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Impacts of Dams on Fish Species Assemblage and Functional Trait Composition Within Two Alabama Drainages

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ABSTRACT

Modifications to flow regimes may substantially alter the structure and function of aquatic systems and biotic assemblages. We assessed the impacts of relatively large dams in Alabama, USA, on fish assemblages and functional trait composition at two scales—within one drainage (Bear Creek, BCD) and between two drainages (BCD and Cahaba River, CRD). We collected fishes in shallow waters (< 1 m) of lotic sections of three impounded and two unimpounded streams. Impoundment effects were similar at both scales. Assemblage structure differed up- and downstream of impoundments, but few differences were detected between unimpounded stream sections. Additionally, there were few functional trait composition differences between up- and downstream sections of impounded or unimpounded streams. However, we detected numerous functional trait composition differences between impounded and unimpounded streams, indicating that ecosystem functions may differ in each stream type due to differences in fish functional traits. Fish assemblage and functional trait variations were best explained by the percent cover of aquatic vegetation, temperature, and discharge variation. Fish species that preferred slow-moving waters were indicators of impounded streams, and species that preferred high percentages of vegetation were indicators of unimpounded streams. Species sensitive to habitat degradation, such as leuciscids and percids, were less common, and more tolerant species, such as centrarchids, were more common in the current study than in historical surveys from the 1960s and 2000s. Although we detected assemblage differences by taxa between impounded and unimpounded streams, functional trait composition may give an operational understanding of assemblage changes, allowing managers to target functional groups for conservation efforts, as well as providing a metric that can be applied to other systems.

1 | Introduction

Flow regimes influence the structure and function of aquatic ecosystems, affecting water quality, energy resources, physical habitat, and biotic assemblage composition and interactions (Vannote et al. 1980; Poff et al. 1997). Thus, modifications to flow regimes may substantially impact aquatic biodiversity by altering habitats, fragmenting populations, and altering food sources (Dudgeon 2000; Vörösmarty et al. 2010; Barnett et al. 2020, 2023). Dams and impoundments are one of the most severe and widespread anthropogenic alterations to lotic systems worldwide (Graf 1999; Sayer et al. 2025). Dams and impoundments alter a river's hydrological and temperature regimes, water chemistry, channel geomorphology, habitat

structure (e.g., substrate, woody debris, and vegetation), and floodplain connectivity (Ward 1976; Baxter 1977; Bunn and Arthington 2002; Graf 2006; Helms et al. 2011; Chu et al. 2015; Barnett et al. 2023).

How a dam is managed determines its effects on the flow regime. For example, flood control impoundments stabilize flows, whereas hydroelectric impoundments create more erratic flows. Fish assemblages dependent upon the flow regime are impacted differently by different types of dam management (Bunn and Arthington 2002; Lima et al. 2017; Arantes et al. 2019). Increased flow stability has reduced fish diversity, driven primarily by decreases in lotic taxa, while shifting resource use from benthic toward pelagic nutrients (Bunn and Arthington 2002; Gido et al. 2009; Freedman et al. 2014; Dunn et al. 2024). Flow stabilization has also decreased fish functional diversity, with decreases in species with traits that favor hydrological variation and increases in sedentary species (Pereira et al. 2021). Dams that increase hydrological variability downstream often favor fishes with generalized feeding strategies (Poff and Allan 1995; Bunn and Arthington 2002; Arantes et al. 2019) and cause shifts in fish assemblage structure due to catastrophic downstream drift of macroinvertebrate food sources during peak flow events. Erratic flows can also modify the quality and quantity of habitat available, often stranding fishes in off-channel habitats during rapid flow decreases (Young et al. 2011). Additionally, changes in overall flow variability uncouple the hydrological regime from the seasonal flow patterns with which fish life histories coevolved (Mims and Olden 2012, 2013). Moreover, regional species pools, land use, invasive species, and other disturbances can influence the changes in fish assemblages that result from dams and impoundments (Harding et al. 1998; Johnson et al. 2008; Hubbell et al. 2020; Faucheux et al. 2023).

The southeastern United States (US) is a global hotspot for fish biodiversity, supporting approximately 80% of freshwater fish species in the US and Canada (Jelks et al. 2008; Elkins et al. 2019). Nonetheless, freshwater fishes in this region have been threatened due to the disruption of natural flow regimes and degradation of habitats by dams and impoundments (Dudgeon 2000; Bunn and Arthington 2002; Johnson et al. 2008; Sayer et al. 2025). There are over 17,000 dams in the southeastern US (Graf 1999; NID 2013) impounding streams with varying species pools and stream habitat conditions. Understanding how fish assemblages are impacted by impoundments and what interacting environmental factors may be driving these changes is key to conserving fish diversity within this region. A consistent picture of the impacts of large dams on fish assemblages (Ruhr 1957; Phillips and Johnston 2004a, 2004b; Knothe et al. 2022; Faucheux et al. 2023) and functional traits (Helms et al. 2011; Keck et al. 2014) in the southeastern US is lacking, with some studies finding no assemblage differences up- and downstream of impoundments but others finding differences. Thus, there remains a need for detailed assessments of the impacts of large dams on fishes.

We assessed the effects of relatively large dams on fish species assemblage and functional trait composition in southern Appalachian, Alabama, streams. We compared fish assemblages in up- and downstream sections of impounded and unimpounded streams within and between (two Hydrologic Unit Code [HUC] Level 8) drainages. We addressed four questions (Table 1): (1) Do fish species assemblage and functional trait composition differ between up- and downstream sections of impounded and unimpounded streams and between drainages? (2) Do differences in stream habitat characteristics between impounded and unimpounded streams correlate with differences in fish species assemblage and functional trait composition? (3) Are any fish species strong indicators of up- or downstream sections of impounded or unimpounded streams? (4) Are any fish functional traits strong indicators of up- or downstream sections of impounded or unimpounded streams?

2 | Methods

To assess the effects of large dams (> 15 m height; ICOLD 2011) on the assemblage structure of fishes, we conducted a field survey at two scales in three impounded and two unimpounded streams in the Bear Creek (BCD; Tennessee River Basin) and Cahaba River drainages (CRD; Mobile River Basin) in Alabama (Barnett et al. 2022, 2023). During Year 1 of the study (spring and fall 2015), we assessed within-drainage effects of impoundments on fish assemblages in the BCD. In Year 2 (fall 2016 and spring 2017), we assessed whether impoundment effects were consistent between the BCD and CRD.

2.1 | Study Area

We sampled lotic sections of five streams in the BCD and CRD in the southern Appalachian Mountains of Alabama (Figure 1, see Barnett et al. (2022) for details). Two streams were unimpounded: one in the BCD (Rock Creek [233 km^2 drainage area]) and one in the CRD (Shades Creek [287 km^2 drainage area]). Three streams were impounded by earthen storage dams (17–29 m high), creating reservoirs with surface areas of 425–1700 ha (Appendix S1). Two impounded streams (Little Bear [235 km^2 drainage area] and Cedar [517 km^2 drainage area] creeks) were in the BCD, and one (Little Cahaba River [126 km^2 drainage area]) was in the CRD. The BCD impoundments were flood-control impoundments, and the CRD impoundment stored water for municipal use. All impoundments released water from more than 10 m below full pool levels (see Barnett et al. 2022 for details). Dams in both drainages passed normal inflows via spillways throughout the year. In the BCD, one large impoundment (Pickwick Lake) was located 37, 65, and 68 km downstream of our downstream-most sample sites in Rock, Little Bear, and Cedar creeks, respectively. There was no large impoundment downstream of the CRD streams. Land use in BCD was dominated by forest (80%) and agriculture (12%), while land use in CRD was dominated by forest (69%) and developed lands (22%) (Barnett et al. 2023).

We sampled one unimpounded (Rock Creek) and two impounded (Little Bear and Cedar creeks) streams in the BCD ($N = 24$ sites) during Year 1 of the study. We sampled two unimpounded (BCD—Rock Creek; CRD—Shades Creek) and two impounded streams (BCD—Little Bear Creek; CRD—Little Cahaba River) during Year 2 of the study ($N = 30$ sites). We selected Little Bear Creek to represent BCD impounded streams because its dam and impoundment were most similar

TABLE 1 | Research questions, statistical analyses, and expected results (numbered sequentially with superscripts).

Research question	Statistical analyses	Expected result if impoundments impacted fish assemblages
Question 1: Do fish species assemblage and functional trait composition differ between up- and downstream sections of impounded and unimpounded streams and between drainages?	PERMANOVA	[1]Fish species assemblage and functional trait composition will differ between impounded and unimpounded streams. [2]Fish species assemblages and functional trait composition will differ between up- and downstream sections of impounded streams but not between unimpounded stream sections.
Question 2: Do differences in stream habitat characteristics between impounded and unimpounded streams correlate with differences in fish species assemblages and functional trait composition?	Distance-based linear models	[3]Environmental variables that discriminate between impounded and unimpounded streams will also explain fish assemblage differences between stream types and stream sections.
Question 3: Are any fish species strong indicators of up- or downstream sections of impounded or unimpounded streams?	Indicator value analyses	[4]Certain fish species will be associated only with sections upstream of impoundments, downstream of impoundments, or in unimpounded streams.
Question 4: Are any fish traits strong indicators of up- or downstream sections of impounded or unimpounded streams?	Fourth corner analyses	[5]Fish traits associated with lentic environments will be indicators of impounded streams.

