APPLIED ECOLOGY

Fragmentation of Andes-to-Amazon connectivity by hydropower dams

Elizabeth P. Anderson,[1]* Clinton N. Jenkins,[2,3,4] Sebastian Heilpern,[5] Javier A. Maldonado-Ocampo,[6] Fernando M. Carvajal-Vallejos,[7,8] Andrea C. Encalada,[9,10] Juan Francisco Rivadeneira,[11] Max Hidalgo,[12] Carlos M. Cañas,[13] Hernan Ortega,[12] Norma Salcedo,[12,14] Mabel Maldonado,[15] Pablo A. Tedesco[16]

Andes-to-Amazon river connectivity controls numerous natural and human systems in the greater Amazon. However, it is being rapidly altered by a wave of new hydropower development, the impacts of which have been previously underestimated. We document 142 dams existing or under construction and 160 proposed dams for rivers draining the Andean headwaters of the Amazon. Existing dams have fragmented the tributary networks of six of eight major Andean Amazon river basins. Proposed dams could result in significant losses in river connectivity in river mainstems of five of eight major systems—the Napo, Marañón, Ucayali, Beni, and Mamoré. With a newly reported 671 freshwater fish species inhabiting the Andean headwaters of the Amazon (>500 m), dams threaten previously unrecognized biodiversity, particularly among endemic and migratory species. Because Andean rivers contribute most of the sediment in the mainstem Amazon, losses in river connectivity translate to drastic alteration of river channel and floodplain geomorphology and associated ecosystem services.

INTRODUCTION

Andes-to-Amazon connectivity—facilitated by rivers—supports many natural and human systems in the Amazon. For example, Andean-origin rivers contribute roughly half of the Amazon mainstem's annual flow and export massive quantities of sediment, organic matter, and nutrients to the lowlands (*1*). Consequently, Andean rivers largely control geomorphological processes like river meandering, sediment deposition, and floodplain formation for thousands of kilometers downstream (*2*). These processes create and maintain habitats for many vertebrate and invertebrate species, both terrestrial and aquatic. River connectivity is particularly critical for freshwater fishes (*3*), whose diversity peaks globally in the Amazon with an estimated 3500 to 5000 species [2258 spp. known to date; (*4*, *5*)]. Some Amazonian fishes migrate thousands of kilometers between the Amazonian lowlands and the Andes, including the goliath catfishes (*Brachyplatystoma* spp.), which undergo the longest strictly freshwater migration in the world (*6*). Migratory fishes dominate Amazonian freshwater fisheries and, coupled with floodplain agriculture and riparian forest products, provide a primary source of income or protein for the >30 million people that inhabit the Amazon basin. Rhythms of life, cultural traditions, and indigenous cosmologies are all strongly influenced by Andes-to-Amazon connectivity as well (*7*–*9*).

An unprecedented boom in hydropower development has begun to disrupt the critical linkages between the Andean headwaters and the lowland Amazon, threatening to trigger irreversible change (*10*–*12*). Accordingly, the proliferation of dams in the Andean headwaters of the Amazon was recently identified as one of the top 15 global conservation issues (*13*). Given the strong controls of Andean rivers on the greater Amazon, there is an urgent need for basin and regional-scale analyses to quantify the effects of the proliferation of dams on river connectivity. Environmental impact and licensing protocols for hydropower are typically site-specific and largely ignore the cumulative or synergistic effects of multiple dams on a river network or within a watershed (*10*, *12*). Previous global studies of fragmentation of large rivers show that over half of the world's large river systems are affected by existing dams (*14*), and many large tropical river basins stand to be altered by proposed dams (*12*, *15*). These assessments have helped document general trends but often mask the hierarchical nature of river networks, treat the Amazon basin as a single unit, and do not consider the consequences of losses in Andes-to-Amazon connectivity.

Here, we present a current, regional analysis of river fragmentation by hydropower dams in the Andean headwaters of the Amazon, including one of the first attempts to apply a standard river connectivity index at a regional scale. In particular, we (i) updated previously published data (*10*) on existing and proposed hydropower projects through review of government documents and direct contact with authorities in Colombia, Ecuador, Peru, and Bolivia; (ii) verified the location of existing dams using satellite imagery; (iii) quantified cumulative effects of existing dams and dams under construction on longitudinal river connectivity; (iv) projected potential additive effects of proposed dams on longitudinal river connectivity; and (v) examined river network fragmentation in light of Andes-to-Amazon connectivity and freshwater fish biodiversity.

We defined eight Andean Amazon river basins—major rivers with headwaters in the Andes region >500 m above sea level (masl)—and considered each basin from its origins to discharge in the Amazon mainstem to perform connectivity analyses. Focal basins were the

[1]Department of Earth and Environment and Institute for Water and Environment, Florida International University, Miami, FL 33199, USA. [2]IPÊ—Instituto de Pesquisas Ecológicas, Nazaré Paulista, São Paulo 12960, Brazil. [3]SavingSpecies Inc., Holly Springs, NC 27540, USA. [4]Nicholas School of the Environment, Duke University, Durham, NC 27708, USA. [5]Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, USA. [6]Unidad de Ecología y Sistemática (UNESIS), Laboratorio de Ictiología, Departamento de Biología, Facultad de Ciencias, Pontificia Universidad Javeriana, Bogotá, Colombia. [7]FAUNAGUA, Cochabamba, Bolivia. [8]ECOSINTEGRALES SRL, Cochabamba, Bolivia. [9]Instituto BIOSFERA, Laboratorio de Ecología Acuática, Universidad San Francisco de Quito, Quito, Ecuador. [10]IMAR/MARE, Department of Life Sciences, University of Coimbra, 3001-456 Coimbra, Portugal. [11]Carrera de Biología, Facultad de Ciencias Biológicas, Universidad Central del Ecuador, Quito, Ecuador. [12]Departamento de Ictiología, Museo de Historia Natural–Universidad Nacional Mayor San Marcos, Lima, Peru. [13]Wildlife Conservation Society, Av. Roosevelt 6360, Miraflores, Lima, Peru. [14]Department of Biology, Francis Marion University, Florence, SC 29506, USA. [15]Unidad de Limnología y Recursos Acuáticos, Universidad Mayor de San Simón, Cochabamba, Bolivia. [16]UMR5174 EDB (Laboratoire Evolution et Diversité Biologique), CNRS, IRD, UPS, ENSFEA, Université Paul Sabatier, F-31062 Toulouse, France.
*Corresponding author. Email: epanders@fiu.edu

Caquetá, Putumayo, Napo, Marañón, Ucayali, and Madeira. The large Madeira was subdivided into the Madre de Dios, Beni, and Mamoré sub-basins for analysis. We used HydroSHEDS for river mapping and calculation of connectivity metrics, and applied the dendritic connectivity index (DCI) to further examine the effects of dam-induced fragmentation on tributary networks (*16*, *17*).

