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Assessing conservation priorities of endemic freshwater fishes in the Tropical Andes region

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Abstract

1. Assessing the effectiveness of protected areas for sustaining species and identifying priority sites for their conservation is vital for decision making, particularly for freshwater fishes in South America, the global centre of freshwater fish diversity. Several conservation planning studies have used threatened freshwater fishes or species that are vulnerable to climate change as conservation targets, but none has included both in priority-setting analysis.

2. The objectives of this study were to identify gaps in the coverage of the existing protected areas in representing the endemic freshwater fishes of the Tropical Andes region, and to identify conservation priority areas that adequately cover threatened species and species vulnerable to climate change.

3. Data on 648 freshwater fishes from the Tropical Andes were used to identify gaps in the protected area coverage, and to identify conservation priority sites under three scenarios: (i) prioritize threatened species; (ii) prioritize species that are vulnerable to climate change; and (iii) prioritize both threatened species and species vulnerable to climate change.

4. A total of 571 species (88% of all species) were not covered by any protected areas; most of them are restricted to ≤10 catchments. To represent both threatened species and species vulnerable to climate change in the third scenario, 635 catchments were identified as priority areas, representing 26.5% of the study area. The number of irreplaceable catchments for this scenario is 475, corresponding to 22.5% of the total area.

5. The results of this study could be crucial for designing strategies for the effective protection of native fish populations in the Tropical Andes, and for planning proactive climate adaptation. It is hoped that the identification of priority areas, particularly irreplaceable catchments, will help to guide conservation and management decisions in the Andean region.

development on freshwater biodiversity in the Tropical Andes

1 | INTRODUCTION

Freshwater ecosystems – rivers, lakes, aquifers, and wetlands – occupy less than 1% of the Earth's surface and contain less than 0.01% of the world's water, yet they harbour approximately 10% of all known species and one-third of all vertebrates (Balian, Segers, Lévèque, & Martens, 2008). Freshwater biodiversity plays a vital role in the provision of resources to humans, including food, fibre, and medicines, as well as other indirect services, such as flood control, water filtration, pollution reduction, carbon sequestration, and recreation (Russi et al., 2013; Strayer & Dudgeon, 2010). However, freshwater biodiversity is being affected globally by human pressures that threaten its persistence (Collen et al., 2014; Thieme et al., 2010; Vörösmarty et al., 2010). Indeed, the Living Planet Index shows that the size of monitored freshwater populations decreased on average by 81% between 1970 and 2012, which is more than twice the reduction of terrestrial (38%) and marine species (36%) (World Wide Fund for Nature (WWF), 2016). The main threats affecting these species are habitat loss and degradation, overexploitation, invasive species, pollution, water abstraction, and flow regulation (Dudgeon et al., 2006; Garcia-Moreno et al., 2014). Moreover, the impact of these stressors can be exacerbated by climate change, increasing the susceptibility of freshwater ecosystems (Ormerod, Dobson, Hildrew, & Townsend, 2010; Strayer & Dudgeon, 2010).

Despite the importance of freshwater biodiversity to humans and its high level of threat, the identification of priority areas for the conservation of freshwater biodiversity and ecosystems has lagged behind, relative to the terrestrial and marine realms (Abell, Allan, & Lehner, 2007; Hermoso, Abell, Linke, & Boon, 2016). Indeed, few protected areas have been created primarily for freshwater conservation, and freshwater biodiversity and ecosystems are usually protected only incidentally through the inclusion within terrestrial protected area networks (Herbert, McIntyre, Doran, Allan, & Abell, 2010; Lawrence et al., 2011; Nel et al., 2007; Saunders, Meeuwig, & Vincent, 2002). Only in the past decade have systematic conservation planning approaches been applied to freshwater ecosystems (Carrizo et al., 2017; Esselman & Allan, 2011; Hermoso, Filipe, Segurado, & Beja, 2015a; Linke, Turak, & Nel, 2011; Moilanen, Leathwick, & Elith, 2008; Nel et al., 2009), and only one that we are aware of has included freshwater fishes in South America (Frederico, Zuanon, & De Marco, 2018).

With more than 5100 species, the freshwater fish fauna of South America is one of the most diverse on Earth (Reis et al., 2016), including phylogenetic and functional diversity (Toussaint, Charpin, Brosse, & Villéger, 2016). Most of these species are concentrated in two major basins, the Amazon and the Orinoco, which combined include more than 3000 species, 1240 of which are endemic (Reis et al., 2016). The Tropical Andes region encompasses the headwaters of these basins and several Pacific and Caribbean drainages of Colombia and Ecuador (Anderson & Maldonado-Ocampo, 2011). Together with the western Amazon, the area includes great heterogeneity of landscapes and habitats, with a particular geological history that has resulted in high levels of fish endemism, with more than 600 species found nowhere else (Jiménez-Segura, Ortega, et al., 2016). Many of these species are important for people's livelihoods as a food source, and for economic income; however, more than 16% are globally threatened with extinction (Jiménez-Segura, Ortega, et al., 2016), and 11% are vulnerable to climate change (Carr & Tognelli, 2016).

Assessing the effectiveness of protected areas for sustaining species and identifying priority sites for their conservation is vital for decision making, particularly for freshwater fishes in South America, given the high diversity, imminent threats, and dearth of conservation planning studies. Previously, several conservation planning studies have used either threatened freshwater fishes (Carrizo et al., 2017; Holland, Darwall, & Smith, 2012) or freshwater fishes that are vulnerable to climate change as conservation targets (Bond, Thomson, & Reich, 2014); however, no study has included both threatened species and species vulnerable to climate change as conservation targets in priority-setting analysis. This study aimed to address that need by assessing the conservation priorities of endemic freshwater fishes in the Tropical Andes region of South America. The objectives of the study were two-fold: to identify gaps in the coverage of the existing protected areas in representing the endemic freshwater fishes of the region, and to identify conservation priority areas that adequately cover threatened species and species vulnerable to climate change.

2 | METHODS

2.1 | Study area and data

The study area included the eastern versant of the Andes of Colombia, Ecuador, Peru, and Bolivia (also referred to as the western Amazon basin or Andean Amazon), the Chocó region of Colombia, and the north-western portion of Ecuador (Figure 1). The area includes nine freshwater ecoregions and comprises more than 50 major river systems, most draining into the Amazon basin, with others draining into the Caribbean Sea and the Pacific Ocean. In the Tropical Andes, considerable gradients in topography and climate create a diverse range of aquatic systems and, consequently, numerous distinct habitats to support a rich diversity of freshwater fishes.

