity encapsulated in these two templates is far from marginal (*i.e.* 32 and 39 dams, respectively, for the balanced template; 42 and 87 for the reactive one, see Supplementary materials, Table S5). Further, protection measures would be needed to also limit the important expected increase in deforestation in these two templates (more than 40% of the area impacted for the reactive template in 2050, up to 57% for the balanced one, see Supplementary materials, Table S5). The compromises required to protect fish biodiversity in these two templates appear thus extremely difficult to achieve, provided that any protection measures could be really considered due to political priorities towards the development of small and large hydropower dams projects for energy supply (Latrubesse et al. 2017; Anderson et al. 2018), increase in deforestation for plantations, logging or cattle ranching (Seymour & Harris 2019) and shifts in protected areas policy (Golden Kroner et al. 2019; Visconti et al. 2019; Ferrante & Fearnside 2019). Further, a template focusing only on pristine areas (*i.e.* the proactive 1 template) is clearly not a good option for ecosystem protection because providing, at least in our case, limited biodiversity benefits and thus little conservation value.

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 identified here. These KBAs, which are delineated within sub-basins, are defined as 'sites contributing significantly to the global persistence of biodiversity' (http://www.keybiodiversityareas.org/home; see for example Holland et al. 2012). KBAs can support the strategic expansion of protected area networks by governments and civil society working toward achievement of the Aichi Biodiversity Targets (in particular Target 11 and 12), as established by the Convention on Biological Diversity (CBD 2010). KBAs may also inform private sector safeguard policies, environmental standards, and certification schemes, and support conservation planning and priority-setting at national and regional levels.

Finally, we only focused here on freshwater fishes. Even if this taxon can eventually serve as an umbrella for other freshwater organisms (Tisseuil et al. 2013), it may be interesting to extend the approach to other freshwater taxonomic groups and test the congruence between sub-basins highlighted in our six templates and the ones obtained using these other groups (He et al. 2018).

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Tables and Figures

Table 1: Coverage of protected areas (*i.e.* Protected Areas and Indigenous Lands, RAISG, 2019) and of freshwater habitats in each conservation strategy template (Floodplain areas from Nardi et al., 2019, River Strahler Order categorization from Shen et al., 2017).

	Percentage (Total Surface area in km^2)				Percentage	
Template	Template area	Protected Areas (PAs)	Indigenous Lands (ILs)	Floodplain	River Strahler Order 1-3	River Strahler Order 4-9
pro-active 1	15 (912 830)	28 (256 590)	43 (388 517)	20 (182 289)	85	15
pro-active 2	15 (884 487)	29 (255 726)	46 (409 395)	20 (181 296)	85	15
pro-active 3	18 (1 068 115)	31 (330 604)	39 (417 472)	22 (236 159)	85	15
reactive	18 (1 081 958)	15 (157 810)	23 (247 567)	8 (83 192)	87	13
representative	19 (1 104 674)	21 (235 561)	38 (414 811)	18 (202 415)	86	14
balanced	17 (994 088)	17 (172 680)	27 (264 009)	15 (151 292)	87	13
Amazon Basin	5 896 663	26 (1 529 559)	30 (1 783 229)	16 (962 835)	86	14

Table 2: Biodiversity encapsulated in each conservation strategy template; Biodiversity "protected" (*i.e.* recorded within templates' Protected Areas and Indigenous Lands); and Biodiversity "unprotected" (*i.e.* beneficing of no protection measure at the Amazon basin scale).

	Biodiversity: Percentage (and number)					Biodiversity "protected"		Biodiversity "unprotected"		
Template	Families	Genera	Total species	Amazonian endemic species	IUCN Threatened species	Total species	Amazonian endemic species	Genera	Total species	Amazonian endemic species
pro-active 1	95 (53)	83 (428)	63 (1 487)	50 (676)	3	1 222	524	9	61	48
pro-active 2	95 (53)	89 (456)	71 (1 676)	60 (804)	20	1 408	618	12	108	95
pro-active 3	96 (54)	86 (442)	71 (1 682)	60 (810)	7	1 380	619	12	120	97
reactive	98 (55)	86 (442)	66 (1 552)	57 (770)	41	1 061	485	19	136	116
representative	96 (54)	93 (478)	82 (1 935)	74 (998)	33	1 562	721	15	172	137
balanced	98 (55)	90 (465)	78 (1 830)	70 (949)	30	1 414	654	15	171	142
Amazon Basin	56	514	2 355	1351	43	1 990	1 043	34	365	308

Table 3: Biodiversity threatened in each conservation strategy template, at present and in 2050 (*i.e.* recorded only within threatened sub-basins). By definition, the three pro-active templates have no sub-basin threatened.

