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Vulnerability of the biota in riverine and seasonally flooded habitats to damming of Amazonian rivers

Edgardo M. Latrubesse[1] | Fernando M. d'Horta[2] | Camila C. Ribas[2] | Florian Wittmann[3] | Jansen Zuanon[2] | Edward Park[4] | Thomas Dunne[5] | Eugenio Y. Arima[6] | Paul A. Baker[7]

[1]Asian School of the Environment and Earth Observatory of Singapore (EOS), Nanyang Technological University (NTU), Singapore

[2]National Institute of Amazonian Research (INPA), Manaus, Brazil

[3]Institute of Floodplain Ecology, Karlsruhe Institute of Technology, Rastatt, Germany

[4]National Institute of Education (NIE), Nanyang Technological University, Singapore

[5]Bren School of Environmental Science and Management, University of California (UCSB), Santa Barbara, California, USA

[6]Department of Geography and the Environment, University of Texas at Austin, Austin, Texas, USA

[7]Nicholas School of the Environment, Duke University, Durham, North Carolina, USA

Correspondence
Edgardo Latrubesse, Asian School of the Environment and Earth Observatory of Singapore (EOS), Nanyang Technological University (NTU), Singapore.
Email: elatrubesse@ntu.edu.sg

Abstract

1. The extent and intensity of impacts of multiple new dams in the Amazon basin on specific biological groups are potentially large, but still uncertain and need to be better understood.

2. It is known that river disruption and regulation by dams may affect sediment supplies, river channel migration, floodplain dynamics, and, as a major adverse consequence, are likely to decrease or even suppress ecological connectivity among populations of aquatic organisms and organisms dependent upon seasonally flooded environments.

3. This article complements our previous results by assessing the relationships between dams, our Dam Environmental Vulnerability Index (DEVI), and the biotic environments threatened by the effects of dams. Because of the cartographic representation of DEVI, it is a useful tool to compare the potential hydrophysical impacts of proposed dams in the Amazon basin with the spatial distribution of biological diversity. As the impact of Amazonian dams on the biota of both rivers and periodically flooded riparian environments is severe, DEVIs from different Amazonian tributary basins are contrasted with patterns of diversity and distribution of fish, flooded forest trees and bird species.

4. There is a consistent relationship between higher DEVI values and the patterns of higher species richness and endemism in all three biological groups. An assessment of vulnerability at the scale of tributary basins, the assessment of biodiversity patterns related to DEVI, and the analysis of teleconnections at basin scale, demonstrate that recent construction of dams is affecting the biota of the Amazon basin.

5. The evidence presented here predicts that, if currently planned dams are built without considering the balance between energy production and environmental conservation, their cumulative effects will increase drastically and represent a major threat to Amazonian biodiversity.

1 | INTRODUCTION

The Amazon River system comprises Earth's most complex network of fluvial channels connected to some of the largest, most hydraulically intricate, and most productive wetlands on the planet. The river basin discharges ca. ∼6,600 km^3 y^{-1} (∼16–18% of the planet's freshwater flow) to the Atlantic (Filizola & Guyot, 2009; Meade, Dunne, Richey, Santos, & Salati, 1985). The scales of the Amazon basin's fluvial features are extreme. For example, four of the world's 10 largest rivers are in the Amazon basin (the Amazon, Negro, Madeira, and Japurá), and 20 of the 34 largest tropical rivers are Amazonian tributaries (Latrubesse, 2008, 2015). The Amazon system transfers water, sediments, and solutes across continental distances, constructing and sustaining Earth's most massive continuous belt of floodplains and a mosaic of continental wetlands encompassing more than 1,000,000 km^2 (Latrubesse et al., 2017).

The flood-pulse (Junk, Bayley, & Sparks, 1989), the fluvial styles (fluvial channel and floodplain morphologies) (Latrubesse, 2012), and their spectra of morphodynamic conditions in space and time provide predictable disturbance regimes that result in high habitat diversity for aquatic and non-aquatic organisms within the alluvial landscape (Salo et al., 1986). This is evident in the high α and β biological diversity found in and among these habitats. The Amazon Basin harbours the highest diversity of freshwater fishes in the world, with more than 2,700 species and a still unknown number of undescribed forms (Dagosta & De Pinna, 2019; Oberdorff et al., 2019). This remarkable fish diversity is heterogeneously distributed in the basin, with the species richness by basins being influenced by historical factors such as climatic stability, as well as by current factors such as temperature and energy availability (Oberdorff et al., 2019). Ter Steege et al. (2013) recognized 4,962 tree species in the Amazon basin, of which 2,166 flood-tolerant tree species occur in river floodplains. Between 10 and 30% of all floodplain tree species are estimated to be endemic (Wittmann et al., 2013). Floodplain trees play a major role in the carbon cycle. It has been estimated that methane emissions from Amazon floodplain trees are equivalent to the whole Arctic CH$_4$ source, and represent ∼15% of the global wetland CH$_4$ source (Pangala et al., 2017).

Amazonia also hosts the highest number (in absolute and percentage terms) of vertebrates specialized on or dependent upon flooded habitats. More than 150 species of non-aquatic birds are also restricted to these environments or are highly dependent on them (Cohn-Haft, Naka, & Fernandes, 2007; Laranjeiras, Naka, & Cohn-Haft, 2019; Remsen & Parker, 1983). The majority of Amazonian primate species exhibit some level of dependence on flooded forests, and some are highly dependent (e.g. *Cacajao* spp.) (Haugaasen & Peres, 2005). This high biodiversity, combined with significant carbon storage (Abril et al., 2014) and multiple uses by humans, such as food, timber, and non-timber forest products, including medical uses, ensures that Amazonian large-river wetlands provide more ecosystem services than almost any other large landscape feature worldwide (Castello & Macedo, 2016; Richey, Melack, Aufdenkampe, Ballester, & Hess, 2002; Wittmann & Oliveira Wittmann, 2010).

In a recent article, we provided an analysis of the irreversible consequences for hydrophysical features of Amazon valley environments to be expected at different scales from the more than 400 dams that exist already or are under consideration (Latrubesse et al., 2017). Other recent papers also have drawn attention to the potential impacts of dams at a regional scale, with emphasis on Andean basins and specific biotic groups (Anderson et al., 2018; Castello et al., 2013; Forsberg et al., 2017; Winemiller et al., 2016), or have pointed out more specific impacts (Fearnside, 2013, 2014, 2015, 2016)

Latrubesse et al. (2017) compared vulnerabilities between tributary basins and emphasized the need for a more efficient and integrative legal framework involving all nine of the basin countries for anticipatory assessments of how socio-environmental and ecological impacts of hydropower production can be better managed. To quantify the current and potential impacts of dams within tributary basins, a Dam Environmental Vulnerability Index (DEVI) was developed and applied, based on a multidisciplinary analysis at the basin scale, including geomorphological, hydrological, and land-cover features. It was demonstrated that many rivers of the Amazon basin and the coastal zone of South America are vulnerable to the cumulative and synergistic effects of large dams, and a set of actions was recommended within the existing legal and institutional framework for a transparent, multinational, inclusive decision-making process (Latrubesse et al., 2017).

