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The representativeness of protected areas for Amazonian fish diversity under climate change

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Abstract

1. The Amazon basin has been subjected to extreme climatic events and according to climate change projections this hydrosystem could face changes in the natural dynamic of flood cycles that support the feeding and reproduction of many fish species, threatening aquatic biodiversity.
2. Protected areas (PAs) are the main tools used to safeguard the biodiversity in the long term; however, they are fixed areas that could be subject to climate change, questioning their future efficiency in protecting biodiversity.
3. The Amazon basin currently benefits from a relatively high level of protection as 52% of its catchment area is under the form of true PAs or indigenous lands. However, the capacity of these PAs to protect freshwater biodiversity remains unclear as they have generally been assessed with little regard to freshwater ecosystems and their hydrological connectivity. Here, the aim was to evaluate the effectiveness of PAs in representing the Amazon fish fauna under current and future climatic conditions.
4. A macroecological approach was used to estimate the minimum size of the geographical range needed by each species to achieve long-term persistence, by a combined function of range size and body size, two ecological traits known to influence species extinction risk.
5. In future the Amazon basin could risk losing 2% of its freshwater fish fauna owing to unsuitable climatic conditions, with a further 34% adversely affected. The present Amazon network of PAs will cover the minimum required range for species persistence for more than 60% of the freshwater fish species analysed under the future climate scenario. However, more than 25% of the future susceptible species are currently concentrated in large tributaries and in the central-lower Amazon floodplain where few PAs occur, highlighting the lack of appropriate conservation actions for these specific water bodies.

† *In memoriam.*

KEYWORDS

Amazon basin, climate change, freshwater ecosystem conservation, protected areas, range–body size relationship, riverine fishes, species distribution models

1 | INTRODUCTION

Freshwater ecosystems are highly dependent on the processes occurring in the surrounding landscape (Fausch, Torgersen, Baxter, & Li, 2002), and this characteristic makes them highly susceptible to human pressures (Vörösmarty et al., 2010). These pressures have led to habitat loss or fragmentation and alterations in hydrology, water chemistry and trophic food webs (Reid et al., 2019), and to an increase in the rate of species loss (Dias et al., 2017; Reid et al., 2019). Among the indirect threats, climate change through increasing temperatures can also have significant effects on freshwater species, particularly on those at present living close to their thermal upper tolerance limits (Strayer & Dudgeon, 2010; Tewksbury, Huey, & Deutsch, 2008). In temperate rivers, freshwater fish species have already shifted their ranges upstream in response to climate change (Comte, Buisson, Daufresne, & Grenouillet, 2013), whereas shifts in the distribution of tropical fish species have not yet been thoroughly evaluated, even if most lowland tropical freshwater species are expected to tolerate warmer conditions (Comte & Olden, 2017). Climate change will also lead to hydrological changes owing to modifications in the amount and timing of precipitation (Allan, Palmer, & Poff, 2005), changing the natural dynamic of flood cycles that support the feeding and reproduction of many fish species (Alho, Reis, & Aquino, 2015) and potentially leading to species extinctions (Tedesco et al., 2013).

Protected areas are designed to achieve the long-term conservation of biodiversity, ensuring the persistence of ecosystem services and cultural values (Pittock, Hansen, & Abell, 2008). They also play an essential role in climate change mitigation by slowing deforestation and thus maintaining carbon storage (Nepstad et al., 2006; Ricketts et al., 2010; Soares-Filho et al., 2010). However, PAs are fixed areas in the landscape, making climate change a potential issue for their conservation efficiency (Hannah, 2008). The PAs in tropical ecosystems have mostly been established and designed based on terrestrial organisms and ecosystems, relegating aquatic conservation to the hope that it will converge with terrestrial conservation (Azevedo-Santos et al., 2019; Fagundes, Vogt, & De Marco, 2016; Frederico, Zuanon, & De Marco, 2018; Lawrence et al., 2011). The capacity of these PAs to protect freshwater biodiversity remains unclear, however, as they do not formally take into account hydrological connectivity, an essential component for the dispersal of aquatic organisms. Indeed, given the severe restriction to the dispersal of freshwater organisms within the dendritic river network (Benda et al., 2004; Carvajal-Quintero et al., 2019; Grant, Lowe, & Fagan, 2007), the established PAs may inadequately protect aquatic ecosystems and their associated fauna (Abell, Lehner, Thieme, & Linke, 2017; Frederico et al., 2018).

