Received: 1 October 2019 | Revised: 4 June 2020 | Accepted: 30 June 2020

DOI: 10.1111/gcb.15285

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

The combined effects of climate change and river fragmentation on the distribution of Andean Amazon fishes

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Funding information
MacArthur Foundation, Grant/Award Number: 16-1607-151053-CSD and G-1607-151047; ERANet-LAC, Grant/Award Number: AmazonFish (ELAC2014/DCC-0210); LABEX TULIP, Grant/Award Number: ANR-10-LABX-41; BiodivERsA, Grant/Award Number: ODYSSEUS project; LABEX CEBA, Grant/Award Number: ANR-10-LABX-25-01; Conselho Nacional de Desenvolvimento Científico e Tecnológico; COLCIENCIAS, Grant/Award Number: 44842-519-2015; EDB Lab

Abstract

Upstream range shifts of freshwater fishes have been documented in recent years due to ongoing climate change. River fragmentation by dams, presenting physical barriers, can limit the climatically induced spatial redistribution of fishes. Andean freshwater ecosystems in the Neotropical region are expected to be highly affected by these future disturbances. However, proper evaluations are still missing. Combining species distribution models and functional traits of Andean Amazon fishes, coupled with dam locations and climatic projections (2070s), we (a) evaluated the potential impacts of future climate on species ranges, (b) investigated the combined impact of river fragmentation and climate change and (c) tested the relationships between these impacts and species functional traits. Results show that climate change will induce range contraction for most of the Andean Amazon fish species, particularly those inhabiting highlands. Dams are not predicted to greatly limit future range shifts for most species (i.e., the Barrier effect). However, some of these barriers should prevent upstream shifts for a considerable number of species, reducing future potential diversity in some basins. River fragmentation is predicted to act

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*In memoriam.

jointly with climate change in promoting a considerable decrease in the probability of species to persist in the long-term because of splitting species ranges in smaller fragments (i.e., the Isolation effect). Benthic and fast-flowing water adapted species with hydrodynamic bodies are significantly associated with severe range contractions from climate change.

KEYWORDS

dams, freshwater fish, functional traits, global change, habitat fragmentation, range shifts, species distribution models, tropical Andes

1 | INTRODUCTION

Range shifts are one of the main responses of species to climate change (Pecl et al., 2017). Species are expected to colonize new areas toward higher elevations and latitudes following the shifting envelope of suitable climatic conditions (Lenoir & Svenning, 2015). These changes related to ongoing global warming have already been documented across multiple taxa (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Lenoir & Svenning, 2015). Freshwater organisms (e.g., fishes) are considered particularly vulnerable to climate change. Among other things, because they have limited capacity to regulate body temperature and their dispersal ability is highly constrained by the structure of river networks (Krabbenhoft et al., 2020; Woodward, Perkins, & Brown, 2010). The hydrological network limits movements along river corridors and connected wetlands of fish species under warming conditions, potentially reducing the possibilities for these organisms to find new suitable climatic areas. Species-specific responses to climate change, as the degree of range contraction or expansion, are expected to heavily depend on species' life-history traits that will determine species vulnerability and extinction risk (Lenoir et al., 2010; Pacifici et al., 2015; but see Angert et al., 2011). Recent studies in temperate regions have documented upstream movements of fish species as a response to climate change (Comte & Grenouillet, 2013; Heino, Virkkala, & Toivonen, 2009). However, the potential consequences of climate change on freshwater fishes remains poorly explored compared to other taxa (Pacifici et al., 2015). Furthermore, current knowledge is highly biased toward cold-water fish species from temperate regions (Comte, Buisson, Daufresne, & Grenouillet, 2013; Troia, Kaz, Niemeyer, & Giam, 2019), which conform a small portion of the global fish taxonomic and life-histories diversity compared to tropical environments (Oberdorff et al., 2011; Toussaint, Charpin, Brosse, & Villéger, 2016).

Freshwater ecosystems are also imperiled by multiple human disturbances (Vörösmarty et al., 2010), that are expected to interact heavily with climate change to influence future species ranges (Comte, Hugueny, & Grenouillet, 2016; Radinger et al., 2016). In particular, river fragmentation by dams limits fish dispersal and increases their extinction risk by splitting species ranges (Carvajal-Quintero et al., 2017; Dias et al., 2017). Recent empirical evidence supports the vision that anthropogenic barriers to fish movements (e.g., dams and weirs) have delayed or prevented fishes from reaching upstream suitable climatic conditions (Gibson-Reinemer, Rahel, Albeke, & Fitzpatrick, 2017) and have interacted with ongoing climate change to reorganize fish assemblages in temperate streams (Kuczynski, Legendre, & Grenouillet, 1980). This suggests that these physical barriers must be accounted for when forecasting freshwater fish range shifts as a response to climate change (Radinger et al., 2017; Radinger, Hölker, Horký, Slavík, & Wolter, 2018).

Located in the Neotropics, the Andean Amazon region is characterized by a strong elevation zonation up to 6,000 meters above sea level (m a.s.l.), shifting in a very short distance from the extensive lowland Amazonian habitats to the narrow and steep Andean habitats. This gradient of particular conditions has significantly shaped freshwater species distribution and life histories (De La Barra et al., 2016; Lujan et al., 2013). Specialized fish assemblages with a high degree of endemism have been established throughout the tropical Andes (Anderson & Maldonado-Ocampo, 2011; Carvajal-Quintero et al., 2015; Oberdorff et al., 2019). Highland assemblages display low functional diversity with a high degree of specialization to fast-flowing waters (rheophily), while lowlands are more functionally diverse and less specialized (Lujan & Conway, 2015). Some of the morphological specializations to rheophily include strong compressed or depressed bodies, surface attachment organs (e.g., oral suction discs), and large pectoral fins (Lujan & Conway, 2015). This natural elevational gradient in fish assemblages, also observed in other aquatic taxa, is expected to be heavily influenced by future climate change (Larson et al., 2011; Maldonado et al., 2011; Tognelli et al., 2019) and river fragmentation (Anderson et al., 2018), with potentially great modifications also in ecosystem functioning mediated by aquatic biodiversity (Atkinson et al., 2019; McIntyre et al., 2008). Several studies reviewed by Báez, Jaramillo, Cuesta, and Donoso (2016) suggest that Andean species are likely to migrate upward and suffer severe range contractions as a consequence of both climate change and the pronounced elevation gradient produced by the Andean mountains (although slower climate velocities in mountain streams could mitigate these impacts; Isaak et al., 2016). As a result, high species turnover and assemblage rearrangements are expected due to the steep variation of environmental conditions (Lawler et al., 2009). Additionally, hydropower dam development is becoming a major conservation concern globally and the Andean Amazon is among the tropical regions experiencing the highest rates of dam development (Sutherland et al., 2013; Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015). These high rates of dam construction are expected to continue into the foreseeable future (Carvajal-Quintero et al., 2017; Winemiller et al., 2016; Zarfl et al., 2015) and the Andean Amazon freshwater ecosystems will be particularly affected (Anderson et al., 2018; Finer & Jenkins, 2012).