The extent and intensity of impacts of multiple dams on specific biological groups are potentially significant, but still loosely documented and need to be better understood. River disruption and regulation by dams may affect sediment supplies, river channel migration, floodplain dynamics and, as a major adverse consequence, are likely to decrease or even suppress ecological connectivity among populations of aquatic organisms and of organisms dependent upon seasonally flooded environments, with detrimental consequences for regional human populations. For instance, the reduction in the flood pulse amplitude and consequently in the flooded area along the Amazon River main stem resulting from the construction of six large dams in the Andean Amazon is expected to result in a dramatic decrease in fisheries yield in the Brazilian Amazon, with potential consequences for food security of human riverine populations (Forsberg et al., 2017). This article complements the previous results (Latrubesse et al., 2017) by assessing the relationships between dams, DEVI, and the threatened biota. The impact of

Amazonian dams is mostly focused on the biota of rivers and the periodically inundated environments that border them, so here DEVI values are contrasted with patterns of diversity and distribution of fish, flooded forest tree species, and birds associated with periodically flooded environments. Because of the cartographic representation of DEVI, it is a useful tool to compare the potential hydrophysical impacts of proposed dams in the Amazon basin with the spatial distribution of biological diversity.

2 | METHODS

Information on planned and constructed dams in the Amazon basin was compiled from multiple sources, designated by the Brazilian government classification system (Latrubesse et al., 2017). It is based on energy generation capacity and differentiates small ($1 \leq MW < 30$) and large ($30 \leq MW < 1,000$ MW) hydroelectric power plants (Agência Nacional de Energia Elétrica: ANEEL, 2015). An additional category of megadams ($\geq 1,000$ MW) was incorporated.

The DEVI was created to assess the vulnerability of rivers to dams (Latrubesse et al., 2017). It incorporates threats to the basins that support natural river and floodplain activity, and ecological services (sediment supplies, channel mobility, and the flood pulse) into three sub-indices: Basin Integrity Index (BII), Dam Impact Index (DII), and Fluvial Dynamics Index (FDI). Every index is normalized on a scale of 0–100, with higher values indicating greater vulnerabilities. Details of the methodological aspects of DEVI can be found in Latrubesse et al. (2017).

The BII measures the vulnerability of the basin to erosion and to runoff that may carry pollutants to the rivers, such as fertilizers, sediments, and others. First, the *percentage of basin deforested* (PBD) represents areas that are directly or indirectly (through edge-fragmentation effects) affected by deforestation and other artificial areas (urban centres, roads, etc). Dividing this number by the total area of each basin provides the percentage of basin deforested. The percentage of basin protected is derived by dividing the protected areas by the area per basin. Upstream polygons are delineated by identifying the area and the hydrological network upstream of the dam furthest downstream for each basin.

Thus, the calculated the normalized PBD (NPBD) and normalized PUD (NPUD) for basin *i* is:

$$NPBDi = [PBDi - \min(PBD)] / [(\max(PBD) - \min(PBD)]$$

$$NPUDi = [PUDi - \min(PUD)] / [\max(PUD) - \min(PUD)]$$

Where PBD and PUD denote the percentage of the basin that is at present deforested, and the percentage of the basin that is deforested but located upstream of the dam that is furthest downstream, respectively. Normalized variables range from 0–1. The normalization of protected area variables PBP and PUP requires the inversion of each element *i* because higher percentage values indicate lower vulnerability. This is obtained by switching the min/max values.

Consequently, for the variables PBP and PUP, the normalized value for basin *i* is:

$$NPBPi = [PBPi - \max(PBP)] / [(\min(PBP) - \max(PBP)]$$

$$NPUPi = [PUPi - \max(PUP)] / [(\min(PUP) - \max(PUP)]$$

where PBP and PUP refer to the percentage of the basin within protected areas, and the percentage of the protected area upstream of the dam that is furthest downstream, respectively. The BII is calculated as the sum of each normalized variable, weighted equally, ranging from 0–1 expressed as:

$$BIIi = (NPBPi + NPUPi + NPBDi + NPUDi) / 4$$

The FDI is an indicator of the fluxes of sediment transported by the river flow (as sediment yield, SY), the morphodynamic activity of the rivers (represented here by the average channel migration rates), and the height range of the flood pulse (as mean water stage variability of maximum and minimum stages, WSV). It is calculated as:

$$FDIi = (NSYi + NMRi + NWSVi) / 3$$

where NSY, NMR, and NWSV are the normalized mean SY (Mt km^{-2} yr^{-1}), normalized mean channel migration rates (ch-w yr^{-1}), and normalized average water stage annual variability (m), respectively, for basin *i*. Migration rates are calculated at a multi-temporal scale from remote sensing imagery (in our case, we used Landsat TM) by generating erosional–depositional polygons, and then dividing the polygons by the average channel width for inter-basin comparison. Water level data were supplied from the Hydrogeodynamics of the Amazon Basin and Brazilian National Agency of Water.

The DII is calculated for each basin as:

$$DIIi = (PLUi + PTAi + PNUi) / 3$$

Each term – PLU, PTA, and PNU – denotes a ratio of river length directly affected by dams, a ratio between the number of major tributaries with dams and the total number of major tributaries, and the number of dams (planned and existing) per basin, respectively. The river length directly affected by dams is calculated using the percentage of the total river length affected by dams. It is an indicator of how much 'free' river is available upstream of the uppermost dams and how much is affected downstream of the uppermost dam. The third parameter concerns the percentage of affected tributaries. It is the number of major tributaries with dams (planned and existing) divided by the total number of major tributaries within the basin.

The DEVI for basin *i* is calculated as the sum of all three indices:

$$DEVIi = BIIi + DIIi + FDIi$$

DEVI ranges from 0–3, with higher values indicating higher vulnerability of the basin.

The DEVI and DII were compared with the Dendritic Connectivity Index (DCI), developed by Cote, Kehler, Bourne, and Wiersma (2009) and applied by Anderson et al. (2018) to Andean rivers. To assess the correlations among DCI, DEVI, and DII, a Spearman's rank correlation was used.