The Amazon basin is the largest drainage on Earth with an area of about 6 million km^2 (excluding the Tocantins River) and encompassing parts of seven countries (Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru and Venezuela). Present estimates indicate that 42% of the Amazon catchment area is protected, i.e. hydrological units included within PAs and having their upstream part protected (see Abell et al., 2017 for details). However, as river size increases the degree of protection decreases, reaching only around 20% (Abell et al., 2017). The Amazon fish fauna contains about 15% of the world's fish species (Jézéquel, Tedesco, Bigorne, et al., 2020; Oberdorff et al., 2019; Tedesco et al., 2017). This hyper-diverse ichthyofauna has been imperilled by the growing impacts generated by human activities (Castello et al., 2013). Thus, advancing knowledge on current and future vulnerability levels of the Amazon freshwater fish species can be useful for efficient management and conservation actions.

Evaluating the level of threat of the fish fauna is a challenging task, but quantifying the extent of a species' distributional range within the system of PAs (i.e. species representativeness) has been widely adopted as a rapid and effective tool for evaluating conservation strategies in large areas (Ribeiro, Martins, Martinelli, & Loyola, 2018; Rodrigues et al., 2004; Scott et al., 1993). Another related way is to estimate species' susceptibility, i.e. the species vulnerability limit or the minimum size of the geographical range that each species needs for long-term persistence (Gaston & Blackburn, 1996; Le Feuvre, Dempster, Shelley, & Swearer, 2016). 'Susceptibility limit' is used hereafter in order to avoid confusion with other classifications such as those of the International Union for Conservation of Nature (IUCN). It is widely known in macroecology that small species can have both small and large geographical ranges, whereas large species occupy large geographical areas for maintaining viable populations, owing to their dispersal, habitat and energy requirements (Brown & Maurer, 1987, 1989; Gaston & Blackburn, 1996). These assumptions have been advanced to explain the triangular relationship between species' geographical range and body size, also one of the earliest patterns documented in macroecology (Brown, 1995) and observed across a large number of taxonomic groups and geographical scales, including freshwater fishes (Carvajal-Quintero et al., 2017). The upper boundary of this triangular relationship corresponds to the spatial extent of the study area and the lower boundary corresponds to the susceptibility limit of the species (Figure 1) and represents the minimum range size below which species persistence is not assured (Gaston & Blackburn, 1996). This limit has been widely considered a measure of extinction risk (Agosta & Bernardo, 2013; Carvajal-Quintero et al., 2017; Diniz-Filho, 2004; Diniz-Filho et al., 2005; Gaston & Blackburn, 1996; Le Feuvre et al., 2016; Pyron, 1999; Rosenfield, 2002). Therefore, identifying this low theoretical boundary for the Amazonian fish species is important for estimating species persistence within PAs under future climate change.

Here, an evaluation of the present and future distributions of 1,293 freshwater fish species inhabiting the Amazon basin (out of the

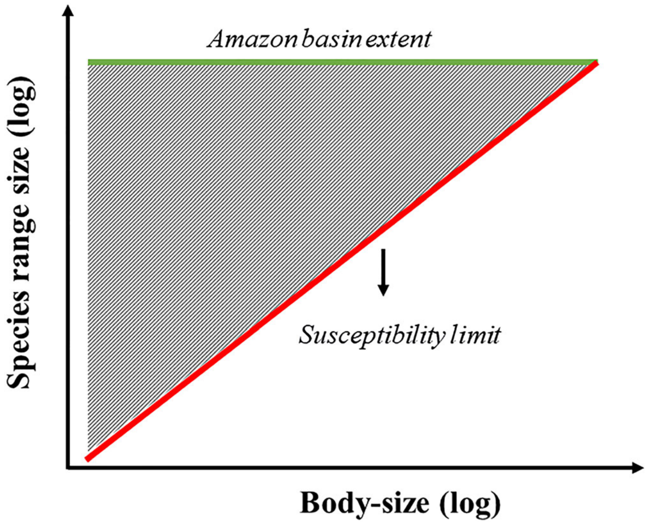

FIGURE 1 Representation of the triangular relationship between species geographical range and body size

2,400 species already recognized) has been performed in order to assess the capacity of the current PA network to protect the fish fauna now and in the near future.