Although the tropical Andes has been recognized as a hotspot for global biodiversity conservation (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000), the region's biodiversity has commonly been neglected from conservation and research efforts (Anderson & Maldonado-Ocampo, 2011). The evaluation of different combined human disturbances still needs further research within this region, especially to detect spatial hotspots of major changes in biodiversity (Jézéquel, Tedesco, Darwall, et al., 2020) and to identify species particularly vulnerable to future global change (Larson et al., 2011). Specifically, the interplay between climate change and river fragmentation in the Andean Amazon might lead to an increased vulnerability of freshwater biodiversity in that region (Castello et al., 2013; Castello & Macedo, 2016; Encalada et al., 2019). In this study, we implemented a species distribution models (SDMs) approach based on the most up-to-date distribution data on fishes of the Andean Amazon to evaluate the combined impact of future climate change and river fragmentation by dams on the species range shifts and their persistence probability of species in relation to the remaining accessible and suitable areas. We further investigate which species as well as which functional traits present the highest levels of vulnerability to future climate change and river fragmentation by dams.

2 | MATERIALS AND METHODS

2.1 | Study area and species

The Andean Amazon is a high-gradient mountain region that contains the primary headwater areas of the Amazon River and harbors numerous endemic fish species (Anderson & Maldonado-Ocampo, 2011). Our study area was defined as the Western Amazon encompassing the entire extension of the six major Andean Amazon basins and contiguous minor drainages (Figure 1). Fish occurrence data were obtained from the AmazonFish project, a collaborative and exhaustive database that includes historical fish species occurrences for the entire Amazon Basin from the literature, biological collections, and recent field expeditions (Jézéquel, Tedesco, Bigorne, et al., 2020). We gathered a total of 9,354 spatial unique sampling points at 1 km^2 resolution for 1,826 fish species within the Western Amazon. To reduce possible inaccuracies in fish sampling points and streams, all the records were snapped to the HydroSHEDS stream network (Lehner, Verdin, & Jarvis, 2008) encompassing 525,600 km^2. Using a 3 km buffer (Domisch, Wilson, & Jetz, 2016), it resulted in a subset of 7,129 spatial unique sampling points at 1 km^2 resolution. In the Western Amazon, 612 fish species presented at least one occurrence above 500 m a.s.l., following the Andean Amazon delimitation (Mcclain & Naiman, 2008). From the 612 species, 483 (78.9%) met the criteria of having 10 or more occurrences to produce reliable SDMs (van Proosdij, Sosef, Wieringa, & Raes, 2016; Wisz et al., 2008). For this final species selection, the time span of our occurrence records, when available, ranges from 1852 to 2018, and 82.6% of these occurrences fit the time span of the climate data used in our SDMs (see Section 2.2).

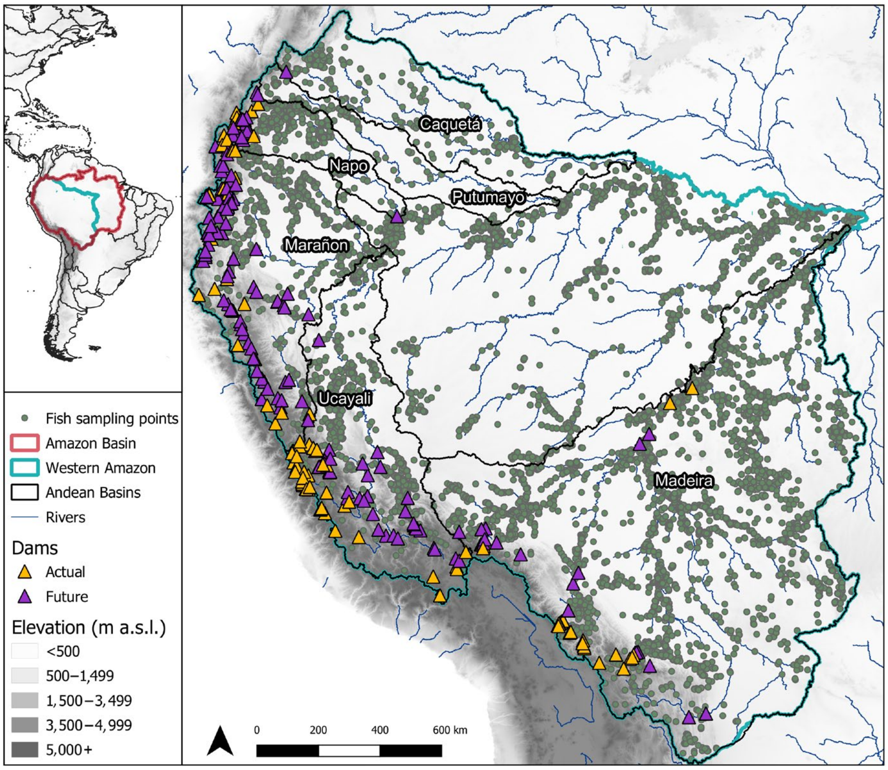


FIGURE 1 The Western Amazon region showing the fish sampling points available from the AmazonFish project (Jézéquel, Tedesco, Bigorne, et al., 2020) and the locations of the dams (Anderson et al., 2018)

2.2 | Environmental variables

The current and future climates were represented by CHELSA v1.2 bioclimatic variables (Karger et al., 2017). The current climate represents 1979–2013 average values. Future forecasts for the 2070s (2060–2080) were drawn from the most optimistic (2.6) and pessimistic (8.5) Representative Concentration Pathways (RCPs) of greenhouse gases from the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC AR5; Collins et al., 2013). Each RCP was described by two General Circulation Models (GCMs; HadGEM2-AO and MIROC5), which represent some of the less biased family models available for South America (Gulizia & Camilloni, 2015). Temperature variables were used at the grid cell scale as they yield similar results than stream field-observed temperature data when fitting fish SDMs in Amazonian fishes (Frederico, De Marco, & Zuanon, 2014). For precipitation-based variables, we computed for each grid cell the accumulated sum of upstream values to better represent the modifications of river drainages under changes in regional rainfall (Domisch, Amatulli, & Jetz, 2015; precipitation seasonality was described by the mean of the upstream values). Topographical variables describing the upstream-downstream gradient included slope (calculated from GMTED2010, Danielson & Gesch, 2011) and the Strahler stream order (Shen, Anagnostou, Mei, & Hong, 2017). Nine soil variables at 0 cm depth from the SoilGrids database (Hengl et al., 2017) were summarized into a principal component analysis (PCA) and its two main axes (44.9% of variation explained) were retained as synthetic variables to represent stream substrate properties. After applying multicollinearity analyses to reduce the number of predictor variables (see Supplementary Methods: Appendix S1 and Figure S1), a subset of seven non-correlated variables were selected to represent current and future environmental conditions: annual mean temperature, isothermality, accumulated annual precipitation (mm), mean accumulated upstream precipitation seasonality, soil PCA axis 2, slope, and the Strahler stream order (Table S1). All environmental variables were used at 30 arc-seconds (~1 km^2) clipped to the HydroSHEDS stream network (Lehner et al., 2008).