Data were collected within the framework of the International Union for Conservation of Nature (IUCN) Red List of Threatened Species to assess the risk of the extinction of species. The Red Listing process was based on two regional workshops that involved the participation of local experts (Tognelli, Lasso, Bota-Sierra, Jiménez-Segura, & Cox, 2016). Species taxonomy and threat categories were based on the Red List. Species in the categories 'Critically Endangered' (CR), 'Endangered' (EN), and 'Vulnerable' (VU) are collectively referred to as 'threatened species'. Species in the other Red List categories – 'Data Deficient' (DD), 'Least Concern' (LC), and 'Near Threatened'
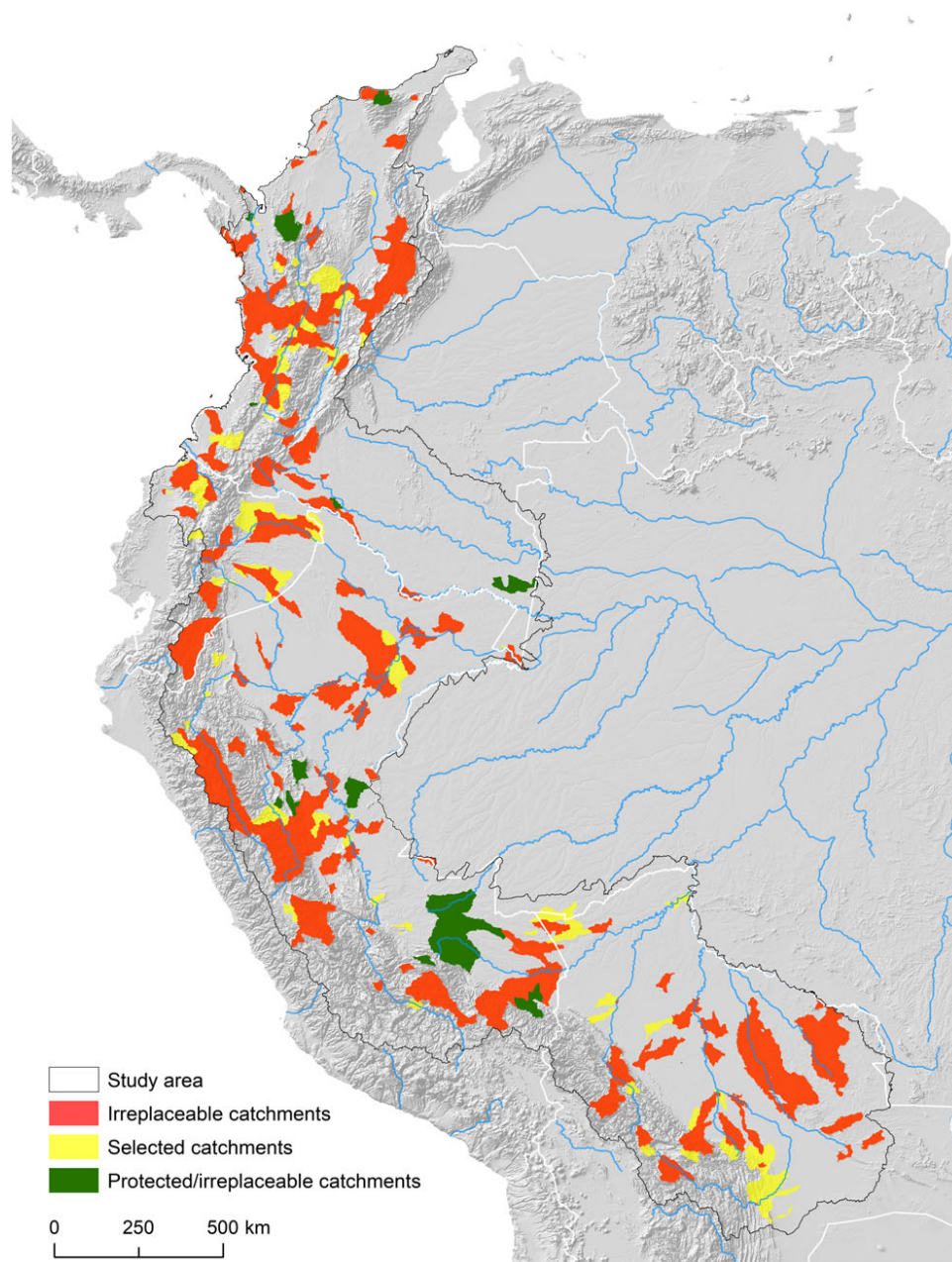
FIGURE 1 Distribution of catchments selected by the best solution in the spatial priority analysis for the first scenario (to prioritize 73 threatened species). Irreplaceable catchments (in red) are those selected in all 1000 runs, selected catchments (in yellow) are those complementing the irreplaceable catchments to achieve the conservation targets, and protected/irreplaceable catchments (in green) are those catchments that are both irreplaceable and protected (≥70% of their area overlap with a protected area)

(NT) – were also included in the analysis. No species were categorized as 'Extinct' (EX) or 'Extinct in the Wild' (EW).

Distribution data on 648 species of freshwater fishes (with the majority endemic to the study area) were compiled during the workshops. The global standardized hydrological database HydroBASINS (Lehner & Grill, 2013), customized to include lake polygons, was used to map species occurrence data to catchment units. HydroBASINS is a series of polygon layers that depict catchment boundaries at different scales in a hierarchically nested manner at a global scale. Of the 12 hierarchical levels of HydroBASINS, level 8 was used in this study. At this level, the total number of catchments or planning units in the study area was 3220, with an average area of 805 km² (median = 489 km²; minimum = 0.38 km²; maximum = 24,590 km²), and with a total area

of 2 595 171 km². Species were considered present in a catchment only when a collecting record overlapped with that catchment (coded as 'Extant' in the Red List). Parts of the distribution of a species that were considered by the experts as probably present in catchments (coded as 'Probably Extant' in the Red List), owing to the availability of adequate habitats, were not included in the analysis. Only species that were coded as 'Native' were included in the analysis, excluding species coded as 'Reintroduced', 'Introduced', 'Vagrant', and 'Origin Uncertain'.

Data on existing protected areas in the region were obtained from the World Database on Protected Areas (UNEP-WCMC 2017, available at www.protectedplanet.net). Only protected areas in the IUCN management categories I–IV were used in the analysis, where only scientific research and, in some cases, tourism are allowed. Protected

areas in these management categories are less modified and more oriented toward protecting biodiversity, in contrast to protected areas in management categories V and VI, which allow human settlement and the sustainable use of natural resources.

2.2 | Gap analysis

A gap analysis consists of assessing the degree to which biodiversity elements (e.g. species and ecosystems) are represented in the existing protected area network (Scott et al., 1993). To identify species represented in the current reserve network, the distribution maps of each freshwater fish were overlain onto the map of protected areas, and a gap analysis was conducted to assess the representation of catchments and freshwater fishes in the network. Catchments were considered adequately protected when at least 70% of their area overlapped with protected areas (Carrizo et al., 2017; Holland et al., 2012). The representation of species in the existing protected area network was based on the proportion of each species conservation target (see below for assignment of conservation targets) within adequately protected catchments. Based on this, species were classified into three categories: (i) 'protected', when 100% of the conservation target was included in adequately protected catchments; (ii) 'partial gap', when only a proportion of the conservation target was included in adequately protected catchments; and (iii) 'gap', when none of the conservation target was included in adequately protected catchments. The representation of fishes in protected areas was also compared with the information provided by the experts during the Red List assessment workshops regarding the presence of species in protected areas.