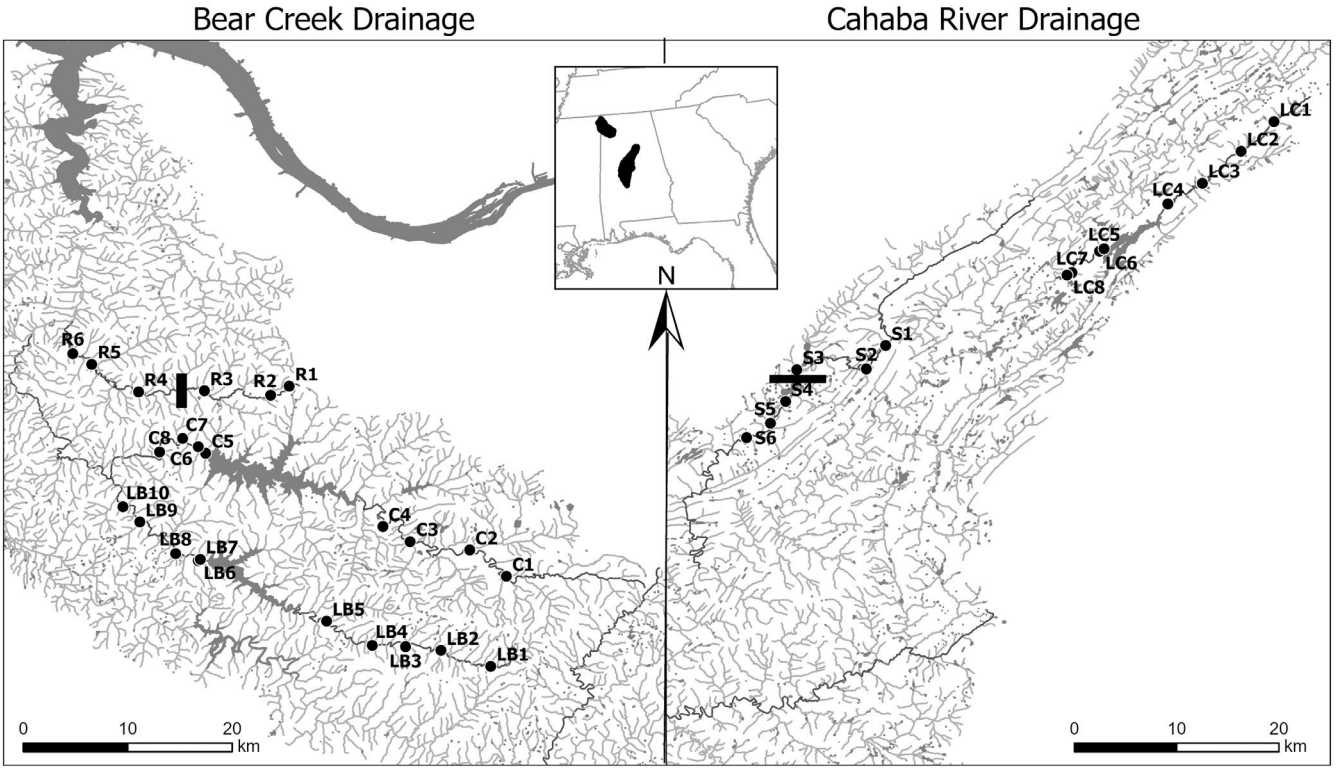

FIGURE 1 | Map of Bear Creek and Cahaba River drainages, Alabama, USA, with collection sites represented by filled circles. Sites are numbered in ascending order from up- to downstream, with letters representing stream names (R = Rock Creek, C = Cedar Creek, LB = Little Bear Creek, S = Shades Creek, and LC = Little Cahaba River). Shaded polygons along Cedar Creek, Little Bear Creek, and Little Cahaba River represent impoundments. Black bars crossing Rock and Shades creeks delineate the midpoint between each unimpounded stream's up- and downstream sections. Inset shows drainage locations within the southeastern USA, with the Bear Creek drainage in the northwest corner and the Cahaba River drainage in the center of Alabama.

in size to those in the Little Cahaba River. We assessed impounded streams in separate sections up- and downstream of impoundments (hereafter, "up- and downstream sections"). In each section, we selected four to five sample sites at set intervals, based on stream distance up- and downstream of impoundments (Barnett et al. 2022). All sites upstream of impoundments were in flowing sections, and the above areas were physically altered by the impoundment. In unimpounded streams, we mimicked those site distributions, using distance from the stream's longitudinal midpoint, but sampled only three sites per section (Figure 1).

2.2 | Fish Collections

At each site, we sampled fishes in a linear reach 30 times the wetted stream width (min = 200 m; max = 500 m; Schaefer et al. 2012). We split each sampling reach into two contiguous subreaches, and two crews simultaneously collected fishes by single-pass electrofishing (3–8 s/m; mean 5 s/m ± 1.2 SD) in the upstream subreach and kick seining (20 plots/100 m, 2 m long × 1.5 m wide) in the downstream subreach (see Barnett et al. 2021). Data from the two subreaches were combined for each site for analyses (see Section 2.5). Because kick seining creates high turbidity and can reduce the visibility needed to collect fishes while electrofishing, we always kick seined downstream of electrofishing subreaches. Because these methods are ineffective in deeper water, we sampled only in depths less than 1 m (≥ 85% of each reach). We determined the target number of kick seines and electrofishing duration based on subreach areas, and stopped sampling once we reached the target sampling effort (Barnett et al. 2021). We recorded the area (m^2) sampled by each method and the species of all fishes captured. We preserved voucher specimens in 10% formalin.

2.3 | Fish Functional Traits

We assigned various ecological and life-history traits to each fish species, per the FishTraits database (Frimpong and Angermeier 2009), as potential indicators of disturbance associated with dams and impoundments. For fish species whose taxonomy has changed, trait information from the past taxonomy was used. We used 23 traits for each species (Appendix S2). These traits included information on: (1) trophic ecology; (2) body size and reproductive ecology; (3) habitat preferences; and (4) temperature tolerances. The FishTraits database provides the mean functional trait value for traits of each species.

2.4 | Environmental Data Collection

Water quality and stream habitat characteristics (i.e., channel characteristics and stream bed composition) (Appendices S3 and S4) were measured during each sampling event. We measured water quality variables (water temperature, conductivity, dissolved oxygen [DO], and pH) with a Hydrolab Quanta (HACH-Hydrolab, Loveland, CO) at one location in each site before sampling fishes. Channel characteristics (wetted width [m], depth [cm], and canopy cover [%]) were measured at four transects that were evenly spaced within the reach. We measured stream depth mid-channel and 10 cm away from the right and left edges. Canopy cover was measured mid-channel with a convex spherical densiometer. We used Wolman pebble count procedures (Wolman 1954; Barnett et al. 2023) to analyze streambed composition across the bankfull channel width. We sampled 10 zig-zag transects, with 10 points from one bank to the other, at each site (100 sampling points/site). At each sampling point, we blindly selected one particle and one piece of woody debris (if present) and measured the maximum dimension (mm) of the particle and the maximum diameter of the woody debris (Bain and Stevenson 1999). Between adjacent sampling points, we visually estimated the percentage of vegetation and small woody debris (SWD, < 10 cm diameter) cover and counted pieces of large woody debris (LWD ≥ 10 cm diameter) (Bain and Stevenson 1999).

We recorded hourly water temperatures with iButton data loggers (Maxim Integrated, San Jose, CA) at each site in the BCD starting in fall 2015 and in the CRD starting in spring 2016, until the completion of the study (details in Barnett et al. 2023). We calculated stream temperature metrics (i.e., temperature variation and mean, max, and minimum water temperatures by season) from hourly data (Appendix S3).

To characterize stream hydrology, during each sampling period, we calculated stream discharge (m^3/s) using the transect method (Harrelson et al. 1994) with a Marsh-McBirney Flo-Mate 2000 and topsetting rod (Hach, Loveland, CO). At each site, we calculated discharge at one transect, taking at least 25 measurements. Using this discharge data, we regressed calculated discharge on distance downstream for up- and downstream sections separately. Using these relationships, we calculated hourly discharges at each site from hourly US Geological Survey (USGS) and Tennessee Valley Authority (TVA) discharge data from one site on unimpounded streams and one site up- and downstream on impounded streams (Appendix S1; Barnett et al. 2023). Because there was no gauge on Rock Creek, we estimated discharge from Cedar Creek impoundment inflow data, due to their close proximity to each other (see Barnett et al. 2023 for details). With these data, we calculated hydrology variables for each season (Appendix S3): maximum discharge, minimum discharge, coefficient of variation (discharge variation); Richard-Baker flashiness index (flashiness; Baker et al. 2004); calendar day with greatest discharge (peak flow day); and number of days with no flow (days zero flow). For clarity, days zero flow do not equal the number of days a stream was dry. Stream drying was not calculated. Discharges were likely underestimated because we did not account for tributary contributions. Discharge data from TVA were unavailable during Year 1 of the study; thus, discharge measurements were only calculated during Year 2.

2.5 | Data Analyses

Our research questions addressed the effects of impoundments on fish species assemblages and functional trait composition (Table 1) at two scales: within one drainage (Bear Creek, BCD) and between two drainages (BCD and Cahaba River, CRD), to assess whether the effects of impoundments in one drainage could be generalized across drainages. To test for differences in fish assemblages between up- and downstream sections of impounded and unimpounded streams, we based our analyses on

a multivariate split-plot design structure. Streams were whole-plot factors, and stream sections up- or downstream of dams or of stream midpoints were sub-plot factors. For all assemblage structure analyses, electrofishing and kick-seining data were characterized as number of fishes collected/100 m^2 and were summed, representing fish relative density at each site. For multivariate models, dispersion did not vary among groups.

2.5.1 | Species Assemblage Comparisons

To test if fish assemblage structure (i.e., relative densities of each species) differed between impounded and unimpounded streams and between up- and downstream sections of streams, we compared assemblage structures among Years 1 and 2 data sets separately using PERMANOVAs (Table 1: Question 1). We constructed models for each year's comparisons and square-root transformed relative densities to reduce the contribution of highly abundant species in the analyses (Anderson et al. 2008). We calculated Bray–Curtis similarity matrices comparing assemblage structures between each pair of sites. For within-drainage comparisons (Year 1), we used PERMANOVAs to test responses of assemblage structures to stream, stream section (up-/downstream), and season (spring/fall), with stream section nested in stream. Because there was only one unimpounded stream assessed in within-drainage comparisons, we did not include stream type (impounded/unimpounded) as a factor. Instead, each stream was treated as a factor, and post hoc pairwise comparisons were then used to assess which streams differed. PERMANOVA models included two-way interactions of stream with stream section and season, as well as three-way interactions with all factors. For between-drainage comparisons (Year 2), BCD and CRD were assessed together. We used PERMANOVAs to test responses of assemblage structures to stream type, drainage (BCD/CRD), stream section, and season, with stream section nested in stream type and stream type nested in drainage. By including drainage as an explanatory variable, we can account for impoundment effects on fish assemblages both between- and within-drainages. In addition, by nesting stream type in drainage, we are informing the model that the fish assemblage of impounded and unimpounded streams in one drainage is unique to that drainage. Thus, the variability among fish assemblages in each drainage's streams is accounted for and assessed in the model. PERMANOVA models included two-way interactions of stream type with season, stream section, and drainage, as well as three- and four-way interactions with all factors. Because we were only interested in assemblage structure differences between stream types and sections, we did not interpret the main effects of season or drainage. Sampling site was a random effect in our models to account for repeated samples at each site, allowing for intercepts to vary among sites. We used pairwise PERMANOVAs to obtain p-values for significant ($p \leq 0.05$) interactive effects. We conducted 2-dimensional non-metric multidimensional scaling (NMDS; Clarke 1993) to visualize differences in assemblage structures identified by PERMANOVA. All data were assessed using the PERMANOVA add-on (Anderson et al. 2008) in PRIMER, with 9999 permutations of residuals in both the main tests and post hoc comparisons. All highly correlated ($r > 30\%$) species were visualized on NMDS plots.

2.5.2 | Functional Trait Comparisons

To test if fish functional trait composition differed between impounded and unimpounded streams and between up- and downstream sections of streams (Table 1: Question 1), we used PERMANOVAs to compare fish trait composition using their community weighted means (CWM) (Lavorel et al. 2008), analyzing Years 1 and 2 data sets separately (Table 1: Question 1). The CWM is based on the mass-ratio hypothesis, which states that numerically dominant species are expected to have the largest impact on the structure and function of communities (Grime 1998; Garnier et al. 2004). Changes in CWM trait composition indicate that the community structure has shifted, often due to environmental changes (Mouillot et al. 2013). Thus, CWM trait composition is a useful detector of changes in community structure based on underlying species dynamics (Ricotta and Moretti 2011). For each site and season, we calculated the CWM for each trait by multiplying the mean functional trait value (see Section 2.3) for each species occurring at a site by the species' relative density at that site and summing across species, using the following equation:

$$\mathrm{CWM} = \sum_{i}^{R} p_i t_i$$

where R is the number of samples, p_i is the relative abundance of species i, and t_i is the mean trait value of species i (Garnier et al. 2004). We normalized data to zero mean and unit variance and constructed PERMANOVA models, analyzing each year separately. In the models, we used Gower distance (Gower 1971), which allows the use of different variable types (i.e., categorical and continuous) because its coefficient generates equal weights for them. Models for within- and between-drainage comparisons were structured the same as the species assemblage models but with functional trait composition (i.e., CWM) as the response variable. All data were assessed using the PERMANOVA add-on (Anderson et al. 2008) in PRIMER, with 9999 permutations of residuals in both the main tests and post hoc comparisons.