2 | METHODS

2.1 | Species distribution models

Species distribution models (SDMs) were used to estimate species geographical ranges from information on the present and future climate. Species occurrence records (presence only) were obtained from the AmazonFish Project database (∼*c*. 2,400 species; Jézéquel, Tedesco, Bigorne, et al., 2020). SDMs were constructed for 1,293 species with more than 10 occurrence points from the AmazonFish project database (nearly 54% of all valid Amazonian species). To model the distribution of species, 19 bioclimatic variables related to temperature and precipitation (averaged for the period 1950–2000) were extracted from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), together with a set of biologically meaningful physical variables: i.e. elevation (Global Digital Elevation Model), elevation range, maximum slope, stream length and flow accumulation (Domisch, Amatulli, & Jetz, 2015). To represent the future climatic conditions, the HadGEM2AO and MIROC5 Global Circulation Models were selected under the representative concentration pathway 'business as usual' – RCP 8.5 (the 'worst-case' scenario of carbon emission) for 2050. These last two models represent the less biased ones available for the Amazon region (Joetzjer, Douville, Delire, & Ciais, 2013). Biological data were aggregated at the grid scale corresponding to the resolution of the bioclimatic dataset (10 km^2). For both bioclimatic and physical variables, the least correlated variables (Pearson's $r < 0.70$) were selected, and the most ecologically meaningful one kept when two variables were correlated with Pearson's $r \geq 0.70$ (Braunisch et al., 2013). Distributions were projected under the BIOMOD2 platform (Thuiller, Lafourcade, Engler, & Araújo, 2009) using five modelling techniques (Generalized Linear Model, Generalized Additive Model, Generalized Boosted Model, Multivariate Adaptive Regression Splines and Maximum Entropy). The procedure comprised three sets of 1,000 randomly selected pseudo-absences with equal weighting for presence and absence. The models were calibrated with 70% of the data selected at random and the predictive performance of each model was evaluated on the remaining 30% with the area under the relative operating characteristic curve and the true skill statistic (TSS) (Jézéquel, Tedesco, Darwall, et al., 2020; Leroy et al., 2014; Oberdorff et al., 2019). This process was repeated three times. To produce robust distributional forecasts, an ensemble forecast method was applied to combine the five modelling techniques (Thuiller et al., 2009). Models with TSS values <0.6 were discarded and the current consensus distributions were obtained by averaging distributions with weights proportional to their TSS values. Probability maps were transformed into maps of suitable vs. non-suitable areas by choosing the probability threshold that maximized the TSS value. A detailed description of model-building procedures and environmental variables used here is given in Oberdorff et al. (2019).

2.2 | Representativeness of protected areas

The overlap between the Amazon PAs and the extent of the predicted range of species was used to evaluate the representativeness of each fish species inside PAs (Scott et al., 1993). This procedure was repeated for present and future climatic conditions. The Amazon PA shapefile was obtained from *The Amazon Geo-Referenced Socio-Environmental Information Network* (https://www.amazoniasocioambiental.org/en/, accessed August 2019).

