ENVIRONMENTAL STUDIES

The changing hydrology of a dammed Amazon

Kelsie Timpe and David Kaplan*

Developing countries around the world are expanding hydropower to meet growing energy demand. In the Brazilian Amazon, >200 dams are planned over the next 30 years, and questions about the impacts of current and future hydropower in this globally important watershed remain unanswered. In this context, we applied a hydrologic indicator method to quantify how existing Amazon dams have altered the natural flow regime and to identify predictors of alteration. The type and magnitude of hydrologic alteration varied widely by dam, but the largest changes were to critical characteristics of the flood pulse. Impacts were largest for low-elevation, large-reservoir dams; however, small dams had enormous impacts relative to electricity production. Finally, the “cumulative” effect of multiple dams was significant but only for some aspects of the flow regime. This analysis is a first step toward the development of environmental flows plans and policies relevant to the Amazon and other megadiverse river basins.

INTRODUCTION

Flow variability is widely recognized as a primary driver of biotic and abiotic conditions in riverine ecosystems (1–4). Along with longitudinal and lateral connectivity (5, 6), maintenance of a natural flow regime is critical for sustaining healthy riverine ecosystems and the services they provide (7–9). While the magnitude, timing, and predictability of river flow vary greatly among river systems, the flood pulse concept (6) predicts that periodic flow pulsing supports productivity, biodiversity, and species adaptation (10). Large, lowland rivers often have extensive floodplains and predictable annual flood pulses, creating recurring spatial and temporal variability as the aquatic/terrestrial transition zone moves up and down the floodplain (11). This dynamic also promotes the exchange of sediments, nutrients, and biota between the river channel and the floodplain (12) and promotes species adaptations to the dynamic environment of frequent, regular flooding, including fish that time their spawning with the flood pulse to use floodplains for feeding and rearing (13) and plants adapted to take advantage of flood-delivered nutrients (14, 15). These dynamic river-floodplain environments (for example, the Amazon, Mekong, Congo, and Yangtze rivers) exhibit some of the highest levels of biodiversity and productivity in the world (16–19).

Dams alter the natural flow regime by changing the magnitude, frequency, duration, timing, and rate of change of flow (1), as well as by modifying the transport of riverine sediments, nutrients, and biota (20). Just upstream of a dam, the creation of a reservoir shifts the environment from lotic to lentic, affecting water quality (21) and potentially increasing atmospheric flux of greenhouse gases from decomposing organic matter (22, 23). Reservoirs generally reduce biodiversity (24) and are specifically detrimental to migratory fish species because the lentic environment of the reservoir can act as a “filter” for species reliant on free-flowing water (25). Reservoirs, even those associated with “run-of-river” dams, trap sediments (26), reducing storage capacity and potentially causing backwater effects (27, 28); downstream, floodplains receive less nutrient and organic matter deposition (2, 28).

In addition to reduced sediment transport, the most conspicuous downstream impact of dam construction and operation is permanent alteration of the flow regime (28–31). Stunted flood pulses and increased base flows reduce floodplain habitat and encourage the encroachment of upland vegetation, resulting in the degradation of floodplain forests and loss of biodiversity (1, 30, 32). Frequent flow reversals and changes in flood timing driven by energy demand can disorient fauna, which rely on predictable flood timing and duration for migration and spawning cues (33). Rapid changes in flow, particularly if coupled with decreased sediment load, can also erode river channels and shorelines, resulting in vegetation disturbance and habitat loss (30, 34).

While the negative environmental impacts of dams are fairly well understood, the development of new hydropower to support growing global energy demand (35) is widely viewed as a sustainable source of electricity (36). Currently, 450 new large dams are planned or in construction in the Amazon, Congo, and Mekong basins (16). In the Brazilian Amazon, >30 large and >170 small dams are planned for construction over the next 30 years as a result of government plans geared toward increased energy security, economic growth, improved living standards, and industrialization (37–39). These efforts are a subset of the Initiative for the Integration of the Regional Infrastructure of South America, which seeks to transform Amazonia into a continental source of hydropower and intermodal hub of roads, waterways, and railroads (40). The rapid pace of planned development, spatial scale of impact, and potential for loss of globally important ecosystem services make this impending hydrological transformation unprecedented (41). As such, hydropower development in the Amazon region is expected to have a cascade of physical, ecological, and social effects at local to global scales (42), many of which will result from dam-induced changes to the hydrologic regime.

In recent decades, the concept of “environmental flows” has been applied to understand and, where possible, mitigate the negative impacts of dams, with a focus on quantifying hydrologic alteration (HA) and subsequent social-ecological impacts (43–46). At its core, the environmental flows concept recognizes that societies benefit directly (for example, via food production) and indirectly (for example, by supporting industry, recreation, and cultural identity) by allowing free-flowing water to support aquatic ecosystems (9). Several pioneering studies have sought to identify the gap between the state of the art globally and within Brazil’s legal framework on the subject of environmental flows (47–49), and some have worked to adapt and apply holistic environmental flows methodologies to specific cases within Brazil (50, 51).

Despite this progress, implementation of environmental flows methods and policies remains in the early stages of development in Brazil (47, 52). Particularly lacking in this context is a basin-wide characterization of the type and magnitude of dam-induced changes to the hydrologic regime and a synthesis of the environmental and management variables that drive alteration. Put simply, we ask: Are existing dams...
causing significant hydrological changes and, if so, in what ways and why? The goals of this work are thus (i) to quantify dam-induced HA across the Brazilian Legal Amazon (Fig. 1), (ii) to identify environmental and management variables that predict the observed magnitude of hydrological alteration to inform future dam siting and operation, and (iii) to quantify the cumulative effects of multiple dams on a river, where applicable. By advancing these goals, we aim to support the establishment of holistic environmental flows methods suitable for the region.

Given the large spatial and temporal scales of analysis and the limited availability of hydrological and biological data in the region, we used a broadly applicable environmental flows method to quantify the type and magnitude of HA induced by Amazon dams and to identify the influence of environmental and management predictor variables on the observed alteration. The Indicators of Hydrologic Alteration (IHA) method (1) uses pre- and post-dam construction flow data (Fig. 2A) to calculate 33 ecologically relevant parameters across five “groups” that describe primary facets of the flow regime: magnitude, frequency, duration, timing, and rate of change of flow (Table 1). The relative differences (percentage) between pre- and post-impact parameter values (Fig. 2B) are then used to assess and compare dam impacts across systems.