2.5.3 | Stream Characteristics Associated With Fish Species Assemblage and Functional Trait Composition

To identify stream characteristics that best distinguished impounded and unimpounded streams, as well as up- and downstream sections of streams, we used canonical analysis of principal coordinates (CAP) (Anderson and Willis 2003). This analysis uncovers the axes in principal coordinates space that best discriminate between a priori groups (up- and downstream sections of impounded and unimpounded streams). All data (i.e., temperature metrics, stream habitat characteristics, water quality parameters, and hydrology metrics; Appendix S4) were $\log_e$ (variable +1) transformed and normalized ([variable $-\bar{x}$]/standard deviation) to zero mean and unit variance so that characteristics had comparable, dimensionless scales. For within- and between-drainage analyses, separately, we calculated Euclidean distance matrices comparing stream characteristics between each pair of sites. Euclidean distance matrices were used in CAP analyses to allocate sites to the a priori classification groups by permutation (9999 permutations). We visualized differences between stream types using ordination plots and quantified separation among impounded

and unimpounded stream sections using leave-one-out (LOO) allocation success (Bloom 1991). We identified stream characteristics with the greatest contribution to the separation among a priori groups by the strength of their correlation to the first two axes generated by CAP, with highly correlated ($r > 30\%$) variables visualized using vector overlays. Analyses were run using PRIMER 7.0 (Quest Research Limited).

To assess if differences between impounded and unimpounded stream characteristics correlated with fish assemblage differences (Table 1: Question 2), we modeled the relationship of stream characteristics to fish assemblage structure (i.e., relative densities of each species) and functional trait composition (i.e., CWM) (Appendix S3) for within- and between-drainage comparisons, separately. We measured the strength and significance of relationships between fish assemblage structure, as well as functional trait composition and stream characteristics by using multivariate, distance-based, linear models (Legendre and Anderson 1999; Jupke and Schäfer 2020). Distance-based linear models use non-Euclidean distance measures to test interaction terms, using nonparametric permutation methods that do not rely on assumptions of multivariate normality and are least influenced by different response types (categorical vs. continuous variables) and sample sizes (Legendre and Anderson 1999, Jupke and Schäfer 2020). Bray–Curtis similarities (assemblage structure) and Gower distances (functional trait composition) were calculated as stated above. All stream characteristics were $\log_e$ (variable +1) transformed and normalized. We used the "Best" selection procedure, where all possible combinations of predictors were tested, and the best combination of parameters for each number of variables was selected. Because sample sizes were small relative to the number of estimated parameters, we based model selection on corrected Akaike information criterion (AIC_c) (Burnham and Anderson 2004). Delta AIC_c values ≤ 2 represented the best-supported models (Hurvich and Tsai 1989). For each predictor variable, relative variable importance was calculated based on the presence of variables in the AIC_c-best models (Burnham and Anderson 2004). The total weight of each variable is summed across all best models, with a value of 1 indicating variables that occur in all models. Predictors with relative variable importance > 0.5 were considered important. Important stream characteristics were plotted as vectors in NMDS ordinations of fish assemblage structures and functional trait composition. Analyses were performed using PRIMER.

2.5.4 | Indicator Species Analyses

To identify the most important and stable species that characterized up- and downstream sections of impounded and unimpounded streams (Table 1: Question 3), we used the indicator index (IndVal) in the *indicspecies* package in R (R Core Team 2022) as proposed by Dufrêne and Legendre (1997). Within- and between-drainage comparisons were made separately. In between-drainage analyses, each drainage was also analyzed separately. The indicator index is determined using an analysis of the relationship between assemblage structure (i.e., relative densities of each species) and stream classification (i.e., up- or downstream of impounded or unimpounded streams). The IndVal is maximum (100%) when all individuals of a species are found in a single group of sites and when the species occurs in all sites within that group. Specificity, the probability that the surveyed site belongs to a target site group given the fact that a certain species has been found there, and fidelity, the probability of finding the species in sites belonging to the site group, were calculated. The index for each species is independent of the presence and relative densities of other species. An IndVal threshold level of 25% was used (Dufrêne and Legendre 1997), which assumes that specificity and fidelity are at least 50%. The statistical significance of the relationship between species and up- and downstream sections of impounded or unimpounded streams was tested using permutation tests with 999 permutations.

2.5.5 | Indicator Fish Trait Assessment

To identify the functional traits that characterized up- and downstream sections of impounded and unimpounded streams (Table 1: Question 4), we quantified the relationship between fish functional trait composition and up- and downstream sections of streams. We used the fourth-corner method to assess differences between functional traits up- and downstream of impounded and unimpounded streams, analyzing within- and between-drainage comparisons separately (Legendre et al. 1997; Dray and Legendre 2008). In between-drainage analyses, each drainage was also analyzed separately. This analysis uses three input matrices: (1) a relative density matrix of species at each site (L), (2) a habitat matrix with each site's stream type and section (e.g., unimpounded upstream) (R), and (3) a matrix containing functional traits for each species (Q). Fourth-corner analysis tests the relationship between functional traits and habitat variables via the site $\times$ species relative density matrix and returns a matrix describing the correlations. First, we performed a correspondence analysis on matrix L. Next, using the scores of the sampling sites and species from the correspondence analysis as weights for the rows, we conducted principal component analyses on matrices Q and R (Legendre and Gallagher 2001; Greenacre 2017). We used the RLQ analysis to maximize the cross-covariance between habitat (i.e., stream type and section) and trait ordinations, resulting in a co-structure between the three matrices, which is quantified through the RLQ axes. The associations between species, traits, and habitat variables along the RLQ axes represent the best compromise between traits and habitat variables through species abundances (Dray et al. 2014). Variables that have the highest positive or lowest negative scores on the RLQ axes are contributing the most to the observed spatial patterns and trait-habitat relationships, while variables with a score close to 0 do not contribute to the observed relationships. We used a Bonferroni correction to adjust p values to test for statistical significance ($p \leq 0.05$). We ran fourth-corner analyses using the *fourthcorner* function in the *ade4* package (Dray and Dufuor 2007) in R.

3 | Results

We collected 20,878 fishes representing 15 families and 88 species, with 69 and 48 species collected in the BCD and CRD, respectively (Appendix S5). Four species were nonnative to the BCD and CRD. Except for eight species, the assemblage was composed mostly of nonmigratory fishes. We collected an average of 186 individuals (SD = 165) and 17 species (SD = 6) per site. The BCD fish community was dominated (based on cumulative

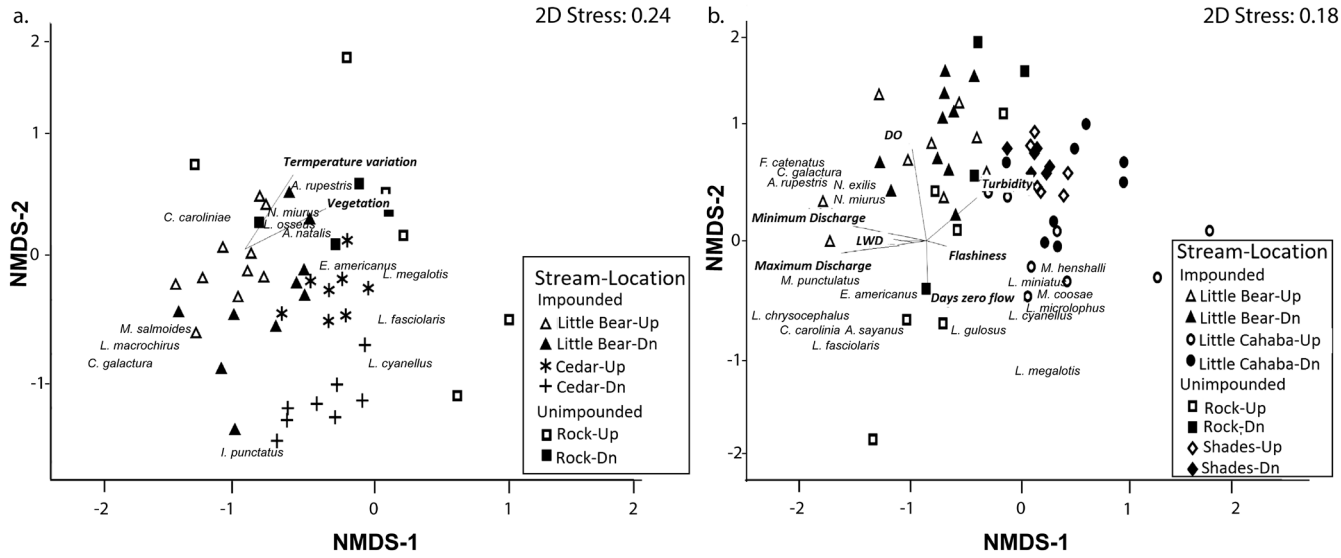

FIGURE 2 | Assemblage structure ordinations (NMDS) based on fish relative densities for within- (a) and between-drainage (b) comparisons. Within-drainage comparisons assessed 2015 measurements of all study streams in the Bear Creek Drainage (BCD). Between-drainage comparisons assessed 2016–2017 measurements of one impounded and one unimpounded stream in the BCD and Cahaba River Drainage. Symbols represent sites from each stream. Some symbols overlap. Stream characteristics that discriminated between impounded and unimpounded streams and were strongly correlated ($r > 30\%$) with the ordination (see Influence of Impoundments on Species Assemblage in Results section) are overlaid. Stream characteristic vectors show the relative association and magnitude of correlation for each variable. All species were included in NMDS but only strongly correlated species were plotted on the ordination plot (see Appendix S5 for list of species names). Discharge data were not included in within-drainage assessments. Dn = downstream; LWD = number of large woody debris pieces; Up = upstream; Vegetation = percent vegetation cover.

abundance) by Largescale Stoneroller *Campostoma oligolepis* (22%), Redline Darter *Etheostoma rufilineatum* (17%), and Snubnose Darter *E. simoterum* (10%). The CRD fish community was dominated by Longear Sunfish *Lepomis megalotis* (15%), Largescale Stoneroller (14%), Banded Sculpin *Cottus carolinae* (9%), Tricolor Shiner *Cyprinella trichroistia* (8%), and Bluegill *L. macrochirus* (8%). Roughly 35% of collected species were uncommon, detected at fewer than five sites across both drainages.