To understand the spatial aspects of threats to biodiversity indicated by DEVI, species richness maps for fish, trees, and birds associated with periodically flooded habitats were generated. These maps allow the analysis of the vulnerability of the biota, based on qualitative comparisons between the DEVI and richness patterns of species associated with aquatic and flooded habitats. Owing to the heterogeneity of the data available for these groups, different approaches to producing the richness maps were adopted. For fishes, published sources were used (Winemiller et al., 2016) augmented by databases from the authors, whereas for upper Andean-foreland rivers, the fish species richness in individual Andean basins was estimated based on the elevation intervals proposed by Anderson et al. (2018) in their table 3. For trees, richness values based on surveys of mean tree α-diversity were assigned for each basin (Fisher, Corbet, & Williams, 1943), considering upland (non-flooded) and floodplain forest inventories compiled from several sources (Assis, Wittmann, Piedade, & Haugaasen, 2015; de Almeida, do Amaral, & da Silva, 2004; Householder, Wittmann, Tobler, & Janovec, 2015; Kurzatkowski, Leuschner, & Homeier, 2015; Luize, Silva, Wittmann, Assis, & Venticinque, 2015; Montero, Piedade, & Wittmann, 2014; Pitman et al., 2014; Targhetta, Kesselmeier, & Wittmann, 2015; Wittmann et al., 2013), and a total of 153 plots from the reviews of Wittmann et al. (2013, 2017) (67 of the plots are 1 ha in extent and the others vary between 0.1 and 0.75 ha) in large river floodplains or associated swamp forest. For birds, polygons of flooded habitat species distribution (BirdLife International & NatureServe, 2014) were overlapped in ArcGIS, and the richness map was obtained using the Count Overlapping Polygons tool.

3 | RESULTS AND DISCUSSION

3.1 | Rivers and DEVI

Because of the variety of geotectonic settings and hydro-geomorphological regimes that characterize the Amazon basin, it is relevant to assess and compare DEVI at the tributary basin scale. The Amazon tributaries were classified according to the dominant geotectonic region from which they drain, as it controls their sediment regimes and biogeochemistry: (a) Andean or Andean-foreland rivers, characterized by high suspended nutrient-rich sediments and solute loads and relatively high pH (so-called 'white water' rivers); (b) cratonic rivers with low suspended load and pH, low nutrient concentration, and often highly enriched in dissolved and particulate organic carbon ('clear' or 'black' water rivers); and (c) lowland rivers draining Cenozoic sedimentary rocks, transporting abundant suspended sediment load and flowing entirely through the tropical rainforest. A fourth mixed-terrain category (Andean-foreland–craton)

is applied only to the Madeira basin because of the complexity of its geotectonic domains. The results show that the construction of dams will affect these rivers and wetlands in different ways owing to the physical and biotic differences among the Amazonian sub-basins. Andean and lowland storage dams will dramatically alter flow regimes and sediment supplies in downstream reaches, whereas run-of-river dams are expected to trap less sediment and produce smaller modifications of the hydrological regime, but cause extensive inundation and flooding of tropical forest with attendant organic loading from decomposing vegetation.

DEVI sub-indices vary among these geotectonic regions (Figures 1 and 2). Andean sub-basins tend to have higher BII, FDI, and DII values than cratonic and lowland basins. Cratonic basins also display low FDI and lower BII and DII values than other basins, with the exception of the Tapajós, which has an exceptionally high number of planned dams and high rates of deforestation (Figures 1 and 2). Despite the relatively low number of planned dams in the Xingu, the vulnerability of this basin stands out among cratonic basins because of the high rate of deforestation (BII).

The Andean rivers most vulnerable to proposed dam constructions are the Marañon and Ucayali, with high values of DEVI, FDI, and BII (Figures 1 and 2). DII is particularly high in the Marañon. Because of its high rates of channel floodplain sediment exchanges (driving channel migration and abandonment), the Ucayali River is the most sensitive Andean river to dam building regarding flow regulation and decrease in sediment load. Reductions of these factors by dam construction pose threats to wetland creation and maintenance. The Marañon River is less dynamic in terms of its sediment regime and morphology but is critically threatened by the larger number of planned and built dams concentrated along most of the mountainous course of its main channel, which threaten to reduce radically both the sediment supplies and inundation potential that maintain floodplain and marshland environments

The morphodynamics and floodplain style of cratonic rivers are different from Andean rivers. Their FDIs reflect the environmental relevance of the flood pulse, but the cratonic rivers have low SYs and low lateral migration rates (Figure 2). However, the DII is very high in some cratonic rivers due to the large number of constructed and planned dams along the main stem and the number of tributaries to be affected (Figure 2).