Amazon PAs were restricted to areas under strict protection (IUCN protection area categories I–IV) or sustainable use (IUCN protection area categories V–VI) and Indigenous Lands, representing about 52% of the Amazon basin surface area (Jézéquel, Tedesco, Darwall, et al., 2020; Figure 2). Combining the protection template with present and future climatic conditions resulted in two representativeness scenarios: (1) current + PAs, based on current species range within the Amazon PAs; and (2) future + PAs, based on future climatic species ranges within Amazon PAs. To build these scenarios, the binary SDM models (see Section 2.1) and the Amazon PA shapefile were rescaled to 1 km pixel resolution rasters, which were then used to calculate the species representativeness within PAs. The species range raster and the PA raster were overlapped to calculate the area of species range inside the PAs. This procedure was repeated for each species under the two scenarios described above. All analyses were performed within the R environment (R Core Team, 2020) using the *raster* package (Hijmans, 2019).

2.3 | Susceptibility analysis

The relationship between log-transformed species geographical range size and body size to provide an estimate of their long-term

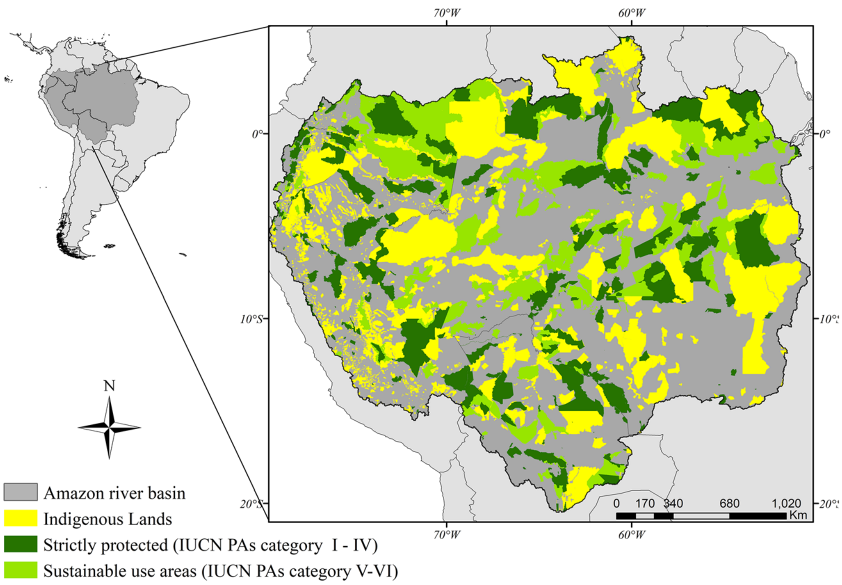

FIGURE 2 Map of the Amazon basin and its protected areas network

persistence probability is a well known macroecological pattern (Brown & Maurer, 1989; Diniz-Filho, 2004; Gaston & Blackburn, 1996). Usually, this relationship shows a triangular shape, where small-bodied species can have both small and large geographical ranges, whereas large-bodied species only occupy large geographical ranges, resulting in a minimum range size exhibited by species that tends to increase with body size. Thus, the lower limit of the triangular relationship represents a minimum range size required by species to achieve long-term persistence, as larger-bodied species require larger geographical range sizes in order to maintain minimum viable population sizes (Brown & Maurer, 1989). This lower limit set by the range size–body size relationship has recently been used in conservation approaches to identify species that are near or below this limit as species facing a higher extinction risk (Carvajal-Quintero et al., 2017; Le Feuvre et al., 2016).

Thus, the relationship between species body size and their geographical range size was determined by log-transforming the species occurrence area (km^2) under each climatic scenario and the data available from FishBase (Froese & Pauly, 2019) for maximum standard body length (cm) to estimate the lower boundary (susceptibility limit) of the triangular relationship. To do so, a quantile regression was applied, setting a fifth quantile to identify the lower limit, i.e. the susceptibility limit (Scharf, Juanes, & Sutherland, 1998). The quantile regression was performed using the *quantreg* package (Koenker, 2019). This lower fifth quantile represents an estimate of the minimum geographical range size that each species needs for long-term persistence (Figure 1). Although the choice of quantile to define the lower boundary is subjective, this framework was the same as previously established by Carvajal-Quintero et al. (2017). The susceptibility limit was further used as a threshold to classify the species as susceptible if their range fell below the 95% confidence interval of the lower limit, or not susceptible if their range fell above the limit (see Figure 1), in both climatic and PA scenarios.