At least one species collected was associated with each of the 23 fish traits assessed. Regarding feeding strategies, 40% and 20% of species were obligate benthic or surface water feeders, respectively, with 40% of species being generalist feeders. Most species (70%) had more than one food preference, with 97% of species eating aquatic and terrestrial invertebrates and larval fishes. Regarding habitat preference, 59% of species preferred lotic habitats, while 35% of species were habitat generalists (both lotic and lentic habitats). Additionally, 85% of species were adapted to three or more microhabitat types (i.e., substrate, vegetation, and LWD), and 69% of species were adapted to three or more substrate types, with sand, gravel, and cobble being the most common substrate traits.

3.1 | Influence of Impoundments on Species Assemblage

3.1.1 | Assemblage Structure Comparisons

For both within- (BCD; Year 1) and between-drainage (BCD and CRD; Year 2) assemblage structure (i.e., relative density of each species) comparisons (Table 1: Question 1), stream type interacted with stream section (PERMANOVAS, within drainage: $F_{2,45} = 5.59$, $p < 0.01$; between-drainage: $F_{1,57} = 2.77$, $p = 0.02$; Figure 2). No other two-, three- or four-way interactions were significant ($p > 0.05$). Assemblage structures differed between up- and downstream sections of both impounded streams in within drainage comparisons (PERMANOVAS, Cedar Creek $-t_{1,12} = 3.09$, $p = 0.001$, Little Bear Creek $-t_{1,16} = 2.12$, $p = 0.001$; Figure 2), but no differences were detected between up- and downstream sections of the unimpounded stream, Rock Creek (PERMANOVA, $-t_{1,6} = 1.35$, $p = 0.15$; Figure 2). Similarly, assemblage structure only differed between impounded streams in between-drainage comparisons (PERMANOVAS, impounded streams $-t_{1,28} = 2.03$, $p = 0.004$; unimpounded streams $-t_{1,14} = 1.45$, $p = 0.07$; Figure 2).

3.1.2 | Fish Species Assemblage Associations With Stream Characteristics

For within-drainage comparisons, stream habitat characteristics differed between up- and downstream sections of both impounded and unimpounded streams (CAP: LOO = 85%). CAP Axis 1 separated all upstream sections from all downstream sections (eigenvalue CAP 1 = 86%), with temperature variation lower, and LWD, minimum temperature, and wood size higher at down- than upstream sites (Figure 3a). CAP Axis 2 separated stream sections upstream of impoundments from those in unimpounded streams (eigenvalue CAP 2 = 77%), with pH and water temperature higher, and percent vegetation cover and turbidity lower upstream of impounded than in unimpounded streams (Figure 3a).

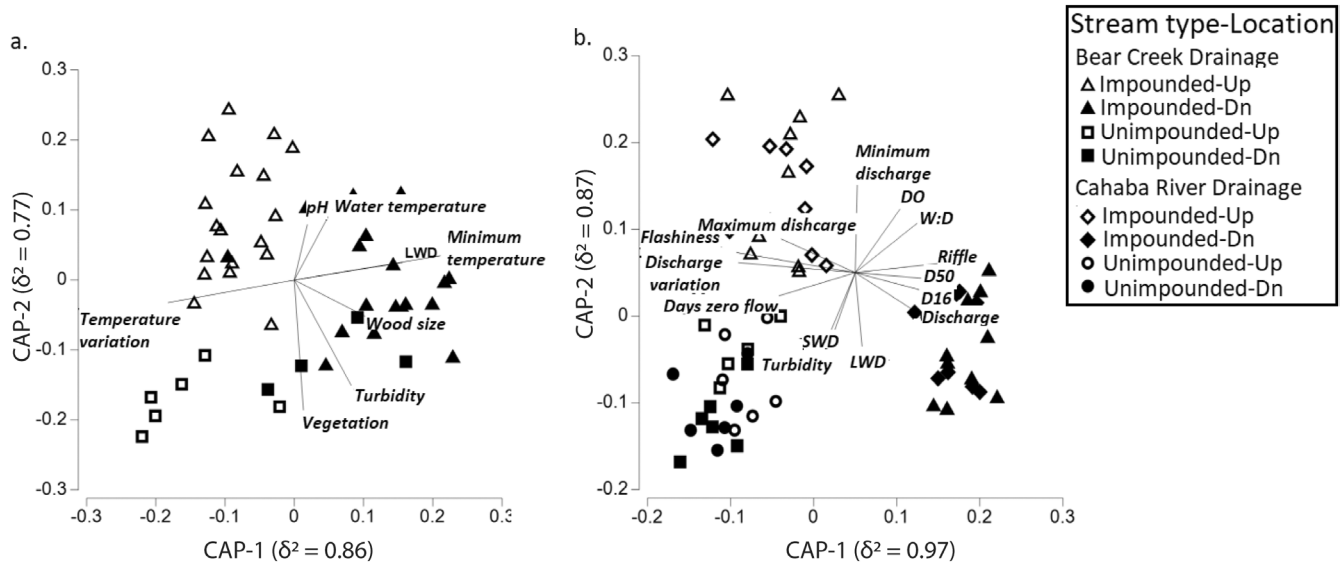

FIGURE 3 | Canonical analysis of principal coordinates (CAP) ordination plots based on impounded and unimpounded stream characteristics for within- (a) and between-drainage (b) comparisons. Within-drainage comparisons assessed 2015 measurements of all study streams in the Bear Creek Drainage (BCD). Between-drainage comparisons assessed 2016–2017 measurements of one impounded and one unimpounded stream in the BCD and Cahaba River Drainage. Symbols represent stream characteristics from spring and fall samples. Some symbols overlap. Black vectors represent raw Pearson correlations of stream characteristics that contributed > 30% to the dissimilarity between up- and downstream sections of impounded and unimpounded streams. Discharge data were not included in within-drainage assessments. D16 = Particle size at which 16% of particles were smaller; D50 = median particle size; Dn = downstream; DO = dissolved oxygen; LWD = number of large woody debris pieces; Riffle = percent of site length containing riffles; SWD = mean percent cover of small woody debris; Up = upstream; Vegetation = percent vegetation cover; W:D = ratio of mean wetted width to mean depth; Wood size = average diameter of woody debris; δ^2 = the canonical correlation or strength of the association between the multivariate data and a priori groups.

Of these stream habitat characteristics, distance-based linear models identified temperature variation, percent vegetation cover, and number of pieces of LWD as the best indicators of a site's fish assemblage, explaining 20% of the total variation among sites (Table 1: Question 2, Table 2, Figure 2a). Differences in fish assemblage between sites upstream in Cedar Creek (impounded) and throughout Rock Creek (unimpounded) vs. sites downstream in Cedar Creek and throughout Little Bear Creek (impounded) were best explained by temperature variation and percent vegetation cover, which were both higher in the former sections. Fish assemblage differences between all Little Bear Creek sites vs. all Rock and Cedar Creek sites were best explained by LWD, with more LWD in Little Bear Creek.

For between-drainage comparisons, stream habitat characteristics differed between up- and downstream sections of impounded, but not unimpounded, streams in both drainages (CAP: LOO = 88%). CAP Axis 1 separated sections upstream of impoundments and all unimpounded stream sections from sections downstream of impoundments (between-drainage CAP 1 = 97%), with discharge variability (i.e., flashiness, discharge variation, and days zero flow higher) higher and percent riffle, substrate size, and total discharge lower in the former sections (Figure 3b). CAP Axis 2 separated all unimpounded stream sections from sections upstream of impoundments (between-drainage CAP 2 = 87%), with percent SWD, turbidity, and LWD higher, and minimum discharge, DO, and width-to-depth ratios lower in unimpounded streams than upstream of impoundments.

The best explanatory stream characteristics (minimum discharge, maximum discharge, number of days with zero flow, flashiness, turbidity, LWD, and DO) identified by distance-based linear models accounted for 49% of the total variation in fish assemblages among sites (Table 1: Question 2, Table 2, Figure 2b). Differences in fish assemblages between BCD and CRD sites were best explained by turbidity and LWD, with higher turbidity and lower LWD in the CRD. Flashiness and minimum discharge best explain differences in fish assemblages between sites upstream in Little Cahaba River (impounded) and all other CRD sites, with flashiness higher and minimum discharge lower upstream in Little Cahaba River. Differences in fish assemblages between Little Bear Creek (impounded) and Rock Creek (unimpounded) sites were best explained by LWD and minimum and maximum discharge, which were all higher in Little Bear Creek.

3.1.3 | Indicator Species

For within-drainage assessments, indicator species analyses revealed Whitetail Shiner *Cyprinella galactura* and Northern Studfish *Fundulus catenatus* were indicators of impounded streams, and Green Sunfish *Lepomis cyanellus*, Scarletfin Shiner *Lythrurus fasciolaris*, and Redfin Pickerel *Esox americanus* were indicators of unimpounded streams (Table 1: Question 3). Additionally, Brindled Madtom *Noturus miurus* was an indicator of sites downstream of impoundments, Bluegill was an indicator of sites upstream of impoundments, and Redfin Pickerel was an indicator of sites downstream in unimpounded streams

TABLE 2 | Distance-based linear model results of stream characteristics that best explained within- and between-drainage fish species assemblage and functional trait composition.

Model	R^2	*N*	Psuedo-*F*	RVI
Assemblage structure				
Within-drainage	0.20	3		
Vegetation			4.09**	1.00
Temperature variation			3.07**	0.67
LWD			2.65*	0.67
Between-drainage	0.49	6		
Maximum discharge			7.69**	1.00
Flashiness			2.20*	0.83
Minimum discharge			7.65**	0.83
Days zero flow			4.23**	0.83
DO			4.15**	0.67
Turbidity			4.64**	0.67
LWD			2.15*	0.50
Functional trait composition				
Within-drainage	0.16	2		
Water temperature			4.91**	1.00
Vegetation			3.80**	0.50
Between-drainage	0.30	3		
Maximum discharge			6.93**	1.00
Minimum discharge			7.31**	0.67
Flashiness			2.65*	0.67
W:D			2.10	0.33

Note: Within-drainage comparisons assessed 2015 measurements from all study streams in the Bear Creek (BCD) Drainage. Between-drainage comparisons assessed 2016–2017 measurements from one impounded and one unimpounded stream in the BCD and Cahaba River drainages. The results include variables from the models that were within two AICc units of the best model. Stream characteristics are listed by decreasing Pseudo-*F* values. *N* = number of models within 2 AICc units of the best model; RVI = relative variable importance (variables with RVI of 1.00 were included in all of the best models); LWD = large woody debris (≥ 10 cm diameter); DO = dissolved oxygen (mg/L); W:D = width-to-depth ratio.
*$p \leq 0.05$.
**$p \leq 0.01$.

(Table 3). There were no indicator species for upstream sections of unimpounded streams.

For BCD between-drainage assessments, indicator species analyses revealed Rock Bass *Ambloplites rupestris*, Northern Studfish, and Whitetail Shiner as indicators of impounded streams and Scarletfin Shiner, Redfin Pickerel, and Warmouth *Lepomis gulosus* as indicators of unimpounded streams (Table 1: Question 3, Table 3). Additionally, Slender Madtom *Noturus exilis* was an indicator of sites upstream of impoundments, and Redfin Pickerel was an indicator of sites downstream in unimpounded streams. For CRD, indicator species analyses revealed Redspotted Sunfish *Lepomis miniatus*, Banded Sculpins, and Redeye Bass *Micropterus coosae* as indicators of impounded streams, and Warmouth as an indicator of unimpounded streams (Table 3). Additionally, Dollar Sunfish *L. marginatus* was an indicator of sites downstream of impoundments.