2.3 | Spatial priority analysis

Three scenarios were considered for the spatial priority analysis: the first was to prioritize all 73 threatened species in the region; the second was to prioritize all 69 species that are vulnerable to climate change (for a detailed explanation of the assessment of species vulnerability to climate change, see Carr & Tognelli, 2016); and the third was to prioritize both threatened species and species that are vulnerable to climate change (133 species in total, nine of which are both threatened and vulnerable to climate change). The conservation priority software MARXAN 2.4.3 (Ball, Possingham, & Watts, 2009) was used to identify the network that meets the targets specified while minimizing the total cost. The area of the catchments (i.e. planning units) in square kilometres was used as a proxy of cost (Moilanen, Wilson, & Possingham, 2009).

Conservation targets for the three scenarios were based on species representation (i.e. the number of catchments of occurrence of a particular species within the prioritization solution). For the first scenario (threatened species scenario), species in any of the threatened categories were assigned conservation targets based on the number of catchments in which they occur (instead of on their threat category, because most of them occur in ≤10 catchments). Species present in 1–10 catchments had a conservation target of 100% of their occurrences, species present in 11–50 catchments had a conservation target of 75% of their occurrences, species present in 51–100 catchments had a conservation target of 50% of their occurrences, and species present

in >100 catchments had a conservation target of 10% of their occurrences. For all other non-priority species, a target of two catchments was specified. The same conservation targets were assigned for species vulnerable to climate change in the second scenario (species vulnerable to climate change scenario), and for both threatened species and species vulnerable to climate change in the third scenario (threatened species and species vulnerable to climate change scenario).

Hydrological connectivity is an important feature in freshwater conservation planning (Hermoso, Kennard, & Linke, 2012) because of the interconnected nature of freshwater ecosystems. In this study, connectivity was considered by using the boundary length modifier (BLM) in MARXAN (Game & Grantham, 2008). The BLM is used to minimize the overall reserve system boundary length to produce a more compact reserve system by selecting neighbouring planning units (Game & Grantham, 2008). To find an optimal BLM, the method recommended in Stewart and Possingham (2005) was used. Each scenario was run, varying the BLM at six levels (0, 0.001, 0.01, 0.1, 1, and 10). In all three scenarios a value of 0.01 of BLM was found to be the most efficient and gave an appropriate level of spatial compactness. Hydrological connectivity was not used in the prioritization because the catchment database did not have a resolved topology. Each MARXAN run was completed with the default parameters for the simulating annealing algorithm, with a random start of 10% of the selectable planning units. Each scenario was run 1000 times and the number of times that a catchment was selected was used as a measure of its irreplaceability (i.e. catchments that were selected 1000 times were considered irreplaceable). For each scenario, the catchments that had ≥70% of their area within protected areas were considered protected and locked in the prioritization analysis.

3 | RESULTS

Distribution data were collected for 648 species of freshwater fishes. Of these, 12 were considered CR, 28 were considered EN, and 33 were considered VU: collectively, these amounted to 73 species referred to as threatened. The number of species of freshwater fishes in the other Red List categories were as follows: NT = 36; LC = 338; and DD = 201. Most of the species had very restricted distributions, with 27% occurring in only one catchment, 52% in five or fewer catchments, and 68% in 10 or fewer catchments.

3.1 | Gap analysis

In total, 100 protected areas in the IUCN management categories I–IV were found within the study area, covering 191 134 km^2 (7.3% of the total area). Fifty-five catchments had at least 70% of their area covered by these protected areas, representing 2.5% of the total area. In total, 571 species (88% of all species) were considered gap species in this analysis (i.e. the catchments in which they occur are not adequately covered by any protected area) (Table 1). The average percentage of species conservation targets protected (i.e. proportion of catchments in adequately protected catchments) was higher for widely distributed species than for restricted species (Table 1). On average, species occurring in 1–10 catchments had 2.9% of their catchments represented in protected areas (Table 1), and most of

TABLE 1 Number of species, number of threatened species, number of species vulnerable to climate change (CC), the average percentage of species conservation targets protected (i.e. the proportion of catchments in adequately protected catchments), and the number of gap, partial gap, and protected species for each conservation target (percentage of species in each group in parentheses). The conservation targets are based on species occurrences in catchments: 10%, >100 catchments; 50%, 51–100 catchments; 75%, 11–50 catchments; 100%, 1–10 catchments

Conservation targets	No. of species	Threatened	Vulnerable to CC	Average % of target	Gaps	Partial gaps	Protected
10%	31	5	0	31.7	19 (61.3)	3 (9.7)	9 (29.0)
50%	8	1	0	28.1	5 (62.5)	1 (12.5)	2 (25.0)
75%	168	8	18	15.6	126 (75.0)	27 (16.1)	15 (8.9)
100%	441	59	51	2.9	421 (95.5)	14 (3.2)	6 (1.4)
Total	648	73	69	7.9	571 (88.1)	45 (6.9)	32 (4.9)
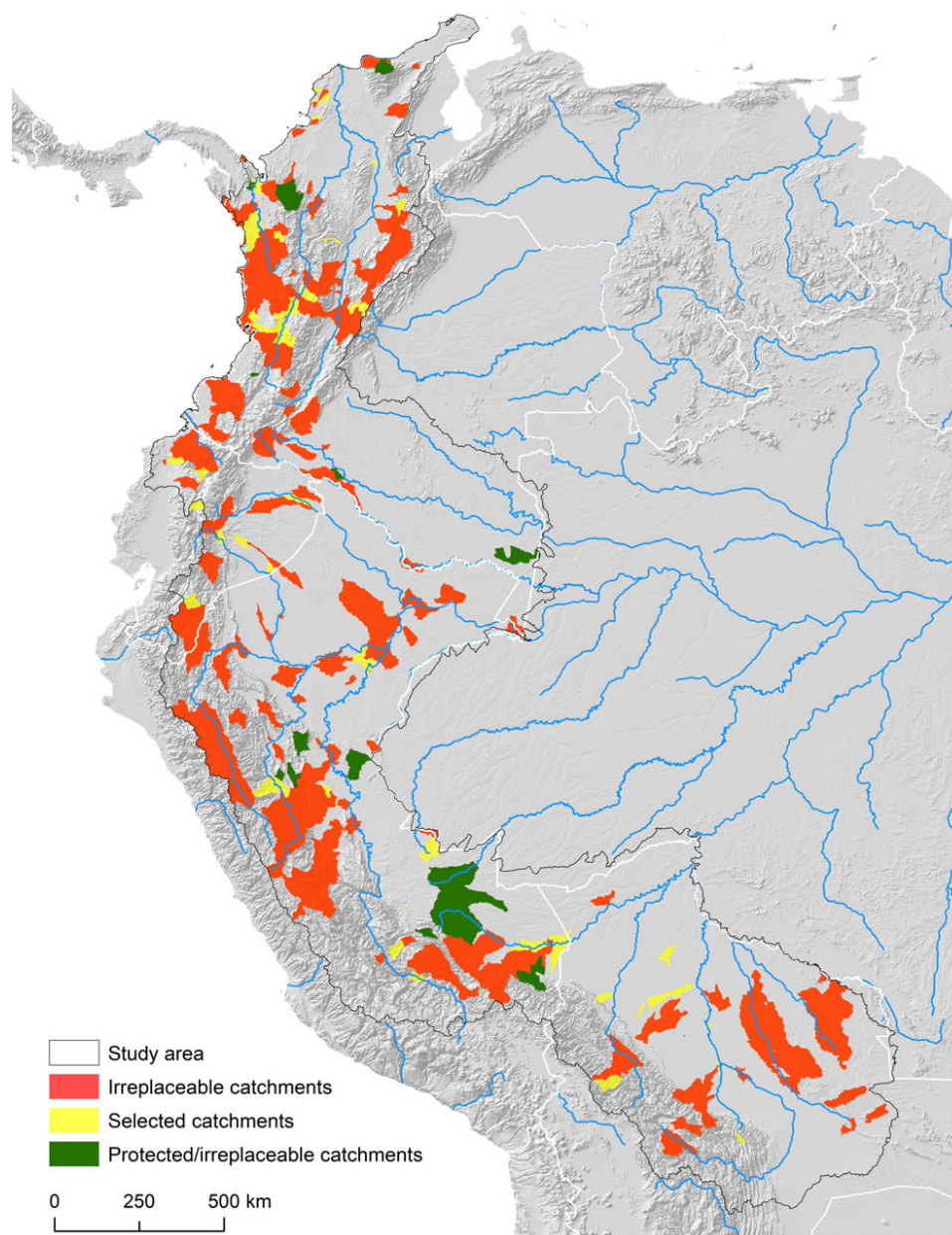
FIGURE 2 Distribution of catchments selected by the best solution in the spatial priority analysis for the second scenario (to prioritize 69 species vulnerable to climate change). Irreplaceable catchments (in red) are those selected in all 1000 runs, selected catchments (in yellow) are those complementing the irreplaceable catchments to achieve the conservation targets, and protected/irreplaceable catchments (in green) are those catchments that are both irreplaceable and protected (≥ 70% of their area overlap with a protected area)

