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Assessment of dam effects on streams and fish assemblages of the conterminous USA

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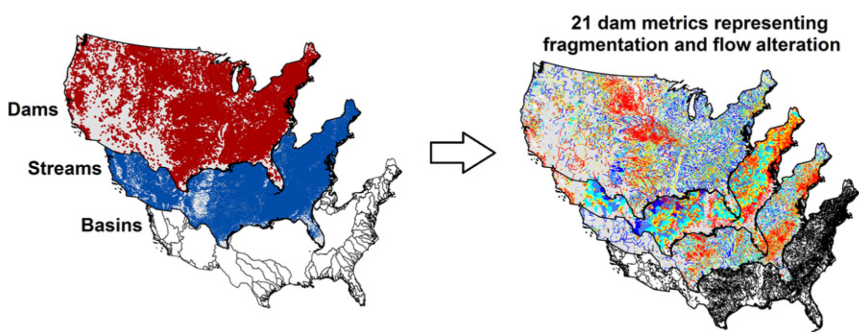
HIGHLIGHTS

- Developed 21 metrics of stream fragmentation and flow alteration by dams in the USA.
- Dams have increased stream fragments by 801% and significantly altered flows.
- Dam influences on streams and fishes differ by ecoregion and stream size.
- Dams have affected fishes as much or more than other anthropogenic stressors.
- Diverse dam metrics are needed to aid in dam policy and management decisions.

GRAPHICAL ABSTRACT



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ABSTRACT

Despite the prevalence of damming as a global disturbance to river habitats, detailed reach-based assessments of the ecological effects of dams are lacking, particularly across large spatial extents. Using data from nearly 50,000 large dams, we assessed stream network fragmentation and flow alteration by large dams for streams of the conterminous USA. We developed 21 dam metrics characterizing a diversity of dam influences operating at both localized (e.g., distances-to-dams) and landscape scales (e.g., cumulative reservoir storage throughout stream networks) for every stream reach in the study region. We further evaluated how dams have affected stream fish assemblages within large ecoregions using more than 37,000 stream fish samples. Streams have been severely fragmented by large dams, with the number of stream segments increasing by 801% compared to free-flowing streams in the absence of dams and a staggering 79% of stream length is disconnected from their outlet (i.e., oceans and Great Lakes). Flow alteration metrics demonstrate a landscape-scale disturbance of dams, resulting in total upstream reservoir storage volumes exceeding estimated annual discharge volumes of many of the nation's largest rivers. Further, we show large-scale changes in fish assemblages with dams. Species adapted to lentic habitats increase with dams across the conterminous USA, while rheophils, lithophils, and intolerant fishes decrease with dams. Overall, fragmentation and flow alteration by dams have affected fish assemblages as much or more than other anthropogenic stressors, with dam effects generally increasing with stream size. Dam-induced stream fragmentation and flow alteration are critical natural resource issues. This study emphasizes the importance of considering dams as a landscape-scale disturbance to river habitats along with the need to assess differential effects that dams may have on river habitats and the fishes they support. Together, these insights are essential for more effective conservation of stream resources and biotic communities globally.

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1. Introduction

Aquatic habitat degradation resulting from anthropogenic disturbances is a major source of freshwater biodiversity loss globally (Dudgeon et al., 2006), contributing to population declines in imperiled fishes (Jelks et al., 2008). Many studies have demonstrated how anthropogenic disturbances can operate both locally and over landscapes to change stream habitats, with local disturbances including those that directly change the stream channel (e.g., channelization and bank hardening) and landscape-scale disturbances including those that can operate throughout catchments (e.g., urbanization, agriculture, deforestation). Often, localized and landscape-scale disturbances can act in concert, having multiple, cumulative effects on aquatic habitat (Degerman et al., 2007; Schinegger et al., 2012). Dams are an example of a disturbance known to have a diversity of effects on streams, inducing localized changes that alter the continuum of stream temperature, water chemistry, energy, and sediment (i.e., serial discontinuity concept; Ward and Stanford, 1983) as well as having landscape-scale influences including stream network connectivity loss and system-wide changes in flow and temperature regimes (Nilsson et al., 2005).

Despite the prevalence of damming, few detailed reach-based assessments have been conducted investigating landscape-scale consequences stemming from the cumulative effects of dams over large spatial extents. This cumulative aspect is important as dams not only affect streams as individual disturbances, but also in conjunction with all other dams located throughout stream networks (Segurado et al., 2013). Because stream networks consist of longitudinally-connected fluvial habitat patches constrained within dendritic networks (Fagan, 2002), habitats as well as organisms therein are particularly susceptible to network-wide disturbances such as damming, which alter boundaries, size, quality, and connections among habitats. This is particularly true for stream fishes that use disparate habitats for reproduction, growth, and survival (Schlosser and Angermeier, 1995; Fausch et al., 2002), as dams can influence species assemblage structure, richness, and abundance (e.g., Cheng et al., 2016; Cooper et al., 2016). Further, dams can also affect macroinvertebrate communities (Van Looy et al., 2014), an important food source for many stream fishes. Due to these factors, studies focusing on dams that lack network-wide measurements for all streams or have only considered a single aspect of fragmentation provide a limited view of dam effects on river systems and aquatic biota throughout entire stream networks.

In the USA and globally, there is a need to understand the scale and magnitude of dams as a landscape-scale disturbance and to evaluate large-scale influences of dams on fish communities, particularly when compared to other prominent landscape disturbances. This study meets these needs. We first develop 21 dam metrics characterizing stream network fragmentation and flow alteration which we use to describe regional patterns in dam influences across the vast and heterogeneous region comprising the conterminous USA. Next, we evaluate relationships between fish assemblage traits and dam metrics, considering how these relationships vary by stream size and by ecoregion. Finally, we test the relative influence of dams on stream fishes in comparison with other major landscape-scale stressors to better understand the potential for dams to act as a landscape-scale disturbance to stream fish assemblages.

2. Methods

2.1. Describing dam conditions for the conterminous USA

2.1.1. Dam database

We utilized a comprehensive and spatially consistent large dam database for the conterminous USA, the National Anthropogenic Barrier Dataset (NABD; USGS, 2013). The NABD includes spatially-verified dam locations attributed to the 1:100,000 scale National Hydrography Dataset Plus Version 1 stream network (described below; NHDPlusV1; USEPA and USGS, 2005) as well as dam attributes including reservoir storage volume (Fig. 1). NABD dams were derived from the 2009 U.S. Army Corps of Engineers National Inventory of Dams (NID; USACE, 2009) and meet the following criteria: 1) dam hazard potential is considered either high or significant or 2) dams exceed 7.62 m in height and 1.85 hectare-meter of storage or exceed 1.83 m in height and 6.17 hectare-meter of storage (USACE, 2009). To create the NABD, we overlaid dams from the NID and the stream network of the NHDPlusV1 with satellite imagery from Google Earth™. We matched locations of dams from the NID with dam locations represented in Google Earth™ by conducting searches of reservoir or dam names and through visual verification based on Google Earth™ imagery to identify locations of dams in reference to the NHDPlusV1 stream network. Dams from the NID that fell directly onto the NHDPlusV1 stream network were linked to the appropriate spatial location. Dams from the NID that could not be associated with a location on the NHDPlusV1 stream network were not incorporated into the NABD database. This process resulted in 49,298 NID dams linked to the NHDPlusV1 that were used in this study from the NABD database. To ensure that large dams were not missing from the resulting dataset, dams greater than 7.62 m from the USFWS Fish Passage Decision Support System (USFWS, 2008) were checked against NABD dams. This process identified 170 dams that we added to NABD that were not included in the 2009 NID. The final dam data layer includes 49,468 dams linked to the NHDPlusV1 streams throughout the conterminous USA (Fig. 1).