The hydrologic parameters in Table 1 were chosen specifically because of their relationships to ecological functions, such as population dynamics and habitat suitability (30). Given their structuring influences on ecosystems (53), half of the IHA parameters seek to characterize different aspects of event extremes, such as the magnitude and duration of flood/drought events. For example, IHA parameters in group 2 include 1-, 3-, 7-, 30-, and 90-day maxima and minima; number of zero flow days; and base flow index. Group 3 parameters describe the timing of annual minima and maxima. Group 4 parameters quantify the number/duration of high and low pulses. Event extremes affect river morphology and physical habitat conditions, availability of floodplain habitats, soil moisture and anaerobic stress in plants, magnitude of channel-floodplain nutrient exchange, distribution of plant communities, spawning cues for migratory fish, and compatibility with aquatic organism life cycles, among others (5). The remaining parameters focus on the magnitude of average flow (group 1; average monthly flows) and the rate of change of water conditions (group 5; rise/fall rate and number of reversals). Monthly flows influence the reliability of water supplies for terrestrial animals and habitat availability for aquatic organisms, whereas the rate of change of flow can affect spawning cues and the trapping of organisms on islands or within floodplain lakes (Table 1).

Using a pre-/post-analysis such as IHA to quantify HA in the absence of an experimental control requires assumptions about the length of record (LOR) needed to characterize the hydrologic regime. Previous studies suggested using >20 years of pre- and post-impact data (54); however, this guidance was developed for temperate systems and would preclude IHA application for many Amazonian dams, given their relatively recent construction and a lack of long-term hydrological data in the region (55). To overcome this challenge, we modified the approach of Richter et al. (54) to characterize the uncertainty associated with the application of shorter record lengths when data were limited. This LOR analysis was used to determine how many years of data were required to achieve a specified level of statistical certainty for any flow gauging station. This LOR method guided station selection for IHA analysis (see Methods). Using this approach, we identified 40 flow stations associated with 33 dams that had sufficiently long records for analysis (tables S1 and S2), allowing us to assess the impacts of both individual and multiple dams. A complete description of hydrology and dam data sets, which have since been published in a larger social-ecological database (56), is given in Methods.

Fig. 1. Map of the study area, which encompasses the Brazilian Legal Amazon, the Tocantins/Araguaia basin, and parts of the Paraná and North Atlantic basins, illustrating the distribution of existing small and large dams and highlighting those used in this study. Large dams are referred to as UHEs and have a production capacity of ≥30 MW; small dams are PCHs and have a production capacity of 1 to 30 MW. Streamflow stations used in the LOR analysis and to calculate IHA are also shown. Note that only major rivers are depicted.
RESULTS

LOR analysis

Results from the LOR analysis (Figs. 2 and 3 and table S3) served as a guideline for record length requirements when identifying flow gauging stations to use in the IHA analysis. This approach also allowed us to characterize the statistical uncertainty associated with the application of shorter record lengths when data were limited (tables S4 to S6). In contrast to Richter et al. (54), we found that fewer than 20 years of data could be used to yield statistically significant IHA results for a number of rivers across the Amazon. Figure 3 illustrates the results of the LOR approach for two stations with different flow regimes. The Seringal Fortaleza station (Fig. 3A) is located on the Rio Purus in the west central Amazon lowlands, and the Aruanã station (Fig. 3B) is located on the Rio Araguaia in the south central Cerrado. Due to consistent intra- and interannual flow variation at the Seringal Fortaleza station over the period of record (57), only 2 years of data are needed to be within 10% of the long-term mean annual flow maximum with 90% confidence; 7 years are required to be within 5% of the mean (vertical dashed lines). In contrast, achieving similar statistical confidence for the Aruanã station, which experiences more interannual flow variation (57), would require 15 and 30 years of data to be within 10 and 5%, respectively, of the long-term mean with 90% confidence, demonstrating the wide range of hydrologic regimes (and data requirements) across the region.

Across the entire LOR data set, we found that record lengths between 1 and 28 years would be required to be within 10% of the long-term mean annual flow maximum with 90% confidence (table S3). We found that two closely linked environmental variables were well correlated with the required LOR: mean river flow and station elevation (Fig. 4, A and B). In general, large rivers flowing through lowland forests required shorter record lengths to characterize the flow regime because their discharge, while varying greatly over the year, is relatively predictable from year to year. Smaller rivers in the highlands required longer records because of the higher intra- and interannual variability driven by variability in precipitation. Geographic location may also help to predict the required length of record, as suggested by the clustering of geographic locations in Fig. 4.

Dam-induced HA

Figure 5 synthesizes the overall magnitude and type of dam-induced HA for individual dams across the Brazilian Amazon. All dams were observed to affect the hydrologic regime; however, the magnitude and type of impact varied greatly by dam and station. Mean HA across all dams/stations was 30%, but the most impactful dam (Balbina) had a mean HA of >100% (Fig. 5A). The dams with the highest HA values were mostly large UHEs (usina hidrelétricas; defined as having production of ≥30 MW); however, some smaller PCHs (pequenas centrais hidrelétricas; defined as having a production between 1 and 30 MW) had equivalent or larger impacts, illustrating that dam size and production capacity are not the only drivers of hydrologic impact. Across dams, the most marked shifts in flow regime occurred in HA parameter groups 4 and 5 (Fig. 5B), which correspond to the frequency/duration and frequency/rate of change of high- and low-water conditions (Table 1; see Discussion). Scaling HA by published installed electricity production capacity (Fig. 5C) paints a potentially divergent picture of the “most” and “least” impactful dams (note the log scale on the y axis). While Balbina remains the “worst” large dam (UHE) in our data set, this analysis highlights the outsized impact of small dams (PCHs) relative to their production potential.