the species in this conservation target (95.5%) were considered gaps. Only six species in this group were considered protected, and none of those was threatened or vulnerable to climate change.

In total, 77 species occur in adequately protected catchments and their conservation targets are therefore covered or partially covered by protected areas (Table 1). Only six threatened species and four species vulnerable to climate change had some of their conservation targets covered (i.e. partial gaps). This contrasts with the 206 species identified by the experts as occurring in protected areas during the Red List workshops (nine of these are threatened and 24 are vulnerable to climate change). This implies that 68% (442) of all species were still considered gaps. The difference between the coverage of protected areas in this study and the results from the Red List workshop is most likely the result of excluding all protected areas in IUCN management categories other than I–IV from the analysis, and of the percentage cut-off criterion for a catchment to be considered protected.

3.2 | Spatial priority analysis

In total, 465 catchments were identified in the threatened species scenario as priority areas to achieve the conservation targets set for every species (Figure 1). This represents 21.7% of the total area, of which 2% is already under the protection of the current reserve network. There were 380 catchments assessed as irreplaceable (i.e. they were
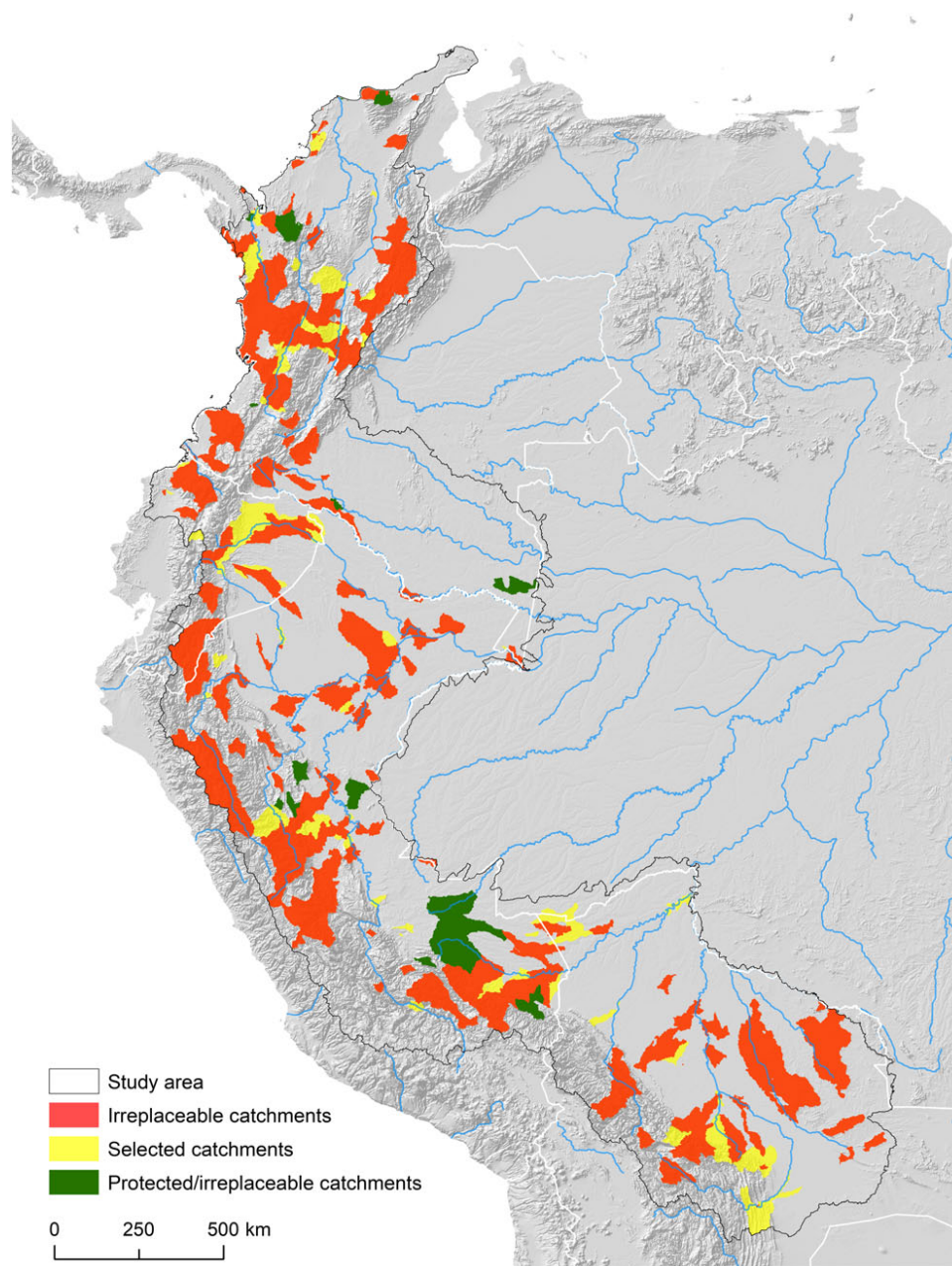
FIGURE 3 Distribution of catchments selected by the best solution in the spatial priority analysis for the third scenario (to prioritize 133 species, including both threatened species (73) and species vulnerable to climate change (69)). Irreplaceable catchments (in red) are those selected in all 1000 runs, selected catchments (in yellow) are those complementing the irreplaceable catchments to achieve the conservation targets, and protected/irreplaceable catchments (in green) are those catchments that are both irreplaceable and protected (≥70% of their area overlap with a protected area)

selected in all 1000 runs), representing 19.6% of the total area. Of these, 42 catchments (2% of the area) are already protected (protected/irreplaceable in Figure 1).