3.2 | Influence of Impoundments on Functional Traits

3.2.1 | Functional Trait Comparisons

For both within- and between-drainage comparisons (Table 1: Question 1), fish functional traits differed between impounded and unimpounded streams (PERMANOVAS, within drainage: $F_{2,45} = 5.59$, $p < 0.01$; between-drainage: $F_{1,59} = 7.57$, $p < 0.01$; Figure 4). Additionally, for within-drainage comparisons, stream and stream section interacted ($F_{2,45} = 2.60$, $p = 0.02$), with no differences detected between the functional traits of fishes upstream in Little Bear and Cedar creeks (impounded streams), whereas functional traits differed among downstream sections of all streams. Within each stream, functional traits did not differ between up- and downstream sections. Additionally, no other two-, three-, or four-way interactions were significant.

3.2.2 | Fish Trait Associations With Stream Characteristics

Of the stream habitat characteristics that best discriminated between up- and downstream sections of impounded and unimpounded streams in within-drainage comparisons (see CAP analyses; Figure 3a), water temperature and percent vegetation cover were the best explanatory variables of fish functional trait composition, explaining 16% of the total variation (Table 1: Question 2, Table 2, Figure 4a). Impounded streams' fish functional trait CWM values were positively associated with water temperature and negatively associated with vegetation cover. Conversely, unimpounded streams' fish functional trait CWM values were negatively associated with water temperature and positively associated with vegetation cover. While functional traits differed among downstream sections of stream (i.e., downstream of Little Bear Creek differs from downstream of Cedar Creek), no stream habitat characteristics correlated with functional trait composition differences between downstream sections of Little Bear and Cedar creeks. In addition, fish functional trait CWM values in downstream sections of Rock Creek were positively associated with vegetation cover, while downstream sections of Little Bear and Cedar Creeks were negatively associated with vegetation cover.

Of the stream habitat characteristics that best discriminated between up- and downstream sections of impounded and

TABLE 3 | Indicator species analyses results, showing significant relationships of fish species to up- and downstream sections of impounded and unimpounded streams.

	Bear Creek Drainage						Cahaba River Drainage					
Species	**I**	**I-Up**	**I-Dn**	**U**	**U-Up**	**U-Dn**	**I**	**I-Up**	**I-Dn**	**U**	**U-Up**	**U-Dn**
Within-drainage												
Cyprinella galactura	+*											
Fundulus catenatus	+*											
Lepomis cyanellus				+*								
Lythrurus fasciolaris				+*								
Esox americanus				+*		+**						
Noturus miurus			+*									
Lempomis macrochirus		+**										
Between-drainage												
Ambloplites rupestris	+**											
F. catenatus	+**											
C. galactura	+*											
L. fasciolaris				+*								
E. americanus				+*		+**						
Lepomis gulosus				+*						+*		
N. exilis		+*										
Cottus caroliniae							+**					
Lepomis miniatus							+**					
Micropterus coosae							+*					
Lepomis marginatus									+*			

Note: I = impounded; U = unimpounded; Up = upstream of impoundment or upstream section of unimpounded stream; Dn = downstream of impoundment or downstream section of unimpounded stream; + = positive relationship; within-drainage = 2015 Bear Creek Drainage comparisons; between-drainage = 2016–2017 Bear Creek and Cahaba River drainage comparisons.
*$p < 0.05$.
**$p < 0.01$.

unimpounded streams in between-drainage comparisons (see CAP analyses; Figure 3b), minimum discharge, maximum discharge, width-to-depth ratio, and stream flashiness were the best explanatory variables of fish functional trait composition, explaining 30% of the total variation (Table 1: Question 2, Table 2, Figure 4b). Minimum discharge and width-to-depth ratios were positively associated with impounded stream fish functional trait composition, while maximum discharge and flashiness were positively correlated with unimpounded stream functional trait composition.

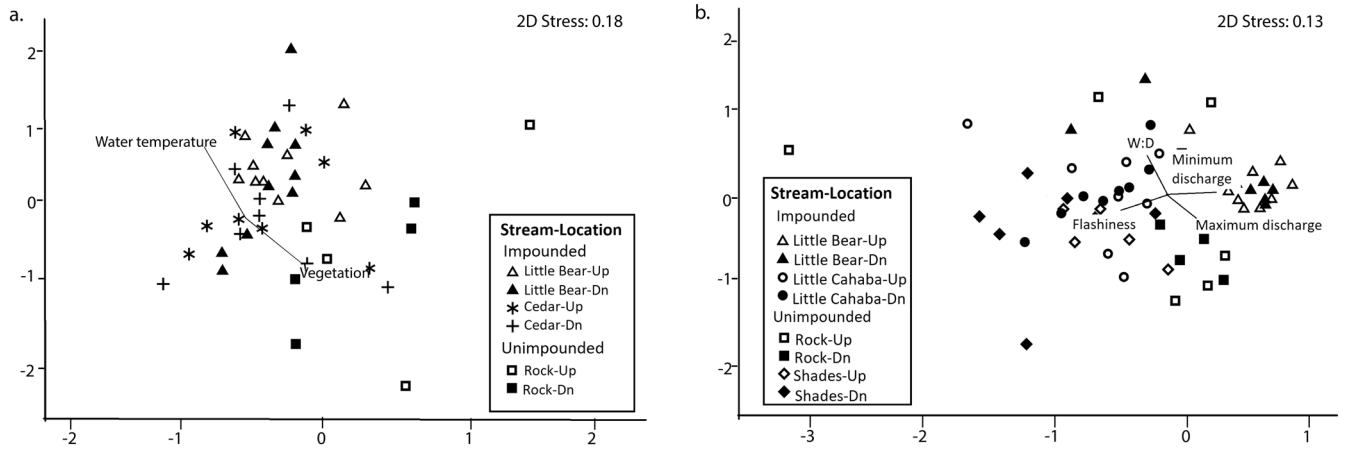

FIGURE 4 | Functional trait ordinations (NMDS) based on trait community weighted means for within- (a) and between-drainage (b) comparisons. Within-drainage comparisons assessed 2015 measurements of all study streams in the Bear Creek Drainage (BCD). Between-drainage comparisons assessed 2016–2017 measurements of one impounded and one unimpounded stream in the BCD and Cahaba River Drainage. Symbols represent sites from each stream. Some symbols overlap. Stream characteristics that discriminated between traits in impounded and unimpounded streams and were strongly correlated with the ordination (see Section 3.2) are overlaid. Stream characteristic vectors show the relative association and magnitude of correlation for each variable. Discharge data were not included in within-drainage assessments. Dn = downstream; Up = upstream; Vegetation = percent vegetation cover; W:D = ratio of mean wetted width to mean depth.

3.2.3 | Indicator Traits

For within-drainage comparisons, fourth-corner analysis extracted five significant relationships among fish traits, stream habitat characteristics, and impounded and unimpounded stream sections (Table 1: Question 4). Surface feeders, as well as fish with longer spawning seasons, were negatively correlated with sites upstream of impoundments, while lithophilic guarders and fish that preferred cobble habitats were positively correlated with sites upstream of impoundments (Table 4). Additionally, fish with longer spawning seasons were positively correlated with downstream sites in unimpounded streams (Table 4). For between-drainage comparisons, fourth-corner analysis extracted three significant relationships. In the BCD, surface feeders, fish that prefer lotic habitats, and habitats with aquatic vegetation were negatively correlated with sites upstream of impoundments. Fish occurring at higher maximum temperatures and fish that prefer habitats with aquatic vegetation were negatively correlated with sites upstream of impoundments, while lithophilic nonguarders were positively associated with sites upstream of impoundments (Table 4).

TABLE 4 | Significant functional trait relationships to up- and downstream sections of impounded and unimpounded streams based on fourth-corner analyses.

	Impounded		Unimpounded	
Comparison	**Up**	**Dn**	**Up**	**Dn**
Within-drainage				
Surface or water column feeder	−**			
Length of spawning season	−**			+**
Guarders, substrate choosers, lithophils	+**			
Cobble or pebble substrate	+**			
Between-drainage				
Aquatic vegetation	−**			
30-year average maximum July temperature	−**			
Nonguarders, brood hiders, lithophils	+**			

Note: Up = upstream; Dn = downstream; within-drainage = 2015 Bear Creek Drainage comparisons; between-drainage = 2016–2017 Bear Creek and Cahaba River drainage comparisons; + = positive relationship; − = negative relationship.
**$p < 0.01$.

4 | Discussion

We used a combination of taxonomic and functional measures to evaluate fish assemblage structure in impounded and unimpounded streams. These measures conveyed somewhat different, yet complementary, information regarding fish responses to impoundments. If impoundments were not impacting fish assemblages, we would expect similar fish assemblages along the stream lengths sampled (range 12–32 km) due to very few stream order changes and no evidence of natural fish faunal breaks (Matthews 1986). This was only supported in our unimpounded streams, with few assemblage differences between up- and downstream sections. We found that fish assemblages differed between up- and downstream sections of impounded streams. Similarly, there were more differences between fish functional traits up- and downstream of impounded than unimpounded streams. We used two analytical approaches to assess fish functional traits. According to the CWM approach, which takes into account the combination and dominance of each trait at a site, no differences were detected between sites up- and downstream

of impounded or unimpounded streams. This indicated that although fish assemblage composition (species presence and abundance at a site) differed between up- and downstream sections of impounded streams, the fish species present in both sections shared similar functional traits. Conversely, according to the RLQ analyses, which assess each trait's relationship with impounded and unimpounded streams individually, there were fish functional traits correlated to sites upstream of impoundments. The difference in findings may indicate that although some traits are associated with a stream section, these traits are not dominant within sites, when compared to the entire suite of traits present at a site, causing no differences to be identified in CWM assessments. Nonetheless, these traits are still important in understanding the impacts of impoundments on fish assemblages. Additionally, fish functional traits differed between impounded and unimpounded streams, indicating that dams and impoundments may alter fish assemblage ecosystem functions throughout streams. Fish assemblages and functional traits differences between sites up- and downstream of impoundments were best explained by temperature and flow regime differences, as well as habitat complexity differences (i.e., LWD, substrate size, and percent vegetation).

