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RESEARCH ARTICLE

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Crayfish assemblages correlate with dam-induced effects on abiotic factors and predatory fish assemblages in Alabama streams

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Abstract

Stream faunal assemblage structure is tied closely to hydrology and associated physiochemical properties. By altering natural flows, dams and their impoundments impact faunal assemblages over long distances. Although numerous studies have assessed the effect of dams on stream fauna, information is lacking for crayfishes. In this study, we characterized the effects of relatively large storage dams on crayfish assemblage structures. Over 2 years, we sampled three impounded and two unimpounded streams across two drainages in Alabama, United States, to identify biotic and abiotic factors correlated with crayfish assemblage metrics. Compared to impounded streams, unimpounded streams had greater habitat complexity (e.g., aquatic vegetation and woody debris), fewer predator fishes, lower minimum temperatures, and more variable discharges. These characteristics correlated with a higher density and diversity of crayfishes and smaller adults in impounded compared to unimpounded streams. Crayfish species assemblages differed between drainages, as did the biotic and abiotic factors affecting crayfish assemblages in each drainage, suggesting that these factors were species-specific in their effects. Additionally, analysis of land uses suggested that factors other than dams may have also contributed to the observed differences in assemblage structures between impounded and unimpounded streams. For instance, in the more urbanized drainage, crayfish assemblages were more similar between up and downstream sections in all streams, regardless of impoundment. Our results indicate that large dams alter stream crayfish assemblage structure, with potentially cascading effects in trophic and organic matter dynamics both up and downstream.

KEYWORDS
crayfish assemblage structure, impoundments, land use changes, predator fish, stream environmental characteristics

1 | INTRODUCTION

The defining characteristic of lotic systems is flowing water (Poff et al., 1997), yet in over half of the world's rivers, natural flow patterns are disrupted (McAllister et al., 2001). Dams and impoundments are one of the most prevalent and extreme alterations to lotic systems (Grill et al., 2015) and cause changes to a river's hydrological regime, temperature regime, chemistry, channel geomorphology, and floodplain connectivity (Baxter, 1977; Chu et al., 2015; Graf, 2006; Helms et al., 2011; Ward, 1976). These

alterations to lotic systems modify the quality, distribution, and access to key habitats which may detrimentally affect some species and favor others, impacting local community structure and function (Stanford et al., 1996; Turgeon et al., 2019). Habitat generalists and predatory fishes tend to tolerate altered river conditions and are often associated with impounded rivers, where they are stocked for sport fisheries. (Phillips & Johnston, 2004; Taylor et al., 2001; Turgeon et al., 2019). Predatory fishes play a large role in structuring freshwater systems through top-down effects (Batzer, 1998; Diel, 1995), impacting densities, size-structure, and species composition of prey communities, with crayfishes as a primary prey for many game fishes (Dorn & Mittlebach, 1999). The elevated abundance of top predators can lead to an imbalance between predator consumption and prey abundance (Eby et al., 2006; Ploskey & Jenkins, 1982), causing changes in food web structures and potentially creating trophic cascades.

Numerous studies have examined the impacts of dams and impoundments on different faunal groups, but only three assessed impacts on crayfish assemblages, and two of those focused on small dams or weirs (Adams, 2013; Joy & Death, 2001). No prior study has assessed how changes to stream abiotic properties and predator fish assemblages induced by relatively large dams and associated impoundments (dam height >15 m, impoundment area >400 ha) impact crayfishes (Barnett & Adams, 2021; Barnett, Adams, et al., 2020a). This is a significant omission in our understanding of the riverine trophic structure, as crayfishes are important not only as prey, but also as predators and processors of organic matter (Dorn & Mittlebach, 1999; Hanson et al., 1990; Statzner et al., 2003).

Barnett et al. (2022) assessed differences in crayfish assemblages between streams without dams and those with relatively large dams in the Bear Creek (BCD) and Cahaba River (CRD) drainages, Alabama, United States. Assemblages in unimpounded streams were composed of both habitat generalists and habitat specialists, and gradually shifted in composition downstream. Conversely, crayfish assemblages were similar up and downstream of large dams, with habitat generalist species numerically dominant. Other differences were drainage-specific, with juvenile density and assemblage structures differing between unimpounded and impounded streams only in the BCD. While Barnett et al. (2022) determined that crayfish assemblage structures differed between impounded and unimpounded streams, they did not assess how dam-induced changes to stream characteristics were associated with crayfish assemblages.