2.3 | Determining range shifts induced by climate change

We based our workflow on an ensemble modeling approach combining two high-performance SDMs machine learning techniques—boosted regression trees (BRT; Elith, Leathwick, & Hastie, 2008) and MaxEnt (ME; Phillips, Anderson, Dudík, Schapire, & Blair, 2017) to fit presence-only SDMs, allowing us to obtain a consensus out-performing single SDM projection of species ranges (Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009). All analyses and data management were performed under R v3.4.0. environment (R Core Development Team, 2018). We applied an “All Target Group” approach, where all the fish sampling points within the study area were used as pseudoabsences to reduce sampling bias and spatial autocorrelation effects (Phillips, 2009). Additionally, pseudo-absences within a 10 km buffer from a presence were discarded to reduce commission errors conservatively, a strategy recommended on museum collections data (Mateo, Croat, Felicísimo, & Muñoz, 2010). For each species, full SDMs, using all available occurrence data for training, were fitted using BRTs and ME for current conditions with default settings in the *biomod2* package (Thuiller, Georges, Engler, & Breiner, 2016). Then, we projected these full SDMs under the different climate scenarios (Current, RCP 2.6 and RCP 8.5). See Supplementary Methods (Appendix S2) for further details on the predictive evaluation and projections of our SDMs.

Species distribution models may overpredict species ranges if, for instance, a suitable habitat exists but is not accessible because of biogeographical barriers that have limited dispersal and colonization historically (Alexander et al., 2018; Cooper & Soberón, 2018). For each species, we applied two range constraints to reduce the potential overprediction in our SDMs projections for current and future climatic conditions. For current conditions, we calculated the convex hull polygon defined by species occurrences and its overlap with major basins (HydroBASINS at level 5; Lehner & Grill, 2013), defining those basins where a species could be present in the current climate. For future climate conditions, we implemented an approach using species-specific dispersal capacities based on Radinger and Wolter (2014) to distinguish between the suitable future area and the effectively reachable area. Although this dispersal model is based on a global meta-analysis including mostly North American and European taxa, it represents the most comprehensive model currently available to estimate freshwater fish dispersal capacities. See Supplementary Methods (Appendix S3) for details on our implementation of this dispersal model to produce maximum dispersal distances determining future accessible areas.

Expected species range shifts between current and future dispersal-constrained ranges were quantified applying six metrics as follows: range extirpation (% of range size loss), range colonization (% of range size gained), range shift (% of overall loss or gain in range size), changes in range center (differences in mean elevation), changes in the lower limit (differences in elevation values at the 5th percentile), and changes in the upper limit (differences in elevation values at the 95th percentile). To test for differences between current and future climate conditions in expected species range shifts, paired Student's t tests were applied distinguishing between contracting and expanding species. To describe the spatially differential impacts of climate change across the Andean Amazon, for each future climate scenario, we averaged the range shifts values of all species predicted to be present at each 1 km^2 grid cell in the current distribution.

2.4 | Impacts of river fragmentation by dams

We estimated the future impact of river fragmentation by dams on Andean Amazon fishes using dam locations from Anderson et al. (2018).

The original locations were manually snapped to the HydroSHEDS stream network (Lehner et al., 2008). Those dams occurring in small streams not represented in the HydroSHEDS stream network could not be considered, resulting in a subset of 113 from 142 current (constructed or under construction) dams and 151 from 160 future (planned or proposed) dams. We evaluated two contrasting future river fragmentation scenarios: (a) "Constant": only current dams and (b) "Increased": current plus future dams. The impacts of river fragmentation were coupled with climate change leading to four different future scenarios—climate change (RCP 2.6 and RCP 8.5) × river fragmentation (Constant and Increased). For these future scenarios, two different impacts on fish distribution were evaluated: (a) the "Barrier effect," where the dams act as physical barriers preventing future species range shifts; and (B) the "Isolation effect," where dams affect the fish species persistence in their future projected distribution by splitting species ranges into isolated fragments of smaller sizes.

The Barrier effect was estimated as the percentage loss of colonizable areas comparing future ranges with and without dams. Dams were included as stopping points when calculating the future areas accessible by dispersal capacities with a vector network analysis (see Appendix S3). Since specific information was not available for each dam, they were all considered impassable for both upstream and downstream movements. Dams located in the Andean Amazon correspond mostly to hydropower with no fish passage facilities allowing upstream movement, and many of them also have high capacity turbines limiting downstream movement (Finer & Jenkins, 2012). The rationale to estimate the Barrier effect of fragmentation by dams on future species ranges was that the current presence of a species in a given fragment generated by a dam allowed that species to colonize future suitable areas within the fragment. If the species was absent from a fragment, any future suitable habitat within the fragment was assumed to be unavailable to colonize under any future scenario.

The Isolation effect was evaluated using an approach based on the triangular relationship between body size and range size commonly observed in vertebrates (Gaston & Blackburn, 1996) including freshwater fishes (Carvajal-Quintero et al., 2017; Le Feuvre, Dempster, Shelley, & Swearer, 2016). In this macroecological pattern, large-bodied species display only broad range sizes, while smaller species have a diversity of range sizes (Figure S2). The lower bound of this triangular relationship is interpreted as the minimum range size that species can naturally have for a given body size. Deviations below this vulnerability limit, like those potentially generated by fragmentation, can be interpreted as an increase in vulnerability to extinction. Following Carvajal-Quintero et al. (2017), we estimated this vulnerability limit for the Andean Amazon fishes fitting a quantile regression (0.05 quantile) of the relationship between the log-transformed maximum body length and the log-transformed current range size using the *quantreg* package (Koenker, 2018). Then, we adjusted a normal distribution of species deviations from the fitted vulnerability limit, using mean equal to zero and variance defined by the residuals of the quantile regression fit. We used this distribution function to calculate the probability of a species with a given body length and range size to be above the vulnerability limit (ranging from vulnerable, 0, to not vulnerable, 1). Using current species ranges, this probability can be interpreted as a natural probability to persist. Our approach assumes that dams split species ranges into totally isolated fragments that no longer represent the original species range. These stream fragments were calculated using the Barrier Analysis Tool (http://www.geodata.soton.ac.uk/geodata/gis/project173). For each species, we calculated all the probabilities to persist based on the number of stream fragments occupied in one future scenario. For each future scenario, these probability values were averaged to represent the overall probability to persist within all the future projected range of a species. The Isolation effect for each species was measured as the change in the probability to persist between natural and future ranges. Differences between future scenarios were tested using paired Student's *t* tests.

To evaluate the role of climate change and both the Barrier and Isolation effects of river fragmentation at the species level, we performed a nonparametric two-way analysis of variance with a robust estimation based on rank estimators (Kloke & Mckean, 2012). In addition, we mapped both effects to visualize the spatial distribution of their impacts across the Western Amazon. For the Barrier effect, we calculated the future suitable but inaccessible areas and the number of species blocked by contrasting future projections with dams and without dams for each one of the species (RCP × Fragmentation). For the Isolation effect, current ranges were averaged and weighted by the change in the species probability to persist between natural and future ranges (RCP × Fragmentation).

