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LETTER

Damming Fragments Species' Ranges and Heightens Extinction Risk

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Abstract

Tropical rivers are experiencing an unprecedented boom in dam construction. Despite rapid dam expansion, knowledge about the ecology of tropical rivers and the implications of existing and planned dams on freshwater-dependent species remains limited. Here, we evaluate fragmentation of fish species' ranges, considering current and planned dams of the Magdalena River basin, Colombia. We quantify the relationship between species' range and body sizes and use a vulnerability limit set by this relationship to explore the influence that fragmentation of species' ranges has on extinction risk. We find that both existing and planned dams fragment most fish species' ranges, splitting them into more vulnerable populations. Importantly, we find that migratory species, and those that support fisheries, are most affected by fragmentation. Our results highlight the dramatic impact that dams can have on freshwater fishes and offer insights into species' extinction risk for data-limited regions.

Introduction

Nearly two-thirds of the world's largest rivers were fragmented by dams at the start of this century (Nilsson *et al.* 2005), and the remaining proportion of free-flowing rivers are rapidly declining (Finer & Jenkins 2012; Zarfl *et al.* 2014; Winemiller *et al.* 2016). Despite diverse impacts from dams on freshwater ecosystems, tropical and subtropical regions of South America, Africa, and Asia are experiencing booms in dam construction due to growing human population, economic development, and demand for low-carbon energy sources (Finer & Jenkins 2012; Kareiva 2012; Zarfl *et al.* 2014). At the same time, our understanding about the consequences of dams on species' extinction risk remains limited. Numerous studies have focused on impacts to species' diversity post dam construction (Poff *et al.* 2007), but approaches are needed that quantify potential consequences of new dams prior to their implementation. Such approaches could be particularly useful in regions where dam expansion is

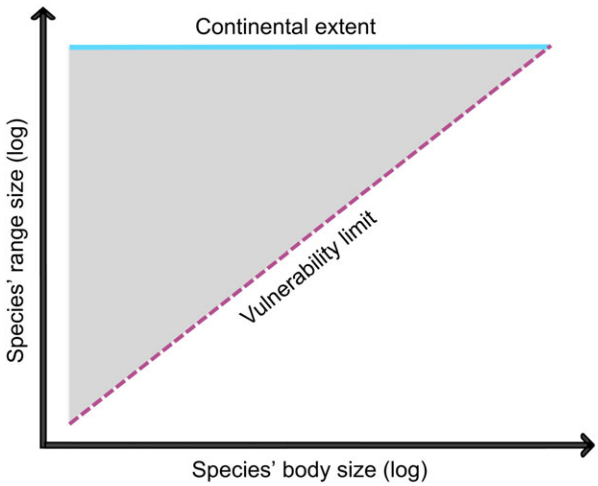

Figure 1 Representation of the theoretical constraint envelope described by the interspecific functional relationship between species' body size and geographical range size (modified from Brown & Maurer 1987). Note that small-bodied species show both small and large range size (high variance), whereas large-bodied species show only large range size (low variance). The solid line indicates the absolute space constraint, whereas the dashed line (referred to here as a vulnerability limit) is commonly associated with a minimum viable population size that is necessary for species' persistence. Based on the vulnerability limit, larger-bodied species are highly sensitive to fragmentation, because they require large range sizes for their persistence (i.e., to maintain sustainable population sizes), and so too are smaller-bodied species with restricted range sizes.

imminent (Kareiva 2012; Zarfl *et al.* 2014; Winemiller *et al.* 2016), and where biological information for species remains limited (Meyer *et al.* 2015).

Expanding fundamental macroecological relationships between species' range and body sizes (primarily documented in terrestrial vertebrates to date) could help us to better understand the potential impacts that dams can have on the vulnerability of freshwater-dependent species. The range-body size relationship commonly forms an approximate triangular shape (Gaston & Blackburn 1996); the spatial extent of the study area sets the upper limit of the triangle, and forms the upper limit of species' range size (Figure 1). The slope of the lower bound of this relationship forms because smaller species have a variety of range sizes, but larger-bodied species only have relatively large range sizes. Across assemblages, the minimum range size required for a given species, based on body size, generates a "probabilistic" vulnerability limit in bivariate space (Figure 1), whereby any species that is near or beyond this limit is prone to extinction or has a low probability of persistence through time (Gaston & Blackburn 1996). In this way, the triangular constraint space formed between range and body size could change as species' range size changes. Such changes could occur because of natural processes or because of dams or other human-induced factors that influence habitat loss or fragmentation. Indeed, changes in range size have quite consistently been shown to be a strong predictor of extinction risk (DiMarco *et al.* 2015).