In the species vulnerable to climate change scenario, 561 catchments were needed to achieve the conservation targets set for every species, representing 23.5% of the total area (Figure 2). Of these catchments, 396 (19.7% of the total area) were identified as irreplaceable, and 42 (2% of the area) are already covered by protected areas (protected/irreplaceable in Figure 2). Only 294 of the irreplaceable catchments were common to both the first and second scenarios.

When trying to represent both threatened species and species vulnerable to climate change in the third scenario, 635 catchments were identified as priority areas to achieve the conservation targets set for all species, representing 26.5% of the total area (Figure 3). The number of irreplaceable catchments for this scenario is 475, amounting to 22.5% of the total area, of which 2% is covered by protected areas. The distribution of selected and irreplaceable catchments throughout the region is relatively homogeneous (Figure 3). It is surprising that very few catchments were selected in the middle and lower Magdalena River and the Amazon basin in Colombia. The average area of catchments in this scenario was 1085 km^2 (median = 627 km^2; minimum = 1.23 km^2; maximum = 24,591 km^2).

4 | DISCUSSION

This study has provided the first comprehensive assessment of the effectiveness of existing protected areas to represent endemic freshwater fishes of the Tropical Andes region. The results suggest that the protected area network fails to provide sufficient coverage to safeguard all freshwater fishes assessed, as 88% of the species are not adequately represented in any protected area. Most of these are species restricted to one or a few catchments and include the majority of species that are threatened and vulnerable to climate change. Indeed, the large number of irreplaceable catchments in all three scenarios is a result of the high number of range-restricted species. The poor spatial coverage of protected areas in the Tropical Andes in covering habitats for freshwater fishes is probably because most protected areas have not been designed with freshwater biodiversity in mind. Similar problems have been identified for freshwater species elsewhere (Carrizo et al., 2017; Chessman, 2013; Darwall et al., 2011; Herbert et al., 2010; Hermoso, Filipe, Segurado, & Beja, 2015b; Lawrence et al., 2011; Raghavan, Das, Nameer, Bijukumar, & Dahanukar, 2016). If the effective conservation of freshwater fishes is a goal of current conservation frameworks in the Tropical Andes, protected areas need to be designed and managed specifically for freshwater species (Chessman, 2013).

A novelty of this study is the inclusion of both threatened species and species vulnerable to climate change in the conservation planning process. This is important because susceptibility of freshwater fishes to climate change in the Tropical Andes does not appear to be related to their level of threat, as only 11% of the threatened species are also vulnerable to climate change (Carr & Tognelli, 2016). This mismatch between the current conservation status of a species and its vulnerability to emerging climate-related threats has also been reported for

fishes in California (Moyle, Kiernan, Crain, & Quiñones, 2013), the Brazilian Amazon (Frederico, Olden, & Zuanon, 2016), and globally (Comte & Olden, 2017). Species that are vulnerable to climate change but are not currently threatened could easily go under the conservation radar, as there are no current imminent threats to them, suggesting that perceptions of current extinction risk do not necessarily provide insight into future risks associated with climate change (Frederico et al., 2016). In this regard, the results of this study can be crucial in advocating the protection of native fish populations in need, and for proactive climate adaptation planning, such as restoration, land purchases, and management actions tending to enhance the resilience of riverine ecosystems, and to minimize the impacts (Palmer et al., 2009).

Freshwater species may be among the species on Earth most vulnerable to climate change because of the relatively high fragmentation and isolation of inland aquatic habitats (Strayer & Dudgeon, 2010). Most studies investigating the effects of climate change on freshwater fishes have focused on forecasting potential distributional shifts in response to projected climate scenarios (Bond et al., 2014; Comte, Buisson, Daufresne, & Grenouillet, 2013; Markovic et al., 2014). This assumes that species may be able to migrate to more suitable areas. Unlike terrestrial species, however, aquatic organisms have fewer dispersal opportunities, and natural and man-made barriers may impede migration in linear dendritic networks (Myers et al., 2017). Indeed, river connectivity from the Andes to the Amazon is already fragmented by dams, and with twice the present number of dams projected to be built in the region, this fragmentation is only expected to increase (Anderson et al., 2018; Forsberg et al., 2017). Moreover, for species restricted to rare habitats, there may not be sufficient suitable habitat to move amongst as the climate changes (Heller & Zavaleta, 2009). This is the case of the freshwater fishes in the Tropical Andes, where 74% of the species that are vulnerable to climate change are restricted to fewer than 10 catchments, and 40% are known from only one catchment. The strategy for conserving these species, then, is to improve their ability to cope with climate change within their existing range through habitat management (Greenwood, Mossman, Suggitt, Curtis, & Maclean, 2016). For instance, a recent study in the upper Condamine River in Australia showed that riparian restoration can offset predicted population consequences due to climate change in a threatened fish species (Turschwell et al., 2018). Protected areas will achieve their potential for freshwater conservation only if coupled with intensive management to abate threats (Chessman, 2013).

The results of this study have implications not only for the conservation of freshwater fishes, but also for the protection of a resource upon which many people rely. For example, inland fisheries in the Tropical Andes mainly exploit migratory species, and they represent an important source of food and provide livelihoods for many local communities (Jiménez-Segura, Ortega, et al., 2016). Indeed, the Tropical Andes contain the spawning grounds of the great Amazonian migratory catfishes (Barthem et al., 2017). The recruitment of these fish populations depends on the health and connectivity of rivers, floodplain lagoons, and their connection channels (Barthem et al., 2017; Jiménez-Segura, Galvis-Vergara et al., 2016). Freshwater fishes in the Andean region are also an important source of wild-caught species for the global aquarium trade, representing an important source of

income for rural people (Mancera-Rodríguez & Álvarez-León, 2008; Moreau & Coomes, 2007). For instance, in 2015 over 16 million ornamental fishes were exported from Colombia for a total value of $25 000 000 (Autoridad Nacional de Acuicultura y Pesca (AUNAP), 2016). Twenty-nine per cent of the total number of species included in this study are being used, either for food consumption or in the ornamental trade, and another 18% are probably being used for other activities (their use could not be confirmed) (Tognelli, Mesa, & Lasso, 2016).

Achieving the conservation targets set for all fish species when prioritizing for threatened species and species vulnerable to climate change would involve adding almost one-quarter of the study area to the existing protected area network. This study is a good starting point for identifying priority catchments for conservation to expand the current protected area network in the Tropical Andes, but it can be developed further in different ways. For instance, some of the catchments identified may be subject to intensive land use, habitat loss and degradation, fragmentation by the presence of dams, or other pressures that may make them suboptimal for protection. In the absence of socioeconomic data for the entire region, we used catchment area as cost in our analysis, on the (unlikely) assumption that conservation actions cost the same everywhere (Carwardine et al., 2008). Future studies, at a finer scale, can incorporate socio-economic and vulnerability data to minimize conflict, or opportunity costs, with human activities.