2.5 | Species traits and vulnerability under future scenarios

All species were characterized by a set of seven unitless functional traits (BE, body elongation; BLS, body lateral shape; RES, relative eye size; RML, relative maxillary length; OGP, oral gape position; PP, pectoral fin position; PS, pectoral fin size) representing distinct ecological attributes and derived from 10 ecomorphological measures obtained from a global database (Toussaint et al., 2016). For species with unmeasured traits (i.e., 3.6% of the traits), missing values were filled with the mean trait value from congeneric species occurring in the Amazon basin, or available elsewhere in the Neotropics for monospecific genera (37 out of the 483 considered species; 7 from 483 species were excluded because the trait values were still missing even after this filling procedure). All seven functional traits transformed to *z*-scores were used as predictor variables for each one of the impact metrics using multivariate linear mixed models accounting for species relatedness with genera, family, and order as nested random intercepts, obtaining comparable regression coefficient among predictors. To test for the relationship between functional traits and our metrics of species impacts from climate change and river fragmentation, we used a multimodel inference approach with the *dredge* function in MuMIn package (Barton, 2019). Models from all possible combinations of functional traits were fitted and judged based on the Akaike information criterion (AIC) as a measure of goodness-of-fit. The bests models, those with ΔAIC < 4, were used to produce weighted average regression coefficients, including zeros when a predictor was missing (Grueber, Nakagawa, Laws, & Jamieson, 2011).

3 | RESULTS

3.1 | Range shifts induced by climate change

A final subset of 458 species (94.8% of the species with more than 10 occurrences) presented satisfactory performances on SDMs (AUC mean, $\mu = 0.843$, and standard deviation, $\sigma = 0.07$) that were considered for further analysis. Accounting for species dispersal capacities, our projections show that climate change will promote range contractions in most of the Andean Amazon fish species. Under RCP 2.6, 276 species (60%) were predicted to experience range contraction ($\mu = 68.5\%$, $\sigma = 32.03$) and 182 species (40%) were predicted to experience range expansion ($\mu = 109.45\%$, $\sigma = 267.38$). In RCP 8.5, 313 species (68%) would contract ($\mu = 82.6\%$, $\sigma = 26.79$), while 145 species (32%) would expand ($\mu = 165.7\%$, $\sigma = 549.53$; Figure S3). Among those species predicted to contract their ranges, 30 species (6%) and 78 species (17%) were predicted to completely lose suitable areas, respectively under RCP 2.6 and RCP 8.5.

Species current range center was positively related to their degree of expected range contractions (RCP 2.6: $R_s = 0.51$, $p < .001$; RCP 8.5: $R_s = 0.32$, $p < .001$; R_s = Spearman correlation), while negatively related to the projected degree of range expansion (RCP 2.6: $R_s = -0.37$, $p < .001$; RCP 8.5: $R_s = -0.38$, $p < .001$; Figure 2a). Species predicted to experience future range contraction were significantly distributed at higher elevations (RCP 2.6: $\mu = 377.6$, $\sigma = 409.95$; RCP 8.5: $\mu = 362.26$, $\sigma = 452.84$) compared to species predicted to expand their ranges (RCP 2.6: $\mu = 232.25$, $\sigma = 389.54$; RCP 8.5: $\mu = 228.32$, $\sigma = 266.69$) in both climatic scenarios (RCP 2.6: Student $t(401.11) = 3.82$, $p < .001$; RCP 8.5: $t(430.84) = 3.95$, $p < .001$; Figure 2b,c). Species range loss was significantly higher in the RCP 8.5 scenario ($t(457) = -10.57$, $p < .001$), but species range gain was predicted to be similar between both climatic scenarios ($t(457) = -0.91$, $p > .05$). The contracting species are predicted to significantly shift their range center and their lower range limit toward higher elevations in both future climatic scenarios, but their upper range limit only in the RCP 8.5 scenario (Figure 2a–c; Table S2). The expanding species will also significantly shift their upper range upward but by maintaining their range center and their lower limit relatively constant (Figure 3d–f; Table S2).

3.2 | Impacts of river fragmentation by dams

Our projections of future species range shifts combined with the effects of river fragmentation scenarios by dams showed heterogeneous results. The Barrier effect of dams is expected to prevent range shifts principally for those species distributed at lower elevations (100–500 m a.s.l.). The species loss of future colonizable areas was significantly influenced by the river fragmentation scenario ($F = 2{,}664.87$, $p < .0001$) and to a lesser degree by the climate change scenario ($F = 1{,}782.15$, $p < .0001$). River fragmentation and climate change intensity are expected to drive an increased loss of colonizable areas (Figure 4a,b). We further found a significant interaction between the barrier effect of river fragmentation and climate

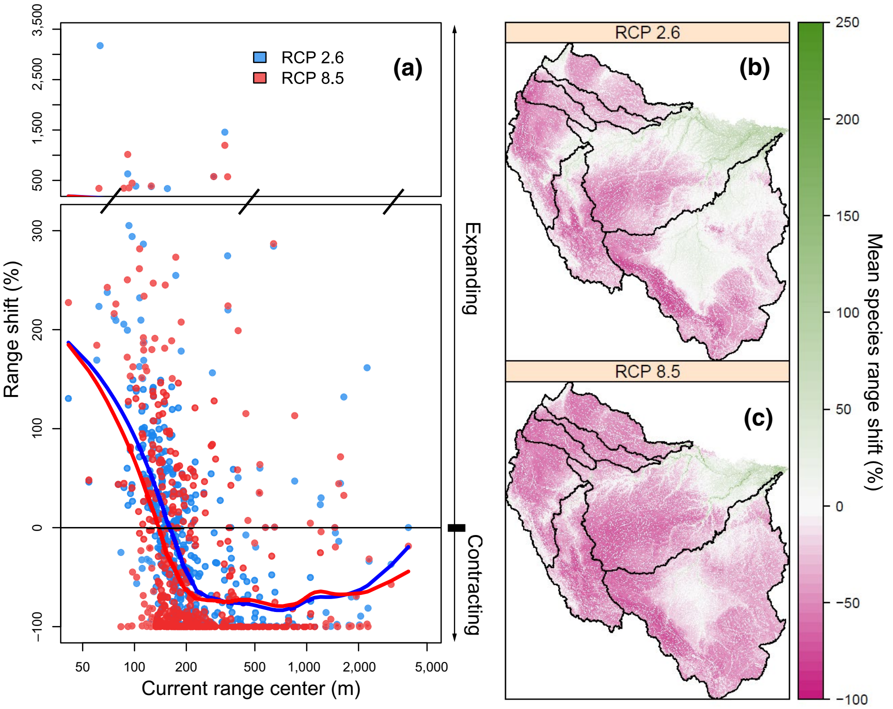


FIGURE 2 Expected species range shifts accounting for species dispersal capacities in Andean Amazon fishes predicted under climate change scenarios for expanding and contracting species for the 2070s (a): RCP 2.6 (blue dots) and RCP 8.5 (red dots). Lines indicate best-fit lines from locally weighted scatterplot smoothing (LOWESS). Mean species range shifts across the Andean Amazon under RCP 2.6 (b) and RCP 8.5 (c) Each grid cell is the averaged range shift of all species currently distributed in that place