Table 1. Existing and proposed dams on Andean-origin rivers in the Amazon basin, classified according to major basin, country, size (installed generation capacity, based on available data), and freshwater ecoregion (*20*).

	Existing/ in construction		Proposed	
	Number	Total MW (≥)	Number	Total MW
Basin				
Caquetá	0	0	1	687
Putumayo	0	0	0	0
Napo	9	1669	22	2949
Marañón	36	2723	82	25,785
Ucayali	67	1873	37	11,852
Madre de Dios*	25	965	11	8595
Beni	20	625	3	5000
Mamoré	5	279	6	3871
Madeira†	32	7693	18	15,466
Country				
Colombia	0	0	1	687
Ecuador	31	3766	64	10,710
Peru	86	2838	84	32,482
Bolivia	25	903	11	12,861
Brazil‡	2	6450	—	—
Size (MW)				
No data	51	—	0	—
1–10	37	207	21	111
11–100	35	1268	57	2608
101–1000	17	3457	67	25,801
1001–4500	4	9025	15	28,219
Ecoregion				
Amazonas High Andes	141	7502	123	23,325
Western Amazon Piedmont	1	6	16	12,487
Ucayali-Urubamba Piedmont	0	0	10	7271
Mamoré-Madre de Dios Piedmont	0	0	9	8507
Others	2	6450	2	3150

*The Madre de Dios estimates include the Beni River basin. †The Madeira estimates include the Madre de Dios, Beni, and Mamoré river basins. ‡The Brazil estimate includes only the Santo Antônio and Jirau dams.

RESULTS

Here, we report four major findings. First, the footprint of hydropower development in the Andean Amazon has been severely underestimated. We documented 302 hydropower dams or projects in the region, corresponding to 142 dams in operation or under construction and 160 dams in various stages of planning (Table 1 and Fig. 1). The number of dams in operation or under construction is nearly two times higher than previously reported (*10*, *12*, *15*), a consequence of hydropower development over the past 5 years and our procurement of new data. Two additional mega dams were completed in 2012 on the Madeira River in Brazil (Santo Antônio and Jirau) outside of the Andean Amazon region. We included these dams in our connectivity analyses because they fragment the Madeira's Andean headwaters from the downstream Amazon.

Of the four Andean Amazon countries, Peru has the highest numbers of both existing and proposed dams (see Table 1 and the Supplementary Materials). Most existing dams in Peru are small projects (<50 MW) located high in the Andes, apart from a few dams in the size range of 100 to 1000 MW. In contrast, most proposed dams in Peru are between 100 and 1000 MW, and at least six projects under consideration could exceed 1000 MW installed generation capacity. Bolivia shows similar trends to Peru. Existing dams tend to be small- or medium-sized projects <50 MW, whereas proposed dams, although fewer in number, nearly all exceed 100 MW installed capacity. In Ecuador, most existing dams also tend to be <50 MW, apart from a handful of older dams and the Coca Codo Sinclair project (~1500 MW), which recently began operation in the Napo River basin. Colombia is the only country with no hydropower dams currently in operation or under construction in the Andean Amazon. However, the hydropower scenario could change significantly in the future, given Colombia's recently signed peace accords and the related increase in security, access, and business interest in the Amazon region (*18*, *19*).

Second, most existing hydropower development has affected tributary networks of the Andean Amazon, but not river mainstems. Of the eight Andean Amazon river basins we analyzed, six have hydropower dams in operation or under construction (Fig. 1). The Ecuadorian regions of the upper Marañón River basin—including the Pastaza and Santiago sub-basins—have many existing hydropower projects, as do the tributaries of the upper Ucayali (Peru) and Beni (Bolivia). The only Andean Amazon basins currently unaffected by existing hydropower dams are the Caquetá (Colombia-Brazil) and the Putumayo (Colombia-Peru-Brazil). Application of the DCI showed that the Marañón and Ucayali tributary networks have already experienced moderate fragmentation by existing dams—reflecting losses of approximately 20% of network connectivity in each basin (Table 2).

This situation is likely to change if proposed dams are constructed. Our analysis suggests that the Putumayo may soon be the only major river system unimpeded by hydropower dams in the entire Andean Amazon region. Under future dam development scenarios, losses in network connectivity could increase by >50% in the Marañón, Ucayali, and Beni and by >35% in the Madre de Dios and Mamoré (Table 2 and Fig. 2). Significant mainstem fragmentation is a possibility for five of eight major Andean Amazon rivers (Fig. 2). Of these, the Napo, Beni, and Mamoré have proposed dams near the mouth of the mainstem, which would isolate almost the entire upstream river network from