Changes to stream habitat characteristics by large impoundments caused shifts in fish assemblages up- and downstream of impoundments, with only lotic species indicators of sites downstream of impoundments, but lotic, lentic, and generalist species indicators of sites upstream. Changes in fish communities can be attributed to abiotic changes in the ecosystem (Jackson et al. 2001; Kraft et al. 2015), as well as to biotic interactions among lentic and lotic fish fauna (Pringle et al. 2000; Jackson et al. 2001; Šmejkal et al. 2023). Anthropogenic abiotic changes often increase suitable habitats for lentic and generalist species, thereby increasing interactions among lentic and lotic species. Additionally, fisheries management agencies often stock and introduce piscivorous game fishes to impoundments, which increases the number of generalist species in impounded streams (ADCNR 2024). Native fishes are often extirpated from impounded streams and replaced by macrohabitat generalists and Centrarchids (e.g., *Lepomis* spp.) (Taylor et al. 2001; Herbert and Gelwick 2003; Guenther and Spacie 2006; Šmejkal et al. 2023). Similarly, surveys from 2000 (post-impoundment) in the BCD documented a decrease in sensitive fish species, such as leuciscids and percids, and an increase in species tolerant to environmental changes and impoundments (i.e., centrarchids) compared to historical surveys before streams were impounded (Walls 1968; Phillips and Johnston 2004a). Likewise, most species that were collected previously, either pre-impoundment (Walls 1968) or post-impoundment (Phillips and Johnston 2004a), but not in the current study, were sensitive leuciscids and percids (Appendix S6). We also collected more tolerant Centrarchidae and Leuciscidae species compared to previous studies (Walls 1968, Phillips and Johnston 2004a). Although there is no pre-impoundment fish data for Little Cahaba River, comparison of our data to those collected post-impoundment downstream of the dam in 1962 suggests changes in fish assemblages similar to those in the Bear Creek Drainage, with fewer cyprinids and percids and more centrarchids collected in the current study than historically (May 1963) (Appendix S6). Species richness may differ between studies due to differences in sites sampled and in collection methods, with electrofishing and kick seining used in this study and seining used in previous studies (May 1963; Walls 1968; Phillips and Johnston 2004a). Because of these differences, formal comparisons between current and historical data were not made.

Seasonal movement of some species (e.g., certain catostomids and clupeids) is well documented, but most of the species we collected are not considered migratory (Boschung and Mayden 2004). Nonetheless, dams could decrease recruitment and dispersal of nonmigratory fishes (Ward and Stanford 1995). For instance, in between-drainage comparisons, lithophilic nonguarders were positively associated with sites upstream of impoundments but did not have an association with sites downstream of impoundments, which also had suitable habitat. Fishes in the Leuciscidae (33%), Percidae (57%), and Petromyzontidae (10%) families made up the lithophilic nonguarders in this study. These species often rely on larval drift for dispersal and colonization (Welcomme 2006; Ramler et al. 2016; Nagel et al. 2021). Impoundments may have hindered seasonal movement of these species to downstream sites, and thus, lithophilic nonguarders were more prevalent upstream of impoundments. In addition, lengths of fish spawning seasons differed among stream sections in within-drainage comparisons; fish with shorter spawning seasons tended to occur upstream of impoundments, while those with longer seasons were downstream in unimpounded streams. This pattern may be due to fish with longer spawning seasons moving greater distances longitudinally throughout the stream system; thus, the inability to move longitudinally due to impoundments may restrict the species pool to species that have a shorter spawning period (Kruk and Penczak 2003; Chen et al. 2023).

Dams frequently alter streams' hydrological and temperature regimes, which can substantially impact aquatic biodiversity (Ward 1976; Baxter 1977; Dudgeon 2000; Graf 2006; Barnett et al. 2023). Impoundments in this study were managed for different purposes (i.e., BCD impoundments managed for flood control and CRD impoundment managed for municipal water use). While each impoundment stabilized downstream flow, the timing of water release varied between drainages. Nonetheless, in both drainages, temperature and flow regime parameters were some of the best explanatory variables of fish species and functional trait composition, with the least temperature and discharge variability in sites downstream of impoundments. Fish species that preferred slow-moving rivers (i.e., Northern Studfish, Brindled Madtom, Rock Bass, and Redspotted Sunfish) were indicators of impounded streams. Lower discharge variability not only reduces peak flows but also reduces river-floodplain connectivity, reducing habitat available to fishes and decoupling essential functions of the riverine system (Junk et al. 1989; Hanks 2020). Additionally, fish species associated with higher temperature variations were positively correlated with sites upstream of impoundments and unimpounded stream sites, indicating that dams are reducing the temperature variability at sites downstream of impoundments. Shifts in temperature and hydrology variation and patterns can cause changes and asynchrony with the timing of life history events (e.g., spawning) (Crowder and Magnuson 1983; Bunn and Arthington 2002; Hanks 2020), with negative impacts documented from both hypolimnetic and epilimnetic dam releases (Yeager 1993; Hanks and Hartman 2019).

Dam-induced changes in river hydrology cause major habitat loss and simplification in stream ecosystems (Nilsson et al. 2005), with habitat complexity being one of the most important influences on stream community structure (Angermeier and Karr 1984; Smith et al. 2014; Barnett et al. 2023). Reducing habitat complexity decreases suitable microhabitats for habitat specialists. For instance, in within-drainage comparisons, percent vegetation cover was one of the best explanatory variables of fish assemblage and functional trait composition differences between impounded and unimpounded streams, with unimpounded streams having higher vegetation cover and higher diversities of fish assemblage and functional traits. Similarly, two species that were commonly found in streams with high vegetation (i.e., Green Sunfish and Redfin Pickerel) were indicators of unimpounded streams. Additionally, in between-drainage comparisons, fish associated with aquatic vegetation were negatively correlated with sites upstream of impoundments. Thus, losing aquatic vegetation from streams can drastically change fish assemblages, with aquatic vegetation providing structure and habitat for fishes, as well as reducing stream velocity and thereby increasing the volume of water within stream habitats (Armitage et al. 1994; O'Hare et al. 2010; O'Hare 2015).

We detected functional composition differences between impounded and unimpounded streams, but only a few differences were detected between up- and downstream sections of impounded or unimpounded streams. Most studies assessing functional diversity compare differences pre- and post-impoundment or between impounded and unimpounded streams (Pool et al. 2010; Oliveira et al. 2018; Perônico et al. 2019; Zhang et al. 2020; Pereira et al. 2021; Wang et al. 2021), while relatively fewer studies have assessed differences between sections up- and downstream of impoundments (Helms et al. 2011; Smith et al. 2017; Ticiani et al. 2022; Faucheux et al. 2023). Similar to our findings, most studies comparing pre- and post-impoundment or impounded and unimpounded streams detected differences in functional diversity between stream types, with nonguarders, habitat generalists, detritivores, and limnophilic species often more abundant in impounded streams (Freeman et al. 2005; Kominoski et al. 2018; Oliveira et al. 2018; Perônico et al. 2019; Zhang et al. 2020). Our findings were also similar to those from streams with low-head dams (Helms et al. 2011; Smith et al. 2017), run-of-river dams (Ticiani et al. 2022) and other flood-control impoundments (Faucheux et al. 2023), with functional traits similar between up- and downstream sections of impoundments. These findings indicate that environmental filters up- and downstream of impoundments are selecting for similar traits.

The distribution patterns detected for fish assemblages in this study convey somewhat different, yet complementary, results as crayfish studied in the same streams (Barnett et al. 2020, 2022, 2023). For both fish and crayfish, assemblages differed between impounded and unimpounded streams. Habitat generalist or invasive species were the dominant crayfish species throughout impounded streams, with microhabitat specialists abundant only in unimpounded streams. However, unlike for fishes, impoundments homogenized crayfish species assemblages, with no differences in crayfish species assemblages up- and downstream of impoundments, but differences were detected between up- and downstream sections of unimpounded streams (Barnett et al. 2022). In the current study, fish species assemblages differed up- and downstream of impoundments but showed similarities between up- and downstream sections of unimpounded streams. These differences between faunal groups may be due to greater species diversity and distances moved by fishes within streams, allowing many species to be common throughout large portions of the stream system, with fragmentation and other environmental changes (i.e., less aquatic vegetation and less discharge variability) to filter out different groups of species, creating differences between impounded stream sections (Sheldon 1968; Horwitz 1978). Although fish species assemblages differed between up- and downstream sections of impounded streams, there were few fish functional composition differences between up- and downstream sections, with functional composition variations detected only in RLQ analyses. This indicates that fish functional diversity may be homogenized by impoundments just as crayfish species diversity is homogenized. Similarly, habitat complexity, temperature, and discharge variation were the key environmental characteristics that explained crayfish and fish assemblages differences among up- and downstream sections of impounded and unimpounded streams (Barnett et al. 2023). Also, impoundments fragmented crayfish populations (Barnett et al. 2020), which may also be occurring in fish populations.

Unimpounded streams were not perfect controls for impounded streams. Impounded streams had higher maximum and minimum flows upstream of impoundments than we observed in unimpounded streams. Nevertheless, during summer months in the BCD, stream drying and isolated pools occurred in upstream sections of impounded and unimpounded streams, indicating similar hydrological patterns. While stream drying was not observed in the CRD, low water depths (average 17 cm for impounded and unimpounded streams) and up to 4 days of no flow were documented through regression analyses of stream gage data in upstream sections of impounded and unimpounded streams in the fall. Nonetheless, we did record stream drying at sites, so we could not assess the impacts of stream drying on fish communities. We also sampled a shorter distance along the BCD unimpounded stream (Rock = 23 km) compared to impounded streams (Little Bear = 33 km; Cedar = 32 km). Although geographic distance does play a factor in stream characteristics, within-drainage CAP analyses showed similarities in stream characteristics between downstream sections of impounded and unimpounded streams in the BCD (Figure 3a). This suggests that differences between impounded and unimpounded streams' fish assemblage patterns may not be due to the geographic distances sampled. Similar stream lengths were sampled in the CRD.

Our sampling approach, sampling shallow waters (> 1 m depth), may reduce the impoundment effect detected in this study. This approach may have reduced the number of deepwater/larger-bodied species we collected, potentially limiting our ability to detect impoundment effects. For instance, studies show that fish species such as White Bass *Morone chrysops* and Channel Catfish *Ictalurus punctatus*, which are both common in lakes, are also common in deep pools of rivers (Page and Burr 1973; Guenther and Spacie 2006). Thus, by sampling only shallow water habitats, impounded and unimpounded stream fish assemblages may seem more similar, reflecting more lotic species

and not representing lentic or deepwater species accurately. For instance, 59% of the species we collected preferred lotic habitats, while 35% of species were habitat generalists (both lotic and lentic habitats). In future studies, deepwater habitats should be sampled to more accurately assess the fish assemblage differences between impounded and unimpounded streams.

Overall, impoundments have played a substantial role in shaping aquatic communities (i.e., fish and crayfish) taxonomic and functional trait composition in the studied drainages (Phillips and Johnston 2004a; Barnett et al. 2020, 2022, 2023; Barnett and Adams 2021). Current and historic species assemblages comparisons in the BCD indicated a continued loss of sensitive species and an increase in habitat generalists (Phillips and Johnston 2004a). While differences were detected between fish assemblages up- and downstream of impoundments, fish functional composition assessments may provide a more well-defined and operational understanding of how fish assemblages are changing within systems, allowing managers to target functional groups instead of a few species for conservation efforts, as well as providing a metric that can be applied to other systems. Additionally, increasing habitat structure in streams, as well as increasing stream thermal and discharge variability to mimic natural conditions, could lead to more habitat specialist species and fewer lentic and generalist species.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author, Z.C.B., upon request.

References

ADCNR. 2024. *Freshwater Fish Hacheries*. Alabama Department of Conservation and Natural Resources. https://www.outdooralabama.com/research/freshwater-fish-hatcheries.