In general, hydrologic regimes were more affected downstream of dams than upstream of reservoirs (Fig. 6A). Although the two available gauging stations located directly within reservoir footprints (Estrada BR-163 and Porto Nacional; table S3) were highly affected (mean overall HA, 75%), stations further upstream were primarily affected by backwater effects and were less altered than stations downstream. We also found that overall HA caused by the first dam to be built on a river did not significantly increase with the construction of one or more additional dams (Fig. 6B); however, cumulative effects were significant for HA parameter groups 4 and 5 (frequency/duration and frequency/rate of change of high- and low-water conditions; Table 1). Detailed descriptions of each dam/station combination, including hydrographs for all LOR and IHA flow stations, are given by Timpe (57).
### Table 1. Summary of hydrologic parameters used in IHA and their ecological influences. Adapted from IHA Manual V7 (28).

<table>
<thead>
<tr>
<th>IHA statistics group</th>
<th>Regime characteristics</th>
<th>Ecosystem influences</th>
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<tbody>
<tr>
<td>Group 1: Magnitude of monthly water conditions (12 indices)</td>
<td>Mean or median value for each calendar month</td>
<td>Habitat availability for aquatic organisms</td>
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<td></td>
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<td>Soil moisture availability for plants</td>
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<td></td>
<td>Availability of water for terrestrial animals</td>
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<td></td>
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<td>Availability of food/cover for fur-bearing mammals</td>
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<td>Reliability of water supplies for terrestrial animals</td>
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<td></td>
<td>Access by predators to nesting sites</td>
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<td></td>
<td></td>
<td>Water temperature, oxygen levels, and photosynthesis in water column</td>
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<tr>
<td>Group 2: Magnitude and duration of annual extreme water conditions (12 indices)</td>
<td>Annual minima, 1-day means</td>
<td>Balance of competitive, ruderal, and stress-tolerant organisms</td>
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<td></td>
<td>Annual minima, 3-day means</td>
<td>Creation of sites for plant colonization</td>
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<td></td>
<td>Annual minima, 7-day means</td>
<td>Structuring of aquatic ecosystems by abiotic versus biotic factors</td>
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<td>Annual minima, 30-day means</td>
<td>Structuring of river channel morphology and physical habitat conditions</td>
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<td>Annual maxima, 1-day means</td>
<td>Soil moisture stress in plants</td>
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<td></td>
<td>Annual maxima, 3-day means</td>
<td>Dehydration in animals</td>
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<td></td>
<td>Annual maxima, 7-day means</td>
<td>Anaerobic stress in plants</td>
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<td>Annual maxima, 30-day means</td>
<td>Volume of nutrient exchanges between rivers and floodplains</td>
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<td>Annual maxima, 90-day means</td>
<td>Duration of stressful conditions such as low oxygen and concentrated chemicals in aquatic environments</td>
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<td></td>
<td>Number of zero flow days</td>
<td>Distribution of plant communities in lakes, ponds, and floodplains</td>
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<td></td>
<td>Base flow index</td>
<td>Duration of high flows for waste disposal and aeration of spawning beds in channel sediments</td>
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<td>Group 3: Timing of annual extreme water conditions (2 indices)</td>
<td>Julian date of each annual, 1-day maximum</td>
<td>Compatibility with life cycles of organisms</td>
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<td></td>
<td>Julian date of each annual, 1-day minimum</td>
<td>Predictability/avoidability of stress for organisms</td>
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<td>Access to special habitats during reproduction or to avoid predation</td>
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<td>Spawning cues for migratory fish</td>
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<td>Evolution of life history strategies and behavioral mechanisms</td>
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<td>Group 4: Frequency and duration of high and low pulses (4 indices)</td>
<td>Number of low pulses within each water year</td>
<td>Frequency and magnitude of soil moisture stress for plants</td>
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<td></td>
<td>Mean or median duration of low pulses (days)</td>
<td>Frequency and duration of anaerobic stress for plants</td>
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<td>Number of high pulses within each water year</td>
<td>Availability of floodplain habitats for aquatic organisms</td>
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<td></td>
<td>Mean or median duration of high pulses (days)</td>
<td>Nutrient and organic matter exchanges between river and floodplain</td>
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<td>Soil mineral availability</td>
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<td></td>
<td></td>
<td>Access for waterbirds to feeding, resting, and reproduction sites</td>
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<td></td>
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<td>Bed load transport, channel sediment textures, and duration of substrate disturbance (high pulses)</td>
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<tr>
<td>Group 5: Rate and frequency of water condition changes (3 indices)</td>
<td>Rise rates: Mean or median of all positive differences between consecutive daily values</td>
<td>Drought stress on plants (falling levels)</td>
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<tr>
<td></td>
<td>Fall rates: Mean or median of all negative differences between consecutive daily values</td>
<td>Entrapment of organisms on islands and floodplains (rising levels)</td>
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<td></td>
<td>Number of hydrologic reversals</td>
<td>Desiccation stress on low-mobility stream edge organisms</td>
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### Fig. 3. Sample LOR results for Seringal Fortaleza (A) and Aruana (B) stations. Solid black horizontal lines represent the long-term mean annual maximum flow for each station. Dashed black and gray horizontal lines represent 5 and 10% of the long-term mean, respectively. Solid green, red, and blue curves represent the 85, 90, and 95% confidence intervals (CIs). Dashed vertical lines indicate the number of years of data required to characterize the annual maximum flow within 5 and 10% of the long-term mean with 90% confidence. LOR results illustrate that widely varying hydrologic regimes yield different LOR requirements to provide similar statistical inference (see text).
Fig. 4. Number of years of flow data required to be within 10% of the long-term mean with 90% confidence across all LOR flow stations regressed against station elevation (A) and mean station discharge (B).