From a conservation perspective, the lower boundary of the range-body size relationship is an important feature because it has been shown to represent a lower limit of range size (from here "vulnerability limit") below which species have heightened extinction risk (Figure 1; Brown & Maurer 1989; Gaston & Blackburn 1996). Furthermore, to our knowledge, the range-body size relationship has not yet been used to quantify potential effects of anthropogenic fragmentation on species' extinction risk. With this in mind, we draw on the range-body size relationship to evaluate fragmentation caused by current (fully constructed and under construction) and current + planned dams (under consideration or proposed) on the range sizes of 179 freshwater fish species in the Magdalena River basin. We further evaluate whether range-size fragmentation, and subsequent reduction in range size results in species shifting closer to the vulnerability limit, and subsequent extinction risk. For both current and current + planned damming, we summarize species' extinction risk at two scales: (1) within fragments of species' natural ranges, which we consider the "population" level and (2) across all fragments created within a species' natural range, which we considered the species level. Finally, we evaluate whether fragmentation from both current and current + planned damming differentially affects certain ecological traits or human-dependency factors.

Methods

Study area, species' ranges, and dam occurrences

We compiled a comprehensive data set of fish species' occurrence records for the Magdalena River basin, Colombia. The Magdalena River is the main fluvial ecosystem of northwest South America (1,540 km long; 7,100 m^3/s discharge), and is a major source of hydropower (Jiménez-Segura *et al.* 2016) and economic development in Colombia (Galvis & Mojica 2007; Barletta *et al.* 2015).

Our data set included occurrence records from 1940 to 2014, with 11,571 occurrence records for 204 fish species (Supporting Information: Dataset). We represented range size for each fish species as the extent of occurrence *sensu* International Union for Conservation of Nature (IUCN 2016). Range size was represented as the area (kilometer^2) falling within the convex hull formed around each species' occurrence records in the Magdalena River basin (Supporting Information: Methods and Figure S1). Species with less than three occurrence records were excluded from our analyses (25 species, see Supporting Information: Dataset), and all subsequent analyses were undertaken for 179 fish species. We further checked the distribution of each species based on an updated freshwater fish checklist that is in progress for Colombia (Maldonado-Ocampo *et al.* 2008) and the Colombian fisheries catalog (Lasso *et al.* 2011). This additional step allowed us to corroborate the narrow distribution of species with a small number of records (<10), certifying that these were rare and locally endemic species. Importantly, given the intensification of human-induced changes to the land- and waterscapes of the Magdalena River basin over the last several decades, it is possible that our range size estimates are conservative.

The geographic location and construction status of large impassable dams (>20 MW hydropower capacity) either those known to occur, or planned for, the Magdalena River basin were obtained from Lehner *et al.* (2011), Opperman *et al.* (2015), and The Nature Conservancy (TNC, unpublished data). We focused our assessment on these large dams because they have been shown to prohibit fish species' dispersal (e.g., Pelicice & Agostinho 2008; Winemiller *et al.* 2016). Our assessment included a total of 29 current (fully constructed and under construction) and 29 planned (under consideration or proposed) dams, respectively.

Ecological traits and human-dependency attributes

We collected information on maximum body length (millimeters) for each of the 179 fish species from FishBase (Froese & Pauly 2016) and published literature (Supporting Information). When different sources provided different values, we used the largest body size, and used maximum body length as a measure of body size. We collected additional information about each fish species ecological characteristics and human dependences, including: (1) species' endemicity to the Magdalena River basin, (2) species' demographic strategy, (3) species' functional group and (4) whether a species is used as resource, commercially or for subsistence, including migratory species (Table S1).