The Tapajós with 32 constructed and planned dams, and thus a high DEVI of ∼65, is the most vulnerable basin among cratonic rivers. The Xingu river concentrates more localized impacts, such as the recently constructed gigantic run-of-river Belo Monte megadam, with 11,233 MW of installed capacity. This dam is the fourth largest dam ever constructed in terms of installed capacity and is promoted as a project of low environmental impact by the Brazilian government and the Consortium Norte Energia (https://www.norteenergiasa.com.br/pt-br/sustentabilidade). However, Belo Monte has produced dramatic socio-environmental and socio-economic impacts on the local and indigenous population (Fearnside, 2017; Lima, Kaplan, & Rodrigues da Costa Doria, 2017), and its run-of-river project is characterized by the uncommon impact of causing a
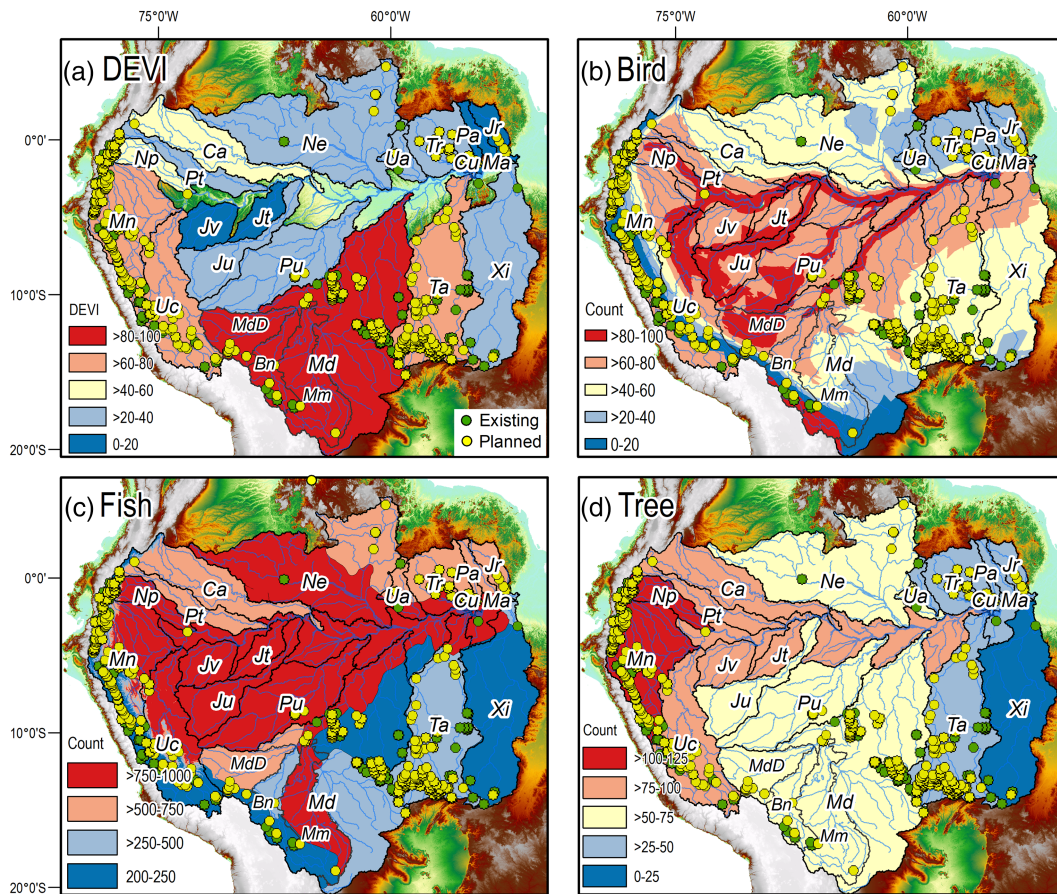
FIGURE 1 Dam Environmental Vulnerability Index (DEVI) (Latrubesse et al., 2017) and species richness pattern of Amazonian river basins. Colour scale from blue (low) to red (high) represents the number of species. Coloured dots indicate the planned and constructed dams ≥1 MW. Abbreviations: Marañon (*Mn*), Ucayali (*Uc*), Napo (*Np*), Putumayo (*Pt*), Caqueta-Japura (*Ca*), Jari (*Jr*), Paru (*Pa*), Curuapenema (*Cu*), Maricuru (*Ma*), Tapajós (*Ta*), Xingu (*Xi*), Trombetas (*Tr*), Negro (*Ne*), Uatumã (*Ua*), Madeira (*Md*), Jurua (*Ju*), Purús (*Pu*), Jutai (*Jt*), Javari (*Jv*). The sub-basins MdD (Madre de Dios), Bn (Beni), and Mm (Mamoré) are tributaries of the Madeira basin and DEVI is calculated for the whole basin
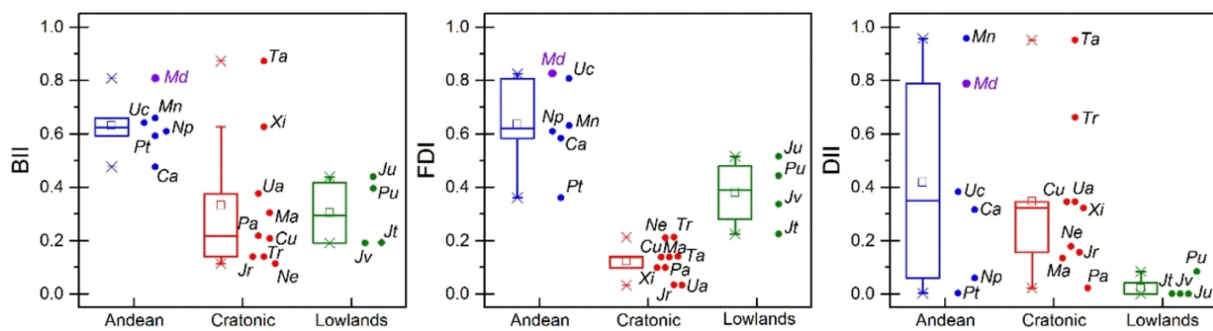

FIGURE 2 Basin Integrity Index (BII), Fluvial Dynamics Index (FDI), and Dam Impact Index (DII) values (dots) of the 19 tributary basins grouped by river types. Boxplots (max, 25 percentile, mean, median, 75 percentile, min) for each river type (Andean, cratonic, and lowland rivers draining Cenozoic sedimentary rocks) (from Latrubesse et al., 2017, SI-Figure 3). For abbreviations, refer to Figure 1 caption

dramatic reduction of water discharge in ~130 km stretch of the river by diverting most of the flow downstream through a canal. This has important consequences, including suppression of processes dependent upon periodic flooding, including fish survival and reproduction, and drastic consequences for connectivity along the Xingu River (Zuanon et al., 2019).

3.2 | Integrating DEVI and the impacts on the biota

3.2.1 | Patterns of species richness

There is a consistent relationship between higher DEVI values and the patterns of higher species richness of fish and floodplain trees and

birds. Except for the Tapajós, the highest DEVI values are observed in Andean-foreland river basins (Madeira, Ucayali, and Marañon). Despite some differences in the diversity patterns observed for different biological groups, there is a general trend towards greater diversity associated with white-water river basins (Figure 1), and a higher rate of fish endemism in the sub-basins of the western portion of the Amazon basin (Oberdorff et al., 2019). Among other factors, the diversity patterns are determined by high habitat heterogeneity and high productivity of these ecosystems (Oberdorff et al., 2019).

Andean-foreland rivers have high bio- and geo-diverse fluvial habitats, related to the high values of FDI (Figures 1 and 2). The high values of FDI in Andean-foreland rivers relate to high nutrient-rich SYs, high channel migration rates and moderate to high flood pulses, all fundamental components of the connectivity of rivers with their huge floodplains. Sediment supply and channel migration modulate the reshaping of the floodplain (Constantine, Dunne, Ahmed, Legleiter, & Lazarus, 2014). Large-scale natural disturbance is caused by high rates of migration and channel shifting of the major rivers. These dynamic landscapes generate high aquatic and alluvial habitat heterogeneity expressed by intricate mosaics formed by river meanders, marginal lakes, sediment banks, beaches, islands, and vegetation at different stages of succession. By contrast, the remarkable nutrient concentration in white-water rivers (mainly of Andean-foreland rivers) results in higher biological productivity when compared with those of cratonic sub-basins (e.g. Furch & Junk, 1997; Junk, Piedade, Schöngart, & Wittmann, 2012).

For fishes, the highest diversity values are reported in Andean-foreland basins and, also, in the Negro and lower Amazon cratonic basins (Figure 1), which agrees with recent findings (Beltrão, Zuanon, & Ferreira, 2019; Oberdorff et al., 2019). Trees exhibit a clear east-to-west gradient of increasing diversity, reaching the highest diversity value in the Marañon basin. Andean-foreland rivers have the highest tree diversity compared with any floodplain forests on Earth, including up to 30 % endemic tree species (Wittmann et al., 2013). Except in the Negro basin, birds specialized in seasonally flooded environments exhibit a pattern consistent with that reported for fishes, i.e. highest diversity in Andean-foreland and Madeira basins, which also sustain a remarkable number of endemic species of fish and birds (Haugaasen & Peres, 2005; Lees & Peres, 2008; Mittermeier, Wilson, & Rylands, 2013; Remsen & Parker, 1983; Vale, Cohn-Haft, Bergen, & Pimm, 2008) (Figure 1).