	Current			Percentage (and number)		2050			Percentage (and number)	
Template	Number of sub-basins (Area in km2)	Families	Genera	Total species	Amazonian endemic species	Number of sub-basins (Area in km2)	Families	Genera	Total species	Amazonian endemic species
pro-active 1	0	0	0	0	0	0	0	0	0	0
pro-active 2	0	0	0	0	0	0	0	0	0	0
pro-active 3	0	0	0	0	0	0	0	0	0	0
reactive	10 (762 410)	3	64	30 (463)	42 (327)	15 (1 075 768)	8	197	66 (1021)	81 (627)
representative	3 (236 972)	0	9	6 (122)	10 (102)	4 (278 410)	0	34	12 (233)	18 (181)
balanced	8 (658 995)	3	39	20 (370)	32 (301)	10 (705 695)	3	69	29 (535)	44 (414)

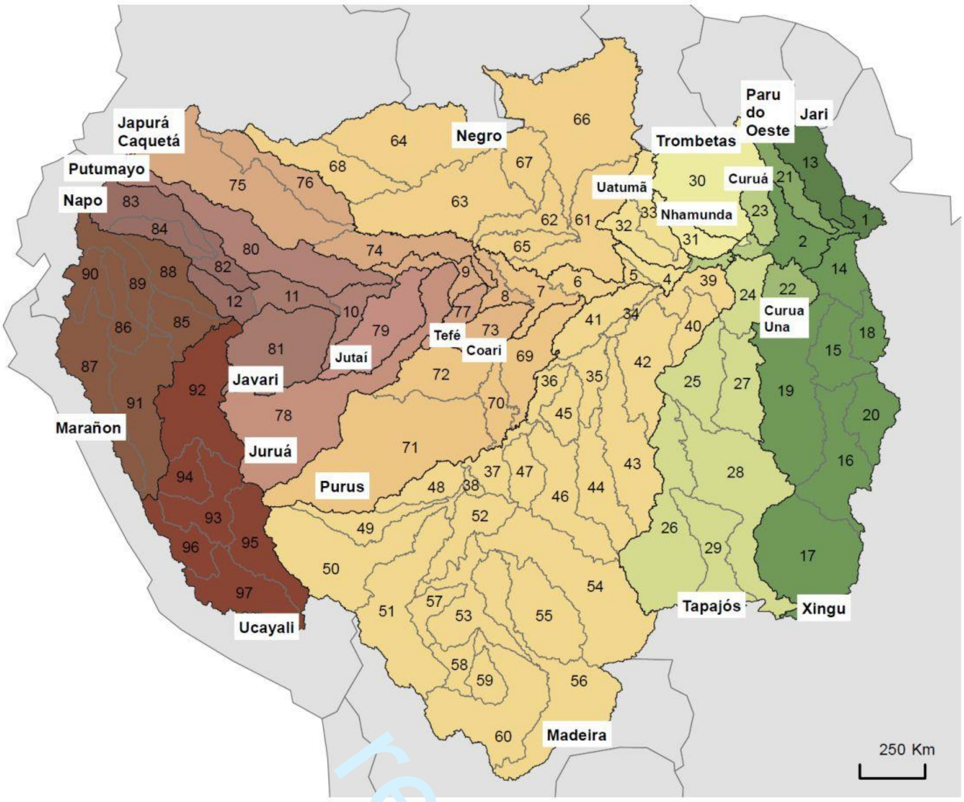

Figure 1: Delimitation and codes of the 97 sub-basins used in the study (see corresponding names in Table S1), based on a modified version of HydroBASINS (see methods). The Main tributaries of the Amazon basin are represented in different colours and their name is added in bold.