Here, we clarify the impacts of large impoundments on crayfishes in streams studied by Barnett et al. (2022) by examining relationships of crayfish assemblage structures to stream physiochemical characteristics and predator fish abundances in impounded and unimpounded streams. We address two primary questions: (1) Do stream fish communities and abiotic characteristics differ between impounded and unimpounded streams within a drainage, and if so, are differences consistent between drainages? (2) Do differences in stream characteristics correlate with differences in crayfish assemblages? Additionally, we evaluate whether any land use differences between drainages might confound the interpretation of dam effects.

2 | METHODS

2.1 | Study area

We sampled lotic sections of three impounded and two unimpounded streams in the southern Appalachian Mountains of Alabama (Figure 1, see Barnett et al. (2022) for details). In the BCD (Tennessee River Basin), we sampled two impounded (Little Bear and Cedar creeks) and one unimpounded (Rock Creek) stream. In the CRD (Mobile River Basin), we sampled one impounded (Little Cahaba River) and one unimpounded (Shades Creek) stream. Each impounded stream had one earthen storage dam (17–29 m high), creating 425 to 1700 ha impoundments (Appendix S1). The BCD impoundments were flood-control impoundments, with water released from outlets more than 19 m below full-pool levels from November until February and during heavy rain events. The CRD impoundment stored water for municipal use, with water released from outlets more than 10 m below full-pool levels when river water levels were insufficient to meet water municipal demands. Dams in both drainages pass normal inflows via spillways throughout the year.

2.2 | Data collection

To assess the association between environmental effects of large dams and the assemblage structure of stream crayfishes, we conducted a two-scaled field survey in two impounded and three unimpounded streams in the BCD (24 sites) and CRD (14 sites). We sampled streams in the spring and fall of 2015 to assess the within-drainage effects of impoundments on crayfish assemblages in the BCD (Barnett et al., 2022). During the second sampling year (fall 2016 and spring 2017), we sampled streams in the BCD and CRD to assess whether impoundment effects were consistent between drainages. During within-drainage comparisons, we sampled one unimpounded (Rock Creek) and two impounded (Little Bear and Cedar creeks) streams in the BCD ($N = 24$ sites). During between-drainage comparisons, we sampled one unimpounded and one impounded stream in both the BCD ($N = 16$; Rock [unimpounded] and Little Bear [impounded] creeks) and CRD ($N = 14$; Shades Creek [unimpounded] and Little Cahaba River [impounded]). We selected three to five sites at set intervals, based on stream distance up and downstream of impoundments (hereafter, "up and downstream sections"). In unimpounded streams, we mimicked those site distributions, using distance from headwaters to identify the stream's longitudinal midpoint (Figure 1).

2.2.1 | Land use

As in Barnett et al. (2022), we used imagery from Landsat 8 Operational Land Imager to quantify recent (2014 and 2015) land use for each stream's HUC level 11 watershed. Supervised classifications in ERDAS Imagine (v. 16) processing software were used to classify land