Data analyses

We used quantile regression (with "quantreg" package; Koenker 2015) in R statistical software (R Core Team 2013) to determine the relationship between species' natural range and body sizes, and to define the lower (0.05 quantile) and upper boundaries (0.95 quantile) of the relationship (Scharf *et al.* 1998). Two statistical analyses were implemented to verify that the relationship between species' natural range and body sizes is actually triangular, testing for a significant slope parameter of the lower boundary. First, we fitted linear quantile mixed models (LQMMs; using "lm4" package; Bates *et al.* 2014) considering quantiles 0.05 and 0.95 with genus, family and order as random factors to account for the taxonomic relatedness of species. Second, we quantified the significance of the lower boundary (0.05 quantile) with a randomization test procedure where body size values were permuted 4,999 times resulting in a null distribution of slope values.

After determining the relationship between range and body size, and respective thresholds, we determined those species that either did or did not fall below the upper limit of the 95% confidence interval of the lower boundary (as defined by the 0.05 quantile). Scharf *et al.* (1998) demonstrated that quantile regression produces robust estimates, and that the 0.05 quantile produces a similar, but more conservative, estimate than the 0.10 quantile, which is also frequently used. For all subsequent analyses, we considered this limit to be the vulnerability limit, as suggested by Le Feuvre *et al.* (2016).

To determine fragmentation of species' ranges by current and current + planned dams, we overlaid each species' geographic range (i.e., the range we considered to be their natural range) with the fragments resulting from the subdivision of the whole drainage basin by both current and planned dams (Figures S1 and S2). Fragmentation from planned dams was accounted for by including all current and all planned dams. The intersection of species' natural geographic ranges with the fragmented drainage basin resulted in multiple occupied fragments, and subsequently, these fragmented ranges were assumed to be independent populations because of dam size and the impossibility of dispersal between dams. These fragmented ranges combined with the vulnerability limit, as defined by species' natural ranges, resulted in a binary output of populations that we considered to either have heightened extinction risk (i.e., with ranges occurring below the vulnerability limit defined by species' natural range-body size relationship) or not. This "lower boundary rule", applied to each of the 179 species, produced (1) a mean value of the fragmented geographic range and (2) a proportion of endangered "populations" for each species, respectively.

To determine the relative importance and effect of the ecological and human-dependency attributes, we fitted generalized linear mixed models (GLMMs) with "binomial" distribution errors to the two extinction risk measures using "lm4" package (Bates *et al.* 2014). We ran