2.1.2. Stream network dataset

The 1:100,000 scale National Hydrography Dataset Plus Version 1 (NHDPlusV1; USEPA and USGS, 2005) was the stream network used

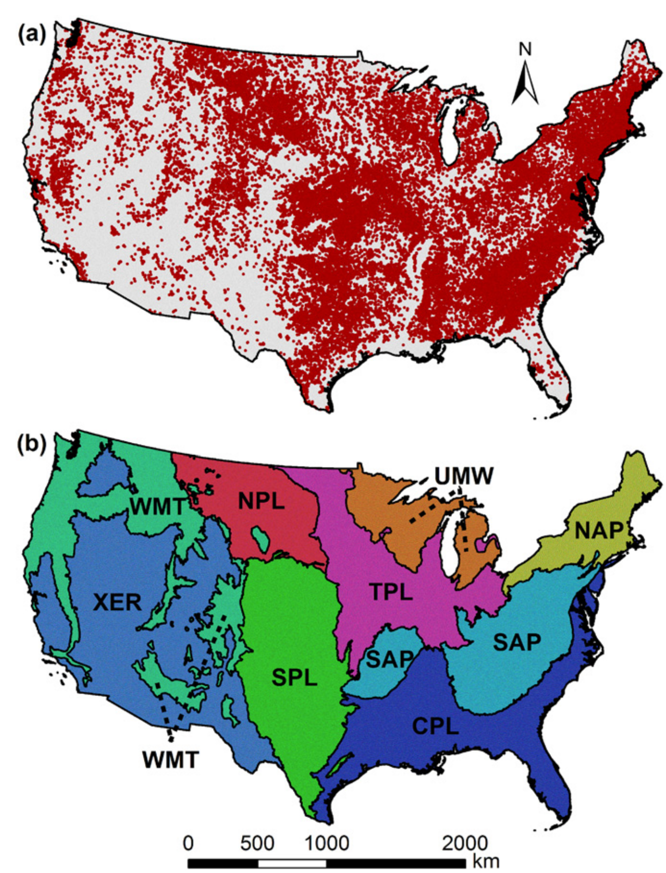

Fig. 1. Distribution of large dam locations (a; $n = 49{,}468$) and nine ecoregions (b) for the conterminous USA. Ecoregions include: Northern Appalachians (NAP), Southern Appalachians (SAP), Upper Midwest (UMW), Coastal Plains (CPL), Temperate Plains (TPL), Northern Plains (NPL), Southern Plains (SPL), Western Mountains (WMT), and Xeric (XER) (USEPA, 2006).

in this study. The NHDPlusV1 includes stream reaches, lake/reservoir polygons, and local catchment boundaries encompassing the land area draining directly to stream reaches. Stream reaches are defined as confluence-to-confluence stream sections, with confluences occurring at stream junctions, inlets/outlets of lakes and reservoirs, and terminal ocean or Great Lake outlets. Local catchment variables were summarized for the land area draining directly to a stream reach whereas network catchment variables were summarized for the entire upstream land area draining to a given reach, including a reach's local catchment (see Wang et al., 2011a).

2.1.3. Dam metric development and assessment

To facilitate generation of fragmentation and flow alteration measures, some modifications of the NHDPlusV1 were necessary. Dam locations were used to split stream reaches when dam locations did not already coincide with a reach junction in the NHDPlusV1 (Cooper, 2013). Using elevation data available with the NHDPlusV1 and the Watershed function in ArcGIS 9.3, stream reach catchments of the NHDPlusV1 were subdivided for dams that were located more than 100 m away from existing reach junctions, resulting in catchments corresponding to dam locations. The resulting database comprised approximately 2.3 million reaches reflecting hydrologic or dam-induced break points and their corresponding catchments for the conterminous USA.

Using a specialized program developed in Python (PSF; Beaverton, OR) that accounted for complex stream network configurations including braided stream reaches and loops, we quantified 21 dam metrics for 2.3 million stream reaches within the conterminous USA (Table 1) falling into four main categories:

Segment-based metrics (3)

Alterations to stream network accessibility and spatial arrangement of habitats can affect dispersal and population dynamics (Fausch et al., 2002; Campbell-Grant et al., 2007) or increase likelihood of species extirpation or extinction (Fagan, 2002). To account for this, we developed stream segments, defined as adjacent sets of stream reaches that are bounded by dams, representing fragmented subdivisions of both the stream network and its corresponding catchment (Fig. 2). In the simplest case, one dam within a stream network would result in two stream segments, with multiple dams located within a stream network (n) typically resulting in $n+1$ stream segments. Stream segment metrics include total stream length, mainstem length (specific to each segment), and catchment area as measures of stream network availability and size (Table 1).

Count and density metrics (9)

Previous studies have shown the number and density of dams located throughout river networks to be influential to stream fishes over large spatial extents (Wang et al., 2011b; Van Looy et al., 2014; Cooper et al., 2016), and we calculated count and density dam metrics to account for their cumulative influence (Table 1). We identified the total number of dams upstream of each stream reach located throughout the stream network and along the upstream mainstream flow path, with the upstream mainstem flow path being identified as the longest upstream pathway above each stream reach. Metrics developed with these data include count and density of upstream dams both along the mainstem and along all upstream paths. Similarly, we identified the number of dams along the downstream mainstem flow path, defined as the shortest pathway below each reach to the ocean, Great Lake, or terminal node in the stream network to create metrics including count and density of downstream mainstem dams for each reach in the dataset.

Distance-based metrics (6)

We calculated distances to the nearest upstream mainstem dam above each reach and downstream mainstem dam below each reach if present (Table 1). These distances were then used to generate total mainstem distance between dams, as well as the percentage of upstream, downstream, and total mainstem lengths free of dams for each stream reach. These metrics provide longitudinal measures of habitat availability, which can be critically important for certain fishes, particularly those that are migratory (potadromous, anadromous, etc.) or have reproductive strategies requiring long river mainstems (e.g., Perkin and Gido, 2011).

Cumulative reservoir storage metrics (3)

Stream flow alteration is known to greatly influence in-stream habitat and aquatic biota adapted to natural flow regimes (Poff et al., 1997; Bunn and Arthington, 2002). We calculated cumulative upstream reservoir storage volume above each reach and expressed it per unit network stream length, network catchment area, and as a percentage

Table 1
Descriptions of 21 dam metrics developed for the conterminous USA.