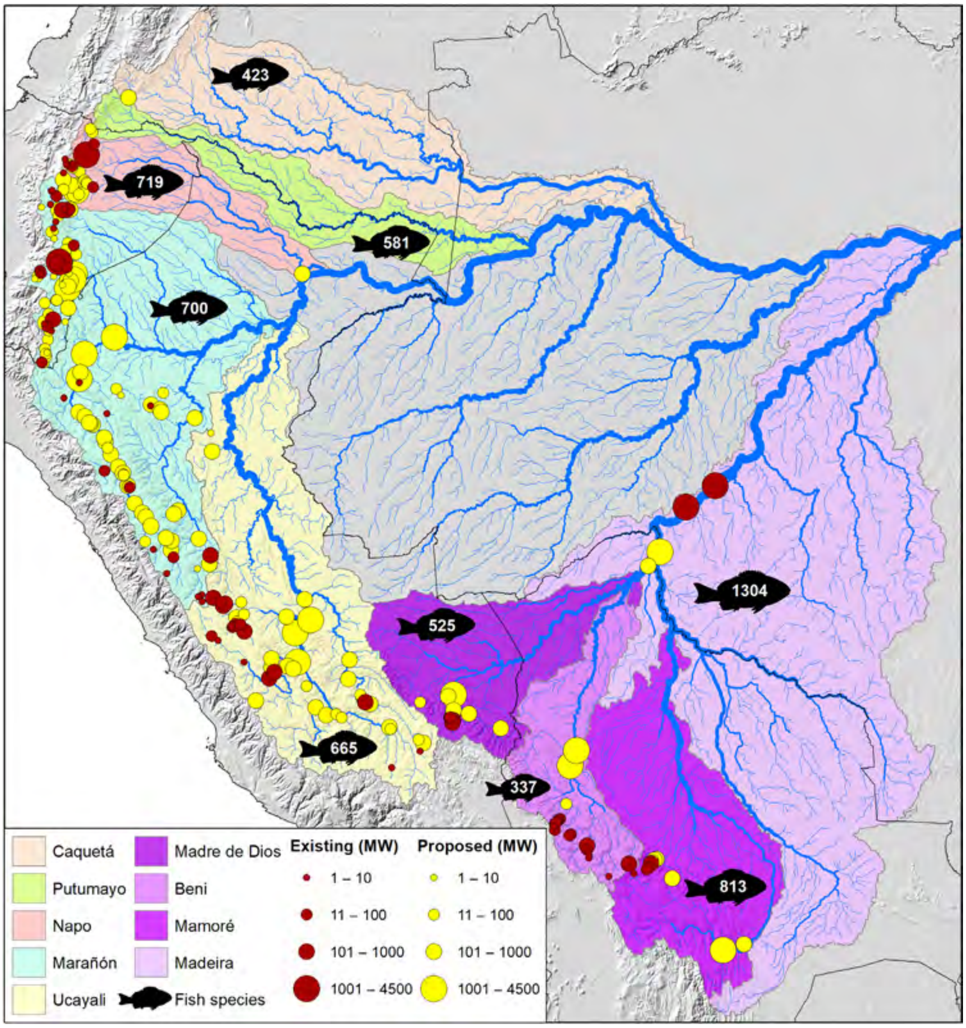

Fig. 1. Dams existing or under construction (red) and proposed (yellow) in Andean Amazon river basins. Estimated fish species richness for each basin is depicted by the fish symbol; fish data were provided by the Amazon Fish Project (*4*).

Table 2. Fragmentation of the Andean tributaries of the Amazon by existing and proposed hydropower dams. River network length and longest continuous river reach (km) are based on river lengths in HydroSHEDS (*48*). For fragmentation metrics, the Mainstem and Tributary Connectivity scores follow the approach of Dynesius and Nilsson (*54*). The DCI follows Cote *et al.* (*16*) and Grill *et al.* (*17*), where 100 equals full connectivity.

Basin	River network length (km)	Longest continuous mainstem river reach (km)	Longest reach (km)—existing dams	Longest reach (km)—existing and proposed dams	Mainstem connectivity—existing dams	Mainstem connectivity—existing and proposed dams	DCI—existing dams	DCI—existing and proposed dams
Caquetá	46,871	2216	2216	2216	100.0%	100.0%	100	99.60
Putumayo	21,165	1952	1952	1952	100.0%	100.0%	100	100
Napo	17,999	1108	1108	981	100.0%	88.5%	92.63	82.01
Marañón	61,619	1656	1551	1135	93.7%	68.5%	82.40	28.17
Ucayali	59,747	2463	2376	1879	96.5%	76.3%	79.68	32.65
Madre de Dios	48,324	1417	1417	1346	100.0%	95.0%	97.09	53.49
Beni	20,103	1260	1260	767	100.0%	60.9%	97.18	39.13
Mamoré	42,010	2048	2048	1427	100.0%	69.7%	99.56	61.16

the lowland Amazon. A similar situation has already occurred on the mainstem Madeira River in Brazil, where the Santo Antônio and Jirau dams—just downstream from the confluence of the Madre de Dios, Beni, and Mamoré rivers—have introduced physical barriers that disrupt longitudinal river connectivity between all three of these river basins and downstream areas of the Amazon (Fig. 2).

Third, dams threaten previously unrecognized freshwater fish diversity and endemism in the Andean Amazon. Freshwater Ecoregions of the World (FEOW) established four divisions for the Andean Amazon region: Amazonas High Andes, Western Amazon Piedmont, Ucayali-Urubamba Piedmont, and Mamoré-Madre de Dios Piedmont (*20*). Both existing and proposed hydropower development is heavily concentrated in the Amazonas High Andes (Fig. 2). This ecoregion harbors numerous fish species that are morphologically adapted to survive in fast-flowing, high-gradient mountain rivers, and it is characterized by high species assemblage turnover along short elevational gradients (*21*, *22*). Nevertheless, Andean Amazon river systems—especially the Caquetá, Putumayo, and upper Marañón mainstem—remain understudied. Our synthesis of existing data from fish collections at sites >500 masl yielded a total of 671 species, the first estimate for the Andean Amazon region (Table 3) (*4*). Dams alter the habitat for these species and create insurmountable barriers to their movement along river corridors; these impacts will be exacerbated by future climate change and predicted contraction of species ranges. Studies from other regions have confirmed the biological relevance of the DCI for freshwater fishes, linking declines in alpha (local) and beta (river network) diversity with incremental increases in river fragmentation (*23*, *24*). On the basis of the projected decreases in DCI values with ongoing hydropower development, we anticipate similar declines in alpha and beta diversity of fishes in the Andean Amazon—particularly the Marañón, Ucayali, Beni, Mamoré, and Madre de Dios basins (Table 2).