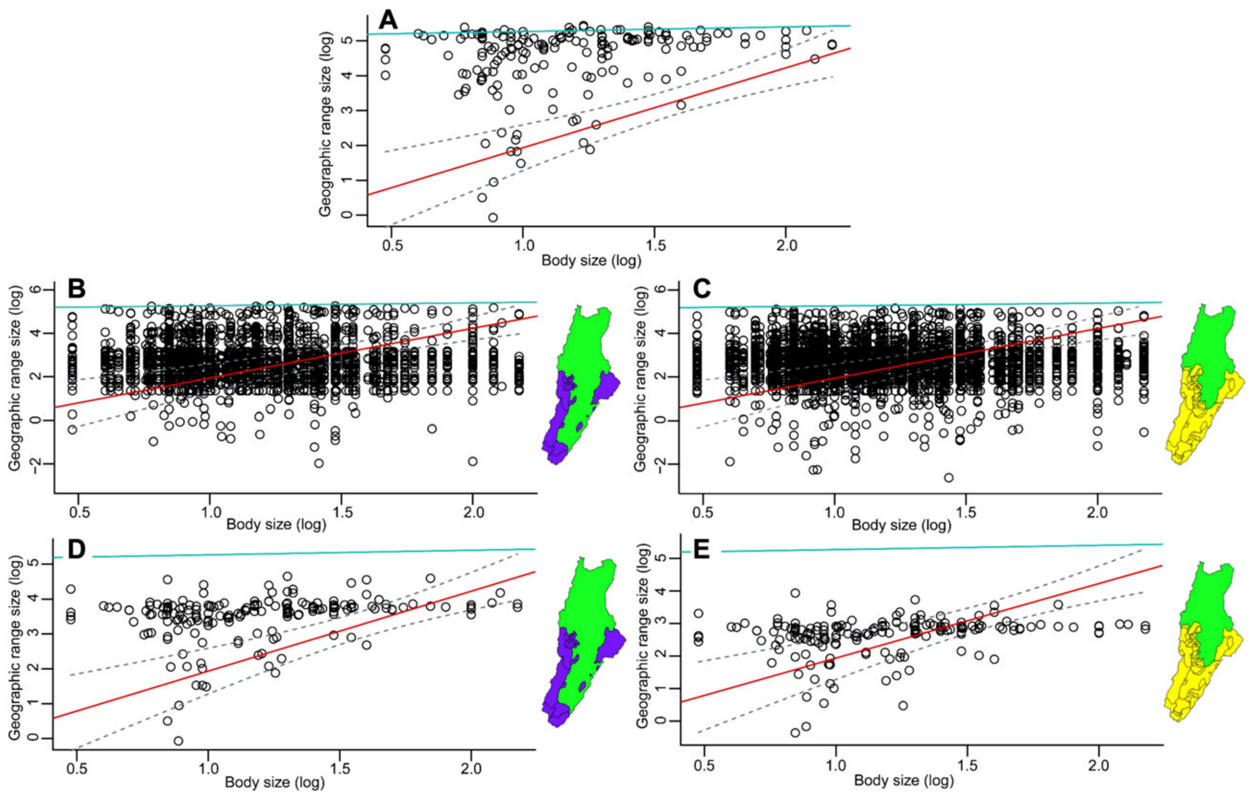

Figure 2 Range and body size relationship for 179 freshwater fish species of the Magdalena River basin. The blue solid line represents the regression of the 95th quantile. The red solid line represents the regression of the 5th quantile, and the dashed lines the 95% confidence intervals. The upper confidence interval (the red line) represents the species' vulnerability limit, built from the natural scenario (without fragmentation; A). For each of the 179 species, range size is shown for each fragmented population caused by damming (current [B] and current + planned [C]), and the species-level range size, which is the mean range size of all species' fragmented populations (current [D] and current + planned [E]). On the right side of each plot is a map to illustrate the scenario of fragmentation evaluated.

models for all possible combinations of the explanatory variables and then performed model averaging based on the "Akaike Information Criterion" (AIC). As a cut-off criterion to delineate a "top model set" providing average parameter estimates, we used models with ΔAICc <2 (Grueber *et al.* 2011). As with the LQMMs, we included genus, family and order as random factors in the GLMMs to account for the taxonomic relatedness of species and to avoid pseudoreplication.

Results

At the species level, the triangular relationship, based on species natural range and body sizes was stronger than could be predicted by chance ($P = 0.0042$; Figure 2A). The LQMM accounting for the taxonomic relatedness of species also revealed a significant positive slope for the lower bound of the relationship between range and body sizes ($P = 0.01$). Based on natural range and body sizes, 11% (~20) of species in the Magdalena River basin have intrinsically heightened extinction risk (Figure 2A).

Current dams subdivide the Magdalena River basin into 30 fragments (~8,700 km^2/fragment on average; Figure S2). Consequently, fish species' natural ranges are split into multiple smaller disconnected fragments. We found that, on average, species' natural ranges in the Magdalena River basin are currently split into nine (±8) fragments by large dams. On average, each species currently has 60% (±21%) of their fragmented populations falling below the vulnerability limit based on the range-body size relationship. Put another way, based on current damming, at least 74% (132) of fish species in the Magdalena River basin have at least half of their fragmented populations falling below the vulnerability limit (Figure 2B).

Looking to the future, the potential doubling of current dams through planned dams (for a total of 58 large dams) would again double the number of fragments (i.e., 59 fragments) dividing the Magdalena River basin, and decrease average fragment size (~4,400 km^2/fragment on average; Figure S2). Subsequently, planned dams would greatly increase the average number of fragmented