Category	Metric	Description	Units
Segment-based	STOT[a]	Total segment length	km
	SMST[a]	Segment mainstem length	km
	SCA[a]	Segment catchment area	km^2
Count and density	UMCT	Upstream mainstem dam count	#
	UMD	Upstream mainstem dam density per unit upstream mainstem length	#/100 km
	UNCT	Total upstream dam count	#
	UNDR[ab]	Upstream network dam density per unit stream network length	#/100 km
	UNDC	Upstream network dam density per unit network catchment area	$\#/km^2$
	DMCT	Downstream mainstem dam count	#
	DMD[b]	Downstream mainstem dam density per unit downstream mainstem length	#/100 km
	TMCT	Total mainstem dam count	#
	TMD	Total mainstem dam density per unit total mainstem length	#/100 km
Distance-based	UM2D	Distance to upstream mainstem dam	km
	UMO[b]	Percentage of open upstream mainstem	%
	DM2D[ab]	Distance to downstream mainstem dam	km
	DMO	Percentage of open downstream mainstem	%
	TM2D	Total mainstem distance between upstream and/or downstream mainstem dams	km
	TMO	Total percentage of open mainstem	%
Cumulative reservoir storage	USR	Upstream reservoir storage volume per unit stream network length[c]	ha-m/100 km
	USC	Upstream reservoir storage volume per unit stream network catchment area[c]	$ha\text{-}m/km^2$
	UDOR[ab]	Percentage of estimated annual discharge stored in upstream reservoirs[cd]	%

[a] Metrics used to describe stream fragmentation and flow alteration patterns.
[b] Metrics used in boosted regression tree models.
[c] Normal reservoir storage volumes taken from the National Anthropogenic Barrier Dataset (NABD).
[d] Annual discharge estimates from the National Hydrography Dataset Plus Version 1 (NHDPlusV1) unit runoff method (USEPA and USGS, 2005).
Dam metrics can be accessed from USGS ScienceBase at http://dx.doi.org/10.5066/F7FN14C5

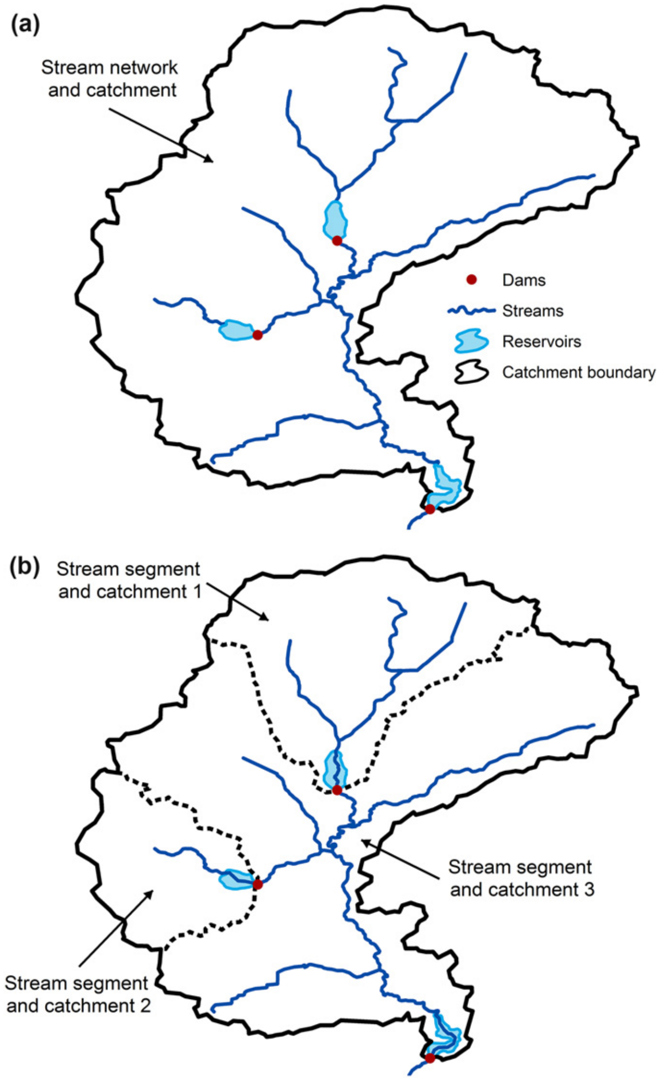

Fig. 2. An example stream network and catchment (a) compared to an alternative set of stream segments and catchments defined by the locations of dams (b). Dashed boundaries in (b) represent subdivisions of the example stream network and catchment in the development of stream segments corresponding to dam locations. Dams were identified as bounding individual stream segments in either the upstream or downstream direction, or in limited cases, were classified as internal to stream segments when alternative flow paths allowed for stream network connectivity around dams.

of estimated annual stream discharge volume (Table 1; hereafter referred to as "degree of regulation"; *sensu* Lehner et al., 2011), following similar assessments conducted at a global scale (Nilsson et al., 2005; Lehner et al., 2011). These metrics were viewed as a coarse approximation of flow alteration by dams, with higher values representing increased capacity for dams to alter the timing and magnitude of downstream flows (Lehner et al., 2011).

Based on previous analyses identifying 1) minimally redundant metrics, and 2) metrics associated with fish responses (Cooper et al., 2016), we chose a subset of six metrics to describe a diversity of dam influences from the four dam metric categories; segment-based, count and density, distance-based, and cumulative reservoir storage (Table 1). To better understand fragmentation and flow alteration nationally, we examined dam metrics by stream size and by ecoregions. Stream size strata were based on catchment area (A; Wang et al., 2011a) and comprised headwaters (HW; $A \le 10$ km^2), creeks (CR; $10 < A \le 100$ km^2), small rivers (SR; $100 < A \le 1{,}000$ km^2), medium rivers (MR; $1{,}000 < A \le 10{,}000$ km^2), large rivers (LR; $10{,}000 < A \le 25{,}000$ km^2), and great rivers (GR; $A > 25{,}000$ km^2). The nine ecoregions in this study were acquired from the U.S. Environmental Protection Agency's Wadeable Stream Assessment program, and have been utilized for continental-scale stream condition assessments (USEPA, 2006; Herlihy et al., 2008; Fig. 1). Ecoregions include: Northern Appalachians (NAP), Southern Appalachians (SAP), Upper Midwest (UMW), Coastal Plains (CPL), Temperate Plains (TPL), Northern Plains (NPL), Southern Plains (SPL), Western Mountains (WMT), and Xeric (XER). Dam metrics representing count and density, distance-based, and cumulative reservoir storage categories were mapped to display regional variability in dam influence patterns and stacked bar graphs showing the percent of stream length within metric classes were developed to describe differences in dam metrics by stream size. Segment-based metrics were compared to those from stream networks in the absence of dams to assess the extent that damming may have fragmented stream networks relative to pre-dam conditions.

2.2. Examining associations between dams and fish assemblages

2.2.1. Fish assemblage metrics

To evaluate the extent to which dams may influence fish assemblages, we assembled stream fish assemblage samples collected using comparable methods from state agencies, universities, and federal programs spanning 1990–2013 (Daniel et al., 2015). A total of 37,107 stream reaches across the conterminous USA had fish samples, from which 49 fish metrics describing taxa richness and relative abundances of functional traits (reproductive, trophic, and habitat preference; Frimpong and Angermeier, 2009), family-level taxonomic classification, and anthropogenic stress tolerance (Esselman et al., 2013; Daniel et al., 2015) were developed (Table A1). To account for regional differences in distributions of fishes and differences in sensitivities to environmental stressors, we conducted metric selection and subsequent analyses by ecoregion and stream size. Due to the distribution of samples across stream size classes, we aggregated samples into broader size classes that included creeks (includes creek and headwater size strata described above) and rivers (all larger size strata). Due to a lack of sufficient fish samples, analyses for the NPL ecoregion were not stratified by size. A subset of fish metrics were selected following an approach developed by Stoddard et al. (2008). This process identifies a subset of metrics that: 1) have enough variability in values among sites to indicate a wide range in possible states, 2) are temporally stable, 3) are responsive to anthropogenic stress gradients, and 4) are statistically independent from other metrics. This allowed for the selection of metrics that were both widely distributed by ecoregion and stream size class and were robust indicators of anthropogenic influences.