The potential for protected areas to work as freshwater ecosystem refugia and to be effective is highly dependent on the broader context in which they are located (Juffe-Bignoli et al., 2016). Given the highly connected nature of freshwater systems, they are particularly vulnerable to the propagation of threats from upstream and upland activities (Fausch, Torgersen, Baxter, & Li, 2002; Poff et al., 1997). Therefore, when designing conservation area networks for freshwater biodiversity the connectivity of the system is essential for maintaining the ecological and hydrological processes that support biodiversity (Hermoso et al., 2012; Linke et al., 2011). Although we used BLM in our analysis to account for some connectivity, this did not take longitudinal connectivity into account. An important extension of this study will be to include the connectivity of the river network to ensure the adequate protection of upstream catchments.

This study focused on identifying conservation priority areas for freshwater fishes; however, an emphasis on a single taxonomic group can lead to biases in conservation planning (Darwall et al., 2011). Several studies have shown that the level of surrogacy (i.e. the extent to which a particular set of biodiversity features effectively represents another in conservation planning) of some freshwater groups may not be adequate for other freshwater or terrestrial groups (Bush, Theischinger, Nipperess, Turak, & Hughes, 2013; Darwall et al., 2011; Hermoso et al., 2015b; Lawler, White, Sifneos, & Master, 2003; Rodrigues & Brooks, 2007). A more taxonomically comprehensive analysis would be valuable in order to identify conservation priority areas for broader freshwater biodiversity in the Tropical Andes region.

The analyses in this study are dependent upon, and subject to, bias within the underlying taxonomic data used. The taxonomic data in this study were based on Tognelli, Lasso, et al. (2016) and may not represent the most up-to-date taxonomy for some species, but were retained for consistency with the information that appears on the IUCN Red List website. It is unlikely that the main patterns of distribution and conservation priority sites selected are affected by any slight discrepancies in sources. Research throughout the study region remains highly fragmentary and incomplete, however, and the bias in taxonomic surveys and discovery of species may mask areas of conservation concern. Nevertheless, the urgency for identifying conservation priority areas in the region is too great to wait until better data become available, and the results of this study can be refined and improved when new data emerge.

Although this is a preliminary broad-scale analysis, we expect that the identification of these priority areas, particularly of irreplaceable catchments, will help to guide conservation and management decisions in the region, considering that poor management and legislation harmful to freshwater fishes are pervasive in the Neotropics (Pelicice et al., 2017). The results can help address Biodiversity Aichi Target 11, which states that at least 17% of terrestrial and inland water areas are adequately conserved and managed by 2020 (Convention on Biological Diversity (CBD), 2010). These results can also help public and private sector organizations to comply with environmental safeguards in the region, particularly in light of a new wave of mining activities (Asner, Llactayo, Tupayachi, & Ráez Luna, 2013; Swenson, Carter, Domec, & Delgado, 2011), oil and gas projects (Finer, Jenkins, Pimm, Keane, & Ross, 2008), and hydropower development (Anderson et al., 2018; Carvajal-Quintero et al., 2017; Finer & Jenkins, 2012; Forsberg et al., 2017; Jiménez-Segura et al., 2014). Given the rapid and increasing rate of development in the Tropical Andes, it is critical to capitalize on the freshwater conservation potential of the current protected area network, improve its efficacy through a holistic and proactive management approach, and identify new areas that can act as refugia for freshwater biodiversity.

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REFERENCES

Abell, R., Allan, J., & Lehner, B. (2007). Unlocking the potential of protected areas for freshwaters. *Biological Conservation*, *134*, 48–63.

Anderson, E. P., Jenkins, C. N., Heilpern, S., Maldonado-Ocampo, J. A., Carvajal-Vallejos, F. M., Encalada, A. C., … Tedesco, P. A. (2018). Fragmentation of Andes-to-Amazon connectivity by hydropower dams. *Science Advances*, *4*, eaao1642.

Anderson, E. P., & Maldonado-Ocampo, J. A. (2011). A regional perspective on the diversity and conservation of tropical Andean fishes: Fishes of the Tropical Andes. *Conservation Biology*, *25*, 30–39.

Asner, G. P., Llactayo, W., Tupayachi, R., & Ráez Luna, E. (2013). Elevated rates of gold mining in the Amazon revealed through high-resolution monitoring. *Proceedings of the National Academy of Sciences*, *110*, 18454–18459.

Autoridad Nacional de Acuicultura y Pesca (AUNAP) (2016). El mercado de las especies ornamentales está en alza. http://www.aunap.gov.co/el-mercado-de-las-especies-ornamentales-esta-en-alza/ [9 February 2018].

Balian, E. V., Segers, H., Lévèque, C., & Martens, K. (2008). The freshwater animal diversity assessment: An overview of the results. *Hydrobiologia*, *595*, 627–637.

Ball, I. R., Possingham, H. P., & Watts, M. (2009). Marxan and relatives: Software for spatial conservation prioritisation. In A. Moilanen, K. A. Wilson, & H. P. Possingham (Eds.), *Spatial conservation prioritisation: Quantitative methods and computational tools* (pp. 185–195). Oxford, UK: Oxford University Press.

Barthem, R. B., Goulding, M., Leite, R. G., Cañas, C., Forsberg, B., Venticinque, E., … Mercado, A. (2017). Goliath catfish spawning in the far western Amazon confirmed by the distribution of mature adults, drifting larvae and migrating juveniles. *Scientific Reports*, *7*, 41784.

Bond, N. R., Thomson, J. R., & Reich, P. (2014). Incorporating climate change in conservation planning for freshwater fishes. *Diversity and Distributions*, *20*, 931–942.

Bush, A., Theischinger, G., Nipperess, D., Turak, E., & Hughes, L. (2013). Dragonflies: Climate canaries for river management. *Diversity and Distributions*, *19*, 86–97.

Carr, J., & Tognelli, M. F. (2016). Evaluación de la vulnerabilidad al cambio climático de las especies de agua dulce de los Andes Tropicales. In M. F. Tognelli, C. A. Lasso, C. A. Bota-Sierra, L. F. Jiménez-Segura, & N. A. Cox (Eds.), *Estado de Conservación y Distribución de la Biodiversidad de Agua Dulce en los Andes Tropicales* (pp. 127–155). Gland, Suiza, Cambridge, UK y Arlington, USA: UICN.

Carrizo, S. F., Lengyel, S., Kapusi, F., Szabolcs, M., Kasperidus, H. D., Scholz, M., … Cardoso, A. C. (2017). Critical catchments for freshwater biodiversity conservation in Europe: Identification, prioritisation and gap analysis. *Journal of Applied Ecology*, 1209–1218.

Carvajal-Quintero, J. D., Januchowski-Hartley, S. R., Maldonado-Ocampo, J. A., Jézéquel, C., Delgado, J., & Tedesco, P. A. (2017). Damming fragments species' ranges and heightens extinction risk. *Conservation Letters*, *10*, 708–716.