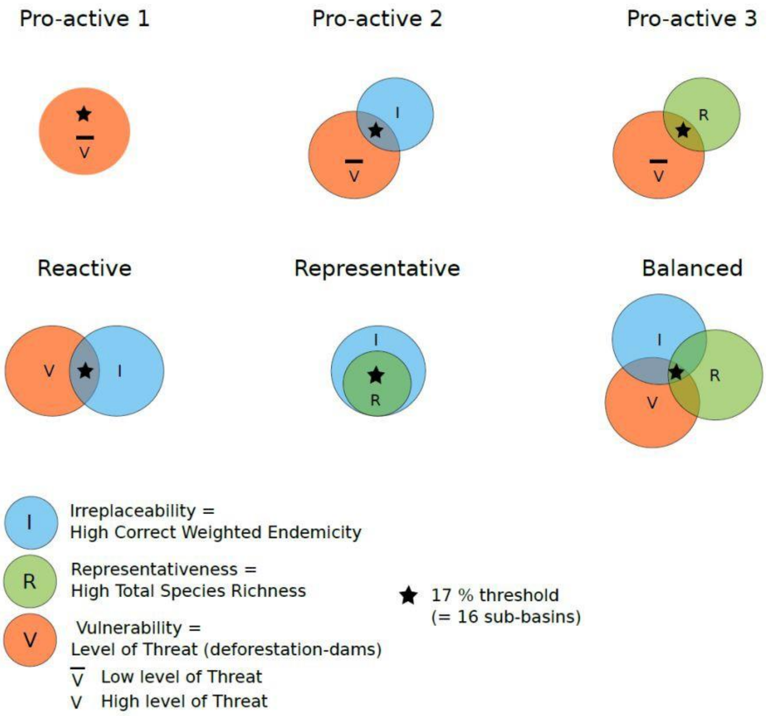

Figure 2: Schematic vision of the six conservation strategy templates and the three criteria involved. The size of the circles is proportional to the importance of each criterion as defined in each conservation strategy template.

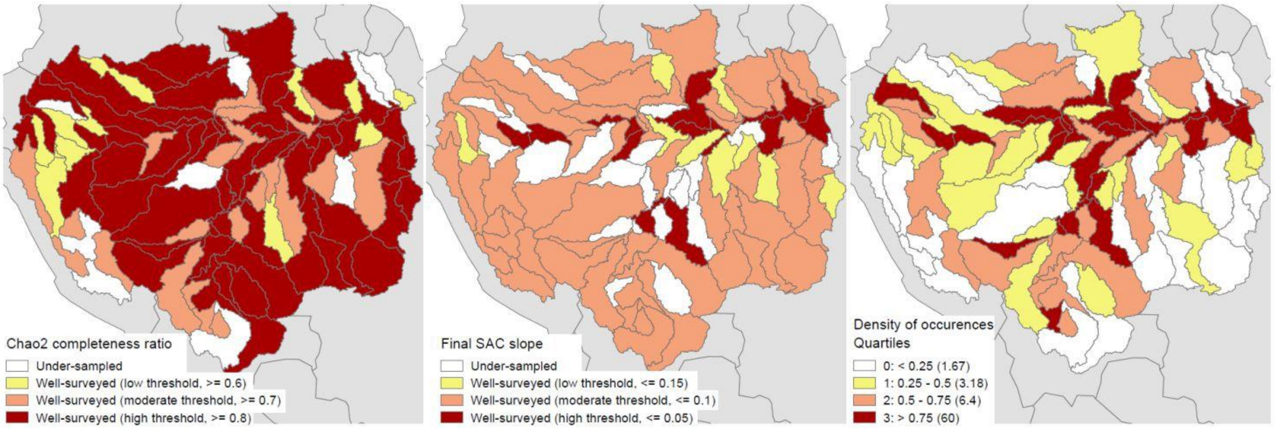

Figure 3: Distribution of the "well-surveyed" and under-sampled sub-basins (using the Chao2 completeness ratio, the right end of the slope of species accumulation curve (SAC) and the density of occurrences). The colour classification is based on Troia & McManamay (2016), with low (i.e. liberal), moderate and high (i.e. conservative) thresholds to define the well-surveyed sub-basins.