3 | RESULTS

3.1 | Climate change effects

The SDMs developed under current climatic conditions resulted in species geographical range sizes varying from 8,779 to 2,041,782 km^2 (Supporting Information Table S1). According to climate change projections for 2050, the Amazon basin will become warmer and dryer, and this trend will be more pronounced in the eastern part of the basin. In this scenario, 24 (2%) of the 1,293 Amazonian freshwater fish species analysed could lose all of their suitable climatic area. Furthermore, more than 34% of the species (436 species) would see at least a 50% decrease in their suitable climatic habitat while 39% (512 species) would experience an increase.

Applying the susceptibility limit (i.e. the lower boundary of the relationship of the range–body size) under the current climate, about 8% of the species (108 species) fell below the limit (Figure 3a). Thus, around 8% of the Amazon freshwater fish species analysed can be considered as currently susceptible. These species belong mainly to the Characidae (22 species), Cichlidae (18 species) and Loricariidae (27 species). Under future climatic conditions, the percentage of species classified as potentially susceptible (i.e. species falling below the susceptibility limit) is nearly double (228 species, ~17%; Figure 3b).

3.2 | Effects of protected areas

At present, the species distribution area covered by PAs varies from 2 to 50%. Applying the susceptibility limit as a threshold for species range representativeness within PAs, the current + PAs scenario shows that 362 species (28%) fall below the susceptibility limit, meaning that these species do not have sufficient area covered by PAs to ensure their long-term persistence (Figure 3c). In this

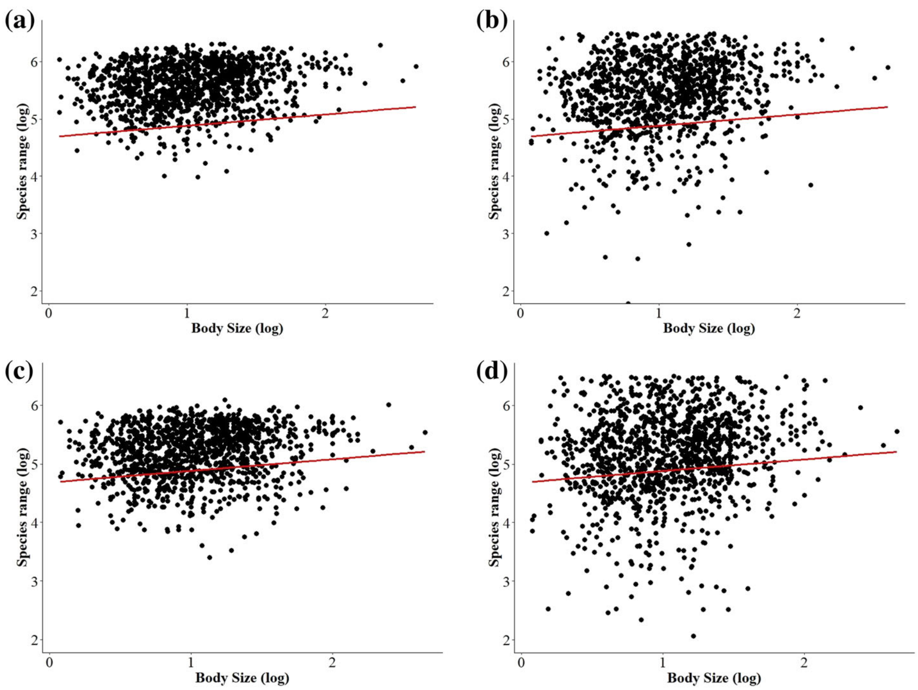

FIGURE 3 Relationship between body size and species range and susceptibility limit (red line) according to climate and protected area scenarios. (a) Current geographical species distribution. (b) Species distribution as influenced by climate change impacts, RPC 8.5 for 2050. (c) Current geographical species distribution within the Amazon protected area (current + PAs). (d) Future geographical species distribution within the Amazon protected area (future + PAs)

scenario, the most susceptible species belong to the Characidae (50% of species identified as susceptible), Loricariidae (22%) and Cichlidae (14%). In the future scenario (future + PAs), the number of susceptible species increases, with more than 36% (471 species) falling below the susceptibility limit (Figure 3d). The families showing an increase in species susceptibility are the same as in the current scenario.