Carwardine, J., Wilson, K. A., Watts, M., Etter, A., Klein, C. J., & Possingham, H. P. (2008). Avoiding costly conservation mistakes: The importance of defining actions and costs in spatial priority setting. *PLoS ONE*, *3*, e2586.

Chessman, B. C. (2013). Do protected areas benefit freshwater species? A broad-scale assessment for fish in Australia's Murray-Darling Basin. *Journal of Applied Ecology*, *50*, 969–976.

Collen, B., Whitton, F., Dyer, E. E., Baillie, J. E. M., Cumberlidge, N., Darwall, W. R. T., … Böhm, M. (2014). Global patterns of freshwater species diversity, threat and endemism: Global freshwater species congruence. *Global Ecology and Biogeography*, *23*, 40–51.

Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. *Freshwater Biology*, *58*, 625–639.

Comte, L., & Olden, J. D. (2017). Climatic vulnerability of the world's freshwater and marine fishes. *Nature Climate Change*, *7*, 718–722.

Convention on Biological Diversity (CBD) (2010). Convention on Biological Diversity's Strategic Plan for 2020 CBD: Montreal. www.cbd.int/sp [8 February 2018].

Darwall, W. R. T., Holland, R. A., Smith, K. G., Allen, D., Brooks, E. G. E., Katarya, V., … Vié, J.-C. (2011). Implications of bias in conservation research and investment for freshwater species: Conservation and freshwater species. *Conservation Letters*, *4*, 474–482.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z., Knowler, D. J., Naiman, R. J., … Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*, 163–182.

Esselman, P. C., & Allan, J. D. (2011). Application of species distribution models and conservation planning software to the design of a reserve network for the riverine fishes of northeastern Mesoamerica: Freshwater protection areas for the fishes of northeastern Mesoamerica. *Freshwater Biology*, *56*, 71–88.

Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes: A continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat. *Bioscience*, *52*, 483–498.

Finer, M., & Jenkins, C. N. (2012). Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. *PLoS ONE*, *7*, e35126.

Finer, M., Jenkins, C. N., Pimm, S. L., Keane, B., & Ross, C. (2008). Oil and gas projects in the Western Amazon: Threats to wilderness, biodiversity, and indigenous peoples. *PLoS ONE*, *3*, e2932.

Forsberg, B. R., Melack, J. M., Dunne, T., Barthem, R. B., Goulding, M., Paiva, R. C., … Weisser, S. (2017). The potential impact of new Andean dams on Amazon fluvial ecosystems. *PLoS ONE*, *12*(8), e0182254.

Frederico, R. G., Olden, J. D., & Zuanon, J. (2016). Climate change sensitivity of threatened, and largely unprotected, Amazonian fishes: Climate change in Amazonian fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*, 91–102.

Frederico, R. G., Zuanon, J., & De Marco, P. (2018). Amazon protected areas and its ability to protect stream-dwelling fish fauna. *Biological Conservation*, *219*, 12–19.

Game, E. T., & Grantham, H. S. (2008). *Marxan user manual: For Marxan version 1.8.10*. St. Lucia, Queensland, Australia, Vancouver, BC, Canada: University of Queensland, Pacific Marine Analysis and Research Association.

Garcia-Moreno, J., Harrison, I. J., Dudgeon, D., Clausnitzer, V., Darwall, W., Farrell, T., … Tubbs, N. (2014). Sustaining freshwater biodiversity in the Anthropocene. In A. Bhaduri, J. Bogardi, & M. Sina (Eds.), *The Global Water System in the Anthropocene* (pp. 247–270). Bonn, Germany: Springer.

Greenwood, O., Mossman, H. L., Suggitt, A. J., Curtis, R. J., & Maclean, I. M. D. (2016). Using in situ management to conserve biodiversity under climate change. *Journal of Applied Ecology*, *53*, 885–894.

Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, *142*, 14–32.

Herbert, M. E., Mcintyre, P. B., Doran, P. J., Allan, J. D., & Abell, R. (2010). Terrestrial reserve networks do not adequately represent aquatic ecosystems. *Conservation Biology*, *24*, 1002–1011.

Hermoso, V., Abell, R., Linke, S., & Boon, P. (2016). The role of protected areas for freshwater biodiversity conservation: Challenges and opportunities in a rapidly changing world. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(S1), 3–11.

Hermoso, V., Filipe, A. F., Segurado, P., & Beja, P. (2015a). Filling gaps in a large reserve network to address freshwater conservation needs. *Journal of Environmental Management*, *161*, 358–365.

Hermoso, V., Filipe, A. F., Segurado, P., & Beja, P. (2015b). Effectiveness of a large reserve network in protecting freshwater biodiversity: A test for the Iberian Peninsula. *Freshwater Biology*, *60*, 698–710.

Hermoso, V., Kennard, M. J., & Linke, S. (2012). Integrating multidirectional connectivity requirements in systematic conservation planning for freshwater systems. *Diversity and Distributions*, *18*, 448–458.

Holland, R. A., Darwall, W. R. T., & Smith, K. G. (2012). Conservation priorities for freshwater biodiversity: The Key Biodiversity Area approach refined and tested for continental Africa. *Biological Conservation*, *148*, 167–179.

Jiménez-Segura, L. F., Galvis-Vergara, G., Cala-Cala, P., García-Alzate, C. A., López-Casas, S., Ríos-Pulgarín, M. I., … Álvarez-León, R. (2016). Freshwater fish faunas, habitats and conservation challenges in the Caribbean river basins of north-western South America. *Journal of Fish Biology*, *89*, 65–101.

Jiménez-Segura, L. F., Ortega, H., Chuctaya, J., Jiménez Prado, P., Carvajal-Vallejos, F. M., Rivadeneira, J. F., … Tognelli, M. F. (2016). Estado de conservación y distribución de los peces de agua dulce de los Andes Tropicales. In M. F. Tognelli, C. A. Lasso, C. A. Bota-Sierra, L. F. Jiménez-Segura, & N. A. Cox (Eds.), *Estado de conservación y distribución de la biodiversidad de agua dulce en los Andes tropicales* (pp. 36–69). Gland, Suiza, Cambridge, UK y Arlington, USA: UICN.

Jiménez-Segura, L. F., Restrepo-Santamaría, D., López-Casas, S., Delgado, J., Valderrama, M., Álvarez, J., & Gómez, D. (2014). Ictiofauna y desarrollo del sector hidroeléctrico en la cuenca del río Magdalena-Cauca, Colombia. *Biota Colombiana*, 15, 3–25.

Juffe-Bignoli, D., Harrison, I., Butchart, S. H., Flitcroft, R., Hermoso, V., & Jonas, ... van Soesbergen, A. (2016). Achieving Aichi Biodiversity Target 11 to improve the performance of protected areas and conserve freshwater biodiversity: Elements needed to meet a global target for protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26, 133–151.

Lawler, J. J., White, D., Sifneos, J. C., & Master, L. L. (2003). Rare species and the use of indicator groups for conservation planning. *Conservation Biology*, 17, 875–882.