To identify fish metrics that were responsive to anthropogenic stress gradients we used t-tests (R 2.15, R Core Team). First, we identified metrics responsive to urban and agricultural land uses and mine densities (Table A2), using the 10th percentile and 90th percentile values to compare sites falling under low and high levels of each stress variable. Next, we tested for overall responsiveness to dams, following Esselman et al. (2013) by ranking each of the five selected dam metrics (Table 1), then averaging across metric rankings to produce an overall rank. We used 10th percentile and 90th percentile overall rank values to identify sites falling under low and high levels of fragmentation and flow alteration respectively. Directionality of t-test statistics were used to interpret overall response direction (positive or negative) to dam influences. Directionality was also used to facilitate interpretation of boosted regression tree analyses (described below). For all t-tests, metrics were deemed responsive at $p < 0.05$.

2.2.2. Accounting for spatial autocorrelation among fish assemblage sites

We tested for spatial autocorrelation among stream reaches with fish sample sites within U.S. Geological Survey six-digit hydrologic unit basins (HUC 6) using the Spatial Analysis in Macroecology program (SAM, Version 4.0; Rangel et al., 2010). We conducted a simultaneous autoregressive (SAR) analysis in SAM of latitude and longitude coordinates versus a set of natural stream features at sampling locations.

Natural variables included four network catchment variables (catchment area, groundwater index, mean annual air temperature, mean annual precipitation) and two local catchment variables (mean catchment slope and maximum catchment elevation) (Table A2). Use of latitude and longitude coordinates represents a conservative method for testing for spatial autocorrelation, as distances along stream networks would likely be longer than Euclidean distances between sample points, potentially resulting in less spatial autocorrelation. The resulting Moran's I values from the SAM procedure were graphed using correlograms and inspected for positive autocorrelation (Schabenberger and Gotway, 2005). In cases where positive autocorrelation was found among sample locations within a basin (Moran's I > 0.2), a set of eigenvector-based spatial filters were applied to remove as much autocorrelation among sample sites as possible.

2.2.3. Boosted regression tree model development

To identify associations between fish metrics and dam metrics, and to compare the influence of dams with natural and non-dam anthropogenic factors, we developed boosted regression tree (BRT) models. BRTs combine regression techniques with a machine learning approach, iteratively generating regression trees trained on the residuals of the previous tree until a minimum amount of predictive deviance is achieved (Elith et al., 2008). We identified natural and non-dam anthropogenic factors established in the literature as having strong influences on fluvial organisms (e.g., Allan, 2004) such as catchment area, precipitation, urbanization, and agriculture. BRT models were developed for each fish metric using 16 total variables split into three variable groups: natural ($n = 6$), non-dam anthropogenic ($n = 5$), and dam ($n = 5$; Tables 1 & A2). We quantified the total importance of the three major variable groups by summing the relative importance of all variables within each respective variable group and reported model deviance explained based on 10-fold cross validation. BRT learning rates were altered to produce a final model developed with a minimum of 1,000 trees using a tree complexity of 5 and a bag ratio of 0.5. BRT models were developed using R statistical software (R 2.15, R Core Team) with the 'gbm' package (see Elith et al., 2008).

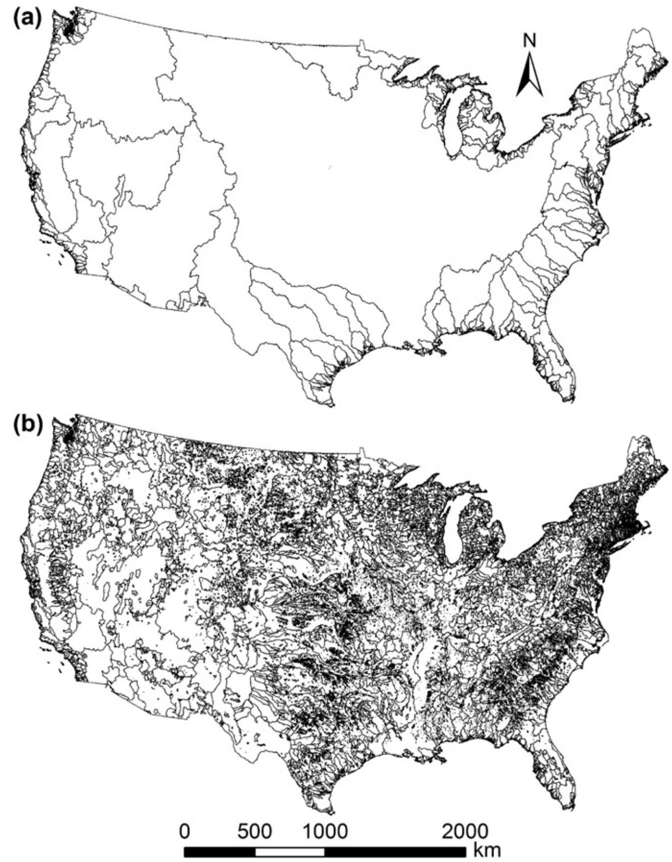

Fig. 3. Stream network catchment boundaries in the absence of dams (a; $n = 6{,}007$) and resulting stream segment catchments when accounting for dams (b, $n = 54{,}120$).

3. Results

3.1. Dam conditions for the conterminous USA

Comparison of catchment boundaries between stream segments fragmented by dams and stream networks in the absence of dams highlights the degree to which dams have fragmented streams as well as their catchments throughout the conterminous USA (Fig. 3). A total of 54,120 segments were identified using the stream network and NABD dam datasets compared to 6,007 connected stream networks that would exist in the absence of dams. This constitutes an increase of 801% in the number of stream segments when dams are present, with increases across different stream size strata ranging from 703% for small rivers to 1,188% for large rivers (Table 2). In comparing stream networks in the absence of dams and stream segments with dams, median total stream lengths and catchment areas of large and great rivers were an order of magnitude smaller due to damming (Table 2). For example, median total stream length decreased from ~28,000 km to ~2,400 km for great rivers when accounting for dams. Conversely, headwater and creek systems were the least affected according to all three segment-based size measures. In total, only 1.9% of overall stream length in the conterminous USA occurs within drainages that do not contain large dams, predominately coinciding with smaller coastal stream systems.

Examination of patterns in degree of regulation, distance to downstream mainstem dam, and upstream network dam density revealed distinct patterns for the conterminous USA. Degree of regulation (i.e., the percentage of annual stream flow volume stored in all upstream reservoirs) increased as a function of stream size, emphasizing the cumulative nature of reservoir storage throughout river networks (Fig. 4a). Rivers in the central and southwest USA (e.g., NPL, SPL, and XER ecoregions) were highly regulated (>100% or one year's annual flow volume), indicating substantial flow alteration from large dams in these regions. Degree of regulation was generally low in the eastern conterminous USA despite the high upstream network dam densities in the region. Distances from stream reaches to downstream mainstem dams indicated that more than 20% of streams in the conterminous USA were within 50 km of a downstream mainstem dam; this result was consistent across all size strata (Fig. 4b). Conversely, only 21% of stream length in the conterminous USA did not have an existing downstream mainstem dam, highlighting the massive degree (79% of total stream length) to which streams are disconnected from their outlets (i.e., oceans and Great Lakes). Upstream network dam densities increased with stream size, but small rivers had the greatest amount of length with the highest densities. Large areas of the eastern and south central USA (e.g., NAP, SAP, and SPL ecoregions) had high upstream network dam densities, while densities in the western USA (e.g., WMT) were comparatively low (Fig. 4c). The large variability in conditions across the conterminous USA among the degree of regulation, distance to downstream mainstem dam, and upstream network dam density metrics underscores the need for multiple metrics in assessing dams across large spatial extents. A diverse set of metrics can help describe each river's unique "dam profile" (Fig. 5), improving understanding of network-wide dam effects, highlighting the interplay between individual and cumulative dam influences and informing management actions and restoration opportunities pertaining to dams. Additional dam metric summaries along with a table containing main dam purpose by ecoregion and stream size are available in the supplemental file (Tables A3 & A4).