Mapping only susceptible species shows a convergence among the scenarios, with the majority of susceptible species being concentrated in large rivers (Figure 4). Looking at the future climatic scenario, >11% of susceptible species are concentrated in the medium to lower Amazon river main stem (Figure 4a and b). Taking into account the climate + PAs scenario (current + PAs and future + PAs), the susceptible species increase in the Amazon floodplain, in the larger tributaries of the upper and lower Amazon and in the medium to lower Amazon river main stem (Figure 4c and 4d).

4 | DISCUSSION

In the Amazon basin, climate change is expected to change precipitation patterns, with the predominance of severe and long droughts in the eastern portion of the basin, and increased precipitation in its western portion (Sorribas et al., 2016), and to increase the average water temperatures (Castello et al., 2013; Castello & Macedo, 2016; Gloor et al., 2015). These new conditions could lead species to expand or contract their natural ranges to maintain their optimal habitat requirements (Oberdorff et al., 2015). According to the projections identified here, the Amazon basin could risk losing around 2% (24 species) of the species analysed owing to future unsuitable conditions. Furthermore, around 34% of the fauna could become more susceptible to extinction owing to potential habitat shrinking. These results should be considered conservative, as this study assumed a free dispersal of species to track suitable climatic conditions, without considering other factors such as potential dispersal barriers to migration (e.g. waterfalls, rapids or dams) and the differential dispersal abilities of species (e.g. long distance migratory species). Moreover, it is highly probable that projections of species susceptibility are also substantially underestimated as many small-range species have been left out because of an insufficient number of occurrences for running SDM projections.

Among the species with a high risk of extinction owing to future climate change are the loricariids *Baryancistrus niveatus* and *Scobinancistrus aureatus* and the cichlid *Crenicichla urosema*. It should be noted that these three species are already classified as Critically Endangered, Vulnerable and Endangered, respectively (ICMBio, 2018 following the IUCN classification and criteria). Frederico, Olden, & Zuanon (2016) have already shown that freshwater fish in the Amazon are highly sensitive to climate change impacts and largely unprotected owing to gaps in the representativeness of PAs. Moreover, about 17% of the fish species analysed could be at risk of having their suitable climatic areas reduced below the minimum range size requirement for their long-term persistence in 2050. For example, *Parancistrus nudiventris* is an endemic species from the Xingu River with a restricted range <10,000 km^2 (Nogueira et al., 2010). Less than 50% of its geographical range is covered by PAs, and it is already classified as Vulnerable owing to habitat loss (ICMBio, 2018). However, despite the negative impacts of future climate change for some species, the results also showed that ~39% of the Amazon freshwater fish species analysed may increase their geographical distribution by 2050. Among them are the giant catfish *Brachyplatystoma filamentosum* (Pimelodidae) and the tambaqui or black pacu *Colossoma macropomum*