Fig. 5. Summary of the overall magnitude (A) and type (B) of dam-induced HA observed across all dams and stations (see table S4 for dam/station naming conventions; U and D indicate upstream and downstream, respectively). Bars with the same color represent multiple stations affected by the same dam. (C) Scaling HA by electricity production capacity shows hydrologic impact (%) per megawatt, illustrating outsized impact of small dams (unfilled bars) and relative efficiency of particular dams, for example, Tucurui (TU) versus Lajeado (LA), on the Tocantins River.
Predicting alteration

The best predictors of hydrological impact were reservoir area and volume (positive correlation) and dam elevation (negative correlation), but the strength and significance of these associations varied by station location (upstream versus downstream) and HA category (Fig. 7). For downstream stations, dam elevation was a consistently significant predictor of dam-induced alteration, explaining 55% of the variance in overall station HA. Elevation was also a good predictor of HA in parameter groups 2, 4, and 5. Upstream, HA values were significantly correlated with multiple predictor variables. Reservoir area and volume were the best predictors of overall HA upstream (reservoir area explained 81% of HA variance across dams), and reservoir area/volume, SD of discharge, production, and dam elevation were all significant predictors of HA in parameter groups 1 and 2. Distance was negatively correlated with HA (that is, impacts decreased with distance from the dam), but not significantly.

DISCUSSION

The synthesis of dam-induced HA across the Brazilian Legal Amazon demonstrates the extensive impact of hydroelectric dams on a range of ecologically relevant hydrologic parameters. Using publicly available data, we characterized the type and magnitude of hydrological changes brought about by dam construction and operation across the Amazon and provide insight into the physical and management drivers of these impacts. These results highlight substantial alteration to critical aspects of the flood pulse as a primary ecohydrological implication of observed hydrologic changes. The diversity of dams and rivers in our data set additionally allowed us to highlight the outsized impact of small hydropower systems relative to their electricity production capacity and add to the discussion of the cumulative impacts of dams. As a critical first step, our LOR analysis expanded the robustness of statistical inference that can be drawn from IHA and other indicator analyses in data-scarce regions. Overall, this study supports the utility of IHA in quantifying HAs for region-wide comparisons, which we believe are important for the creation of scientifically based environmental flows management plans and policies.

Dam-induced HA in the Amazon

Globally, dams are well known to alter the hydrologic regime (29, 30, 58), often with severe ecological (59–61) and social (62–64) consequences. However, dam-induced ecohydrological impacts vary widely based on dam size, design, operation, and geographic setting (64–66). The dams in our study are located across diverse physiographic regions, ranging from lowlands to highlands, and were built over decades of changing design standards, operational protocols, and monitoring regimes. Perhaps unsurprisingly given this heterogeneity, dam-induced HA varied widely across the dams in this study (Fig. 5A). All dams had some impact on the hydrologic regime, however, highlighting their pervasive effects on a range of hydrologic processes. A similar result was found by Magilligan and Nislow (30), who performed a regional study of dam-induced hydrologic impacts across the continental United States.
While each dam-station pair in this study offers a unique case study in HA driven by differences in environmental and management variables (57), several general trends stood out among IHA results. First, although all elements of the flow regime were affected by dam construction and operation in the Amazon, the largest changes are associated with elements of the flow regime related to the frequency, duration, and rate of change of high- and low-water conditions (IHA parameter groups 4 and 5; Table 1) (Figs. 5B and 6A). High values of HA in these parameter groups are indicative of dam operation for energy production (that is, peaking operations). These results point to a substantial impact of Amazonian dams on flood pulse dynamics, which play an important role in structuring river and floodplain geomorphology and biodiversity in tropical rivers (11). Dam-induced alterations in the flood pulse affect riverine sediment transport and the exchange of nutrients, organic matter, and plant/animal propagules between the river and floodplain (6). Impacts on sediment transport are particularly alarming considering the large number of planned dams within the Andean Amazon, where most of the rivers carry large sediment loads (67). Specifically, changes in the frequency/duration of pulse events (group 4) influence soil moisture and anaerobic stress for plants and the availability of floodplain habitat for aquatic organisms (29). Changes in the frequency/rate of pulse events (group 5) can trap aquatic organisms in floodplain lakes and strand terrestrial organisms on floodplain islands (68). Reduced flood duration also reduces fish recruitment, juvenile fish diversity, and floodplain macroinvertebrate abundance (69).

In contrast, changes in mean monthly flows (group 1), the magnitude and duration of annual extremes (group 2), and timing of annual low- and high-water conditions (group 3) were relatively low (Figs. 5B and 6A). Changes to these parameters are generally driven more by the maintenance of large reservoir reserves and water withdrawals for agriculture or domestic use (70) or during the initial stages of reservoir filling (71) rather than by hydropower generation. In this sense, many of the dammed rivers in our study maintained their coarse (that is, monthly) scale mean behavior despite substantial alteration to other aspects of the flow regime, although several large dams (for example, Balbina, Manso, Guaporé, and Serra da Mesa) did have significant impacts on one or more of these parameter groups. Where present, impacts to monthly flows were worse in the dry season for most dams, a finding supported by previous studies on the Manso and Ponte de Pedra dams (72, 73).

We also found that hydrologic regimes downstream of dams were significantly more affected than those upstream (Fig. 6A). Mean overall station HA values for downstream stations were twice as high as those for upstream stations (40 and 20%, respectively). However, it is important to note that these results group all stations upstream and downstream of all (individual) dams together and thus do not take distance from dam into account. Only two dams in our study had both upstream and downstream stations with sufficient data to directly compare HA values. Cachoeira do Lavrinha on the Rio das Almas in the Tocantins/Araguaia basin had equidistant upstream and downstream stations (57 and 54 km, respectively) with low and approximately equal HA (17 and 19%, respectively). These stations’ distance from the dam, coupled with its low production capacity (~3 MW), make it hard to draw conclusions about the magnitude of upstream versus downstream impacts. In contrast, stations upstream and downstream of the Tucuruí dam on the Tocantins River did have different overall HA, with greater impacts downstream (39% at the Tucuruí station) than upstream (25% at the Itupiranga station). However, the downstream station is only 9 km away from the dam, whereas the upstream station is nearly 50 km upstream of the reservoir, again making it difficult to draw robust conclusions about upstream versus downstream impacts of a specific dam.