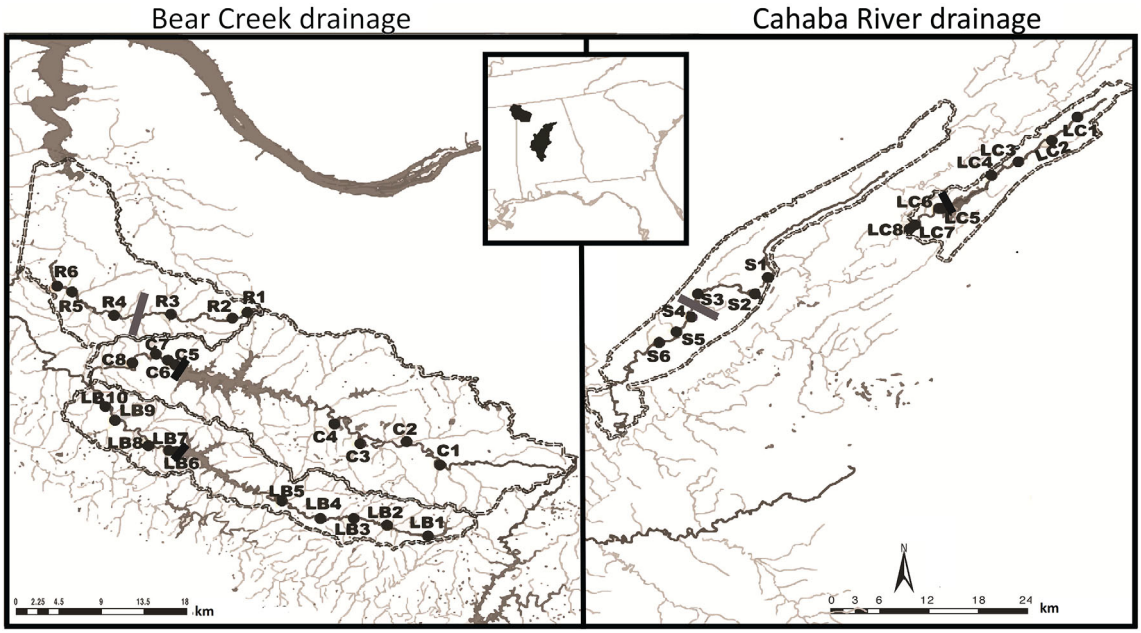

FIGURE 1 Bear Creek (BCD) and Cahaba River (CRD) drainages, Alabama, with collection sites represented by labeled circles. All BCD streams were assessed in within-drainage comparisons. All streams except Cedar Creek were assessed in between-drainage comparisons. Sites are numbered in ascending order 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). Dashed lines delineate each stream's watershed. Solid lines crossing streams delineate stream's up and downstream sections. Inset shows drainage locations within the southeastern United States, with the BCD in the northwest corner and the CRD in the center of Alabama. [Color figure can be viewed at wileyonlinelibrary.com]

use as forest, water, agriculture (including grasses), barren, or developed. The overall classification accuracy (mean = 90%) and Kappa statistics (mean = 0.81) showed that supervised classifications were suitable for this assessment (Congalton & Green, 1999; Tso & Mather, 2001).

2.2.2 | Environmental data

Channel and water quality characteristics (Appendix S4 and S5) were measured at each site during spring and fall sampling. We first measured water quality parameters (temperature, conductivity, dissolved oxygen [DO], and pH) with a Hydrolab Quanta (HACH-Hydrolab, Loveland, CO) at one location in each site. We estimated the percentage of each site containing riffles. We also measured channel characteristics (wetted width [m], depth [cm], and canopy cover [%]) at four evenly spaced transects. Stream depth was measured mid-channel and 10 cm away from right and left edges. The canopy cover was measured mid-channel with a convex spherical densiometer.

Using Wolman pebble count procedures (Barnett et al., 2020b; Wolman, 1954), we analyzed streambed composition across the bankfull channel width. Ten zig-zag transects were sampled at each site. We sampled 10 points from one bank to the other in each transect (100 sampling points/site). At each sampling point, we measured the substrate and woody debris (if present). Between adjacent substrate sampling points, we visually estimated the percentage of streambed covered by vegetation and small woody debris (SWD) (Bain & Stevenson, 1999), and counted pieces of large woody debris (LWD). Streambed composition was used as a measure of habitat complexity, with larger substrate sizes and woody debris, as well as more vegetation and SWD, indicating sites with greater habitat complexity.

We recorded hourly water temperatures with iButton data loggers (Maxim Integrated, San Jose, CA) in the BCD and CRD from fall 2015 and spring 2016, respectively, until the completion of the study and calculated stream temperature metrics (Appendix S4). Because we did not have hourly water temperature data for spring 2015, we estimated spring 2015 stream temperature metrics using linear regressions of the relationship between our measured (fall 2015–spring 2017) water temperatures and air temperatures (Muscle Shoals, AL, KMSL, NOAA weather station). We used the resulting linear regression to estimate spring 2015 water temperatures from NOAA air temperatures over the same period.

We assessed stream discharge throughout the study period using discharge measured at each site during sampling, as well as United States Geological Survey (USGS) and Tennessee Valley Authority (TVA) discharge data from one location on each stream. During each sampling period, we measured 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 one transect per site, with at least 25 measurements taken at each transect. For each stream, we regressed measured discharge on distance downstream. Linear relationships were calculated separately for up and downstream sections of impounded streams. We used these relationships to calculate hourly discharges at each site from USGS

and TVA discharge data. We calculated discharge metrics from one site on unimpounded streams and one site up and downstream (Appendix S1) on impounded streams using hourly TVA impoundment inflow and outflow discharge data and USGS data for BCD and CRD streams, respectively. Because there was no gauge on Rock Creek, we estimated discharge at site R1 (furthest upstream Rock Creek site) by using linear regressions to evaluate the relationship between discharge measured during sampling at site R1 and Cedar Creek impoundment inflow data, due to their close proximity to each other. Discharges were likely underestimated because we did not account for tributary contributions. TVA discharge data was unavailable for within-drainage comparisons.