Significantly, these most vulnerable zones that encompass Andean-foreland and Madeira sub-basins overlap wetlands protected by (a) conservation units and sites of the Ramsar Convention of Wetlands of International Importance, such as the Pacaya–Samiria National Reserve, the Abanico del Pastaza Wetlands Complex, also identified as of high risk by Anderson et al. (2018); (b) the Llanos de Moxos wetlands in the Upper Madeira basin (Bolivia), considered the largest Ramsar site in the world; and (c) indigenous territories in Brazil, Bolivia, Peru, Ecuador, and Colombia.

The Marañon basin holds around 700 species of fish, the highest tree diversity among Amazon sub-basins, and more than 50% of flooded-habitat birds reported in the Amazon. This basin also exhibits the largest value of DII (0.87), which indicates strong habitat fragmentation by proposed dams that will disrupt and modify the hydrosedimentological regime of a large portion of the total river length and tributary basins.

The Ucayali basin holds more than 650 species of fish, between 90 and 110 species of floodplain trees, and more than 80 species of floodplain birds. Although the potential direct impact by dams on the Ucayali is smaller (DII ∼ 0.38) than in the Marañon, the highest FDI of the Ucayali (0.8) raises the DEVI to 0.6, and, despite the relatively lower number of proposed dams, indicates that this river is particularly susceptible to dam installation.

Because it crosses geotectonic domains (Andean, foreland, and cratonic), the Madeira River basin is considered a mixed-terrain fluvial basin. It provides ∼40–50% of the total sediment load of the Amazon river (Dunne, Mertes, Meade, Richey, & Forsberg, 1998; Park & Latrubesse, 2019; Vauchel et al., 2017), so impacts of dams leading to reductions in sediment load and nutrients can result in very damaging consequences for downstream biodiversity, especially in the complex floodplains of the Lower Amazon (Park & Latrubesse, 2017, 2019).

After integrating all the indices from Andean-foreland and cratonic tributaries, the Madeira basin is found to be the basin most threatened by dam building in the Amazon (DEVI > 80) because the basin presents high BII (0.8), FDI (0.82) and DII (0.85) values (Figures 1 and 2). The high DEVI value of the Madeira sub-basin is especially alarming as it harbours high biological diversity associated with its fluvial habitats, such as 1,304 species of fish (Queiroz et al., 2013), 50–60 floodplain tree species and more than 80 species of floodplain birds (at least 10 endemic) (Vale et al., 2008). More than 800 fish species are recorded upstream of the Santo Antônio and Jirau dams in Brazil, with a high concentration of species in the Mamoré sub-basin (Mm in Figure 1). The rivers from the upper Madeira basins are at risk from the potential construction of 16 dams in the Andes and the Bolivian lowlands, upstream of the already installed Jirau dam. The cratonic tributaries of the Madeira basin in Brazil are also vulnerable, with 30 dams already constructed or under construction and an additional 26 dams proposed.

3.2.2 | Effects on habitats and connectivity loss

DEVI and river connectivity
River connectivity describes the degree to which matter and organisms can move among spatially defined units over diverse temporal and spatial scales (Amoros & Roux, 1988; Wohl, 2017). River–floodplain connectivity is described in longitudinal, lateral, and vertical dimensions, and also has a temporal dimension (seasonal, annual, decadal, and beyond). Thus, connectivity is related to water and sediment fluxes, floodplain hydrogeomorphological characteristics, channel pattern style and mobility, shaping habitats for different types of organisms, including fish (Pouilly & Rodríguez, 2004; Rodríguez & Lewis, 1997). In large rivers, connectivity links a dominant agent (e.g. the flood pulse) with various dependent habitat characteristics (e.g. riparian vegetation) and the type and degree of the connections

between lotic and lentic environments as conditioned by the hydro-geomorphological complexity of the channel–floodplain system (Drago, Paira, & Wantzen, 2008; Park & Latrubesse, 2017; Stevaux, Corradini, & Aquino, 2013).

Dams are considered the most disruptive direct impact on the ecological connectivity of a river as they interrupt and regulate the river flow. Diverse methods exist for assessing the role of connectivity, the consequences of human impacts and the search for alternatives to guarantee sustainable ecological functions and ecological services along the fluvial corridors of large rivers (Drago et al., 2008; Hudson & Colditz, 2003; Junk et al., 1989; Junk & Wantzen, 2006; Marchetti, Latrubesse, Pereira, & Ramonell, 2013; Montero & Latrubesse, 2013; Neiff & Poi de Neiff, 2003; Park & Latrubesse, 2017; Stevaux et al., 2013). DEVI incorporates various influences on river connectivity in its sub-indices DII and FDI. DII is an indicator of how much free-flowing river there is upstream of the uppermost dam, and how much habitat is affected downstream of the uppermost dam. As detailed in the methods section, fundamental components of connectivity are included in the FDI because it is an indicator of the fluxes of sediment transported by the river (SY), the morphodynamic activity (represented by average channel migration rates, and the height range of the flood pulse (mean WSV).

Regarding the assessment of river connectivity, Anderson et al. (2018) applied the DCI to the Andean rivers. DCI is a parameter defined by Cote et al. (2009) that is used as an abiotic metric to assess the probability of an organism being able to move freely between two random points of the drainage network. The DCI developed by Anderson et al. (2018) is partially comparable to and inversely correlates with DII (Figure 3), which assesses the disruption of tributary networks and the main stem caused by dams, and identifies the Andean sub-basins most vulnerable to current and proposed dam construction. A decrease in DCI relates to an increase in DEVI and DII. However, the combined inclusion of the seasonal flow range and channel–floodplain mobility and connectivity in FDI, and thus in DEVI,

provides a more integrative, multi-dimensional approach for anticipating these dam-related threats to habitat values (Figure 3).

Dams, DEVI, and habitats

River fragmentation by dams, combined with an interruption of sediment supply, modification of channel migration rates, and alteration of the hydrological regime will trigger loss of habitat (β-diversity), cause disconnection among populations, and put endemic species of fishes, birds and the riverine vegetation at risk, especially in the Madeira, Ucayali, and Marañon Rivers, in addition to compromising fisheries yield in the Amazon main stem (Forsberg et al., 2017).