Table 2
Comparison of counts and median size characteristics between stream networks lacking dams (Network) and stream segments (Segment) by stream size stratum for the conterminous USA with percent increase (Inc.) or decrease (Dec.) in measures. HW = headwater, CR = creek, SR = small river, MR = medium river, and GR = great river.

	Count			Total length (km)			Catchment area (km^2)			Mainstem length (km)		
Stratum	Network	Segment	% Inc.	Network	Segment	% Dec.	Network	Segment	% Dec.	Network	Segment	% Dec.
HW	3,810	35,017	819	2.4	1.7	30	2.3	2.1	8	2.4	1.7	30
CR	1,535	13,280	765	15.3	11.8	23	23	17.9	22	6.4	4.4	31
SR	456	3,661	703	135	87.9	35	222	146	34	17.4	11	37
MR	147	1,531	941	1,362	350	74	2,207	691	69	56.8	20.9	63
LR	26	335	1,188	9,918	553	94	13,983	845	94	91.1	20.2	78
GR	33	296	797	28,049	2,445	91	42,016	3,562	92	282	71.2	75

3.2. Associations between dam metrics and fish community traits

The fish metric selection process resulted in between 2 and 5 metrics for each ecoregion/stream size class, with a combined total of 62 metrics evaluated (Table 3). The amount of deviation in fish metrics explained by BRT models ranged from 13.6 to 54.3% among metrics, with natural variables generally explaining the greatest amount of deviation (36.1–76.4%) compared to the dam metrics (8.2–45.1%) and non-dam

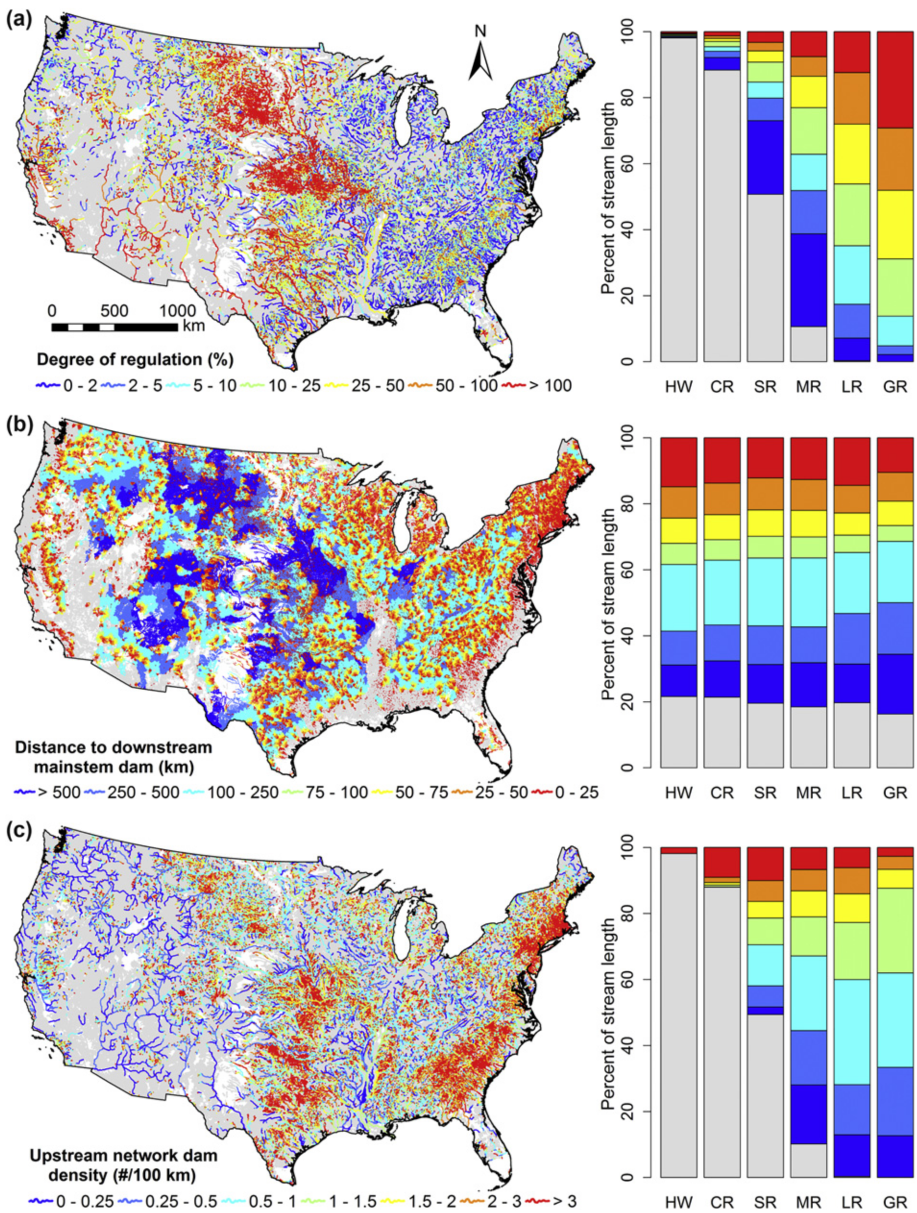

Fig. 4. Maps for three dam metrics; degree of regulation (a), distance to downstream mainstem dam (b), and upstream network dam density (c). Stacked bar graphs show percent of stream length within each class by stream size. Gray portions of maps and graphs represent regions not influenced by a given dam metric. Class breaks for degree of regulation were adapted from Lehner et al. (2011). Classes for distance to downstream mainstem dam and upstream network dam density were determined by maximizing variability across the conterminous USA. HW = headwaters, CR = creeks, SR = small rivers, MR = medium rivers, LR = large rivers, and GR = great rivers.