Basin-wide, Amazonian fishes display a range of movement or migration patterns linked mainly with reproduction or feeding (*6*, *25*–*27*). The well-known migrations of Siluriform and Characiform fishes, notably *Prochilodus*, sustain Amazonian fisheries and influence ecosystem processes in Andean rivers, often without functional redundancy (*28*, *29*). In addition, a recent uptick in river research in the Andean Amazon has documented remarkable movements in small-bodied species; this is

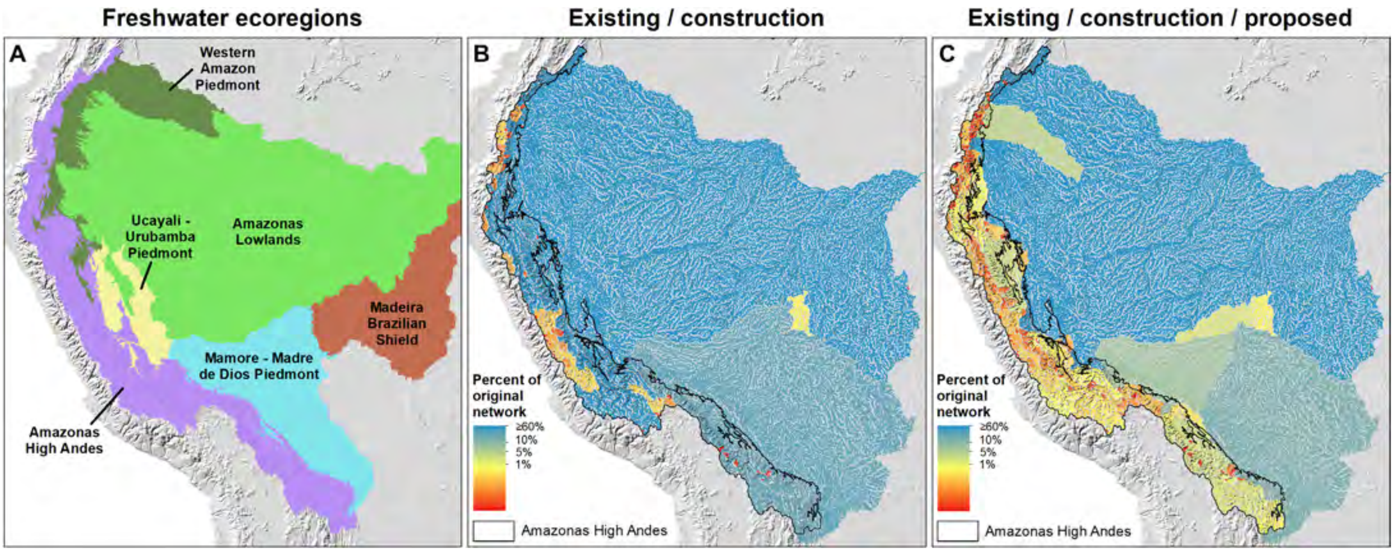

Fig. 2. Fragmentation of Andes-to-Amazon connectivity by hydropower dams. (**A**) Freshwater ecoregions of the Andean Amazon (*20*), where most existing and proposed dams are concentrated in the Amazonas High Andes ecoregion. (**B** and **C**) Fragmentation for individual sub-basins under two scenarios: (B) dams existing and under construction and (C) all dams existing, under construction, and proposed. Color gradation from blue to red denotes increasing fragmentation, represented by decreasing total length of the individual river network. That is, fragmentation is increasing as rivers go from blue (big, connected river networks) to red (small, isolated river networks).

Table 3. Breakdown of hydropower development and estimated fish species richness by elevation range. Data on fish species are provided by the Amazon Fish Project (*4*).

Elevation range (masl)	Existing dams/under construction	Proposed dams	Estimated number of fish species
>4000	52	1	65
3000–4000	23	10	35
2000–3000	29	24	69
1000–2000	30	57	257
500–1000	7	41	602
<500	3	27	1549

exemplified by *Trichomycterus barbouri*, a small-bodied Andean catfish whose juveniles migrate en masse upstream over distances >300 km in the Bolivian Amazon (*26*). Dams interrupt both migration corridors and cues because they present physical barriers and their operations create an unnatural hydrograph, with fluctuations in flow that occur out of sync with historical and/or seasonal patterns. Hydroclimatologic factors play important roles in cueing Characiform and Siluriform fishes at different stages of their migrations (*25*, *30*). Therefore, dams far upstream may influence the migratory behavior of these fishes by disrupting the hydrological signals to which they have responded for thousands of years. Further, water temperature changes associated with dams have the potential to affect viability of larval fishes for both migratory and nonmigratory species (*31*).

Fourth, the presence of hydropower dams in the Andean headwaters will affect multiple downstream natural and cultural processes dependent on Andes-to-Amazon connections. Current estimates suggest that 93% of sediments in the Amazon River are derived from an Andean source (*32*), as is most particulate nitrogen and phosphorus (*33*). Sediment from the Andes drives annual channel migration rates, meandering, and formation of oxbow lakes in the lowland Amazon (*2*), processes that, in turn, influence habitat and resource availability for fishery species, navigation by river, floodplain agriculture, and cultural practices (*8*, *34*, *35*). Our data indicate that Andean dams typically operate as storage dams or water diversion projects, different from lowland Amazonian dams like Santo Antônio and Jirau on the Madeira River, which are run-of-river projects. Consequently, Andean dams are projected to trap as much as 100% of sediment (*36*). Although many Andean dams may be geographically distant from Amazonian lowlands, their profound alteration of sediment and flow regimes is likely to transform coupled human-natural systems downstream.