When compared with regional IHA analyses from temperate and arid zones (30, 31, 74), our results suggest general similarities between dam-induced hydrological alteration across climates (for example, reduced peak flows and increased base flows and flow reversals), although some differences are apparent. For example, as noted above, we observed relatively small changes in mean monthly flows (group 1 parameters) because dams in the Amazon are built primarily for hydropower, with minor abstraction for domestic or agricultural supply. Changes in the timing of extreme events were also relatively low in our data set, because strongly seasonal rainfall in the Amazon is the primary driver of intra-annual flow variation, even in these dammed systems. In contrast, Magilligan and Nislow (30) and Pyron and Neumann (74) observed significant reductions in monthly flows in temperate and arid regions due primarily to agricultural abstraction, which also caused extreme shifts in the timing of flow maxima and minima in some dammed rivers. The magnitude of overall HA across our studied dams (8 to 108%) was within the range of the Richter et al. (31) study (33 to 87%) but considerably lower than the most affected rivers in arid regions reported by Magilligan and Nislow (30) (>250%). We note that the lowest values we observed were generally for small dams (PCHs) and upstream stations, which were not included in these other studies.

Regardless of magnitude, the impact of hydrologic alterations on ecological function can differ between watersheds whether or not they are within the same climatic region (75). One obvious difference between temperate and tropical regions is the high level of biodiversity and productivity in the tropics (76, 77). When considered alongside global climate regulation and other ecosystem services provided by these systems (78), these differences suggest that the impacts of dam-induced HA in tropical river systems may be more detrimental than in temperate systems in terms of biodiversity, productivity, and ecosystem service provisioning, even at lower absolute levels of alteration.

**HA versus electricity production capacity**

Critically, the dams associated with the most severe HAs in our data set have vastly different installed electricity production capacities. Of the three most impactful dams (Fig. 5A), Serra da Mesa produces nearly six times as much energy as Balbina or Manso (table S1) yet has lower mean HA. To better understand the balance between production capacity and impact across dams, we scaled mean station HA by each dam’s published installed production capacity, yielding hydrologic impact (percentage) per megawatt of electricity produced (Fig. 5C). This “scaled HA” suggests that Balbina and Manso have an order of magnitude greater hydrologic impact than Serra da Mesa per unit of installed electricity generation capacity. We note that published installed capacities for hydropower dams within Brazil are often large overestimates of actual energy production (71), making these values low estimates of scaled impact. Although HA is not the only indicator of a dam’s environmental impact, this analysis points to a widely divergent range of ecological impacts relative to economic (that is, energy) benefits. For example, Tucuruí’s large published installed generation capacity (8535 MW) and moderate HA (39% at the closest downstream station) combined to make it the most “efficient” dam in our data set, despite its widely recognized environmental and social impacts (63, 79).

In contrast, despite having relatively low HA values overall (Fig. 5A), the four small dams (PCHs) in our data set had the highest scaled HA values (Fig. 5C). These results are concordant with other studies showing that small hydropower systems can have environmental impacts equal.
to or greater than large systems per unit of power generation capacity (80–83). The high relative impact of these small dams on the hydrologic regime is troubling, given plans for the construction of hundreds of similar systems in the Amazon in the coming decades (40), coupled with minimal environmental licensing requirements for most dams with a production capacity of <10 MW (16). Currently, there are plans to build >400 small hydropower plants within Brazil, many of which will fall within the Brazilian Legal Amazon (84). The impacts of small dams are similar in kind to those of large dams (for example, hydrologic regime alteration, water quality degradation, habitat conversion, and subsequent social-ecological effects) (85), and previous analyses have assumed that the magnitude of these impacts scales with dam size, discounting small dam impacts as “minimal” (86). Despite the widely accepted view that small-scale hydropower is a potential source of “clean” or “green” energy (87), there is growing evidence that the environmental impacts of small dams have been vastly underestimated (83, 87), especially at the potential scale of their application. Of particular concern is the contradiction between the potential impacts of small dams on greenhouse gas emissions and climate change policies that promote small hydropower systems as a climate mitigation strategy (88). An additional challenge is the lack of an internationally agreed upon definition of “small” hydropower, blurring the lines between small and large systems in terms of policy, permitting, implementation, and management (84, 88).

Cumulative impacts of multiple dams
Understanding the cumulative impacts of multiple dams remains a challenge in both the scientific and management communities (16). Only a few studies have assessed how multiple dams affect specific ecological functions. Several authors have found that multiple dams fragment riparian flora relative to free-flowing rivers, leading to increased habitat fragmentation, exacerbated loss of primary vegetation, reduced vegetation complexity, and increased sedimentation relative to single dam systems (89–91). In contrast, a study on low head dams (<15 m height) found uniform disturbance along a river with multiple dams, with no apparent cumulative downstream ecological effects (92). Critically, there are few existing studies that compare the effects of single versus multiple dams on the hydrologic regime (93), leaving several fundamental questions unanswered (for example, are the effects of multiple dams additive, multiplicative, or largely insignificant? Is it better to build several dams on a single river or distribute them across the landscape?). Due at least in part to this lack of knowledge, the cumulative effects of multiple dams remain undervalued in environmental planning and decision-making for both new and existing dams (94, 95).

Our analysis of cumulative impacts for six rivers in the Brazilian Legal Amazon with multiple dams showed that, although overall HA did not significantly increase with the construction of additional dams, alteration within specific parameter groups did (Fig. 6B). Mean HAs in parameter groups 1 to 3 (Table 1) were relatively low (for the reasons discussed above) and nearly identical whether calculated during periods with single or multiple dams along a river. Because group 1 parameters represent the magnitude of monthly flows and group 3 parameters represent the timing of peak and low flows, it may be expected that adding additional hydropower dams (that is, with minimal long-term storage or abstraction) would be unlikely to further alter these aspects of the flow regime. In contrast, cumulative impacts were significantly higher than single dam impacts for parameter groups 4 and 5, which represent the frequency and duration of high and low pulses and the rate and frequency of water condition changes, respectively (Table 1). Although derived from a small data set, these findings imply that multiple dams may magnify the hydrological impacts to critical aspects of the flood pulse that are central to the ecological health of lowland tropical rivers (27). Further studies are needed to elucidate the potential influences of differing dam sizes, types, and geoclimatic regions on the accumulation of impacts from multiple dams.