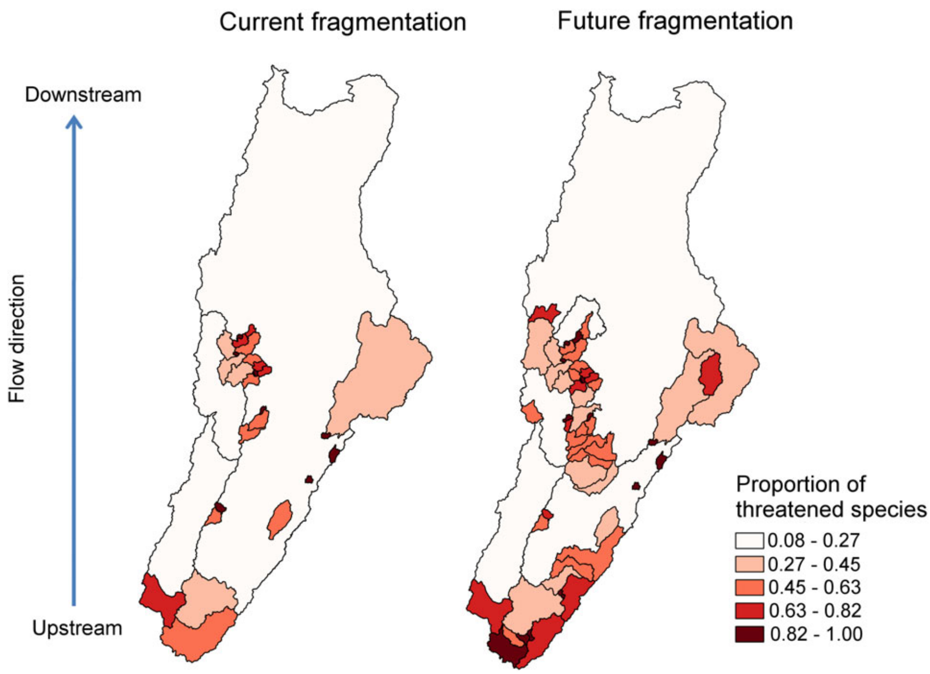

Figure 3 The Magdalena River basin with fragments based on current (left) and planned (right) dams. The shade of each fragment reflects the proportion of threatened species based on their body size, fragment size, and the vulnerability limit as defined by the relationship between species' ranges and body sizes.

populations (29 ± 18.7) per fish species, and result in 79% (141) of fish species having at least half of their fragmented populations falling below the vulnerability limit (Figure 2C, Supporting Information: Dataset). On average, across the 179 fish species, 64% (±20%) of the fragmented populations are projected to fall below the vulnerability limit if all planned dams are implemented along the Magdalena River.

We also found that both current and planned damming heightens extinction risk at the species level (where each new species-level fragmented range size is the average size of their "populations"). Current damming reduces the range size for the majority of species (92%) and increases the percentage of species that fall below the vulnerability limit by 11% (Figure 2D). Similarly, we found that construction of planned dams in addition to current dams would further heighten extinction risk at the species level; all 179 fish species would have reduced range size and 41% of fish species would shift below the vulnerability limit (Figure 2E). Regardless of the damming scenario considered, we found that the proportion of species falling below the vulnerability limit increased as fragment size decreased (Figure 3).

We found that under natural conditions, endemic and "opportunistic" species have heightened extinction risk (Figure 4), and endemic species are significantly closer to the vulnerability limit than others (Table S2). At the population level, we found no particular species trait or human-dependency factor to be more affected by current and planned dams than another (Table S3). However, we found that regardless of ecological traits or human-dependency factors, fragmentation of species' ranges caused by both current and planned dams increases the percentages of species falling below the vulnerability limit (Figure 4). We also found a notable and significant increase in extinction risk for both migratory species and known fisheries species (Figure 4; Table S2) when considering both current and current and planned dams, respectively.

Discussion

Drawing on the macroecological relationship between fish species' range and body sizes, we determined the extent to which current and planned dams fragment fish species' ranges, and the effect that this fragmentation has on species' extinction risk. Our findings solidify the sensitivity of freshwater-dependent species to fragmentation caused by damming (Fagan 2002).

We found that fish species endemic to the Magdalena River basin are inherently under heightened extinction risk compared to non-endemic species. We also found