The upper Amazon River, near the confluence of the Marañón and Ucayali rivers in Peru, exemplifies the susceptibility of interconnected human and natural systems in lowland Amazonia to Andean hydropower development. Here, fluvial dynamics have influenced historical patterns of vegetation in the most carbon-dense ecosystem in the Amazon basin: the peatland pole forests of the Pastaza-Marañón foreland. These forests cover an estimated 35,600 km^2 and have peat up to 7.3 m thick (*37*–*39*). High levels of biodiversity in the Pacaya Samiria National Reserve in Peru have also been linked to the interaction of water and sediment at the confluence of the Marañón River—an anabranching river system, with several channels and islands—and the Ucayali River—a meandering river system, marked by high sinuosity (*40*, *41*). The Kukama, who inhabit this region, consider oxbow lakes as sacred waters and distinguish culturally important features on the mainstem Marañón, such as entrances to underwater cities (*8*). Not far upstream, a ~4500-MW mega dam is currently proposed for the Pongo de Manseriche—a ~12-km canyon on the Marañón River often called the gate between the Andes and the Amazon. The anticipated hydrogeomorphological effects of this project threaten to fundamentally alter the carbon storage capacity of the Pastaza-Marañón foreland region, the viability of Pacaya Samiria as a protected area, and the cultural connections to the Marañón critical to the Kukama's survival. Similar stories are being foreseen for other regions of the western Amazon, where Andes-to-Amazon connectivity acts as a master control for human and natural systems.

DISCUSSION

Our data set and quantification of Andean Amazon river fragmentation emphasize how the Amazon hydropower boom must be examined in detail beyond just the number of dams. We argue that the Andean region's strong controls on coupled human-natural systems in much of the greater Amazon highlight the importance of regional analyses—especially because hydropower development in the Andean Amazon has been previously underestimated. Data on dams can be difficult to obtain in Andean Amazon countries because they are often housed in different places depending on the dam's status, ownership, operation, size, or location. Proposed dams—even at advanced development stages—sometimes change name or construction plans, making them even more challenging to track. If the same trend applies to tropical Africa and Asia—where dam data can also be difficult to obtain and plans frequently change—then existing assessments may underestimate the tropical hydropower boom at a global scale. Although we examined cumulative effects of dams on longitudinal river connectivity, we also note that hydropower development in the Andean Amazon and elsewhere across the tropics occurs alongside many other landscape or social transformations. In addition, the indirect effects of increased availability of hydroelectricity could be considerable for Amazonian ecosystems and human populations because new or cheaper electricity could stimulate road construction, mining, or forest clearing in the absence of strong controls (*42*). Our data could be combined with other information from the region—for example, biodiversity data, climate change analyses, forest cover, fisheries, and areas of cultural importance—to set priorities and examine trade-offs between hydropower and other ecosystem services, as has been done in other parts of the world (*43*, *44*).

In our data set, proposed dams include projects at a range of stages—from concept to advanced planning to preconstruction—and it is unlikely that all of the proposed projects documented here will be constructed. Whether or not an individual proposed dam moves forward is influenced by energy demand as well as political and economic conditions. In Brazil, for example, the recent economic downturn and corruption scandals have implications for dam building at home and in Andean countries, where numerous recently completed dams were built by Brazilian companies (for example, Odebrecht) or partly financed by Brazilian capital. In Peru, a recent change of administration—combined with the Brazilian economic downturn—has temporarily slowed interest in development of new mega hydropower projects in the lowland Amazon region and seems more likely to favor proposals for smaller dams high in the Andes (*45*). Changing political and economic climates in Peru could also favor other kinds of infrastructure projects, such as the Hidrovía Amazónica, which involves dredging and channelization of long stretches of the Marañón, Ucayali, and mainstem Amazon rivers to facilitate increased navigation of goods in and out of the western Amazon. In addition, as experiences globally have shown, dam projects on hold can resurface and be brought to completion years or decades after their original proposal (*46*).

Our results underscore the need for consideration of cumulative and synergistic effects of multiple dams, as well as other infrastructure projects like the Hidrovía Amazónica, on Andean Amazon rivers. Only one of eight major Andean Amazon river systems—the Putumayo—is currently unaffected by existing and proposed dams. Further, our analysis has shown the potential for extensive river fragmentation in one freshwater ecoregion—Amazonas High Andes—characterized by a highly endemic and understudied aquatic fauna. The absence of regional perspectives or cumulative effects assessments of hydropower dams and other infrastructure projects masks conditions that could transform ecological and social dynamics in the western Amazon. Because individual countries typically govern environmental impact assessment and licensing, cumulative effects assessments should be undertaken at a country level, at a minimum. Ideally, these assessments would be realized through a series of nested studies, beginning with the river basin where the dam is located, and then successively scaling up to the level of the entire Amazon basin. This kind of process would provide the opportunity to consider the impacts of an individual dam and its potential for additive or interactive effects on social, economic, and ecological systems in the greater Amazon.

Further, our analysis emphasizes the urgent need for greater international cooperation and transboundary water management, something that is currently uncharacteristic of hydropower planning in the Amazon. For example, no Amazon country has ratified the UN Watercourses Convention (UNWC) (United Nations Convention on the Law of International Watercourses). This convention applies to uses of international watercourses for purposes other than navigation and works to promote measures of protection, preservation, and management of international waters. If Amazonian countries became signatories, then the UNWC could provide a legal basis to encourage sustainable, transboundary water management in light of hydropower development, including protection of shared freshwater ecosystems, frameworks for conflict resolution, and mechanisms for information exchange. Similarly, the existing Amazon Cooperation Treaty (ACT) could provide a vehicle for improving transboundary water management between Amazonian countries, if specific protocols or amendments were introduced as related to international water governance and protection of freshwater ecosystems.

Globally relevant efforts to protect the biological and cultural richness of the Andean Amazon—involving multilateral collaboration, major philanthropic foundations, millions of dollars, and thousands of scientists—have focused on the creation and maintenance of a network of protected areas and indigenous territories in Andean Amazon countries. The ability of protected areas or indigenous territories to conserve biodiversity, cultural diversity, and indigenous livelihoods could be thwarted by river and landscape alterations related to hydropower development. However, rivers, their biodiversity, and the unique ecosystem processes and services they provide are often not considered in protected area design or management (*47*). In addition, the implications of flow alterations from existing and proposed dams should be considered in places with potential for strong hydrological controls on forests or peatland carbon storage.