Predictors of dam-induced HA
Reservoir area and volume and dam elevation were consistently significant predictors of the observed HA (Fig. 7). Even without taking dam type or operational rules into account, these simple bivariate relationships allow us to make general predictions about the strongest drivers of dam-induced HA across the Brazilian Amazon. In general, we found that lowland dams with large reservoirs affect the hydrologic regime more than higher elevation dams with smaller reservoirs. This is exemplified by comparing the two highest HA dams in our data set: Balbina, built on the Uatumá River in the northern Amazonian lowlands [32 m above sea level (masl)], and Serra da Mesa, built on the Tocantins River in the central Cerrado (451 masl). The rivers that these dams impound have comparable average annual flow; however, Balbina created a ~4400-km² reservoir due to the region’s flat topography. In contrast, Serra da Mesa flooded ~1250 km² in the hillier Cerrado landscape. The impacts of Serra da Mesa on the hydrologic regime were substantial (overall HA, 48%), but Balbina’s impact was more than twice as high (overall HA, 108%) and would likely be even greater if the reservoir filling period (that is, zero flow) and initial water releases (missing data) were included in the post-dam analysis.

While elevation and reservoir area were the best univariate predictors of downstream and upstream HAs, respectively, there are inherent relationships among predictor variables. For example, elevation plays a clear role in defining reservoir sizes and flow magnitude; lowland rivers tend to be large because of their large catchments, and dams built in these lowlands create extensive reservoirs due to large flows and flat topography. Moreover, these large, lowland rivers are most strongly characterized by periodic flood pulses, the dynamic we found to be most affected by dam construction (that is, groups 4 and 5 in Fig. 5B). Building dams on these rivers threatens ecologically important floodplain systems that rely on the flood pulse (96) and can have landscape level impacts that are difficult to predict (91). Highland rivers, on the other hand, generally have smaller catchments, lower flows, and “flashier” flood pulses. Although ecological functions in highland rivers are similarly tied to the flood regime, we found dam-induced HA in these systems to be less severe than in lowland rivers. Additionally, dams built on highland rivers generally create smaller reservoirs, leading to (relatively) lower ecological impacts, particularly on fish and macrobenthos (21, 24).

We expected HA to decrease with station distance from dams as dam operation effects and reservoir backwater effects diminish. Although we found a negative correlation between HA and the distance between a dam and an upstream or downstream flow station, the associations were not statistically significant (Fig. 7). These results are similar to those reported by Jiang et al. (97), who found overall HA on the Yangtze River (China) to decline with increasing distance downstream of the Three Gorges Dam, but not monotonically. These authors attributed this decline primarily to inflows from undammed large tributaries and interaction with large natural lakes. Given the potential correlation among predictor variables and a small number of observations across multiple river systems in our study (total of eight upstream and six downstream stations), we limited our analysis of the distance effect to
univariate regression; however, multivariate regression on a larger data set may further elucidate the threshold of upstream/downstream distances beyond which the hydrologic effects of dams become negligible.

**Study limitations and application**

This study has several limitations. First, IHA is a simple analytical tool that relies only on observed flow data to make predictions about potential ecohydrological impacts to river-floodplain systems. Although the method’s simplicity allows rapid calculation of HA across broad spatiotemporal scales, it lacks site-specific calibration in the prediction of impacts to hydrogeomorphology, floodplain characteristics, sediment transport, and other ecological functions. Our application of IHA across diverse river basins with widely varying physiographic characteristics (hydrologic regime, geology and morphometry of the drainage basin, land use types, sediment yield, morphodynamics, sediment transport, floodplain form, etc.) means that similar magnitudes of HA may have different relative impacts. However, because impacts are quantified in relative terms (that is, percent change), we believe that these results still allow useful comparisons between and among dam-affected rivers.

A second limitation of this study was the challenge of identifying streamflow stations with sufficient record lengths to apply hydrologic indicator methods. Although our LOR analysis allowed us to justify using shorter record lengths in several cases (particularly for high-flow, lowland rivers), many dammed rivers had no nearby flow gauging stations or stations with only short or incomplete records. We excluded three UHEs and approximately 100 PCHs from the study because of this lack of data. Missing pre-dam flows may be estimated using remote sensing and other hydrologic tools developed for ungauged basins (98); however, deriving post-dam flows without direct measurement will likely be difficult. Additionally, several newly constructed Amazon dams (for example, the Santo Antônio and Jirau dams on the Madeira River) were built too recently to characterize post-dam hydrology. This data limitation speaks to the need for improvements and expansion of hydrological monitoring across the region, particularly in watersheds with new, under-construction, and planned dams (for example, Tapajós, Xingu, and Madeira). While we support improved monitoring of dam impacts across all components of the social-ecological system, we strongly advocate for improved hydrological monitoring as a relatively cost-effective way to deduce ecological impacts via methods such as IHA.

One possible way around the “new-dam” data challenge is to model post-dam flows and apply the IHA method to compare observed pre-dam data and predicted post-dam data. This approach requires a physically based hydrologic model for each river and dam, as well as extensive parameterization and assumptions to characterize dam operations. This approach is feasible on a dam-by-dam basis and is the general approach taken to predict dam impacts on hydrology via the Environmental Impact Assessment process (99). For example, these models have been used to project an annual streamflow decrease of 80% in the ecologically significant “Big Bend” of the Xingu River (100) and should be further applied to understand how altered hydrology is likely to affect riverine ecohydrology on this and other Amazonian rivers with new or planned dams, such as the Madeira River, where reduced flood pulses may affect connections to floodplain lakes that are critical to support fisheries production (101). Although this intensive modeling approach is beyond the scope of this work, which looks to assess hydrologic impacts from existing dams across a wide spatiotemporal domain, our results do provide guidance on the likely range of impacts from recently built and future dams based on a set of environmental and management variables (Fig. 7).

Additionally, while the LOR analysis approach is useful for assessing HA in the Amazon and other poorly gauged basins, it does have several methodological caveats. First, the long-term means for the parameter values are only estimates of the true mean, given record lengths (23 to 45 years) relative to multicadal and longer time-scale climate variability (102, 103). Thus, the LOR and IHA approaches implicitly assume climate and land use stationarity (104). Second, we only applied the LOR analysis to one IHA parameter, annual 1-day maximum flow, and thus do not characterize the statistics of all 33 metrics of hydrologic variability at all stations; pursuing this approach is computationally feasible but unlikely to provide a more robust estimate of required record lengths. Nevertheless, the LOR analysis presented here improved the quality of our IHA analysis by providing (i) a better understanding of natural system variability, (ii) guidance for the minimum LOR required to perform IHA, and (iii) a quantitative measure of uncertainty around the statistical significance of hydrologic impacts. The method is transferable to other systems and may help to provide support for IHA and other hydrologic indicator analyses in developing basins with limited data.