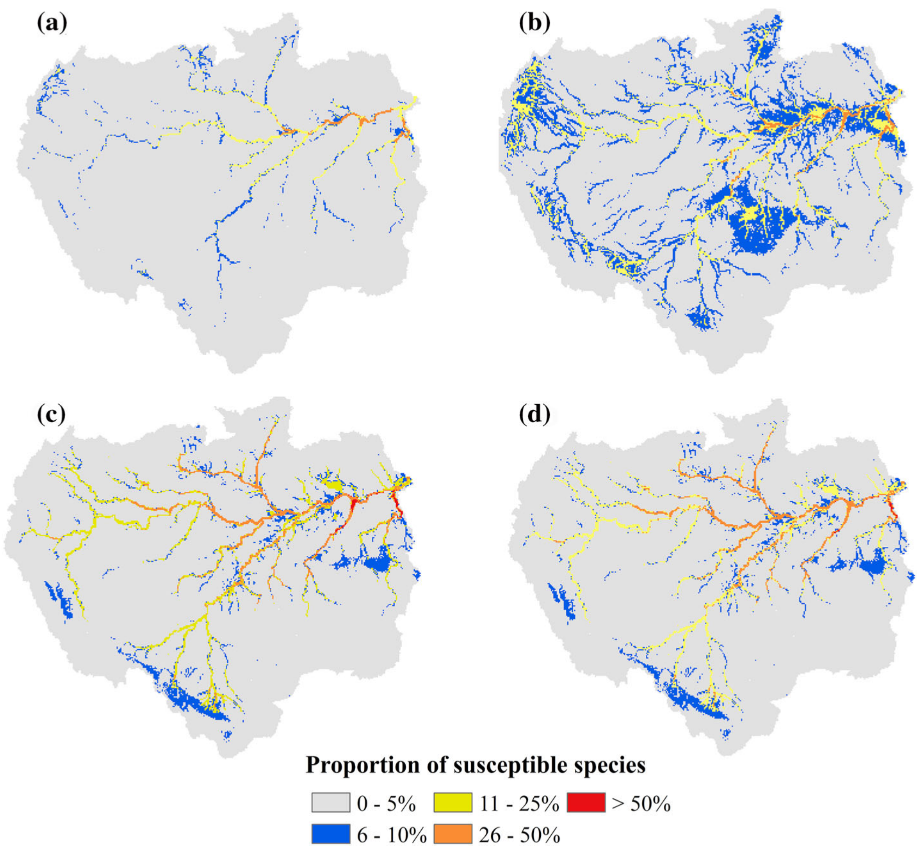

FIGURE 4 Percentages of susceptible species for each scenario analysed: (a) the current susceptible species, 'natural susceptibility'; (b) the susceptible species in the face of climate change only; (c) the current susceptible species according to the current + PAs scenario; and (d) the future susceptible species according to the future + PAs scenario

(Serrasalmidae), both widespread in the Amazon basin and important commercially, but suffering from over-exploitation and habitat fragmentation (Mojica, Oviedo, León, & Lasso, 2012).

The present Amazonian PAs cover the minimum range required for long-term persistence of about 72% (present) and 64% (2050) of the fish species analysed, which makes PAs an important mechanism to prevent fish species decline in the basin. Most of the susceptible species detected here, however, are found in areas with a low cover of PAs, i.e. large rivers and their associated floodplains, including the medium to lower Amazon main stem itself (Abell et al., 2017; Figure 4). Large rivers and their floodplains are highly productive systems that support a high diversity of fishes by providing habitat heterogeneity, food and shelter for individuals (Castello et al., 2018; Reis et al., 2017; Reis, Hermoso, Hamilton, Bunn, Fluet-Chauinard, et al., 2019). Yet these river floodplains have been suffering high rates of deforestation in the past 30 years owing to the lack of formal protection (Castello et al., 2013; Renó, Novo, Suemitsu, Renno, & Silva, 2011), with more than 50% of their area already deforested (Renó, Novo, & Escada, 2016). The land conversion in these systems has already adversely affected fish biomass and functional diversity (Arantes et al., 2019), affecting the productivity of fisheries and the livelihoods they sustain (Castello et al., 2018). Thus, there is an increasing need for more ecologically meaningful conservation planning for these systems by addressing their hydrological complexity (Reis, Hermoso, Hamilton, Bunn, Fluet-Chauinard, et al., 2019, Reis, Hermoso, Hamilton, Bunn, & Linke, 2019).

This study shows that the current system of PAs is potentially suitable for most of the freshwater fish species analysed. However, the Amazon basin still needs effective conservation actions to safeguard freshwater biodiversity, mostly in large rivers and their floodplains. These actions should include systematic conservation planning and appropriate methods based on freshwater ecological characteristics to design an effective series of freshwater PAs (Hermoso, Kennard, & Linke, 2012; Jézéquel, Tedesco, Darwall, et al., 2020; Linke, Turak, & Nel, 2011; Reis, Hermoso, Hamilton, Bunn, et al., 2019).

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CONFLICT OF INTEREST

The authors state that there is no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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