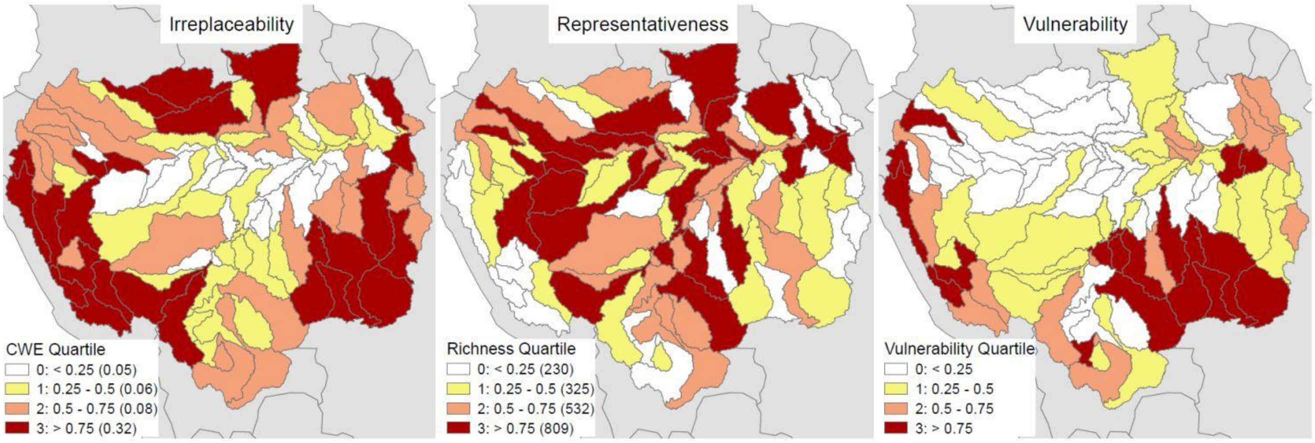

Figure 4: Distribution of the three criteria included in our conservation strategy templates: Irreplaceability ("corrected weighted endemicity", CWE), Representativeness (total species richness) and Vulnerability (level of threat based on the degree of deforestation and habitat fragmentation by dams) using the quartiles discretisation with the relative values in brackets.

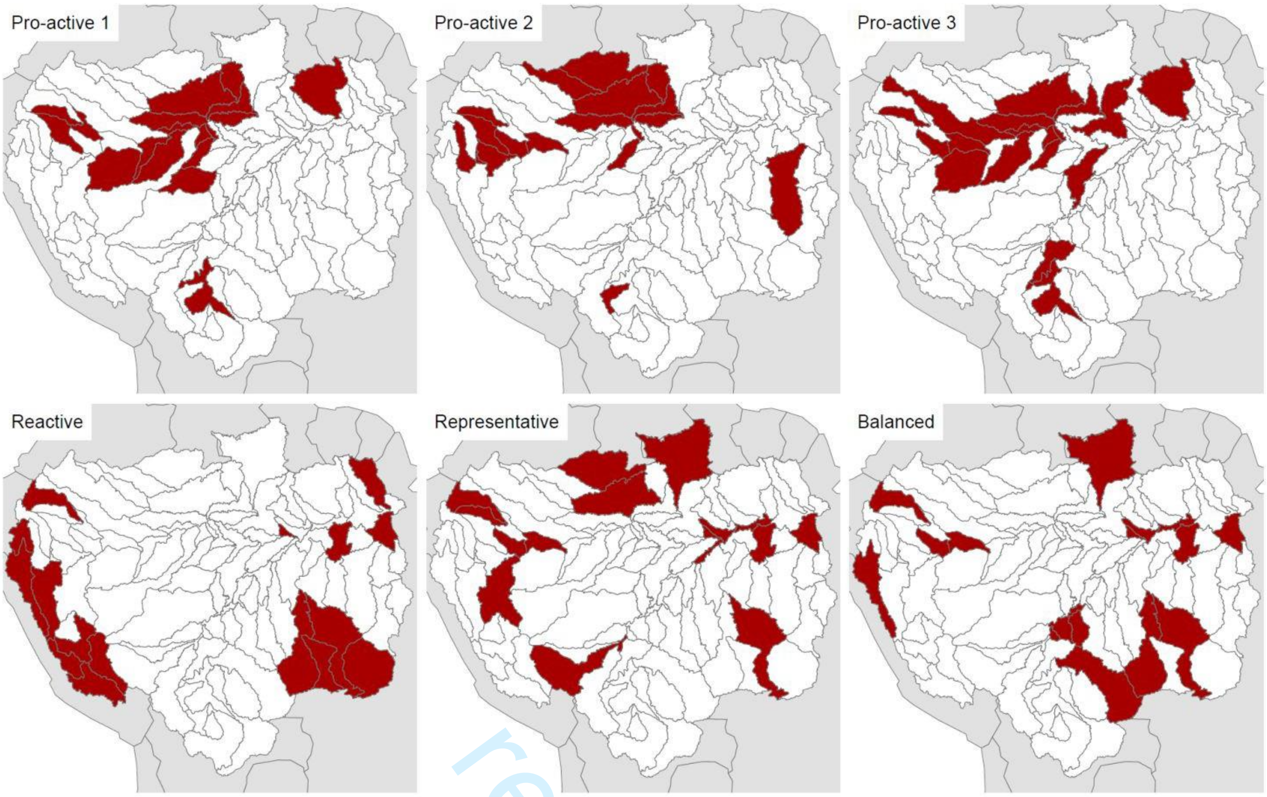

Figure 5: The 16 sub-basins selected (in brown) by each conservation strategy template (Pro-active 1-2-3, Reactive, Representative and Balanced).