A general limitation of this study is that the changes in hydrologic regime synthesized here are limited to the Brazilian Legal Amazon and describe only one of the many ecohydrological impacts of Amazonian dams. Notably, our analysis does not assess how dams and reservoirs affect biotic connectivity. Even in the absence of altered hydrology, dams and dam networks can severely disrupt medium- and long-distance fish migration (16). Along with the physical disruption caused by dams, reservoirs can act as environmental filters for migratory fish, which require stretches of free-flowing river and floodplain habitat for nurseries (21). On rivers with multiple dams, fish can become trapped (21), leading to local extirpation or extinction. Critically, fish ladders have often failed in the Amazon (105, 106). Together, the looming loss of Andes-Amazon connectivity (67), coupled with the severe and widespread HA illustrated here, threatens to devastate some of the planet’s most biodiversity fish communities (107), and further work is needed to adequately assess these combined ecohydrological impacts.

Hydropower development in the Amazon has myriad hydrological, ecological, and social effects (108), and critical questions about its overall sustainability remain unanswered at a variety of scales (67, 109, 110). Given the many impacts of Amazonian hydropower expansion, an alternative to building new generation capacity would be to implement “demand-side” energy policy solutions, such as energy conservation (111); however, with strong political and economic pressure to harness the Amazon’s hydropower potential, this is likely unfeasible. Taking steps to reduce the environmental impacts of dams could be considered the “next-best” practice, including optimizing dam operations to reduce hydrologic regime alterations and improving our understanding of the links between altered hydrology and impacts to ecological and social systems. This work quantified the hydrological impacts of 33 small and large dams across the Brazilian Legal Amazon, providing insight into the physical drivers of dam impacts and highlighting the important ecohydrological implications of the observed hydrologic changes. We believe that this type of regional hydrologic analysis is an important first step toward the development of environmental flows management plans and policies relevant to the Amazon and other megadiverse tropical river basins. Critically, the application of environmental flows methods requires integrative analyses to understand the drivers of hydrological alteration and ecological impacts on aquatic systems in periods before dam implementation (110). These studies thus serve as a baseline from which to isolate anthropogenic impacts from natural variability (4) and to derive post-dam conservation and mitigation strategies. This type of analysis is
difficult in areas where there is a shortage of continuous data, hindering communities and governments in these regions from taking appropriate and sustainable decisions (112).

**METHODS**

**Study area**

This study focuses on existing hydroelectric dams within the Brazilian Legal Amazon and the Tocantins/Araguaia basin (Fig. 1). The “Legal Amazon” covers 5217 km² (61% of Brazil’s territory) and fully encompasses seven states (Amazonas, Pará, Acre, Amapá, Roraima, Rondônia, and Tocantins), along with portions of two others (Maranhão and Mato Grosso). Hydrologically, the Legal Amazon includes the entire Amazon basin and parts of the Tocantins/Araguaia, Paraná, Paranaíba, and northeast Atlantic basins. We included the entire Tocantins/Araguaia basin in our assessment because of the large number of hydroelectric dams in the watershed. Information on dams in the study is summarized in table S1.

The study area includes three biomes (Amazon forest, Cerrado, and Pantanal), various terrain types, and altitudes ranging from near sea level to >600 m. The region’s rivers range from small, mountainous streams to large, meandering lowland rivers with expansive floodplain forests. Some rivers, such as the Madeira in the southwest Amazon, are “white-water rivers” that originate in the Andes Mountains and carry heavy sediment loads. Others, such as the Tocantins in the southeastern portion of the study area, are clear-water rivers that originate in the weathered Brazilian and Guianan shields and have low sediment loads but are rich in dissolved minerals. Black-water rivers, such as the Uatumã in the northern Amazon, carry few suspended sediments but are highly acidic and high in tannins because they drain nutrient-poor sandy soils of the central Amazon (110, 113).

**Data collection and preparation**

To initiate our study, we developed a hydrological database of river flow and stage at 1062 stream gauge stations across the study area. All hydrological data were publicly available and downloaded from the Agência Nacional de Águas (ANA; Brazil’s National Water Agency) using the Hydroweb platform (www.ana.gov.br). Data gaps, when present, were filled whenever possible using linear interpolation, interpolation correlations ($R^2 > 0.8$), and/or stage-discharge curves, as deemed most appropriate. Next, we added information about existing hydroelectric dams to the database (table S1). Information on hydroelectric dams was obtained from the Agência Nacional de Energia Elétrica (ANEEL; Brazil’s National Agency of Electric Energy) and the Sistema Nacional de Informações sobre Recursos Hídricos (SNIRH; Brazil’s National System of Water Resources Information). Dams were divided into two groups: those with an electricity production capacity greater than or equal to 30 MW (referred to as UHEs) and those with a production capacity between 1 and 30 MW (referred to as PCHs). Using the compiled databases, we identified hydrological stations on dammed rivers with sufficient streamflow data for IHA analysis (table S2). These databases were coupled with other hydrological, environmental, social, and economic data of Tucker Lima et al. (56) and also made available on the website of the Amazon Dams Network/Rede Barragens Amazônicas (http://amazondamsnetwork.org/amazon-databases/).

**LOR analysis**

Characterizing natural and altered flow regimes using IHA or other statistical methods requires a flow record that captures intra- and interannual flow variations driven by climate variability. Huh et al. (114) concluded that 20 to 30 years of data are required on either side of an impact to characterize changes in flow variability in southeastern (United States) rivers, and Richter et al. (54) suggested a minimum of 20 years based on three U.S. streams with varying hydrology. Other U.S. studies have found that 10 to >40 years of data are required to detect streamflow trends (114, 115). Given this uncertainty, additional work was needed to robustly define the LOR required to detect statistically significant changes in hydrologic regime due to dam construction and to assess whether guidance derived in temperate and arid systems applied in the Amazon.