Anderson, M., R. N. Gorley, and R. K. Clarke. 2008. *Permanova+ for Primer: Guide to Software and Statistical Methods*. Primer-E Limited.

Anderson, M. J., and T. J. Willis. 2003. "Canonical Analysis of Principal Coordinates: A Useful Method of Constrained Ordination for Ecology." *Ecology* 84, no. 2: 511–525.

Angermeier, P. L., and J. R. Karr. 1984. "Relationships Between Woody Debris and Fish Habitat in Small Warmwater Stream." *Transactions of the American Fisheries Society* 113: 716–726.

Arantes, C. C., D. B. Fitzgerald, D. J. Hoeinghaus, and K. O. Winemiller. 2019. "Impacts of Hydroelectric Dams on Fishes and Fisheries in Tropical Rivers Through the Lens of Functional Traits." *Current Opinion in Environmental Sustainability* 37: 28–40.

Armitage, P. D., J. H. Blackburn, J. M. Einder, and J. F. Wright. 1994. "Impact of Vegetation Management on Macroinvertebrates in Chalk Streams." *Aquatic Conservation: Marine and Freshwater Ecosystems* 4, no. 2: 95–104.

Bain, M. B., and N. J. Stevenson. 1999. *Aquatic Habitat Assessment: Common Methods*. American Fisheries Society.

Baker, D. B., R. P. Richards, T. T. Loftus, and J. W. Kramer. 2004. "A New Flashiness Index: Characteristics and Applications to Midwestern Rivers and Streams." *Journal of the American Water Resources Association* 40: 503–522.

Barnett, Z. C., and S. B. Adams. 2021. "Review of Dam Effects on Native and Invasive Crayfishes Illustrates Complex Choices for Conservation Planning." *Frontiers in Ecology and Evolution* 8: 621723.

Barnett, Z. C., S. B. Adams, J. D. Hoeksema, G. L. Easson, and C. A. Ochs. 2022. "Effects of Impoundments on Stream Crayfish Assemblages." *Freshwater Science* 41: 125–142.

Barnett, Z. C., S. B. Adams, C. A. Ochs, and R. C. Garrick. 2020. "Crayfish Populations Genetically Fragmented in Streams Impounded for 36–104 Years." *Freshwater Biology* 65: 768–785.

Barnett, Z. C., C. A. Ochs, G. L. Easson, and S. B. Adams. 2023. "Crayfish Assemblages Correlate With Dam-Induced Effects on Abiotic Factors and Predatory Fish Assemblages in Alabama Streams." *River Research and Applications* 39: 1537–1550.

Barnett, Z. C., C. A. Ochs, J. D. Hoeksema, and S. B. Adams. 2021. "Not All Methods Are Created Equal: Assessment of Sampling Methods for Crayfishes and Fishes in Southern Appalachian Streams." *Hydrobiologia* 848: 1491–1515.

Baxter, R. M. 1977. "Environmental Effects of Dams and Impoundments." *Annual Review of Ecology and Systematics* 8: 255–283.

Bloom, N. S. 1991. "On the Chemical Form of Mercury in Edible Fish and Marine Invertebrate Tissue." *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1010–1017.

Boschung, H. T., and R. L. Mayden. 2004. *Fishes of Alabama*. Smithsonian Books.

Bunn, S. E., and A. H. Arthington. 2002. "Basic Principles and Ecological Consequences of Altered Flow Refimes for Aquatic Biodiversity." *Environmental Management* 30: 492–507.

Burnham, K. P., and D. R. Anderson. 2004. "Multimodel Inference: Understanding AIC and BIC in Model Selection." *Sociological Methods & Research* 33, no. 2: 261–304.

Chen, Q., Q. Li, Y. Lin, et al. 2023. "River Damming Impacts on Fish Habitats and Associated Conservation Measures." *Reviews of Geophysics* 61: e2023RG000819.

Chu, L., W. Wang, R. Zhu, Y. Yan, Y. Chen, and W. L. 2015. "Variation in Fish Assemblages Across Impoundments of Low-Head Dams in Headwater Streams of the Qingyi River China: Effect of Abiotic Factors and Native Invaders." *Environmental Biology of Fishes* 98: 101–112.

Clarke, K. R. 1993. "Nonparametric Multivariate Analyses of Changes in Community Structure." *Australian Journal of Ecology* 18, no. 1: 117–143.

Crowder, L. B., and J. J. Magnuson. 1983. "Cost–Benefit Analysis of Temperature and Food Resource Use: A Synthesis With Examples From the Fishes." In *Behavioral Energetics: The Cost of Survival in Vertebrates*, edited by W. P. Aspey and S. I. Lustick, 189–222. Ohio State University Press.

Dray, S., and A. B. Dufuor. 2007. "The ade4 Package: Implementing the Duality Diagram for Ecologists." *Journal of Statistical Software* 22, no. 4: 20.

Dray, S., and P. Legendre. 2008. "Testing the Species Traits-Environment Relationships: The Fourth-Corner Problem Revisited." *Ecology* 89: 3400–3412.

Dray, S., P. Choler, S. Doledec, et al. 2014. "Combining the Fourth-Corner and the RLQ Methods for Assessing Trait Responses to Environmental Variation." *Ecology* 95: 14–21.

Dudgeon, D. 2000. "Large-Scale Hydrological Changes in Tropical Asia: Prospects for Riverine Biodiversity the Construction of Large Dams Will Have an Impact on the Biodiversity of Tropical Asian Rivers and Their Associated Wetlands." *Bioscience* 50: 793–806.

Dufrêne, M., and P. Legendre. 1997. "Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach." *Ecological Monographs* 67, no. 3: 345–366.

Dunn, C. G., D. A. Schumann, M. E. Colvin, et al. 2024. "Using Resiliency, Redundancy, and Representation in a Bayesian Belief Network to Assess Imperilment of Riverine Fishes." *Ecosphere* 15, no. 1: e4738.

Elkins, D., S. C. Sweat, B. R. Kuhajda, A. L. George, K. S. Hill, and S. J. Wenger. 2019. "Illuminating Hotspots of Imperiled Aquatic Biodiversity in the Southeastern US." *Global Ecology and Conservation* 19: e00654.

Faucheux, N. M., L. E. Miranda, J. M. Taylor, and J. Farris. 2023. "Impact of Dams on Stream Fish Diversity: A Different Result." *Diversity* 15: 728.

Freedman, J. A., B. D. Lorson, R. B. Taylor, R. F. Carline, and J. R. Stauffer Jr. 2014. "River of the Dammed: Longitudinal Changes in Fish Assemblages in Response to Dams." *Hydrobiologia* 727: 19–33.

Freeman, M. C., E. R. Irwin, N. M. Burkhead, B. J. Freeman, and H. L. Bart. 2005. "Status and Conservation of the Fish Fauna of the Alabama River System." *American Fisheries Society Symposium* 45: 557–585.

Frimpong, E. A., and P. L. Angermeier. 2009. "FishTraits: A Database of Ecological and Life-History Traits of Freshwater Fishes of the United States." *Fisheries* 34: 487–495.

Garnier, E., J. Cortez, G. Billès, et al. 2004. "Plant Functional Markers Capture Ecosystem Properties During Secondary Succession." *Ecology* 85: 2630–2637.

Gido, K. B., J. F. Schaefer, and J. A. Falke. 2009. "Convergence of Fish Communities From the Littoral Zone of Reservoirs." *Freshwater Biology* 54: 1163–1177.

Gower, J. C. 1971. "A General Coefficient of Similarity and Some of Its Properties." *Biometrics* 27: 857–871.

Graf, W. L. 1999. "Dam Nation: A Geographic Census of American Dams and Their Large-Scale Hydrologic Impacts." *Water Resources Research* 35: 1305–1311.

Graf, W. L. 2006. "Downstream Hydrologic and Geomorphic Effects of Large Dams on American Rivers." *Geomorphology* 79: 336–360.

Greenacre, M. 2017. "'Size' and 'Shape' in the Measurement of Multivariate Proximity." *Methods in Ecology and Evolution* 8: 1415–1424.

Grime, J. P. 1998. "Benefits of Plant Diversity to Ecosystems: Immediate, Filter and Founder Effects." *Journal of Ecology* 86: 902–910.

Guenther, C. B., and A. Spacie. 2006. "Changes in Fish Assemblage Structure Upstream of Impoundments Within the Upper Wabash River Basin, Indiana." *Transactions of the American Fisheries Society* 135: 570–583.

Hanks, R. D. 2020. "Dams." In *Encyclopedia of the World's Biomes*, 169–179. Elsevier.

Hanks, R. D., and K. J. Hartman. 2019. "Evaluation of the Influences of Dam Release Types, Land Use, and Habitat Affecting Abundance, Richness, Diversity, Andcommunity Structure of Larval and Juvenile Fish." *Canadian Journal of Fisheries and Aquatic Sciences* 76, no. 8: 1388–1397.

Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and B. D. Jones III. 1998. "Stream Biodiversity: The Ghost of Land Use Past." *Proceedings of the National Academy of Sciences of the United States of America* 95: 14843–14847.

Harrelson, C. C., C. L. Rawlins, and J. P. Potyondy. 1994. *Stream Channel Reference Sites: An Illustration Guide to Field Techniques*, 61. US Department of Agriculture.

Helms, B. S., D. C. Werneke, M. M. Gangloff, E. E. Hartfield, and J. W. Feminella. 2011. "The Influence of Low-Head Dams on Fish Assemblages in Streams Across Alabama." *Journal of the North American Benthological Society* 30: 1095–1106.

Herbert, M. E., and F. P. Gelwick. 2003. "Spatial Variation of Headwater Fish Assemblages Explained by Hydrologic Variability and Upstream Effects of Impoundment." *Copeia* 2003: 273–284.

Horwitz, R. J. 1978. "Temporal Variability Patterns and the Distributional Patterns of Stream Fishes." *Ecological Monographs* 48: 307–321.

Hubbell, J. P., J. F. Schaefer, P. Flood, J. Warren, L. Melvin, and K. A. Sterling. 2020. "Fragmentation Alters Ecological Gradients and Headwater Fish Assemblage Composition Relative to Land Use in a Dendritic River System." *Canadian Journal of Fisheries and Aquatic Sciences* 77: 1281–1291.

Hurvich, C. M., and D. L. Tsai. 1989. "Regression and Time Series Model Selection in Small Samples." *Biometrika* 76: 298–307.

ICOLD. 2011. *Constitution Statuts*, 21. International Commission on Large Dams.

Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. "What Controls Who Is Where in Freshwater Fish Commuities—The Roles of Biotic, Abiotic, and Spatial Factors." *Canadian Journal of Fisheries and Aquatic Sciences* 58: 157–170.

Jelks, H. L., S. J. Walsh, N. M. Burkhead, et al. 2008. "Conservation Status of Imperiled North American Freshwater and Diadromous Fishes." *Fisheries* 33: 372–407.

Johnson, P. T. J., J. D. Olden, and M. J. V. Zanden. 2008. "Dam Invaders: Impoundments Facilitate Biological Invasions Into Freshwaters." *Frontiers in Ecology and the Environment* 6: 357–363.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. "The Flood Pulse Concept in River-Floodplain Systems." In *Proceedings of the International Large River Symposium*, Canadian Special Publications of Fisheries and Aquatic Sciences 106, edited by D. P. Dodge, 110–127. NRC Research Press.