The major issue for floodplain trees is that they are adapted to the predictable duration and timing of the flood pulse over evolutionary time scales and that their leaf physiology, flowering and fruiting phenology, and growth are linked to the seasonality of flooding (Parolin, Lucas, Piedade, & Wittmann, 2010; Schöngart, Wittmann, Piedade, Junk, & Worbes, 2005). Once downstream flood regimes are modified in amplitude or timing, the highly flood-adapted species either lose their ecological niche (when low water regimes are higher than before) or are outcompeted by terrestrial species (when high water regimes are lowered). Where loss of unique floodplain habitat leads to the extinction of its specialist tree community, it is not clear how floodplain forests and their ecosystem services might be restored: no other tree species on Earth are likely to be capable of filling these niches (Wittmann & Householder, 2017). In addition, the loss of floodplain forest is likely to cascade down to planktonic communities, benthic organisms, food webs, and fish communities, as many Amazonian fish species depend on arboreal fruits during the high water-levels (Correa et al., 2015; Gottsberger, 1978; Goulding, 1980). Thus, the fishery yields based on floodplain-forest specialist fishes are likely to decrease (Araujo-Lima, Goulding, Forsberg, Victoria, & Martinelli, 1998).

In the Madeira basin, it has been shown that dams disrupt migratory routes of many fish species (e.g. *Brachyplatystoma, Brycon,*
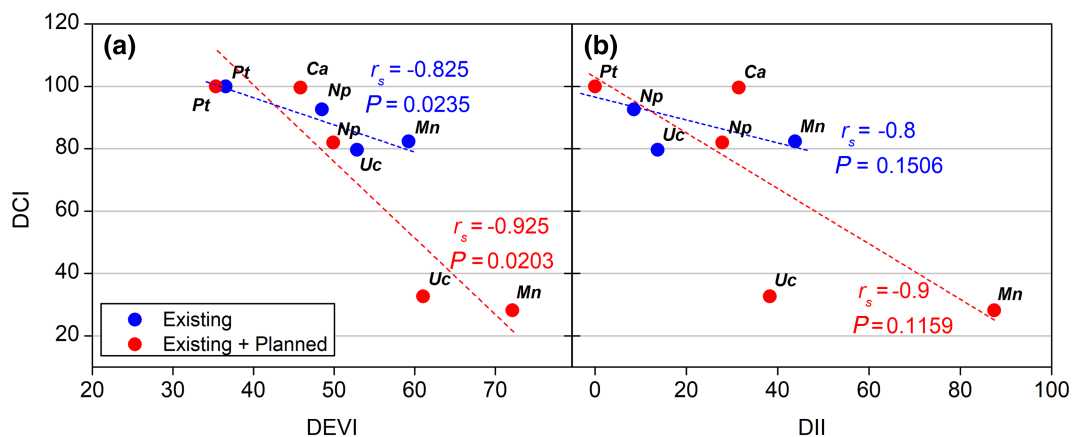
FIGURE 3 Spearman's rank correlation between Dendritic Connectivity Index (DCI) and Dam Environmental Vulnerability Index (DEVI), and DCI and Dam Impact Index (DII), for both existing and planned (including existing) dam scenarios. *P*-values for each case are reported to assess the significance of the trend, as well as r_s values showing the negative trends for all cases. Trend line derived from linear regression is given in each case. For abbreviations, refer to Figure 1 caption

and *Prochilus*), as these species would be losing their access to breeding sites in the western Amazon (Hauser et al., 2018). This disruption has consequences for human populations, as the migratory fish constitute important sources of food and income (Cella-Ribeiro et al., 2015; Lima, Carvalho, Nunes, Angelini, & da Costa Doria, 2020; Santos, Pinto-Coelho, Fonseca, Simões, & Zanchi, 2018).

In cratonic rivers, such as the Xingu, Tapajós, and Trombetas, lateral migration rates and sediment supply are low; thus, the most sensitive element of the FDI to dams is the regulation of the hydrological regime, which triggers changes in the water stage variability and flow duration (flood pulse). For example, the low-productivity igapó-flooded forests of the Negro River and other cratonic rivers are extremely vulnerable to flood pulse modifications (Junk, Wittmann, Schöngart, & Piedade, 2015; Montero & Latrubesse, 2013; Wittmann et al., 2013). On cratonic rivers of the Amazon and Cerrado biome (Brazilian savanna), large and small dams already alter the frequency, duration, and rate of change of high- and low-water conditions (Timpe & Kaplan, 2017). Examples and lessons on the ecological consequences of dams in cratonic rivers are already provided by dams such as Balbina, built in the 1980s in the Uatumã River. Although the BII and FDI are low in the Uatumã basin, DII is large enough to predict severe impacts on the fluvial system and related ecosystems. Balbina Hydroelectric Dam inundated 3,129 km^2 of primary forests, created a mosaic of 3,546 islands, and triggered tree mortality even of seasonal-flood-adapted species, alterations in forest composition (Assahira et al., 2017; de Sousa Lobo, Wittmann, & Piedade, 2019), and a large reduction in the diversity of vertebrates (Benchimol & Peres, 2015). Studies of riparian vegetation in the Belo Monte dam area indicate that 90% of pioneer plant communities on the Xingu River floodplain are currently affected and that the same is likely to happen in the Tapajós basin if the proposed dams are constructed (Cunha & Ferreira, 2012; Ferreira, Cunha, Chaves, Matos, & Parolin, 2013).

Although not as diverse as Andean-foreland and Madeira basins, the Tapajós and Xingu rivers exhibit high diversity, including many endemic species of fish (65 endemics in Tapajós basin and 47 in Xingu basin) (Dagosta & De Pinna, 2019), trees (Ferreira & Prance, 1998; Salomão et al., 2007), and birds (Laranjeiras et al., 2019). Thus, the potential impact of disturbing the highly diverse flooded environments of these basins is enormous. For the cratonic basins, the major threats are fragmentation of the aquatic/alluvial habitats, the elimination of rapids (Winemiller et al., 2016; Zuanon, 1999), and the disturbance of the flood pulses/hydrological regime. Large zones of shallow rapids harbour a high diversity of strictly rheophilous fishes and high rates of fish endemicity, and also support some species of birds and bats that depend on rapids. For example, from the 61 species threatened by hydroelectric dams as identified by the Ministry of the Environment of Brazil (MMA, 2014), the Xingu supports 28% (17 spp) and the Tapajós is the habitat for 20% (12 species; Table 1). Furthermore, it is important to note that the extinction risk assessed according to the International Union for Conservation of Nature (IUCN) criteria does not include the pervasive and potentially synergistic detrimental effects of the continuing climate change on the survival odds of those endangered species. This points to even more dramatic effects of fish diversity loss resulting from the combined disturbances generated by dam construction and environmental modifications derived from climate change (Frederico, Olden, & Zuanon, 2016).

The Belo Monte run-of-river dam causes a huge reduction of ~80% of the water discharge in a downstream stretch of about 130 km of the Xingu River called Volta Grande, by diverting downstream, through an artificial canal, most of the flow in that section of the river. Endemicity was especially high in the Volta Grande, where Belo Monte Dam was constructed and is currently operating; of the 12 fish species endemic to the Xingu River and officially considered threatened (MMA, 2014) seven (58%) only occur in that rapid stretch. The resulting loss of connectivity suppresses populations of aquatic and flood-adapted organisms in a long reach of the river, threatening extinction of local populations and fragmentation of species ranges (Zuanon et al., 2019).