2.2.3 | Crayfish assemblage data

At all sites, crayfishes were sampled in a linear reach 30 times the wetted stream width, or a minimum or maximum length of 200 and 500 m, respectively (Barnett et al., 2022). Crayfishes were collected from riffles and runs by simultaneously single-pass electrofishing (3–8 s/m; mean 5 s/m ± 1.2 SD) upstream subreaches (half the reach length) and kick seining (20 plots/100 m, 2 m long × 1.5 m wide) downstream subreaches (see Barnett et al., 2021). Because kick seining creates high turbidity and does not depend on seeing target animals like electrofishing does, we always kick seined downstream of electrofishing subreaches. Because these methods are ineffective in pools and deeper water, we did not sample in depths greater than 1 m (≤15% of each reach). Before sampling began, we calculated the total number of kick seines and the electrofishing duration, based on subreach areas. Once we reached the target sampling effort, we stopped sampling (Barnett et al., 2021). We recorded the area (m^2) sampled by each method. For all crayfishes captured, we recorded species, life stage, and postorbital carapace length (POCL; mm). We summarized crayfish assemblages at each site in three ways: assemblage structure (species-by-site matrices of relative densities); adult and juvenile relative densities of all species combined (N/100 m^2); and adult sizes. To assess adult sizes, we calculated the 25th and 75th percentiles of POCLs for each site (combined across seasons) to represent the size of small and large adults, respectively.

2.2.4 | Predator fish assemblage data

While sampling for crayfishes, we also collected fishes. We identified fishes that were crayfish predators (hereafter, "predator fishes") and further defined a subset as "top predators". Fish species were designated as predator fishes if the FishTraits database (Frimpong & Angermeier, 2009) indicated that they ate other fishes, crayfishes, crabs, or frogs. We classified all basses and catfishes (Appendix S3) as "top predator fishes" because greater than 40% of their diets can include crayfishes (Dorn & Mittlebach, 1999). We recorded fish species and total lengths. We preserved voucher specimens in 10% formalin. To confirm that predator fishes were eating crayfishes, we examined fish gut samples from predator fishes collected within BCD impoundments ($N = 99$), and 45% of fish had consumed at least one crayfish.

To estimate predator fish biomass, we conducted additional electrofishing surveys summer 2015–2017 (Barnett, Ochs, et al., 2020b) at 20 of the sampled sites. We recorded the species, total length, and weight of each predator fish. We used length-weight polynomial relationships of predator fishes to calculate the total and average biomasses of predator and top predator fishes collected during crayfish sampling.

2.3 | Data analyses

Our research assessed how differences in stream biotic and abiotic properties in the presence of dams are associated with crayfish assemblage structures. To test for differences in crayfish assemblages between impounded and unimpounded streams, we used split-plot designs with streams as whole-plot factors, and stream sections upstream or downstream of dams or midpoints as split-plot factors. Within- and between-drainage effects were assessed separately for each analysis. Within-drainage effects assessed all study streams in the BCD. Between-drainage effects assessed one impounded and one unimpounded stream in the BCD (unimpounded: Rock Creek, impounded: Little Bear Creek) and CRD (unimpounded: Shades Creek, impounded: Little Cahaba River). We also assessed recent land uses differences among streams to assess land use as a potential confounding factor.

2.3.1 | Assessment of land use differences between drainages

To assess whether land use differences confounded our interpretation of dam effects on crayfish assemblages, we examined whether land uses differed between drainages. We assembled Euclidean distance matrices between land uses of each watershed and used PERMANOVAs to identify land use differences between drainages. If land uses differed, we used multivariate, distance-based linear models (McArdle & Anderson, 2001) to assess what land uses contributed most to the differences. 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 & Anderson, 2004). Delta AIC_c values ≤2 represented the best-supported models (Hurvich & Tsai, 1989). PERMANOVAs and distance-based linear models were performed in PRIMER. Because land use percentages were not calculated for each site or stream section, any land use differences detected were not included in the remaining analyses, but we discuss land use when interpreting findings.