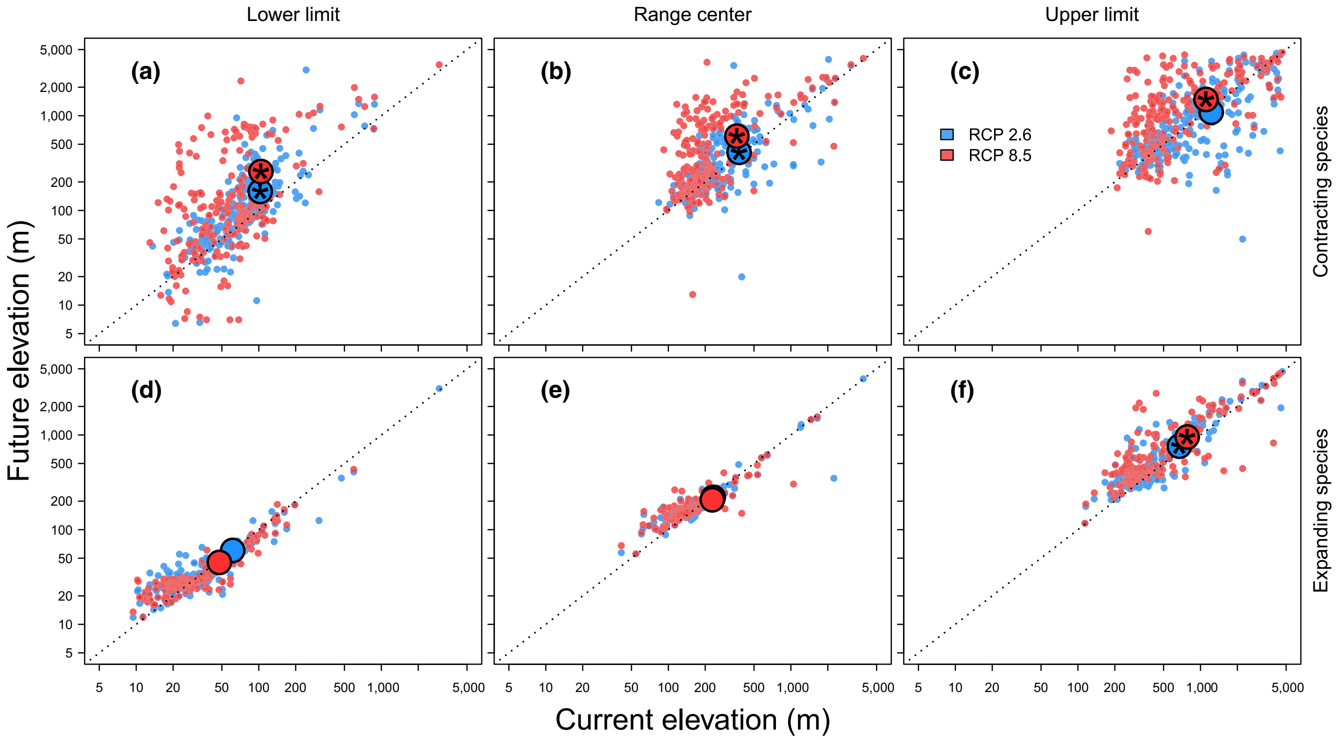
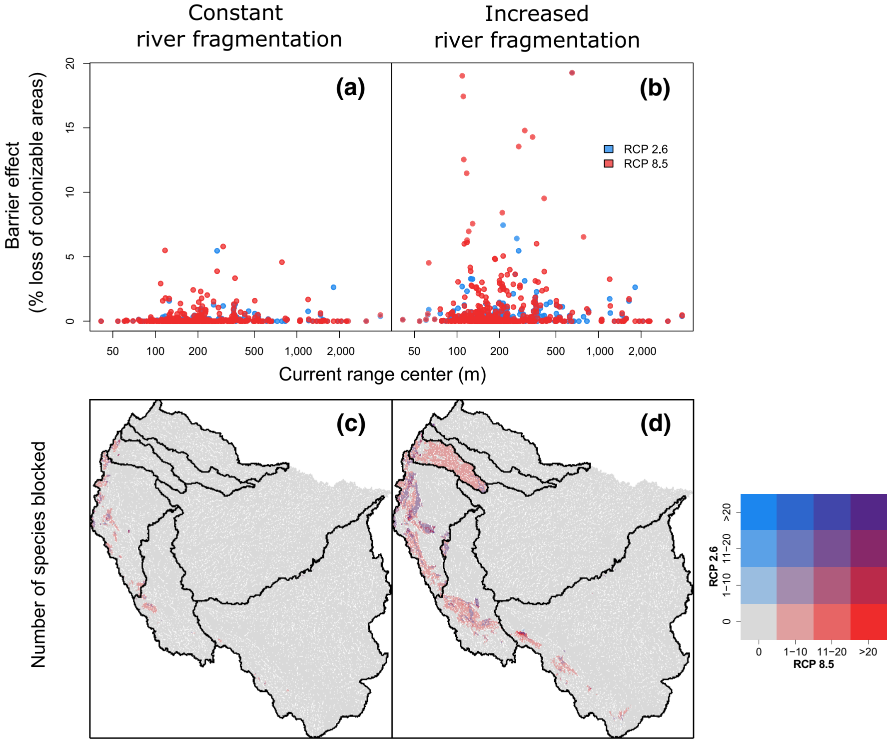


FIGURE 3 Expected range shifts accounting for species dispersal capacities in Andean Amazon fishes expected because of climate change for the 2070s. The upper panel shows range-contracting species and the lower panel shows range-expanding species. Changes in the lower limit (a, d), range center (b, e), and upper limit (c, f). Dot colors indicate climate scenarios: RCP 2.6 (blue) and RCP 8.5 (red). Diagonal black lines represent a 1:1 relationship indicating no change. Big dots represent the mean value and asterisk (*) indicates significant changes between current and future situations (note that the big blue dot in panel [e] has no asterisk)

FIGURE 4 Projected Barrier effect represented as the percentage of loss of colonizable areas of Andean Amazon fishes due to the presence of dams under constant (a) and increased (b) river fragmentation scenarios coupled with climate change (blue, RCP 2.6, and red, RCP 8.5). The maps represent the regions where climate-induced range shifts will be limited by dams, indicating the inaccessible colonizable areas and the number of species blocked, under constant (c) and increased (d) river fragmentation scenarios



change ($F = 1{,}497.74$, $p < .0001$), indicating a synergistic effect of both disturbances in explaining the loss of future colonizable areas. However, most of the species (83%–93%) were not predicted to be severely affected by dams in terms of preventing range shifts, losing between 0% and 5% of future colonizable areas, irrespective of the scenario considered (Figure 4a,b). However, when mapping the

Barrier effect as the number of species limited by dams in their upstream shifts, some basins (e.g., the Napo, with a projected dam at the downstream pour point, see Figure 1) are predicted to suffer from a considerable reduction in their future potential fish diversity under the worst river fragmentation and climate change scenario (Figure 4c,d).