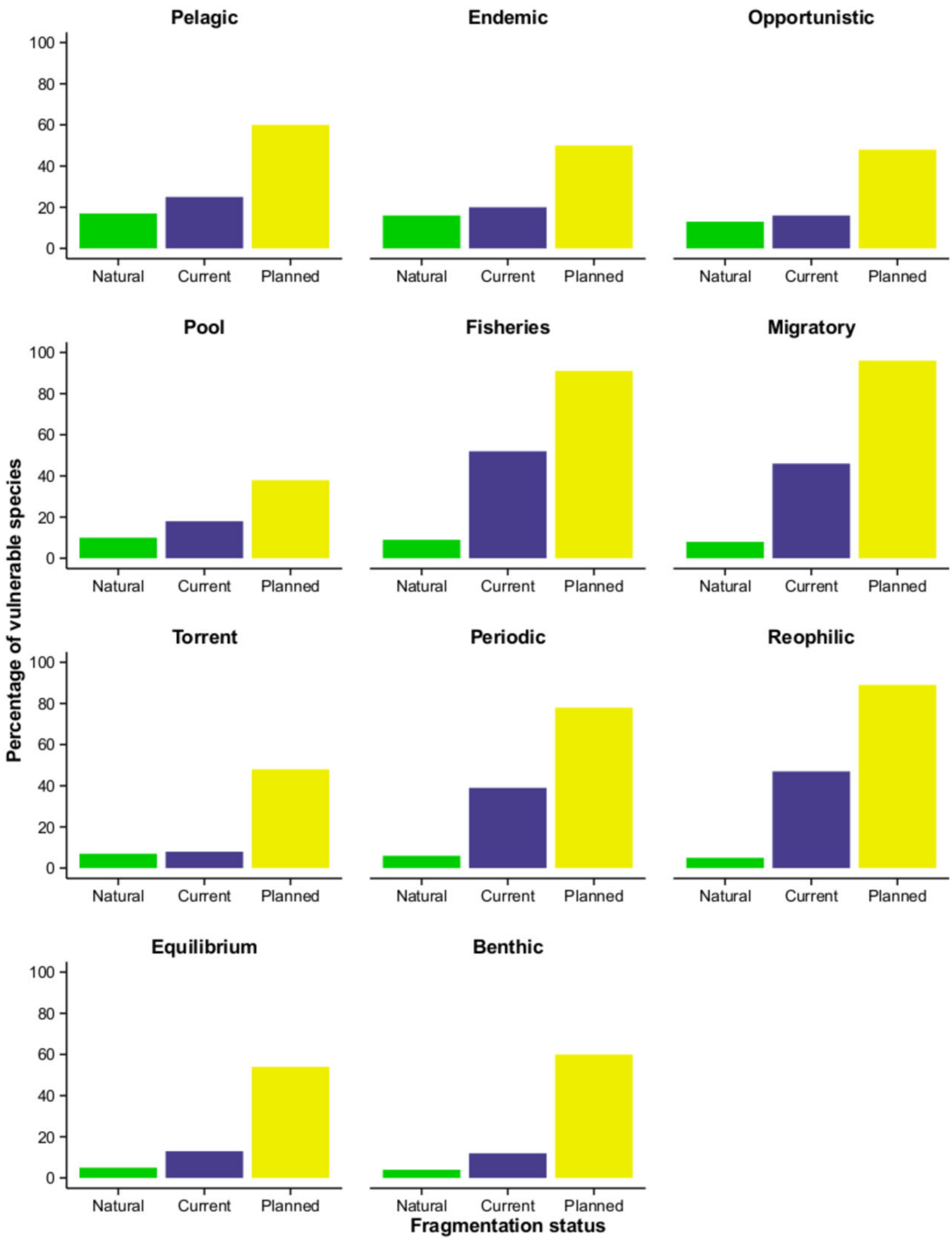

Figure 4 Percentage of vulnerable species for each trait and each scenario of fragmentation evaluated.

that current and planned damming increases the percentage of vulnerable species regardless of the ecological traits considered. Our findings suggest widespread impacts from current damming are likely to have already occurred in the Magdalena River basin. Indeed, under current damming, there is an 11% increase in fish species with heightened extinction risk compared to natural conditions.

The range-body size relationship used in our analyses is particularly relevant for overcoming data limitations that are often faced when making decisions about species' extinction risk (Davidson *et al.* 2009; Bland *et al.* 2012). Around the world, diverse criteria are used to evaluate species' extinction risk, and many assessments, such as those undertaken by the IUCN, are based on changes in range size. By quantifying the impact of current and potential human disturbances on species' range sizes, our approach offers a quantitative approach that complements ongoing efforts to evaluate freshwater species' extinction risk (Carrizo *et al.* 2013), and our analyses could be applied to other regions to improve our understanding about species' extinction risk now and in future. In addition, systematic data on current and future land use, roads or low-head dams were unfortunately not available for our analyses, but such data could be explicitly integrated into future studies. Using these additional data, our approach could also be used to quantify how different human disturbances influence species' extinction risk based on reductions in range size over time. An additional refinement to our approach could include the explicit consideration of species' habitat preferences to reduce any overestimation of fragmentation impacts on species.