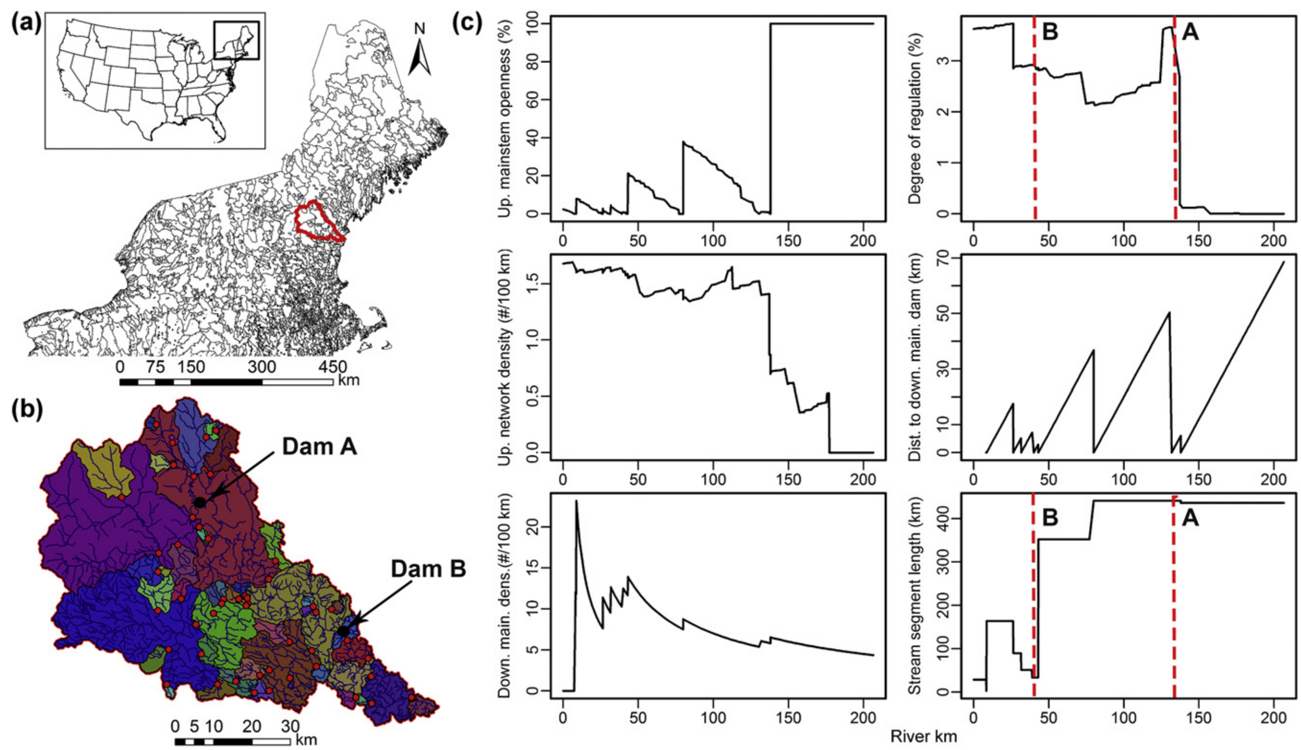

Fig. 5. The widespread availability of dam metrics allows for the investigation of dam influences at any specific scale or stream of interest. Here, an example "dam profile" is shown for the Saco River in Maine and New Hampshire, USA, a basin (a), containing 51 stream segments and their catchments (shown as colored regions in b). Graphs (c) show variation in dam metrics along the ~200 km Saco River mainstem, with river km 0 representing the river outlet. In this example, reservoir storage from Dam A results in a large increase in degree of regulation while not substantially altering stream segment length availability. In contrast, Dam B has minimal influence on degree of regulation while blocking connectivity to a large upstream segment. These differences can suggest differing management actions based on whole-basin dam conditions, such as stream flow remediation (Dam A) or stream connectivity improvements (Dam B).

anthropogenic variables (8.6–32.5%) (Table 3). For creeks, non-dam anthropogenic variables explained more deviation than dam influences for 15 of 26 fish metrics, while for rivers, dam influences explained more deviation than non-dam anthropogenic variables for 23 of 30 fish metrics. Similarly, dam influences explained more deviation in fish metrics for rivers than for creeks for 7 of 8 ecoregions when results were averaged by ecoregion (Fig. 6a), which also shows variation in influences of dams across ecoregions.

Examination of fish metric responsiveness to high levels of fragmentation and flow alteration revealed strong negative responses by intolerant, lithophilic (requiring gravel substrates for spawning), and rheophilic (preferring fast-flowing stream habitats) fishes and strong positive responses by fishes typically associated with impoundment habitats (e.g., lentic, nest guarders, centrarchid species) (Table 3). Variation also occurred within individual fish metrics. For instance, the lithophilic metric was negatively associated with dams, with amount of deviation explained by dam influences varying among ecoregions from 17.8 to 33.8% for the river size class (Fig. 6b). For this metric, there was much greater deviation explained in western and central ecoregions (e.g., WMT and SPL) compared to eastern ecoregions.

4. Discussion

This study showed the pervasive and complex influences of dams on connectivity and stream flows across a very large, heterogeneous region, the conterminous USA. Our evaluation of the dam metrics developed here suggests that certain ecoregions and stream sizes are more affected by dams than others. Further, dams have differential influences on fish communities, having both positive and negative associations with various fish assemblage traits through assessment of multiple dam metrics. Lastly, comparison of the effects of dams with other landscape disturbances indicates that dams can have as much or more influence on fishes than other major stressors, with this information being useful in prioritizing regions for management activities and research pertaining to dams at a national level.

4.1. Patterns in stream fragmentation and flow alteration across the conterminous USA

The differences in fragmentation and flow alteration patterns by stream size identified in this study have strong implications for fluvial habitat. Certain dam influences such as flow alteration and segment-based fragmentation tended to be greater in rivers than smaller creek systems according to our findings. This could perhaps be explained by the differing nature of dams in these systems such as dam purpose and operation (Poff and Hart, 2002). Further, while dams can have large localized influences in creeks, these influences can diminish rapidly when moving downstream through connections to adjoining, unregulated streams (e.g., McCluney et al., 2014). However, the cumulative nature of certain dam influences coupled with high levels of fragmentation found in many river mainstems could lead to greater dam influences in larger systems. The increase in degree of regulation with increasing stream size within ecoregions in this study is consistent with Lehner et al. (2011), who found a similar pattern of increase in a global study of reservoir storage by dams. Lehner et al. (2011) proposed that a 2% degree of regulation leads to flow impairment by dams. Based on that benchmark, 91% of large river reaches and 97% of great river reaches in the conterminous USA would be considered to be flow-impaired. Not only does flow modification alter physical habitats in riverine landscapes, flow modification also disrupts life history events of organisms triggered to flow events (e.g., spring floods; Poff et al., 1997). In addition, segment-based dam metrics demonstrate the extent

Table 3
Boosted regression tree (BRT) and dam responsiveness t-test results for individual fish trait metrics by ecoregion and size class. Dev. exp. = BRT model deviation explained, with Natural (natural variables), Non-dam (non-dam anthropogenic variables), and Dam (dam metrics) representing the percentage of deviance explained by variable grouping. Samples sizes are shown in parentheses for each stratum. Dam response directions based on t-tests are positive (P) or negative (N) with $^{*}p < 0.05$ and $^{**}p < 0.001$. na = not available. See Table A1 for fish trait metric descriptions.