Dams also fragment the future projected species ranges into multiple smaller fragments (i.e., the Isolation effect), considerably shifting them out from the original relationship between body size and range size setting up the vulnerability limit (Figure S4). A considerable proportion of species' fragmented range sizes fell below the vulnerability limit under constant (RCP 2.6:27%, RCP 8.5:31.4%) and increased (RCP 2.6:43%, RCP 8.5:47%) river fragmentation scenarios. This Isolation effect summarizing the changes in range size generated by dam fragmentation and climate change, resulted in a considerable decrease of the overall probability to persist within future distributions for most Andean Amazon fishes under constant (RCP 2.6: $t(427) = 14.68$, $p < .001$; RCP 8.5: $t(379) = 16.77$, $p < .001$) and increased river fragmentation scenarios (RCP 2.6: $t(427) = 20.51$, $p < .001$; RCP 8.5: $t(379) = 22.15$, $p < .001$; Figure 5a,b). The decrease in the probability to persist in the future is principally driven by the river fragmentation scenario ($F = 1{,}347.83$, $p < .0001$), but also the climate change scenario considered ($F = 366.04$, $p < .0001$). The mid and high elevation regions of the Andes will be potentially the most heavily affected, showing a

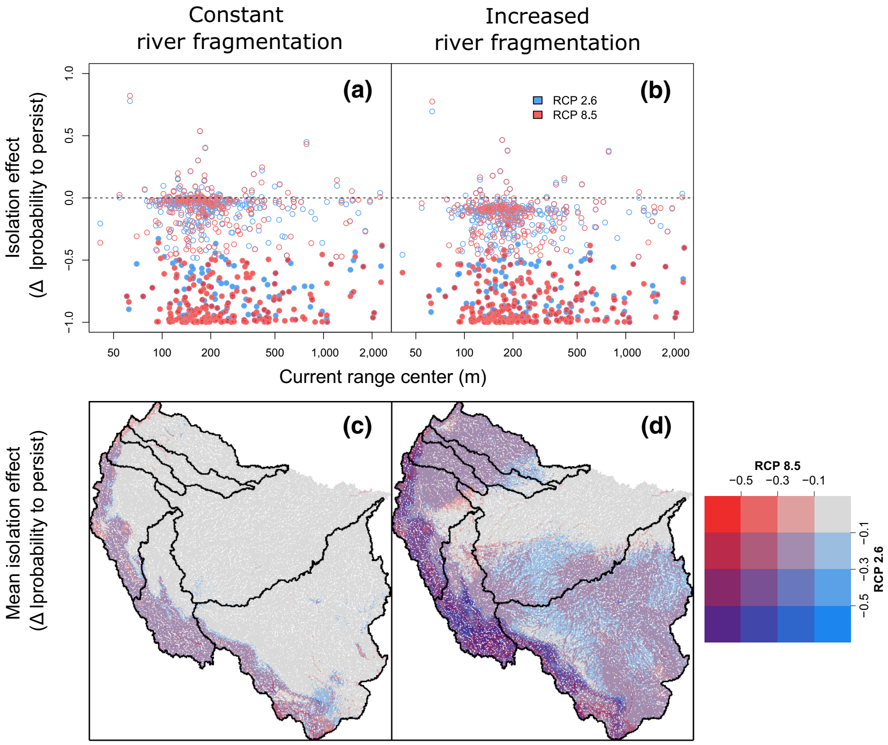


FIGURE 5 Projected isolation effect represented as the changes in the species probability to persist given their future ranges under constant (a) and increased (b) river fragmentation scenarios coupled with climate change (blue: RCP 2.6, and red: RCP 8.5). Filled circles indicate species falling below the vulnerability limit as a consequence of future scenarios, while open circles those that did not. The maps represent the spatial distribution of the mean Isolation effect, under constant (c) and increased (d) river fragmentation scenarios, as the weighted average of current species ranges

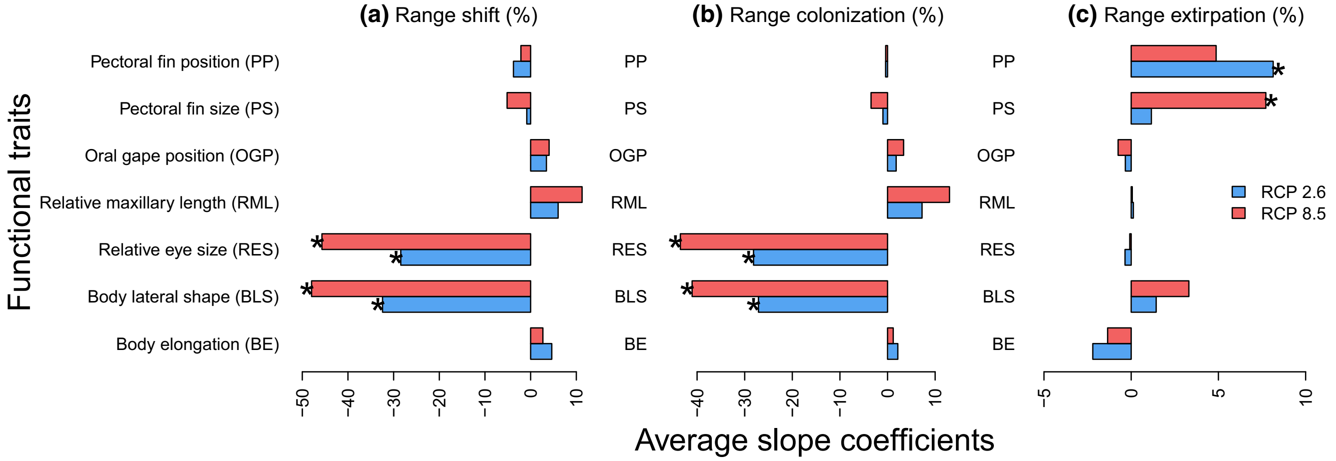


FIGURE 6 Average slope coefficients of functional traits resulting from linear mixed multimodel inference for significant impacts of future climate change scenarios: (a) Range shift, (b) Range colonization and (c) Range extirpation. Asterisk (*) indicates significant effects ($p < .05$). See Figure S5 for results on complementary climate change and fragmentation impact metrics

consistent decrease of the species probability to persist under any of the future scenarios considered (Figure 5c,d).

3.3 | Species functional traits and responses to future scenarios

Among the functional traits considered, body lateral shape, relative eye size, and pectoral fin position—indicating respectively the hydrodynamic shape, visual acuity, and the swimming abilities of species—were the most important predictors in explaining the impacts of climate change in Andean Amazon fishes (Figure 6; Figure S5). Body lateral shape and relative eye size were significantly associated with range shifts and colonization dynamics in both climate change scenarios, suggesting that more hydrodynamically shaped species (i.e., elongated shape with a low ratio of body height over length) and species with low visual acuity will experience more severe range contraction and less colonization of new areas (Figure 6a,b). Furthermore, species with larger and ventrally located pectoral fins (i.e., species inhabiting benthic river habitats) will experience significantly more severe range loss under climate change scenarios (Figure 6c).