The situation is also critical in the Tapajós, which has the largest DII in the whole Amazon basin (0.95). If the planned dams are constructed, the rapids mentioned above will disappear, and the hydrological regime and flood pulse will be greatly altered. The Tapajós and main tributaries would be regulated and transformed into a megalake system through a cascade of large dams extending more than 1,000 km. This pressure on the Tapajós River basin is a consequence of a combination of two main interests: energy production and commercial navigation for soy and meat export. This sequence of dams is equivalent to damming the Mississippi River from Saint Louis to New Orleans, or creating a cascade of reservoirs as long as the distance from Madrid to Paris. Any project like that would raise serious concerns and be considered infeasible in many parts of the world.

Regarding the relationships between vegetation cover/land use, and DEVI, the vulnerability of the Tapajós basin is further enhanced by the high BII (0.87), the highest value for the whole Amazon basin. It reflects widespread land-use changes and limited conservation of forests, particularly upstream of the planned dams. A critical point is that the upper Tapajós extends beyond the Amazon forest, and 22.4% (~110,000 km^2) of the Tapajós basin was originally covered by the Cerrado biome, where the agricultural frontier continues to expand aggressively. This scenario will become even more severe owing to the stimulus the waterway is likely to give to the expansion of agriculture, livestock rearing, and mining. Only fragmented natural Cerrado patches remain because ~50,000 km^2 of Cerrado are already deforested and fragmented, and only 1,901 km^2 are officially protected areas, with ~49,880 km^2 of available remnant natural area without specific legal protection (Latrubesse et al., 2019). Moreover, the effectiveness of the current protected areas may be low for certain groups of organisms such as Amazonian stream-dwelling fishes (Frederico, Zuanon, & De Marco, 2018), which implies the need for innovative strategies for effective conservation of biodiversity (Azevedo-Santos et al., 2018).

In Brazil, although conservation units have been used to protect water springs, to maintain water quality near large urban centres, and to preserve marine biomes and waterscapes of aesthetic value (e.g. rapids and waterfalls; Dean, 1996; Drummond, Franco, & Oliveira, 2010), few were explicitly designed to protect limnological

TABLE 1 Threatened species of fish in Brazilian Amazon tributaries, according to the IUCN criteria and officially considered by Brazil's Ministry of the Environment (MMA, 2014)

Family	Threatened species	Rivers	Tributary basins (Amazon basin)			
			Xingú	Tapajós	Trombetas	Uatumã
Apteronotidae	*Apteronotus lindalvae* de Santana & Cox Fernandes, 2012	Uatumã (*Ua*)				1
Auchenipteridae	*Centromochlus meridionalis* Sarmento-Soares Cabeceira, Carvalho, Zuanon & Akama, 2013	Teles Pires (tributary of the Tapajós basin, *Ta*)		1		
Cichlidae	*Crenicichla heckeli* Ploeg, 1989	Trombetas (*Tr*)			1	
Cichlidae	*Crenicichla urosema* Kullander, 1990	Tapajós (*Ta*)		1		
Loricaiidae	*Harttia depressa* Rapp Py-Daniel & Oliveira, 2001	Uatumã (*Ua*)				1
Loricaiidae	*Harttia dissidens* Rapp Py-Daniel & Oliveira, 2001	Tapajós (*Ta*)		1		
Doradidae	*Hassar shewellkeimi* Sabaj Pérez & Birindelli, 2013	Teles Pire and Juruena (tributaries of the Tapajós basin, *Ta*)		1		
Loricaiidae	*Hopliancistrus tricornis* Isbrucker & Nijssen, 1989	Tapajós (*Ta*)		1		
Lebiasinidae	*Lebiasina marilynae* Netto-Ferreira, 2012	Curuá (tributary of the Tapajós basin, *Ta*)	1			
Lebiasinidae	*Lebiasina melanoguttata* Netto-Ferreira, 2012	Curuá (tributary of the Tapajós basin, *Ta*)	1			
Lebiasinidae	*Lebiasina minuta* Netto-Ferreira, 2012	Iriri (tributary of the Tapajós basin, *Ta*)	1			
Loricariidae	*Leporacanthicus joselimai* Isbrucker & Nijssen, 1989	Tapajós (*Ta*)		1		
Anostomidae	*Leporinus guttatus* Birindelli & Britski, 2009	Curuá (tributary of the Tapajós basin, *Ta*)	1			
Anostomidae	*Leporinus pitingai* Santos & Jégu, 1996	Pitinga (tribuary of the Uatumã basin, *Ua*)				1
Loricariidae	*Lithoxus lithoides* Eigenmann, 1912	Uatumã (*Ua*) and Trombetas (*Tr*)			1	1
Apteronotidae	*Megadontognathus kaitukaensis* Campos-da-Paz, 1999	Xingu (*Xi*)	1			
Crenuchidae	*Melanocharacidium nigrum* Buckup, 1993	Uatumã (*Ua*) and Branco (tributary of the Negro basin, *Ne*)				1
Serrasalmidae	*Ossubtus xinguense* Jégu, 1992	Xingu (*Xi*)	1			
Loricariidae	*Parancistrus nudiventris* Raap Py Daniel & Zuanon, 2005	Xingu (*Xi*)	1			
Loricariidae	*Peckoltia compta* Oliveira, Zuanon, Rapp Py Daniel & Rocha, 2010	Tapajós (*Ta*)		1		
Loricariidae	*Peckoltia snethlageae* (Steindachner, 1911)	Tapajós (*Ta*)		1		
Rivulidae	*Pituna xiguensis* Costa & Nielsen, 2007	Xingu (*Xi*)	1			
Rivulidae	*Plesiolebas altamira* Costa & Nielsen, 2007	Xingu (*Xi*)	1			
Prochilodontidae	*Prochilodus britskii* Castro, 1993	Tapajós (*Ta*)		1		
Characidae	*Rhinopetitia potamorhachia* Netto-Ferreira, Birindelli, Sousa & Menezes, 2014	Teles Pires (tributary of the Tapajós basin, *Ta*)		1		
Doradidae	*Rhynchodoras xingui* Klausewitz & Rossel, 1961	Xingu (*Xi*)	1			
Loricariidae	*Scobinancistrus aureatus* Burgess, 1994	Xingu (*Xi*)	1			
Loricariidae	*Scobinancistrus pariolispos* Isbrucker & Nijssen, 1989	Xingu and Tapajós (*Xi* & *Ta*)	1	1		

(Continues)