Eco.	Size (samples)	Fish trait metric	Dev. exp. (%)	Natural (%)	Non-dam (%)	Dam (%)	Response
NAP	Creek (5,996)	GUARDER_TAXA	33.5	64.9	17.6	17.5	P**
		INTOL_REG_IND	44.6	75.7	8.6	15.6	N**
		LITH_TAXA	40.4	70.5	13.2	16.3	N**
	River (1,711)	INTOL_REG_IND	31.9	43.5	23.6	32.9	N*
		LENTIC_TAXA	42.5	39.4	24.7	35.9	P**
		LG_RIVER_TAXA	43.8	58.3	23.4	18.3	P*
		LITH_NAT_TAXA	45	48.6	21.2	30.3	N**
		PISC_INVERT_IND	28.5	49.9	21.9	28.2	P**
SAP	Creek (5,289)	INTOL_REG_TAXA	48.1	56.2	17.2	26.6	N**
		LENTIC_NAT_IND	29.5	55.4	23.6	20.9	P**
		LITH_TAXA	43.9	69.4	17.1	13.6	N**
		PERCID_TAXA	29.1	52.8	27.3	19.9	N**
		RHEO_NAT_TAXA	37.6	64	17.5	18.6	N*
	River (2,040)	DETRIT_TAXA	39.4	60.2	21.1	18.6	P*
		INTOL_REG_TAXA	54.3	53.8	20.7	25.4	N**
		PISC_TAXA	36.9	36.1	26.8	37.1	P**
		RHEO_NAT_TAXA	44	49.1	23.6	27.3	N**
UMW	Creek (2,736)	DETRIT_TAXA	24.7	50.6	30.4	18.9	P**
		PISC_INVERT_NAT_IND	19.3	56.7	23.5	19.8	N**
		SURF_FEED_TAXA	23.3	59.4	24.3	16.3	N**
		TOL_TAXA	14	54.5	25.8	19.8	P*
	River (1,460)	CENT_TAXA	34.1	49.4	20.2	30.4	P**
		INTOL_REG_TAXA	37.6	47.9	30.3	21.8	P**
		LITH_NAT_TAXA	33.7	45.8	25.5	28.7	N*
		PISC_NAT_IND	26	52.2	20	27.8	P*
CPL	Creek (1,813)	LENTIC_TAXA	52.9	76.4	15.4	8.2	P**
		PISC_NAT_IND	27.6	59.4	26.3	14.3	P*
	River (1,171)	INTOL_REG_TAXA	41.2	53.3	30.4	16.4	N*
		LENTIC_TAXA	50	59.9	26.9	13.2	P*
		LITH_NAT_IND	31.8	49.7	32.5	17.8	N*
TPL	Creek (4,053)	CENT_TAXA	26.9	55.4	21.1	23.5	P**
		DETRIT_NAT_TAXA	31.5	60	19.7	20.4	N**
		SPELEO_NAT_IND	17	56.3	23.9	19.7	N**
		TOL_TAXA	32.4	54.8	23.9	21.4	N**
	River (3,266)	BENTH_INVERT_NAT_TAXA	39.8	57.7	18.4	23.9	N**
		CENT_TAXA	39.5	54.3	20.8	24.8	P**
		LITH_TAXA	49.1	57.3	15.8	26.9	N*
		RHEO_NAT_TAXA	46.5	59.5	19.2	21.3	N**
NPL	na (286)	DETRIT_NAT_TAXA	29.6	59.4	20.1	20.5	P**
		GUARDER_NAT_TAXA	13.6	50.2	23.6	26.2	P*
		INVERT_NAT_IND	28.7	66.6	12.9	20.5	P*
		LITH_TAXA	28.1	50.2	18.5	31.3	N**
		RHEO_IND	25.3	57.7	21.5	20.8	N*
		TOL_TAXA	39	65.2	17	17.8	P*
SPL	Creek (623)	BENTH_INVERT_NAT_TAXA	15.7	58.2	21.9	19.9	N**
		LITH_NAT_IND	33.3	60.5	22.3	17.2	N**
		TOL_IND	28.7	42.5	12.4	45.1	N**
	River (1,819)	BENTH_INVERT_NAT_TAXA	34.1	44.8	14.6	40.6	N**
		LENTIC_IND	32	42.1	27	30.9	P**
		LITH_NAT_IND	51.2	52.4	18.2	29.4	N**
		TOL_IND	38.5	45.9	22.6	31.5	N**
WMT	Creek (2,437)	LITH_TAXA	28.3	57	16.9	26	P*
		RHEO_NAT_IND	36.4	50.2	15.6	34.2	N**
	River (1,101)	INTOL_TAXA	35.9	46	27.8	26.2	N**
		RHEO_NAT_IND	36.8	48.4	22.7	28.9	N**
XER	Creek (460)	HERB_NAT_IND	31.9	50.5	21.1	28.4	P*
		INTOL_REG_TAXA	31.4	60.8	20	19.2	N*
		LITH_TAXA	16.1	54.6	22.6	22.7	N*
	River (846)	HERB_NAT_IND	29.3	45	21.8	33.2	P**
		INTOL_REG_TAXA	47.2	44.5	24.9	30.6	N**
		LITH_TAXA	50.4	41.1	25	33.8	N**
		RHEO_TAXA	52.4	49.5	22.8	27.7	N*

to which larger rivers have been fragmented by dams, resulting in habitat availability that is an order of magnitude smaller in some cases. This emphasizes the importance of considering dams as a landscape-scale disturbance, as dams can act synergistically to affect both flow and connectivity within stream networks.

4.2. Patterns in fish assemblage responses to dams

The study of fish assemblage traits provides a good means to investigate broad-scale patterns in responses to environmental change (Olden et al., 2010; Lima et al., 2016). We found that certain traits

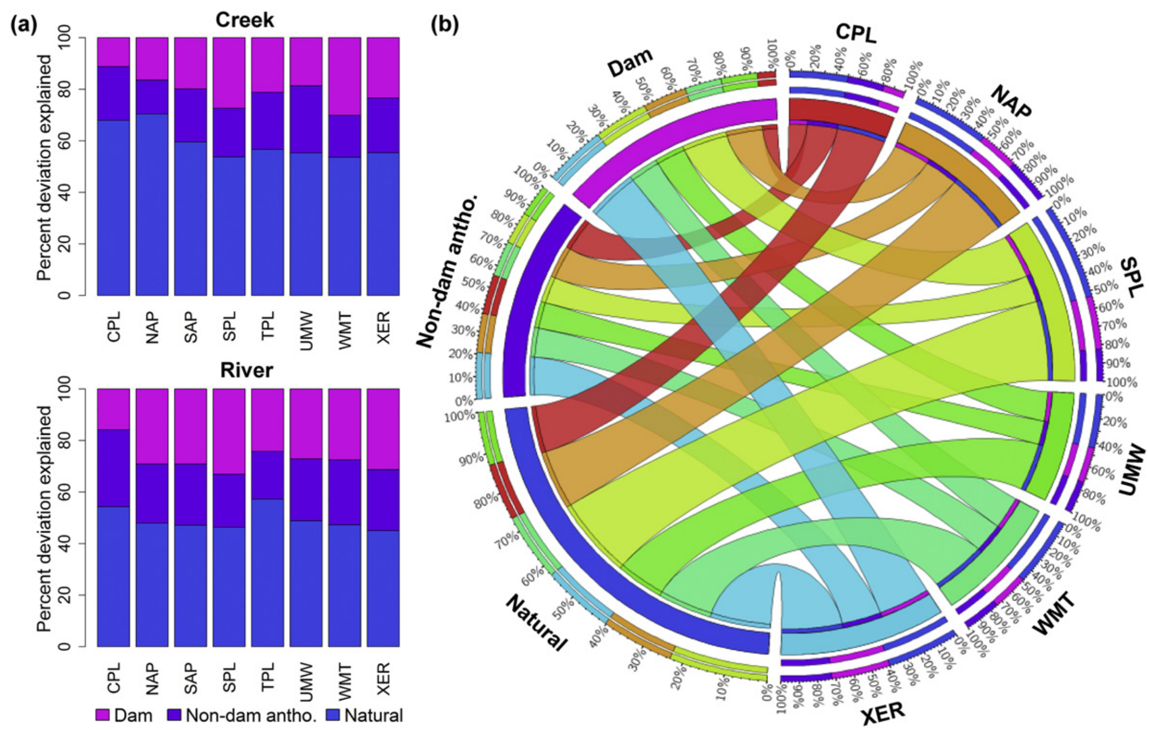

Fig. 6. Deviation explained in boosted regression tree (BRT) models for dam, non-dam anthropogenic, and natural variable groups averaged for each ecoregion/size stratum (a) and for the lithophilic trait metric in rivers (b), a fish metric exhibiting consistent negative associations with dams. Thickness of inner "ribbons" and length of outer ring segments in (b) are proportional to the amount of deviation explained by variable groupings in individual BRT models, while length of inner ring segments are proportional to total model deviation explained (created using Circos software; http://circos.ca/). Ecoregions include: Northern Appalachians (NAP), Southern Appalachians (SAP), Upper Midwest (UMW), Coastal Plains (CPL), Temperate Plains (TPL), Northern Plains (NPL), Southern Plains (SPL), Western Mountains (WMT), and Xeric (XER). See Fig. 1 for ecoregion locations.