2.3.2 | Stream characteristic comparisons

To identify stream characteristics that best separated up and downstream sections of impounded and unimpounded streams, we used canonical analysis of principal coordinates (CAP) (Anderson & Willis, 2003). This analysis uncovers the axes in principal coordinates space that best discriminates between a priori groups. Treatment (impounded vs. unimpounded) and stream section (up vs. downstream) were used as our a priori groups. For each site, we averaged predator fish assemblage, discharge, and channel and streambed characteristics from spring and fall sampling, separately. All data (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).

2.3.3 | Crayfish assemblage associations with stream characteristics

We modeled the relationship of crayfish assemblages to stream characteristics for within- and between-drainage comparisons, separately (Appendix S2). Data for these analyses came from Barnett et al. (2022). Because we were interested in differences between up and downstream sections of impounded and unimpounded streams, only crayfish assemblage and stream characteristics that differed between impounded and unimpounded stream sections (as indicated in Barnett et al. (2022)) were included in the analyses. Dependent variables included assemblage structure (species × site matrices of densities), juvenile and adult densities, and sizes of adult crayfishes. Independent variables were stream characteristics that discriminated between up and downstream sections of impounded and unimpounded streams.

We measured the strength and significance of relationships between crayfish assemblage structure and stream characteristics by using multivariate, distance-based, linear models. After square root transforming crayfish relative densities, we assembled a matrix of Bray-Curtis similarities between pairs of sites. All stream characteristics were $\log_e$ (variable + 1) transformed and normalized. We used the "Best" selection procedure as described above ("assessment of land use differences"). For each predictor variable, relative variable importance was calculated based on the presence of variables in the AICc-best models (Burnham & Anderson, 2004). The total weight of each variable is summed across all best models, with values close to 1 indicating variables that occur in a large portion of models. Predictors with relative variable importance >0.5 were considered important. Important stream characteristics were plotted as vectors in NMDS ordinations of crayfish assemblage structures. Analyses were performed using PRIMER.

We assessed relationships between univariate crayfish assemblage measures (relative density and adult size) and stream characteristics that discriminated between stream sections in impounded and unimpounded streams by using linear mixed-effect repeated-measures (LME) models. We fit LME models with maximum likelihood estimations using the "lmer" function in the *lmerTest* package (Kuznetsova et al., 2015) in R software (version 3.4.2; R Project for Statistical Computing, Vienna Austria). In the models, the assemblage measure was the dependent variable and the site was the random effect. We assessed all within-drainage relationships using the following LME model:

crayfish assemblage measure ~ wood size + turbidity + minimum temperature + temperature variation + median particle size + percent vegetation + top predator biomass + (1|site).

We assessed all between-drainage relationships using the following LME model:

crayfish assemblage measure ~ turbidity + LWD + discharge variation + minimum discharge + maximum discharge + median particle size + top predator biomass + (1|site).

Marginal (variance explained by fixed effects) and conditional (variance explained by fixed and random effects) R^2 were calculated using the "R^2_{GLMM}" function of the *MuMIn* package.

3 | RESULTS

3.1 | Assessment of land use differences between drainages

Land use differed between the BCD and CRD (PERMANOVA $F_{1,9} = 26.20$, $p < 0.01$), with agricultural lands abundant in BCD ($r = 0.92$) and developed lands abundant in CRD ($r = 0.95$) (Table 1; Figure 2).

3.2 | Comparisons between impounded and unimpounded stream characteristics

For within- and between-drainage comparisons of stream characteristics, CAP supported the distinctiveness between impounded and unimpounded streams, as well as the distinctiveness between up and downstream sections of impounded streams (within-drainage: LOO = 89%; between-drainage: LOO = 88%). In within-drainage comparisons, CAP axis 1 separated stream characteristics of upstream sites in unimpounded streams from sites downstream of impoundments, and CAP axis 2 separated stream characteristics of sites upstream of impoundments from sites downstream of impoundments

TABLE 1 Land use percentages for each stream's watershed, and mean drainage land use percentage (% difference from Cahaba River Drainage).