Finally, beyond the need for reform of individual dam-based decision-making processes and regional analyses of hydropower development, we encourage a shift toward greater recognition of the ecological, cultural, and economic linkages to rivers in the Andes and greater Amazon basin. The concept of standing, intact forests as important conservation objects is widely accepted and backed with policies in all Amazonian countries. Similar awareness of and mechanisms for the protection of free-flowing Amazonian rivers are lacking. Future research and advocacy are needed to herald the importance of free-flowing Andean Amazon rivers, especially in light of current trends in hydropower development.

METHODS

Work toward this study began at an international workshop held in Bogotá, Colombia, in June 2015, with representatives from the four Andean Amazon countries and Brazil. Following this workshop, we obtained information on dams in the Andean Amazon from numerous sources in Colombia, Ecuador, Peru, and Bolivia. These included previous studies (*10*, *12*, *15*), government planning documents, and direct correspondence with representatives from government energy authorities. We plotted all existing dams and dams under construction using Google Earth and ArcMap 10.5 to confirm their existence and to verify their location with high-resolution satellite imagery. All fish data came from the Amazon Fish Project (www.amazon-fish.com).

For analyses of river network lengths and fragmentation indices, we used the HydroSHEDS river database (*48*). For calculations of river stretch and overall network lengths, we used the Barrier Analysis Tool (BAT) developed by The Nature Conservancy (*49*). To quantify losses in connectivity, we applied the DCI, developed by Cote *et al.* (*16*) and available for ArcGIS through the Fish Passage Extension (FIPEX) (*50*). River basins were from the Nested Watersheds of South America database, developed by The Nature Conservancy (*48*, *51*–*53*).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/1/eaao1642/DC1

table S1. Hydropower dams existing, under construction, or proposed in Andean Amazon river basins.

REFERENCES AND NOTES

1. M. E. McClain, R. J. Naiman, Andean influences on the biogeochemistry and ecology of the Amazon River. *BioScience* **58**, 325–338 (2008).
2. J. A. Constantine, T. Dunne, J. Ahmed, C. Legleiter, E. D. Lazarus, Sediment supply as a driver of river meandering and floodplain evolution in the Amazon Basin. *Nat. Geosci.* **7**, 899–903 (2014).
3. J. Lessmann, J. M. Guayasamin, K. L. Casner, A. S. Flecker, W. C. Funk, C. K. Ghalambor, B. A. Gill, I. Jacomé-Negrete, B. C. Kondratieff, L. N. Poff, J. Schreckinger, S. A. Thomas, E. Toral-Contreras, K. R. Zamudio, A. C. Encalada, Freshwater vertebrate and invertebrate diversity patterns in an Andean-Amazon basin: Implications for conservation efforts. *Neotrop. Biodivers.* **2**, 99–114 (2016).
4. Amazon Fish Project, www.amazon-fish.com [accessed 14 November 2017].
5. R. E. Reis, J. S. Albert, F. DiDario, M. M. Mincarone, P. Petry, L. A. Rocha, Fish biodiversity and conservation in South America. *J. Fish Biol.* **89**, 12–47 (2016).
6. R. B. Barthem, M. Goulding, R. G. Leite, C. Cañas, B. Forsberg, E. Venticinque, P. Petry, M. L. de B. Ribeiro, J. Chictaya, A. Mercado, Goliath catfish spawning in the far western Amazon confirmed by the distribution of mature adults, drifting larvae and migrating juveniles. *Sci. Rep.* **7**, 41784 (2017).
7. B. Huertas Castillo, M. Chanchari, *Mitos Shawi sobre el Agua* (2012).
8. B. Fraser, L. Tello Imaina, Culture, ecology get short shrift in river plan. *EcoAmericas*, 6–8 (2015).
9. E. P. Anderson, J. C. Veilleux, Cultural costs of tropical dams. *Science* **352**, 159 (2016).
10. M. Finer, C. N. Jenkins, Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. *PLOS ONE* **7**, e35126 (2012).
11. A. C. Lees, C. A. Peres, P. M. Fearnside, M. Schneider, J. A. S. Zuanon, Hydropower and the future of Amazonian biodiversity. *Biodivers. Conserv.* **25**, 451–466 (2016).
12. K. O. Winemiller, P. B. McIntyre, L. Castello, E. Fluet-Chouinard, T. Giarrizzo, S. Nam, I. G. Baird, W. Darwall, N. K. Lujan, I. Harrison, M. L. J. Stiassny, R. A. M. Silvano, D. B. Fitzgerald, F. M. Pelicice, A. A. Agostinho, L. C. Gomes, J. S. Albert, E. Baran, M. Petrere Jr., C. Zarfl, M. Mulligan, J. P. Sullivan, C. C. Arantes, L. M. Sousa, A. A. Koning, D. J. Hoeinghaus, M. Sabaj, J. G. Lundberg, J. Arbruster, M. L. Thieme, P. Petry, J. Zuanon, G. Torrente Vilara, J. Snoeks, C. Ou, W. Rainboth, C. S. Pavanelli, A. Akama, A. van Soesbergen, L. Sáenz, Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* **351**, 128–129 (2016).
13. W. J. Sutherland, S. Bardsley, M. Clout, M. H. Depledge, L. V. Dicks, L. Fellman, E. Fleishman, D. W. Gibbons, B. Keim, F. Lickorish, C. Margerison, K. A. Monk, K. Norris, L. S. Peck, S. V. Prior, J. P. W. Scharlemann, M. D. Spalding, A. R. Watkinson, A horizon scan of global conservation issues for 2013. *Trends Ecol. Evol.* **28**, 16–22 (2013).
14. C. Nilsson, C. A. Reidy, M. Dynesius, C. Revenga, Fragmentation and flow regulation of the world's large river systems. *Science* **308**, 405–408 (2005).
15. C. Zarfl, A. E. Lumsdon, J. Berlekamp, L. Tydecks, K. Tockner, A global boom in hydropower dam construction. *Aquat. Sci.* **77**, 161–171 (2014).
16. D. Cote, D. G. Kehler, C. Bourne, Y. F. Wiersma, A new measure of longitudinal connectivity for stream networks. *Landsc. Ecol.* **24**, 101–113 (2009).
17. G. Grill, C. O. Dallaire, E. F. Chouinard, N. Sindorf, B. Lehner, Development of new indicators to evaluate river fragmentation and flow regulation at large scales: A case study for the Mekong River Basin. *Ecol. Indic.* **45**, 148–159 (2014).