were consistently positively (e.g., lentic) or negatively (e.g., rheophilic/lithophilic) associated with dams, and that these relationships existed largely irrespective of ecoregion and stream size. These could be considered candidate traits used for biomonitoring and assessment (Olden et al., 2010), and specifically in this case, for understanding dam effects more broadly. Fish metrics that can be associated with impoundment environments responded positively to dams, a pattern that could be a result of widespread upstream inundation by reservoirs combined with downstream alteration of the flow regime and geomorphology by dams (Poff et al., 1997). Fish metrics linked to fast-flowing and gravel bottom spawning habitats responded negatively. Van Looy et al. (2014) found a similar negative relationship between multiple dam metrics and both rheophilic and lithophilic fishes for the Loire River, France. Intolerant fishes were also negatively affected, indicating a sensitivity of these fishes to dams in addition to other anthropogenic stressors. For certain fish metrics, fragmentation and flow alteration from dams were as much or more influential than other stressors combined, particularly in larger stream systems. In these cases it is important to consider dam effects in addition to other stressors when assessing condition and restoration opportunities.

Previous studies have demonstrated that anthropogenic stress sources can affect fish differently depending upon the region in which they occur (e.g., Esselman et al., 2013; Daniel et al., 2015). Sabo et al. (2010) found distinct differences in dam density and storage east and west of the 100th meridian (splitting the conterminous USA roughly in half), relating these differences to a higher ratio of non-native to native fish species in the west. We also found regional differences in overall fish assemblage responses to dams, however this is likely reflecting the strong intra-regional variation in dam influences within eastern and western ecoregions. For instance, western regions of the conterminous USA have much lower dam densities and longer distances-to-dams, however degree of regulation is very high. Conversely, in the eastern USA dam densities are greater with comparatively short distances-to-dams and degree of regulation tends to be lower. As a result of this variability, selecting a diverse set of dam metrics that capture a variety of regionally important influences will be vital in representing a range of possible dam effects. Understanding these differences can inform regional management of dams in support of stream biodiversity maintenance (e.g., Poff et al., 2010). For instance, habitat availability in large tributaries plays a crucial role in the maintenance of biodiversity of large river fishes of the Mississippi River (Pracheil et al., 2013), suggesting management actions for dams that increase connectivity to the river's tributaries.

4.3. Implications for stream restoration and dam siting

Dams have limited life spans due to sediment accumulation that restricts water storage capabilities and a physical infrastructure that weakens over time (Poff and Hart, 2002). With an aging set of dams in the conterminous USA (nearly 75% of dams evaluated in this study will be at least 50 years old by 2020), managers will be increasingly confronted with decisions on whether to remove a dam or cope with continued repairs and maintenance. While dam removal decisions can rely heavily on safety and economic considerations (Doyle et al., 2008), the dam metrics presented here can offer an ecological component to the decision-making process by identifying reconnections among habitats or known source populations. For example, a study by Perkin et al. (2015) utilized the segments developed in this study to evaluate the combined influences of fragmentation by dams and stream desiccation due to water extraction on fish community structure in large rivers of the Great Plains. The authors found that rivers with lower fragmentation and less desiccation tended to contain more diverse communities that were dominated by species in the pelagic reproductive guild, while high levels of fragmentation and frequent desiccation resulted in less diverse communities dominated by species in the benthic reproductive guild. Considering dams and other forms of human disturbance to river networks simultaneously could aid in achieving restoration objectives by identifying connections between higher quality, relatively undisturbed habitats, as restoration projects are at risk of failure if the full scope of human-induced changes to river systems are not considered (Palmer et al., 2005).

From an ecological standpoint, the restoration of stream network connectivity is a key motivation for dam removal (Bednarek, 2001), emphasizing the need for a spatial accounting of stream fragmentation and dam influences in the context of other human disturbances across large regions and at multiple scales. When considering these restoration opportunities, moving beyond a simple determination of the amount of river network that will be reconnected and instead evaluating their overall condition will allow for the identification of reconnections between higher quality habitats. For instance, fragmentation and flow alteration metrics could be coupled with land use alteration or climate change projections to identify least-disturbed stream habitats (e.g., Roberts et al., 2013) or used to identify dams that prevent the establishment of non-native species by limiting their dispersal (e.g., Fausch et al., 2009). Similarly, these dam metrics can be incorporated into studies assessing the effects of multiple anthropogenic stressors on stream fishes, informing the prioritization of restoration actions (Schinegger et al., 2016). In certain regions of the world, dam building has increased to meet growing demands for water or hydro-powered energy (Ficke et al., 2007; Winemiller et al., 2016). Accounting for the cumulative impacts of dams would help in siting new dams (Winemiller et al., 2016), as locations could be identified to reduce alteration of physical habitat and disruption of ecological processes (Selinger et al., 2016).

4.4. Biases and limitations

Despite the high degree of fragmentation suggested in this study, only large dams were considered. There are ostensibly millions of other anthropogenic barriers in the conterminous USA (e.g., Graf, 1993, Poff and Hart, 2002), including smaller dams and culverts. Development of a holistic barrier dataset that accounts for these additional barriers (e.g., Januchowski-Hartley et al., 2013) would provide a broader view of fragmentation conditions in the conterminous USA, likely yielding much higher levels of fragmentation than described in the current study. While the measures presented here account for longitudinal dam influences within the riverine landscape, other dam influences exist such as decreased lateral connections with floodplains and hyporheic zones (Bunn and Arthington, 2002). Further, the reservoir storage metrics developed here represent coarse surrogates of flow alteration. We currently lack information on dam management schemes (amount and timing of reservoir releases) at the scale of this study, preventing more detailed evaluation of flow regime alteration. Future representation of these additional aspects would provide a greater accounting of the roles of dams in altering riverine landscapes.

5. Conclusions

Development of multiple dam metrics in this study has provided new insights on the influences of dams on streams in the conterminous USA, demonstrating that large dams have fundamentally changed streams by altering the continuum of flow and connectivity within these systems. Further, dams also have differential effects on fish assemblage traits, and have the potential to influence fish assemblages as much or more than other anthropogenic stressors. This assessment of localized- and landscape-scale stresses from dams for all stream reaches in a very large region provides unprecedented information to conserve and protect stream habitats from dams and to aid in restoration and management decisions at local, regional, and national scales. The approaches developed and lessons learned in evaluating dam-induced stream fragmentation and flow alteration patterns in this study can be used as a guide in conducting similar assessments in other regions of the globe.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2017.02.067. The dam metrics developed for this study are available from USGS ScienceBase at http://dx.doi.org/10.5066/F7FN14C5.

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