Ultimately, species extinction depends on remaining fragment size (Morita & Yamamoto 2002), the minimum viable population of each species supported (Fagan 2002), and potentially, other interacting human disturbances that we were unable to account for here. Depending on the generation time of a species, documenting losses caused by range fragmentation can take years to decades (Tilman *et al.* 1994). However, loss of individual populations, and localized extinctions, could be more frequent than the extinction of an entire species depending on fragment size, the potential for dispersal between fragments, and suitability of remaining habitat (Fagan 2002). Our analyses could be used proactively to identify populations and species with heightened extinction risk because of fragmentation and losses in range size, and to identify those populations in greatest need of conservation action to avoid imminent losses.

Several studies have explored species traits and found that smaller body sizes, migratory behavior, limited ranges, and specialized habitats often explain freshwater fish extinction risk (e.g., Angermeier 1995; Reynolds *et al.* 2005). We found that both migratory fish species and species of fisheries importance are particularly affected by fragmentation from current dams, and will be more greatly affected if planned dams are implemented along the Magdalena River. In tropical river fisheries, like those of the Magdalena River, migratory species are highly valued by local fishers (Orr *et al.* 2012; Winemiller *et al.* 2016). Indeed, the Magdalena River fishery is the most productive in Colombia, and has been increasingly depleted over the last three decades (Galvis & Mojica 2007; Barletta *et al.* 2015). There remains limited understanding, and general lack of quantitative data, to pinpoint the primary causes of fishery decline in the Magdalena River basin (Barletta *et al.* 2015), but our analyses suggest that damming could be a major contributing factor by disconnecting fish populations. Furthermore, our findings highlight that if all dams that are currently planned for the Magdalena River are implemented, fragmentation of species' ranges will increase, further fragmenting fishery species' ranges, and heightening extinction risk.

Our findings support recent calls for more informed and systematic approaches to assessing dam expansion feasibility at basin scales (Lees *et al.* 2016; Winemiller *et al.* 2016), and our analyses begin to address this need, offering a repeatable method to quantify the impacts of current and expanding dams on biodiversity. While our results offer important insights about freshwater-dependent fish species' extinction risk, outputs from our assessment could also be integrated into more formal optimization analyses like those presented by Ziv *et al.* (2012). Outputs from our own, or other similar analyses, could be used to generate scenarios that explore both the allocation and potential removal of individual or groups of dams to minimize fish species' extinction risk while ensuring benefits returned from hydropower. Indeed, integrating our methods and findings within a decision theory framework could reduce regional scale impacts from fragmentation caused by damming to ensure retention of large enough range sizes to support species persistence.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. The Magdalena River basin showing an example of species distribution records (blue dots), the fragments created by current and planned dams (gray and green polygons) and the convex hull formed by the most external species records (orange polygon). Gray polygons are those fragments where the species is considered to be present. The orange polygon represents the area that we measured (in kilometer^2) to obtain the natural geographic range size of a given species. The intersection between orange polygon and each gray polygon represents the areas measured to obtain the fragmented geographic range size of a given species (*Pseudoplatystoma magdaleniatum* in this example).

Figure S2. Maps of three different fragmentation scenarios evaluated for the Magdalena River basin: a natural scenario without human-induced fragmentation (left), a current fragmentation scenario based on current dams (center), and a future fragmentation scenario based on both current and planned dams (right). The main channel of the watershed is represented with the dark blue line (in the left scenario) and tributaries are depicted with light blue lines.

Table S1. Summary of the methodology and the bibliography used to determine different ecological traits and human-dependency attributes.

Table S2. Final most parsimonious generalized linear mixed models (GLMMs) with binomial distribution errors at the species level for natural, current fragmentation caused by damming, and current + planned fragmentation caused by damming. Model parsimony was determined using the AIC value.

Table S3. Final most parsimonious generalized linear mixed models (GLMMs) with binomial distribution errors at the population level for current and current + planned fragmentation. Model parsimony was determined using the AIC value.

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