To do so, we modified the analysis of Richter et al. (54) to develop guidance for the LOR required to characterize streamflow variability within specific statistical bounds and applied it to data sets from 34 streamflow stations within the study area (table S3). Stations were chosen to represent watersheds with the least anthropogenic impact and longest record lengths and were distributed across regions, elevations, and flow magnitudes to assess how hydrogeomorphic factors affected the required LOR. For each LOR station in the analysis, we calculated annual 1-day maximum flow for each year in a data set along with the long-term mean for this parameter. Parameter values were randomly ordered and grouped into record length increments ranging from 2 years to the full LOR. The mean of each record length increment was calculated for comparison to the long-term mean. This process was repeated 50,000 times, from which 95, 90, 85, and 80% CI were calculated. Using these statistics, we calculated the LOR required to be within a given percentage of the long-term mean at a specified level of confidence for each river in the study (table S3). All analyses were performed using R statistical software (116).

**IHA method**

The IHA method (1) is an open-access desktop model developed by the Nature Conservancy that calculates 33 ecologically relevant parameters to characterize hydrologic regime (Table 1). IHA parameters are based on five characteristics of the flow regime listed in Table 1 and were chosen for their close relationship to ecological functions, such as population dynamics and habitat suitability (30). Because of the structuring influence that extreme events have on ecosystems (53), many IHA parameters focus on measuring the characteristics of event extremes, such as timing of extremes (Julian dates), magnitude and duration of events (1-, 3-, 7-, 30-, and 90-day maxima and minima; zero flow days and base flow index; and duration of pulse events), and frequency and duration of events (number/duration of high and low pulses). The remaining parameters focus on the magnitude of average flow (average flow in each month) and the rate of change of water conditions (rise/fall rate and number of reversals).

We used IHA to quantify changes in hydrologic regime due to dam construction and operation by applying IHA to pre- and post-dam periods and comparing the 33 IHA parameters between the two periods. At every station, median values of each IHA parameter were calculated for both the pre- and post-impact periods. Using these statistics, we calculated HA values for each parameter according to the following equation

$$HA\% = \frac{(M_{post} - M_{pre})}{M_{pre}} \times 100$$

where $M_{post}$ is the median for the post-impact period and $M_{pre}$ is the median for the pre-impact period. HA values were calculated for each
Station selection and data analysis

We applied IHA to 40 streamflow stations upstream and downstream of 17 UHE dams and 16 PCH dams in the study area (tables S4 to S6). We categorized the statistical significance of each IHA analysis based on the stations’ pre- and post-impact period record lengths and our LOR analysis of unimpacted stations with similar hydrologic regimes within the geographic area (table S3). Several stations with fewer years of data than identified in the LOR analysis were maintained in our analysis if their hydrographs showed obvious hydrologic impacts after dam construction and they had an extended data set on one side of the impact (that is, were only lacking data in one period).

Some of the rivers in our study area have a single dam, whereas others have a cascade of two or more dams. We thus divided the IHA analysis into two sections to separately assess the impacts of single versus multiple dams on riverine hydroecology (tables S4 to S6). Some dams were included in both analyses if the available data allowed for the isolation of impacts from one dam along a river with multiple dams. This occurred if a dam was the first to be built on a river and remained the only dam for a sufficient period of time for IHA analysis based on the results of the LOR analysis. Depending on data availability, some dams and combinations of dams were analyzed using multiple streamflow stations located upstream, downstream, or upstream and downstream of dams to characterize spatial variation in the ecologically impacts of dam construction (for example, upstream versus downstream impacts and the effect of distance from dams).

For rivers with single dams, we analyzed the impacts of eight UHE dams and four PCH dams using data from 27 streamflow stations (tables S4 and S7). Pre- and post-impact periods were determined on the basis of dam construction, reservoir fill, and operation start dates (table S1). For rivers with multiple dams, we analyzed the cumulative impacts of 14 UHE dams and 12 PCH dams on six rivers using data from 22 streamflow stations (tables S5, S6, and S8). Multiple dams along the same river were grouped together for analysis of cumulative impacts. Because of the complexity of the hydroelectric complex along the Tocantins River, dams on this river were grouped into five combinations based on the dates of dam construction (that is, after the construction of the Tucurui dam in 1984, after the construction of the Lajeado dam in 2001, etc.). If data were available, separate IHA analyses were run using different post-impact periods to reflect the impacts of an increasing number of dams.

Predictor variable analysis

Our study area covered a wide range of hydroclimatic regions, topographies, river types (white, black, or clear water), streamflow magnitudes, dam sizes, and dam types (reservoir, run-of-river, and diversion). Additionally, station locations were not always close to dams, ranging from directly adjacent to hundreds of kilometers away when data were available. To identify the influence of different environmental and management variables on the magnitude and type of dam-induced HA, we performed linear and log regressions between station HA (overall and parameter group mean HA values) and a suite of predictor variables, including the mean, SD, and coefficient of variation of river discharge (Q); electricity production capacity; reservoir area and volume; dam elevation; and station distance from the dam. Regressions were performed separately on upstream and downstream stations to isolate predictor variable effects from inherent upstream versus downstream impact differences (Fig. 6A). For dams with flow data from more than one streamflow station, only the station closest to the dam was used, except when analyzing the effect of distance, when we used all stations.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/11/e1700611/DC1

Table S1. Hydroelectric dams analyzed with supporting information.
Table S2. Streamflow stations used for IHA analysis.
Table S3. Stations used in the LOR analysis.
Table S4. Stations used in the IHA analysis of individual dams, with supporting information.
Table S5. Stations used in the IHA analysis of multiple dams in the Amazon and Paraná basins.
Table S6. Stations used in the IHA analysis of multiple dams in the Tocantins basin.
Table S7. IHA results for streamflow stations in the individual dams analysis.
Table S8. IHA results for streamflow stations in the multiple dams analysis.

REFERENCES AND NOTES


57. K. Timpe, Quantifying the ecohydrological impacts of damming the Amazon. MS Thesis, University of Florida, Gainesville (2016).


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The changing hydrology of a dammed Amazon
Kelsie Timpe and David Kaplan

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