18. A. Regalado, Venturing back into Colombia. *Science* **341**, 450–452 (2013).
19. P. J. Negret, J. Allan, A. Braczkowski, M. Maron, J. E. M. Watson, Need for conservation planning in postconflict Colombia. *Conserv. Biol.* **31**, 499–500 (2017).
20. R. Abell, M. L. Thieme, C. Revenga, M. Bryer, M. Kottelat, N. Nogutskaya, B. Coad, N. Mandrak, S. Contreras Balderas, W. Bussing, M. L. J. Stiassny, P. Skelton, G. R. Allen, P. Unmack, A. Naseka, R. Ng, N. Sindorf, J. Robertson, E. Armijo, J. V. Higgins, T. J. Heibel, E. Wikramanayake, D. Olson, H. L. Lopez, R. E. Reis, J. G. Lundberg, M. H. Sabaj Pérez, P. Petry, Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. *BioScience* **58**, 403–414 (2008).
21. E. P. Anderson, J. A. Maldonado-Ocampo, A regional perspective on the diversity and conservation of tropical Andean fishes. *Conserv. Biol.* **25**, 30–39 (2011).
22. E. De La Barra, J. Zubieta, G. Aguilera, M. Maldonado, M. Pouilly, T. Oberdorff, Qué factores determinan la distribución altitudinal de los peces de ríos tropicales andinos? *Rev. Biol. Trop.* **64**, 157–176 (2016).
23. J. Perkin, K. B. Gido, Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecol. Appl.* **22**, 2176–2187 (2012).
24. S. Mahlum, D. Kehler, D. Cote, Y. F. Wiersma, L. Stanfield, Assessing the biological relevance of aquatic connectivity to stream fish communities. *Can. J. Fish. Aquat. Sci.* **71**, 1852–1863 (2014).
25. C. M. Cañas, W. E. Pine III, Documentation of the temporal and spatial patterns of Pimelodidae catfish spawning and larvae dispersion in the Madre de Dios River (Peru): Insights for conservation in the Andean-Amazon headwaters. *River Res. Appl.* **27**, 602–611 (2011).
26. G. Miranda-Chumacero, G. Álvarez, V. Luna, R. B. Wallace, L. Painter, First observations on annual massive upstream migration of juvenile catfish *Trichomycterus* in an Amazonian river. *Environ. Biol. Fishes* **98**, 1913–1926 (2015).
27. F. Duponchelle, M. Pouilly, C. Pécheyran, M. Hauser, J.-F. Renno, J. Panfili, A. M. Darnaude, A. García-Vasquez, F. Carvajal-Vallejos, C. García-Dávila, C. Doria, S. Bérail, A. Donard, F. Sondag, R. V. Santos, J. Nuñes, D. Point, M. Labonne, E. Baras, Trans-Amazonian natal homing in giant catfish. *J. Appl. Ecol.* **53**, 1511–1520 (2016).
28. J. D. Allan, R. Abell, Z. Hogan, C. Revenga, B. W. Taylor, R. L. Welcomme, K. O. Winemiller, Overfishing of inland waters. *BioScience* **55**, 1041–1051 (2005).
29. B. W. Taylor, A. S. Flecker, R. O. Hall Jr., Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science* **313**, 833–836 (2006).
30. C. M. Cañas, P. R. Waylen, Modelling production of migratory catfish larvae (Pimelodidae) on the basis of regional hydro-climatology features of the Madre de Dios Basin in southeastern Peru. *Hydrol. Process.* **26**, 996–1007 (2012).
31. F. Villamarin, W. E. Magnusson, T. D. Jardine, D. Valdez, R. Woods, S. E. Bunn, Temporal uncoupling between energy acquisition and allocation to reproduction in a herbivorous-detritivorous fish. *PLOS ONE* **11**, e0150082 (2016).
32. N. Filizola, J. L. Guyot, Suspended sediment yields in the Amazon basin: An assessment using the Brazilian national data set. *Hydrol. Process.* **23**, 3207–3215 (2009).
33. A. H. Devol, J. E. Richey, B. R. Forsberg, Phosphorus in the Amazon River mainstem: Concentrations, forms, and transport to the ocean, in *Phosphorus Cycles in Terrestrial and Aquatic Ecosystems* (SCOPE, Saskatchewan Institute of Pedology, 1991), pp. 9–23.
34. O. T. Coomes, Y. Takasaki, C. Abizaid, B. L. Barham, Floodplain fisheries as natural insurance for the rural poor in tropical forest environments: Evidence from Amazonia. *Fish. Manag. Ecol.* **17**, 513–521 (2010).
35. O. T. Coomes, M. Lapointe, M. Templeton, G. List, Amazon river flow regime and flood recessional agriculture: Flood stage reversals and risk of annual crop loss. *J. Hydrol.* **539**, 214–222 (2016).
36. B. R. Forsberg, J. M. Melack, T. Dunne, R. B. Barthem, M. Goulding, R. C. Paiva, M. V. Sorribas, U. L. Silva Jr., S. Weisser, The potential impact of new Andean dams on the Amazon fluvial ecosystem. *PLOS ONE* **12**, e0182254 (2017).
37. O. Lähteenoja, Y. R. Reátegui, M. Räsänen, D. del Castillo Torres, M. Ounonen, S. Page, The large Amazonian peatland carbon sink in the subsiding Pastaza-Marañón foreland basin, Peru. *Glob. Chang. Biol.* **18**, 164–178 (2012).
38. F. C. Draper, K. H. Roucoux, I. T. Lawson, E. T. A. Mitchard, E. N. Honorio Coronado, O. Lähteenoja, L. Torres Montenegro, E. Valderrama Sandoval, R. Zaráte, T. R. Baker, The distribution and amount of carbon in the largest peatland complex in Amazonia. *Environ. Res. Lett.* **9**, 124017 (2014).
39. T. J. Kelly, I. T. Lawson, K. H. Roucoux, T. R. Baker, T. D. Jones, N. K. Sanderson, The vegetation history of an Amazonian domed peatland. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **468**, 129–141 (2017).
40. J. D. Abad, C. Ortals, J. Paredes, J. Vizcarra, The birthplace of the Amazon river, the confluence of the Marañon and Ucayali rivers, paper presented at the American Geophysical Union, San Francisco, CA, 15 to 19 December 2014.
41. A. Mendoza, J. D. Abad, C. E. Frias, C. Ortals, J. Paredes, H. Montoro, J. Vizcarra, C. Simon, G. Soto-Cortés, Planform dynamics of the Iquitos anabranching structure in the Peruvian Upper Amazon River. *Earth Surf. Process. Landf.* **41**, 961–970 (2016).
42. P. E. Little, *Mega-Development Projects in Amazonia* (Derecho, Ambiente y Recursos Naturales, 2014).
43. G. Ziv, E. Baran, S. Nam, I. Rodriguez-Iturbe, S. A. Levin, Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 5609–5614 (2012).
44. J. D. Carvajal-Quintero, S. R. Januchowski-Hartley, J. A. Maldonado-Ocampo, C. Jézéquel, J. Delgado, P. A. Tedesco, Damming fragments species' ranges and heightens extinction risk. *Conserv. Lett.* **10**, 708–716 (2017).
45. M. Dourojeanni, Grandes proyectos en la Amazonía y las prioridades de PPK, *SPDA Actualidad Ambiental* (2016); www.actualidadambiental.pe/?p=41201#_edn5.
46. P. McCully, *Silenced Rivers: The Ecology and Politics of Large Dams* (Zed Books, 2001).
47. L. Castello, M. N. Macedo, Large-scale degradation of Amazonian freshwater ecosystems. *Glob. Chang. Biol.* **22**, 990–1007 (2016).
48. B. Lehner, K. Verdin, A. Jarvis, New global hydrography derived from spaceborne elevation data. *Eos* **89**, 93–94 (2008).
49. Barrier Analysis Tool (BAT), www.geodata.soton.ac.uk/geodata/gis/project173
50. Fisheries and Oceans Canada, *The Fish Passage Extension for ArcGIS (FIPEX)* (Fisheries and Oceans Canada, Habitat Management, Maritimes Region, 2011).
51. P. Petry L. Sotomayor, *Mapping Freshwater Ecological Systems with Nested Watersheds in South America* (The Nature Conservancy, 2009).
52. T. W. Fitzhugh, GIS tools for freshwater biodiversity conservation planning. *Trans. GIS* **9**, 247–263 (2005).
53. J. V. Higgins, M. T. Bryer, M. L. Khoury, T. W. Fitzhugh, A freshwater classification approach for biodiversity conservation planning. *Conserv. Biol.* **19**, 432–445 (2005).
54. M. Dynesius, C. Nilsson, Fragmentation and flow regulation of river systems in the northern third of the world. *Science* **266**, 753–762 (1994).