Jupke, J. F., and R. B. Schäfer. 2020. "Should Ecologists Prefer Model- Over Distance-Based Multivariate Methods?" *Ecology and Evolution* 10, no. 5: 2417–2435.

Keck, B. P., Z. H. Marion, D. J. Martin, et al. 2014. "Fish Functional Traits Correlated With Environmental Variables in a Temperate Biodiversity Hotspot." *PLoS One* 9: e93237.

Knothe, G. J., J. H. O'Connor, and C. T. Mallison. 2022. "Fish Assemblage and In-Stream Habitat Variation in Relation to Dam Structures on the Withlacoochee River, Florida, With Notes on Historical Records." *Southeastern Naturalist* 21: 258–280.

Kominoski, J. S., A. Ruhi, M. M. Hagler, et al. 2018. "Patterns and Drivers of Fish Extirpations in Rivers of the American Southwest and Southeast." *Global Change Biology* 24: 1175–1185.

Kraft, N. J. B., P. B. Adler, O. Godoy, et al. 2015. "Community Assembly, Coexistence and the Environmental Filtering Metaphor." *Functional Ecology* 29: 592–599.

Kruk, A., and T. Penczak. 2003. "Impoundment Impact on Populations of Facultative Riverine Fish." *International Journal of Limnology* 39: 197–210.

Lavorel, S., K. Grigulis, S. McIntyre, et al. 2008. "Assessing Functional Diversity in the Field—Methodology Matters!" *Functional Ecology* 22: 134–147.

Legendre, P., and M. J. Anderson. 1999. "Distance-Based Redundancy Analysis: Testing Multispecies Responses in Multifactorial Ecological Experiments." *Ecological Monographs* 69: 1–24.

Legendre, P., and E. D. Gallagher. 2001. "Ecologically Meaningful Transformations for Ordination of Species Data." *Oecologia* 129: 271–280.

Legendre, P., R. Galzin, and M. L. Harmelin-Vivien. 1997. "Relating Behavior to Habitat: Solutions to the Fourth-Corner Problem." *Ecology* 78, no. 2: 547–562.

Lima, A. C., F. J. Wrona, and A. M. V. M. Soares. 2017. "Fish Traits as an Alternative Tool for the Assessment of Impacted Rivers." *Reviews in Fish Biology and Fisheries* 27: 31–42.

Matthews, W. J. 1986. "Fish Faunal 'Breaks' and Stream Order in the Eastern and Central United States." *Environmental Biology of Fishes* 17: 81–92.

May, M. M. 1963. *A Study of Fishes of the Cahaba River Drainage System of Alabama*. University of Alabama.

Mims, M. C., and J. D. Olden. 2012. "Life History Theory Predicts Fish Assemblage Response to Hydrologic Regimes." *Ecology* 93: 35–45.

Mims, M. C., and J. D. Olden. 2013. "Fish Assemblages Respond to Altered Flow Regimes via Ecological Filtering of Life History Strategies." *Freshwater Biology* 58: 50–62.

Mouillot, D., N. A. J. Graham, S. Villeger, N. W. H. Mason, and D. R. Bellwood. 2013. "A Functional Approach Reveals Community Responses to Disturbances." *Trends in Ecology & Evolution* 28: 167–177.

Nagel, C., M. Mueller, J. Oander, B. C. Stoeckle, R. Khuen, and J. Geist. 2021. "Going With the Flow: Spatio-Temporal Drift Patterns of Larval Fish in a Large Alpine River." *Freshwater Biology* 66, no. 9: 1765–1781.

NID. 2013. "United States National Inventory of Dams Database." United States Army Corps of Engineers.

Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. "Fragmentation and Flow Regulation of the World's Large River Systems." *Science* 308: 405–408.

O'Hare, M. T. 2015. "Aquatic Vegetation – A Primer for Hydrodynamic Specialists." *Journal of Hydraulic Research* 53, no. 6: 687–698.

O'Hare, M. T., C. McGahey, N. Bissett, C. Cailes, P. Henville, and P. Scarlett. 2010. "Variability in Roughness Measurements for Vegetated Rivers Near Base Flow, in England and Scotland." *Journal of Hydrology* 385: 361–370.

Oliveira, A. G., M. T. Baumgartner, L. C. Gomes, R. M. Dias, and A. A. Agostinho. 2018. "Long-Term Effects of Flow Regulation by Dams Simplify Fish Functional Diversity." *Freshwater Biology* 63: 293–305.

Page, L. M., and B. M. Burr. 1973. "Distributional Records for the Crayfishes *Cambarellus puer, C. shufeldti, Procambarus gracilis, P. viaeviridis, Orconectes lancifer, O. bisectus*, and *O. rusticus*." *Transactions of the Kentucky Academy of Science* 34: 51–52.

Pereira, H. R., L. F. Gomes, P. T. Soares, et al. 2021. "Long-Term Responses of Fish Diversity to River Regulation: A Multi-Metric Approach." *Environmental Biology of Fishes* 104, no. 1: 71–84.

Perônico, P. B., C. S. Agostinho, R. Fernandes, and F. M. Pelicice. 2019. "Community Reassembly After River Regulation: Rapid Loss of Fish Diversity and the Emergence of a New State." *Hydrobiologia* 847, no. 2: 519–533.

Phillips, B. W., and C. E. Johnston. 2004a. "Changes in the Fish Assemblage of Bear Creek (Tennessee River Drainage) Alabama and Mississippi: 1968–2000." *Southeastern Naturalist* 3: 205–218.

Phillips, B. W., and C. E. Johnston. 2004b. "Fish Assemblage Recovery and Persistence." *Ecology of Freshwater Fish* 13: 145–153.

Poff, N. L., and J. D. Allan. 1995. "Functional Organization of Stream Fish Assemblages in Relation to Hydrological Variability." *Ecology* 76: 606–627.

Poff, N. L., J. D. Allan, M. B. Bain, et al. 1997. "The Natural Flow Regime." *Bioscience* 47: 769–784.

Pool, T. K., P. Magnan, J. D. Olden, J. B. Whittier, and C. P. Paukert. 2010. "Environmental Drivers of Fish Functional Diversity and Composition in the Lower Colorado River Basin." *Canadian Journal of Fisheries and Aquatic Sciences* 67: 1791–1807.

Pringle, C. M., M. C. Freeman, and B. J. Freeman. 2000. "Regional Effects of Hydrologic Alterations on Riverine Macrobiota in the New World: Tropical–Temperate Comparisons." *Bioscience* 50: 807–823.

Ramler, D., H. Ahnelt, H. L. Nemeschkal, and H. Keckeis. 2016. "The Drift of Early Life Stages of Percidae and Gobiidae (Pisces: Teleostei) in a Free-Flowing Section of the Austrian Danube." *Hydrobiologia* 781, no. 1: 199–216.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Ricotta, C., and M. Moretti. 2011. "CWM and Rao's Quadratic Diversity: A Unified Framework for Functional Ecology." *Oecologia* 167: 181–188.

Ruhr, C. E. 1957. "Effects of Stream Impoundments in Tennessee on the Fish Population of Tributary Streams." *Transactions of the American Fisheries Society* 86: 144–157.

Sayer, C. A., E. Fernando, R. R. Jimenez, et al. 2025. "One-Quarter of Freshwater Fauna Threatened With Extinction." *Nature* 683: 138–145.

Schaefer, J. F., S. R. Clark, and M. L. Warren Jr. 2012. "Diversity and Stability in Mississippi Stream Fish Assemblages." *Freshwater Science* 31: 882–894.

Sheldon, A. L. 1968. "Species Diversity and Longitudinal Succession in Stream Fishes." *Ecology* 49: 193–198.

Šmejkal, M., D. Bartoň, J. Duras, et al. 2023. "Living on the Edge: Reservoirs Facilitate Enhanced Interactions Among Generalist and Rheophilic Fish Species in Tributaries." *Frontiers in Environmental Science* 11: 1099030.

Smith, R. S., E. L. Johnston, and G. F. Clark. 2014. "The Role of Habitat Complexity in Community Development Is Mediated by Resource Availbility." *PLoS One* 9: e102920.

Smith, S. C. F., S. J. Meiners, R. P. Hastings, T. Thomas, and R. E. Colombo. 2017. "Low-Head Dam Impacts on Habitat and the Functional Composition of Fish Communities." *River Research and Applications* 33: 680–689.

Taylor, C. A., J. H. Knouft, and T. M. Hiland. 2001. "Consequences of Stream Impoundment on Fish Communities in a Small North American Drainage." *Regulated Rivers: Research and Management* 17, no. 6: 687–698.

Ticiani, D., C. Larentis, D. R. de Carvalho, A. C. Ribeiro, and R. L. Delariva. 2022. "Dam Cascade in Run-of-River Systems Promotes Homogenisation of Fish Functional Traits in a Plateau River." *Ecology of Freshwater Fish* 32, no. 1: 147–165.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. "The River Continuum Concept." *Canadian Journal of Fisheries and Aquatic Sciences* 37, no. 1: 130–137.

Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, et al. 2010. "Global Threats to Human Water Security and River Biodiversity." *Nature* 467: 555–561.

Walls, B. R. 1968. *Studies on the Fishes of the Bear Creek Drainage of the Tennessee River System*. University of Alabama.

Wang, J., L. Chen, W. Tang, J. Heino, and X. Jiang. 2021. "Effects of Dam Construction and Fish Invasion on the Species, Functional and Phylogenetic Diversity of Fish Assemblages in the Yellow River Basin." *Journal of Environmental Management* 293: 112863.

Ward, J. V. 1976. *Effects of Flow Patterns Below Large Dams on Stream Benthos*. American Fisheries Society.

Ward, J. V., and J. A. Stanford. 1995. "Ecological Connectivity in Alluvial River Ecosystems and Its Disruption by Flow Regulation." *Regulated Rivers: Research and Management* 11: 105–119.

Welcomme, R. L., K. O. Winemiller, and I. G. Cowx. 2006. "Fish Environmental Guilds as a Tool for Assessment of Ecological Condition of Rivers." *River Research and Applications* 22, no. 3: 377–396.

Wolman, M. G. 1954. "A Method of Sampling Coarse River-Bed Material." *Transactions of the American Geophysical Union* 35: 951–956.

Yeager, B. L. 1993. "Impacts on Warmwater Streams: Guidelines for Evaluation." In *Dams*, edited by C. F. Bryan and D. A. Rutherford, 57–113. American Fisheries Society.

Young, P. S., L. C. Thompson, and J. J. Cech Jr. 2011. "Hydropower-Related Pulsed-Flow Impacts on Stream Fishes: A Brief Review, Conceptual Model, Knowledge Gaps, and Research Needs." *Reviews in Fish Biology and Fisheries* 21: 713–731.

Zhang, C., M. Fujiwara, M. Pawluk, H. Liu, W. Cao, and X. Gao. 2020. "Changes in Taxonomic and Functional Diversity of Fish Communities After Catastrophic Habitat Alteration Caused by Construction of Three Gorges Dam." *Ecology and Evolution* 10: 5829–5839.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.