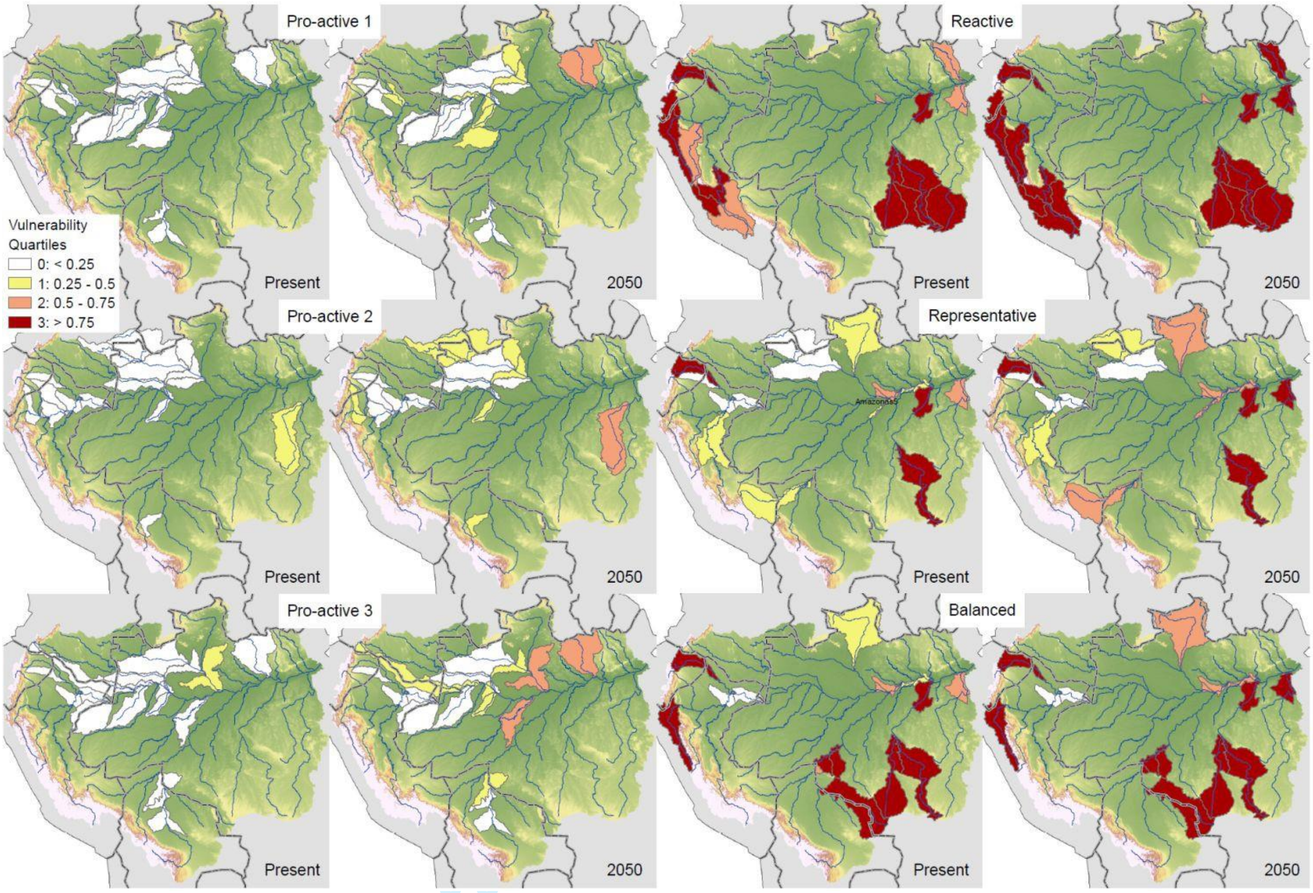

Figure 6: Vulnerability (level of threat: degree of deforestation and habitat fragmentation by dams) using the quartiles discretisation for the 16 sub-basins selected by each conservation strategy template (Pro-active 1-2-3, Reactive, Representative and Balanced) at present and in 2050.