Acknowledgments: This study is the product of an international workshop convened in Bogotá, Colombia, in June 2015, with support from Partners for Conservation in the Colombian Amazon, funded by the U.S. Agency for International Development through Higher Education for Development under the Initiative for Conservation in the Andean Amazon (HED012-9748-LAC-12-03). Fish data were provided by the Amazon Fish Project, through J.A.M.-O. and P.A.T. We are grateful to V. Correa, D. Rosero, C. Bernal, S. Davila, A. Mercado, the National Authority for Water (ANA) in Peru, and the Agency for Regulation and Control of Electricity in Ecuador for assistance with data and information about dams. The manuscript was strengthened by helpful comments from A. Flecker, M. Freeman, M. Montoya, C. Baraloto, and two anonymous reviewers. **Funding:** We received complementary support from the MacArthur Foundation (16-1607-151053-CSD) and the Amazon Fish Project, funded through the European Union Seventh Framework Programme ERANet-LAC (ELAC2014/DCC-0210). We acknowledge support from the French Laboratory of Excellence projects "CEBA" (ANR-10-LABX-25-01) and "TULIP" (ANR-10-LABX-41 and ANR-11-IDEX-0002-02). **Author contributions:** All authors participated in the 2015 workshop, in the study's design, in data gathering, and in review of results and the manuscript. E.P.A., C.N.J., and S.H. analyzed the data and wrote the manuscript. C.N.J. prepared all figures. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 21 June 2017
Accepted 5 January 2018
Published 31 January 2018
10.1126/sciadv.aao1642

Citation: E. P. Anderson, C. N. Jenkins, S. Heilpern, J. A. Maldonado-Ocampo, F. M. Carvajal-Vallejos, A. C. Encalada, J. F. Rivadeneira, M. Hidalgo, C. M. Cañas, H. Ortega, N. Salcedo, M. Maldonado, P. A. Tedesco, Fragmentation of Andes-to-Amazon connectivity by hydropower dams. *Sci. Adv.* **4**, eaao1642 (2018).

Science Advances

Fragmentation of Andes-to-Amazon connectivity by hydropower dams

Elizabeth P. Anderson, Clinton N. Jenkins, Sebastian Heilpern, Javier A. Maldonado-Ocampo, Fernando M. Carvajal-Vallejos, Andrea C. Encalada, Juan Francisco Rivadeneira, Max Hidalgo, Carlos M. Cañas, Hernan Ortega, Norma Salcedo, Mabel Maldonado and Pablo A. Tedesco

Sci Adv **4** (1), eaao1642.
DOI: 10.1126/sciadv.aao1642