4 | DISCUSSION

To our knowledge, this study is the first to quantify the simultaneous effects of future climate change and river fragmentation on freshwater fishes in the Neotropical region, with a focus on the Andean Amazon. Based on our results, we predict significant range shifts for fishes within the Andean Amazon under future climate scenarios, with greatest changes under the most pessimistic scenario (RCP 8.5). A large majority of species are predicted to suffer range contractions related to climate change, and these species are mostly located at mid- and higher elevations in the Andean Amazon. For most species, the Barrier effect of dams is not expected to severely impede these future range shifts, however, dams could considerably impact the probability of species to persist within their future projected distributions by splitting their ranges into smaller isolated fragments. The greater impact from climate change predicted for mid- and high elevation species was further supported by the analysis of functional traits, showing the most severe range contractions for hydrodynamically shaped Andean fish species, inhabiting benthic habitats and adapted to fast flowing rivers and streams.

4.1 | Range shifts induced by climate change

Species range shifts predicted under future climate scenarios are concordant with overall patterns observed for freshwater fishes in temperate regions (Comte & Grenouillet, 2013). Freshwater fishes' general responses to climate change have been related to their thermal preferences; cold-water fish species will experience range contraction and warm water species will experience range expansion (Comte & Grenouillet, 2013). These earlier findings are consistent with our results predicting that Andean Amazon fish species should suffer range contractions, especially those inhabiting higher elevations, which are characterized by colder waters (Lujan et al., 2013). Our findings, therefore, contrast with previous studies not considering climate change as a major threat for most of Amazon freshwater fishes and ecosystems (Oberdorff et al., 2015). Indeed, only a few Amazonian fishes have been assessed as vulnerable to climate change due to their restricted range and limited dispersal ability (Frederico, Olden, & Zuanon, 2016), but those studies were limited to lowland species. Here focusing on Andean species, which also includes a number of species occurring in lowlands (Figure 1), we provide clear evidence suggesting that, within the Amazon basin, highland Andean fishes are the most vulnerable to climate change (Anderson & Maldonado-Ocampo, 2011; Maldonado et al., 2011). Consistent with observed responses to climate change in other taxa across the Andes (Báez et al., 2016) and the globe (Freeman, Lee-Yaw, Sunday, & Hargreaves, 2018), our projections show that high altitude species will move upwards by greatly rising their lower distributional limit but without colonizing new upper areas, experiencing considerable range contraction.

4.2 | Impacts of river fragmentation by dams

Our findings further demonstrate the potential combined effect of river fragmentation by dams and species range shifts induced by climate change in the Andean Amazon. From our findings, the Barrier effect of river fragmentation from damming does not represent a major threat to most of the forecasted species range shifts. Indeed, our results showed that the contraction of ranges is mainly explained by the loss of suitable areas by climate change rather than by the impossibility to colonize new areas because of impassable dams for most species. Furthermore, range expansion was mainly predicted for lowland species in regions that are free of dams or where few dams are planned (Anderson et al., 2019). However, the expected river fragmentation by dams and climate change will considerably disrupt the natural relationship between body size and range size, which results in an overall decrease in the probability of long-term persistence in future ranges. These decreased probabilities to persist are concordant with some empirical evidence showing that the location of dams decreased the probability of fish occurrence over long time periods (Fukushima, Kameyama, Kaneko, Nakao, & Ashley Steel, 2007) and that the isolation degree generated by dams explained some of the observed contemporary extirpations (Kominoski et al., 2017).

Our analysis focused on dams as physical barriers, affecting river stream connectivity for fish movement and distributions. However, several other aspects of river fragmentation by dams potentially affecting Andean Amazon fishes could not be considered here. For instance, we were unable to account for alterations in flow regime caused by operation of dams, as changes in flow discharge and seasonality—two factors that are known to drive the population dynamics and reproduction of a number of tropical freshwater fish species (Tedesco & Hugueny, 2006; Tedesco et al., 2008). Dams also induce upstream and downstream changes in local environmental conditions on freshwater ecosystems affecting fish distribution and assemblage structures (Sá-Oliveira, Hawes, Isaac-Nahum, & Peres, 2015). This is especially true for high elevation species that are strongly adapted to fast-flowing conditions (e.g., high oxygen concentration), which are considerably modified by reservoirs of dams and operation (Arantes, Fitzgerald, Hoeinghaus, & Winemiller, 2019). Dams also trap sediment and nutrient flow movement altering nutrient depositions and the dynamics of river geomorphology downstream (Forsberg et al., 2017)—the essential aspects that drive habitat diversity and availability for downstream fishes in these areas. Furthermore, dams are expected to boost the effect of climate change in fluvial systems by increasing thermal variability (Olden & Naiman, 2010) and altering discharge and water availability patterns (Palmer et al., 2008).

4.3 | Species functional traits and responses to future scenarios

Most of the hydrodynamic species, those species occupying the bottom of the water column and occurring in high elevation gradient and fast flowing waters (e.g., *Trichomycterus*, *Chaestostoma*) were predicted to be more severely affected by climate change. These results confirm that species located in the highlands will be the most affected by climate change. Overall morphology is considered a good proxy of fish ecology in the Andean region (Conde-Saldaña, Albornoz-Garzón, López-Delgado, & Villa-Navarro, 2017). However, other selected morphological traits were not significantly related to climate change effects. This lack of clarity when associating traits with species responses to perturbations has been reported in similar studies and attributed to the complexity of the underlying processes, which call for a more mechanistic understanding (MacLean & Beissinger, 2017). The existing evidence in temperate freshwater fish species suggests that climate-induced shifts in upper or lower range limits seem to involve dissimilar processes. Changes in upper limits have been associated with life-history traits and trophic position, while changes in lower limits have been linked to thermal limits in freshwater fish species from France (Comte, Murienne, & Grenouillet, 2014). In the United States, species with wide niches (e.g., omnivores) have been related to stronger upstream predicted movements than specialized species (e.g., invertivores; Whitney, Whittier, Paukert, Olden, & Strecker, 2017). Considering complementary life-history traits linked to reproduction, trophic regime and growth have shown better explanatory power between species traits and responses to climate change (Chevalier, Comte, Laffaille, & Grenouillet, 2018).