TABLE 1 (Continued)

| Family | Threatened species | Rivers | Tributary basins (Amazon basin) | | | |
			Xingú	Tapajós	Trombetas	Uatumã
Rivulidae	*Spectrolebias reticulatus* (Costa & Nielsen, 2003)	Xingu (*Xi*)	1			
Apteronotidae	*Sternarchogiton zuanoni* de Santana & Vari, 2010	Xingu (*Xi*)	1			
Apteronotidae	*Sternarchorhynchus higuchii* de Santana & Vari, 2010	Uatumã (*Ua*)				1
Apteronotidae	*Sternarchorhynchus inpai* de Santana & Vari, 2010	Trombetas (*Tr*)			1	
Apteronotidae	*Sternarchorhynchus jaimei* de Santana & Vari, 2010	Uatumã (*Ua*)				1
Apteronotidae	*Sternarchorhynchus kokraimoro* de Santana & Vari, 2010	Xingu (*Xi*)	1			
Apteronotidae	*Sternarchorhynchus mareikeae* de Santana & Vari, 2010	Trombetas (*Tr*)			1	
Apteronotidae	*Sternarchorhynchus villasboasi* de Santana & Vari, 2010	Xingu (*Xi*)	1			
Cichlidae	*Teleocichla centisquama* Zuanon & Sazima, 2002	Xingu (*Xi*)	1			
Cichlidae	*Teleocichla prionogenys* Kullander, 1988	Tapajós (*Ta*)		1		

ecosystems (notable exceptions are the Mamirauá Sustainable Development Reserve and the Araguaia National Park). Therefore, the effectiveness of the present system of protected areas for preserving biodiversity may be low for certain groups. Thus, there is room for new areas of conservation to be created, which should be based on well-defined prioritization strategies and criteria (see Jézéquel et al., 2020, as an example for the Amazon fish fauna). The opposite scenario is to continue to make habitats available piecemeal to the voracious policy of deforestation that currently dominates the Brazilian political scene.

The upper Xingu is also in a critical condition, as there is no conservation unit in the portion of the basin situated in the Cerrado biome (Latrubesse et al., 2019). The upper Xingu holds 329 species of fish (Dagosta & De Pinna, 2019), but the impacts on the river have been rampant. In addition to the dams with capacities >1 MW discussed in Latrubesse et al. (2017), more than 40% of the creeks and smaller fluvial systems of the upper Xingu were disrupted by approximately 10,000 impoundments by 2010 (Macedo et al., 2013).

The biotic impacts of dams are not restricted to aquatic and flooded habitats, but also affect upland forests. Studies in the Xingu basin, for example, demonstrated that conversion of forests to pastures and crops decreases annual mean evapotranspiration by approximately one-third (Arantes, Ferreira, & Coe, 2016; Lathuillière, Johnson, & Donner, 2012; Spera, Galford, Coe, Macedo, & Mustard, 2016), increases the annual mean surface temperature locally by more than 5°C, decreases soil moisture by about 30%, and modifies the stream flow of rivers and creeks (Dias, Macedo, Costa, Coe, & Neill, 2015; Hayhoe et al., 2011; Riskin et al., 2017). Among the major consequences are local impacts on flora and fauna, severe losses of plant species diversity, and irreversible impacts on the fauna and food webs.

The environments that make up the Amazon landscapes are deeply connected. For example, many vertebrates considered typical upland species also show high seasonal dependence on flooded habitats (Haugaasen & Peres, 2007), and are essential to floodplain ecological processes such as pollination and dispersal that maintain the biological diversity in flooded and non-flooded environments (Terborgh et al., 2008). The terra firme forests and their drainage systems are intrinsically interconnected, and the disruption of river dynamics will affect Amazonian biota as a whole, with great potential to bring about a massive loss of diversity in these systems.

4 | RECOMMENDATIONS

Our assessment of vulnerability at the tributary basin scale, the assessment of biodiversity patterns, and DEVI, indicate that the recent construction of dams is already affecting the Amazon basin and its biota. The index reflects field research and experience in other dammed river basins indicating that if the planned dams are constructed, their cumulative effects will have further impacts on extensive parts of the river-related ecosystems in the Amazon basin. As noted by Latrubesse et al. (2017), society has to become aware of the magnitude and complexity of the Amazon basin; there is no imaginable mitigation technology to reverse the cumulative impact caused by hundreds of dams.

Our recommendations go further. Countries such as Guyana, Suriname, and France – through the department of French Guiana – and Brazilian states such as Amazonas and Amapá are, as yet, only indirectly threatened by the construction of upstream dams. However, they are not involved at present in the discussions of potential

cumulative and synergistic environmental impacts of dam building upstream of their territories on their own natural and socio-economic resources. Pará state has focused on the impacts of dam building in its own jurisdiction (in the Tapajós and Xingu rivers, for example), ignoring the risks posed to its resources by dam-building in the Madeira basin or in the upper Amazon of Peru and Ecuador.

The existing Amazon Cooperation Treaty (ACT) could provide a vehicle for improving transboundary basin management between Amazonian countries, and for building a new international coalition based on existing legal instruments available in Brazil, such as the Water Management Act (Law 9433/1997), which promotes an integrated catchment management system (see Box 1 in Latrubesse et al., 2017). More scientists echo our claim of the need to revitalize, improve, and expand policy instruments of the ACT Organization (Anderson et al., 2018). The ACT Organization could also catalyse technical and scientific capacity building, consolidate existing programmes, and encourage more active participation of natural and social scientists to engage with stakeholders and decision-makers. Anderson et al. (2018) also point out the significant benefits of signing the United Nations Watercourse Convention and of the legal incentive it can provide to sustainable, transboundary water management, and mechanisms for information exchange. These institutions will be critical in avoiding transboundary tensions and conflicts over freshwater management and use, particularly in the context of future socio-economic growth and changing climate conditions.

Scientists have demonstrated the value of integrating scientific knowledge to subsidize strategies for the sustainable use and conservation of natural resources in the Amazon fluvial and coastal systems. Now is the time for governmental decision-makers to assimilate this understanding and take action and responsibility toward their citizens by considering the cumulative consequences of dam building on their own natural and socio-economic resources, and by their involvement in designing a plan for basin management, even when the dams are far upstream of their borders.

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ORCID

Edgardo M. Latrubesse https://orcid.org/0000-0001-5592-302X
Fernando M. d'Horta https://orcid.org/0000-0003-4747-2892
Camila C. Ribas https://orcid.org/0000-0002-9088-4828
Florian Wittmann https://orcid.org/0000-0001-9180-356X
Jansen Zuanon https://orcid.org/0000-0001-8354-2750
Edward Park https://orcid.org/0000-0002-1299-1724
Thomas Dunne https://orcid.org/0000-0002-5281-6517
Eugenio Y. Arima https://orcid.org/0000-0003-3366-4287
Paul A. Baker https://orcid.org/0000-0001-9438-855X

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