Lawrence, D. J., Larson, E. R., Liermann, C. A. R., Mims, M. C., Pool, T. K., & Olden, J. D. (2011). National parks as protected areas for U.S. freshwater fish diversity: National parks as freshwater protected areas. *Conservation Letters*, 4, 364–371.

Lehner, B., & Grill, G. (2013). Global river hydrography and network routing: Baseline data and new approaches to study the world's large river systems. *Hydrological Processes*, 27, 2171–2186.

Linke, S., Turak, E., & Nel, J. (2011). Freshwater conservation planning: The case for systematic approaches. *Freshwater Biology*, 56, 6–20.

Mancera-Rodríguez, N. J., & Álvarez-León, R. (2008). The trade of ornamental fishes in Colombia. *Acta Biológica Colombiana*, 13, 23–52.

Markovic, D., Carrizo, S., Freyhof, J., Cid, N., Lengyel, S., Scholz, M., ... Darwall, W. (2014). Europe's freshwater biodiversity under climate change: Distribution shifts and conservation needs. *Diversity and Distributions*, 20, 1097–1107.

Moilanen, A., Leathwick, J., & Elith, J. (2008). A method for spatial freshwater conservation prioritization. *Freshwater Biology*, 53, 577–592.

Moilanen, A., Wilson, K. A., & Possingham, H. P. (2009). *Spatial conservation prioritisation: Quantitative methods and computational tools*. Oxford, UK: Oxford University Press.

Moreau, M.-A., & Coomes, O. T. (2007). Aquarium fish exploitation in western Amazonia: Conservation issues in Peru. *Environmental Conservation*, 34, 12–22.

Moyle, P. B., Kiernan, J. D., Crain, P. K., & Quiñones, R. M. (2013). Climate change vulnerability of native and alien freshwater fishes of California: A systematic assessment approach. *PLoS ONE*, 8, e63883.

Myers, B. J. E., Lynch, A. J., Bunnell, D. B., Chu, C., Falke, J. A., Kovach, R. P., ... Paukert, C. P. (2017). Global synthesis of the documented and projected effects of climate change on inland fishes. *Reviews in Fish Biology and Fisheries*, 27, 339–361.

Nel, J. L., Roux, D. J., Abell, R., Ashton, P. J., Cowling, R. M., Higgins, J. V., ... Viers, J. H. (2009). Progress and challenges in freshwater conservation planning. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19, 474–485.

Nel, J. L., Roux, D. J., Maree, G., Kleynhans, C. J., Moolman, J., Reyers, B., ... Cowling, R. M. (2007). Rivers in peril inside and outside protected areas: A systematic approach to conservation assessment of river ecosystems. *Diversity and Distributions*, 13, 341–352.

Ormerod, S. J., Dobson, M., Hildrew, A. G., & Townsend, C. R. (2010). Multiple stressors in freshwater ecosystems. *Freshwater Biology*, 55, 1–4.

Palmer, M. A., Lettenmaier, D. P., Poff, N. L., Postel, S. L., Richter, B., & Warner, R. (2009). Climate change and river ecosystems: Protection and adaptation options. *Environmental Management*, 44, 1053–1068.

Pelicice, F. M., Azevedo-Santos, V. M., Vitule, J. R. S., Orsi, M. L., Lima Junior, D. P., Magalhães, A. L. B., ... Agostinho, A. A. (2017). Neotropical freshwater fishes imperiled by unsustainable policies. *Fish and Fisheries*, 18, 1119–1133.

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., ... Stromberg, J. C. (1997). The natural flow regime: A paradigm for river conservation and restoration. *Bioscience*, 47, 769–784.

Raghavan, R., Das, S., Nameer, P. O., Bijukumar, A., & Dahanukar, N. (2016). Protected areas and imperilled endemic freshwater biodiversity in the Western Ghats Hotspot. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26, 78–90.

Reis, R. E., Albert, J. S., Di Dario, F., Mincarone, M. M., Petry, P., & Rocha, L. A. (2016). Fish biodiversity and conservation in South America. *Journal of Fish Biology*, 89, 12–47.

Rodrigues, A. S. L., & Brooks, T. M. (2007). Shortcuts for biodiversity conservation planning: The effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics*, 38, 713–737.

Russi, D., ten Brink, P., Farmer, A., Badura, T., Coates, D., Förster, J., ... Davidson, N. (2013). *The Economics of Ecosystems and Biodiversity for Water and Wetlands. Executive Summary*. (IEEP London and Brussels.). Gland, Switzerland: Ramsar Secretariat.

Saunders, D. L., Meeuwig, J. J., & Vincent, A. C. J. (2002). Freshwater protected areas: Strategies for conservation. *Conservation Biology*, 16, 30–41.

Scott, J. M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., ... Wright, R. G. (1993). Gap analysis: A geographic approach to protection of biological diversity. *Wildlife Monographs*, 123, 1–41.

Stewart, R. R., & Possingham, H. P. (2005). Efficiency, costs and trade-offs in marine reserve system design. *Environmental Modeling and Assessment*, 10, 203–213.

Strayer, D. L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: Recent progress and future challenges. *Journal of the North American Benthological Society*, 29, 344–358.

Swenson, J. J., Carter, C. E., Domec, J.-C., & Delgado, C. I. (2011). Gold mining in the Peruvian Amazon: Global prices, deforestation, and mercury imports. *PLoS ONE*, 6, e18875.

Thieme, M. L., Turak, E., McIntyre, P., Darwall, W., Tockner, K., Cordeiro, J., & Butchart, S. H. M. (2010). Freshwater ecosystems under threat: The ultimate hotspot. In R. A. Mittermeier, T. A. Farrell, I. J. Harrison, A. J. Upgren, & T. M. Brooks (Eds.), *Fresh water: The essence of life* (pp. 123–151). Arlington, VA: CEMEX and ILCP.

Tognelli, M. F., Lasso, C. A., Bota-Sierra, C. A., Jiménez-Segura, L. F., & Cox, N. A. (2016). *Estado de conservación y distribución de la biodiversidad de agua dulce en los Andes Tropicales*. Gland, Switzerland: IUCN.

Tognelli, M. F., Mesa, S. L. M., & Lasso, C. A. (2016). Síntesis para todos los grupos taxonómicos. In M. F. Tognelli, C. A. Lasso, C. A. Bota-Sierra, L. F. Jiménez-Segura, & N. A. Cox (Eds.), *Estado de conservación y distribución de la biodiversidad de agua dulce en los Andes tropicales* (pp. 157–174). Gland, Switzerland: IUCN.

Toussaint, A., Charpin, N., Brosse, S., & Villéger, S. (2016). Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread. *Scientific Reports*, 6, 1–9.

Turschwell, M. P., Stewart-Koster, B., Leigh, C., Peterson, E. E., Sheldon, F., & Balcombe, S. R. (2018). Riparian restoration offsets predicted population consequences of climate warming in a threatened headwater fish. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28, 575–586.

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., ... Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, 467, 555–561.

World Wide Fund for Nature (WWF) (2016). Living Planet Report 2016. In *Risk and resilience in a new era*. Gland, Switzerland: WWF International.