4.4 | Uncertainties and limitations

In addition to several methodological sources of uncertainty, usual in large-scale predictive studies applying SDMs (Thuiller, Guéguen, Renaud, Karger, & Zimmermann, 2019), different time lags in biotic responses to environmental changes may lead to discrepancies between the realized changes and the expectations resulting from SDMs (i.e., "disequilibrium dynamics" (Lenoir & Svenning, 2015). The time needed for range contractions (i.e., extirpation lag) and expansions (i.e., dispersal and establishment lags) to operate as a response of species to climate change may vary depending on their biological adaptive potential and on species-specific associations to their biotic and abiotic environment, which can either buffer or enhance their vulnerability (Alexander et al., 2018). Altered biotic interactions can influence the probability for a species to establish in new suitable habitats or to be extirpated from those currently occupied. The arrival of a new large-bodied predator, usually presenting higher dispersal abilities, may inhibit the establishment of smaller prey species shifting upstream with a greater dispersal lag. A new predator could also accelerate the extirpation of prey species from downstream places (e.g., Koel et al., 2019), even if prey species, commonly smaller, should benefit from better warming tolerances (i.e., higher physiological thermal maxima; Leiva, Calosi, & Verberk, 2019). Although there is extensive literature on the negative impacts of introduced predator fish on native prey, empirical information from tropical regions is scarce. The example of the expansion of *Arapaima gigas*, a large Amazonian fish predator introduced 60 years ago above the rapids of the Madeira river in southwestern in the Amazon (Peru and Bolivia), provides limited (in a geographic and taxonomic context) evidence that large predators negatively impact native communities (Van Damme et al., 2015).

Interactions between the complex spatial heterogeneity of river networks and the biological features of species can create further delays in the species' responses. For instance, deep zones of the Amazonian mainstems (median depth of 20–30 m in the Solimoes river for instance) may buffer air-temperature changes and serve as thermal refuges, further delaying species responses, while natural barriers like rapids and waterfalls may increase their dispersal lag (Gibson-Reinemer et al., 2017; Torrente-Vilara, Zuanon, Leprieur, Oberdorff, & Tedesco, 2011). Mountain streams, such as in the Andean Amazon, can reduce the dispersal lag and even act as thermal refugia because warming rates and climate velocities in headwater streams should remain low, owing to local temperature gradients related to steep topography (Isaak et al., 2016; Troia et al., 2019). Other additional non-climatic habitat conditions (e.g., habitat size, substrate) may preclude the establishment of species dispersing upstream (Troia et al., 2019).

These interacting sources of uncertainties in species' responses to environmental changes may produce incongruences and delays affecting the likelihood of future range shifts projected by our SDMs. Recent studies from temperate regions where long-term monitoring programs, species-habitat associations, physiological tolerances, or fine physical environmental data are available, were able to integrate some of these sources of uncertainty in their predictive framework (e.g., Alexander et al., 2018; Kearney & Porter, 2009; Troia & Giam, 2019). Despite the lack of information from tropical environments and their biota, contrasting responses to global change results can be expected from tropical fishes. For example, although the thermal tolerances for most neotropical fish species are still unknown (Martínez, Cadena, & Torres, 2016), ecthothermal tropical species tend to display distributions close to their thermal tolerances (Sunday et al., 2019). This is supported by the narrower thermal tolerances found in tropical montane aquatic species when contrasted to their temperate counterparts (Polato et al., 2018). This evidence suggests an expected higher vulnerability of tropical mountain fishes to climate change and partially support our SDMs approach to evaluate their responses. Furthermore, our findings are based on the most complete and available data for the Amazon in terms of fish distribution and traits, climate change and river fragmentation, and further incorporated additional variables such as soil type, slopes, river size and dispersal distances that partly account for some of the uncertainty sources and time lags exposed above.

4.5 | Concluding remarks

Our study highlights the importance to account for the impact of future disturbances in the conservation and management of tropical freshwater ecosystems. The predicted responses of Andean Amazon fishes varied considerably with the severity of climate change and river fragmentation considered. Climate change will produce range contraction and loss for most of the Andean Amazon species, while the operation of current and future dams will potentially decrease the probability of species to maintain future distributions. Furthermore, these two threats are expected to interact with increased consequences for freshwater fishes by reducing their ranges, one of the main species features related to higher extinction risk. In addition, future disturbance scenarios will not affect all species equally, evidenced by differences that depend on the species position along the elevation gradient. This position is also reflected in species traits, at least for the predicted impacts of climate change. We suggest that future conservation efforts should consider species occupying highlands, which are expected to suffer more from climate change, and mid-elevation species, that will be the most threatened by planned dams in the Andean Amazon. Recent efforts on spatial prioritization of future hydropower development in the Amazon drainage suggest that placing dams in higher elevations and smaller streams should be favored to reduce greenhouse gas emissions per unit electricity generated (Almeida et al., 2019). Our species vulnerability assessment should also be implemented in strategic dam planning to consider biodiversity losses and functional reorganization of fish assemblages. The importance of freshwater ecosystems functioning and their biota to the well-being of ecosystems and humans of this region should not be underestimated.

ACKNOWLEDGEMENTS

This manuscript is dedicated to the memory of our friend Dr. Javier A. Maldonado-Ocampo, who passed away in March 2019 on a fieldwork accident in the Vaupes River. GAHR is infinitely grateful to Javier A. Maldonado-Ocampo for all the contributions to his career, constantly supporting him during his master and undergraduate studies. We thank Stephanie Januchowski-Hartley and Juan David Carvajal-Quintero for their time and valuable comments on initial versions of this manuscript. We thank Jonathan Lenoir and an anonymous reviewer for their comments that improved the manuscript. Financial support was provided by the ERANet-LAC project AmazonFish (ELAC2014/DCC-0210), Departamento Administrativo de Ciencia, Tecnología e Innovación -COLCIENCIAS- (44842-519-2015), the BiodivERsA project ODYSSEUS, and the EDB Laboratory, which is part of the French Laboratory of Excellence projects "LABEX TULIP" and "LABEX CEBA" (ANR-10-LABX-41, ANR-10-LABX-25-01). We thank the Field Museum of Natural History in Chicago and the Jhon D. and Catherine T. MacArthur Foundation (Grant G-1607-151047) for having mobilized data for AmazonFish in Colombia, Ecuador, and Peru. EPA and JAM-O acknowledge the Jhon D. and Catherine T. MacArthur Foundation (#16-1607-151053-CSD) for support of the Living Andean Rivers initiative. J.Z. received a productivity grant from Brazil's CNPq.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Fish distribution data that support the findings of this study are available in the public domain: https://doi.org/10.6084/m9.figshare.9923762. Environmental data were derived from the following resources available in the public domain: CHELSA V1.2 (https://chelsa-climate.org/downloads/), HydroSHEDS and HydroBASINS (https://www.hydrosheds.org/), SoilGrids V1.4 (https://soilgrids.org/), and GMTED2010 (https://www.usgs.gov/land-resources/eros/coastal-changes-and-impacts/gmted2010?qt-science_support_page_related_con=0#qt-science_support_page_related_con) and Shen et al. (2017; https://doi.org/10.6084/m9.figshare.c.3302111.v1). Maximum length data are publicly available through FishBase (https://www.fishbase.org). Fish trait data that support the findings of this study are available from Toussaint et al. (2016). Restrictions apply to the availability of these data, which were used under license for this study.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Herrera-R GA, Oberdorff T, Anderson EP, et al. The combined effects of climate change and river fragmentation on the distribution of Andean Amazon fishes. *Glob Change Biol*. 2020;00:1–15. https://doi.org/10.1111/gcb.15285