		Little Bear	Cedar	Rock	Drainage mean
Bear Creek Drainage					
	Agriculture	12.8	14.5	8.2	11.8 (8.9)
	Water	3.0	3.8	1.0	2.7 (1.1)
	Barren	2.3	2.4	2.6	2.4 (−2.3)
	Forest	79.9	74.3	86.2	80.1 (10.8)
	Developed	2.0	5.0	1.9	3.0 (−18.5)
Cahaba River Drainage		Little Cahaba	Shades		
	Agriculture	1.7	4.2		2.9
	Water	2.5	0.6		1.6
	Barren	5.2	4.3		4.7
	Forest	76.0	62.6		69.3
	Developed	14.6	28.3		21.5

and from all unimpounded stream sites (within-drainage: eigenvalue CAP 1 = 0.91, eigenvalue CAP 2 = 0.85) (Figure 3a). Upstream sites in unimpounded streams had lower top predator fish biomass, lower minimum temperature, higher temperature variation, and smaller substrate than sites downstream of impoundments (Figure 3a; Table 2; Appendix S5). Sites upstream of impoundments had less vegetation, lower turbidity, and smaller woody debris than sites downstream of impoundments and all unimpounded stream sites (Figure 3a; Table 2 Appendix S5).

In between-drainage comparisons, CAP axis 1 separated sites downstream of impoundments from sites upstream of impoundment and all unimpounded sites, and CAP axis 2 separated all unimpounded stream sites from sites upstream of impoundments (between-drainage: eigenvalue CAP 1 = 0.93; eigenvalue CAP 2 = 0.82) (Figure 3b). Sites downstream of impoundments had more LWD, higher top predator fish biomass, larger substrate, and lower discharge variation than sites upstream of impoundments and all unimpounded stream sites (Figure 3b; Table 2). Unimpounded stream sites had higher turbidity and lower minimum and maximum discharge than sites upstream of impoundments (Figure 3b; Table 2; Appendix S5).

3.3 | Crayfish assemblage associations with stream characteristics

In the BCD and CRD, seven and eight crayfish species were collected, respectively, including habitat specialists that use both streams and riparian zones and those that are predominately found in one microhabitat (i.e., rocky riffles) (Table 3) (Barnett et al., 2022). Ninety percent of habitat specialist collections were from unimpounded streams. *Faxonius validus* (Faxon, 1914) and *F. erichsonianus* (Faxon, 1898) were most widespread (present in >90% of sites) in the BCD, and *F. virilis* (Hagen, 1870), an introduced species (Hamr, 2002; Hobbs Jr., 1959; Schwarts et al., 1963), was most widespread in the CRD.

Models revealed significant associations between stream characteristics and crayfish assemblage structures (Table 4). For within-drainage comparisons, minimum temperature, top predator biomass, and percent aquatic vegetation were all significant terms in a model that explained 29% of the variation in crayfish assemblage structure (Table 4; Figure 4a). Higher top predator biomass and minimum temperatures in impounded streams, along with more vegetation in the unimpounded stream were correlated with differences between crayfish assemblages in impounded and unimpounded streams (Figures 3a and 4a). In impounded streams, although stream characteristics differed between up and downstream sites, crayfish assemblages were similar. Conversely, unimpounded stream crayfish assemblages differed between up and downstream sites. There were no clear associations between crayfish assemblages and stream characteristics in up and downstream sections of unimpounded streams.

For between-drainage comparisons, minimum and maximum discharge, median particle size (D50), and LWD were all significant terms in a model that explained 29% of assemblage variation (Table 4; Figure 4b). Like within-drainage findings, crayfish assemblage patterns differed from stream characteristic patterns with assemblages differing between up and downstream sections of unimpounded streams but not impounded streams. Larger particle sizes were negatively associated with crayfish assemblages in downstream sections of unimpounded streams, and more LWD and greater discharge variation were positively associated with crayfish assemblages in downstream sections of unimpounded streams. No clear patterns were detected between stream characteristics and crayfish assemblages up and downstream of impoundments.

Stream characteristics were associated with juvenile and adult crayfish relative densities and sizes of adult crayfishes (Table 5). For within-drainage comparisons, juvenile and adult relative densities were negatively associated with top predator biomass and positively associated with aquatic vegetation. Adult relative density was also negatively associated with minimum temperatures. Sizes of small adult crayfishes were negatively associated with aquatic vegetation. For between-drainage comparisons, juvenile crayfish relative density was negatively associated with turbidity. Adult crayfish relative density was negatively associated with top predator biomass and positively

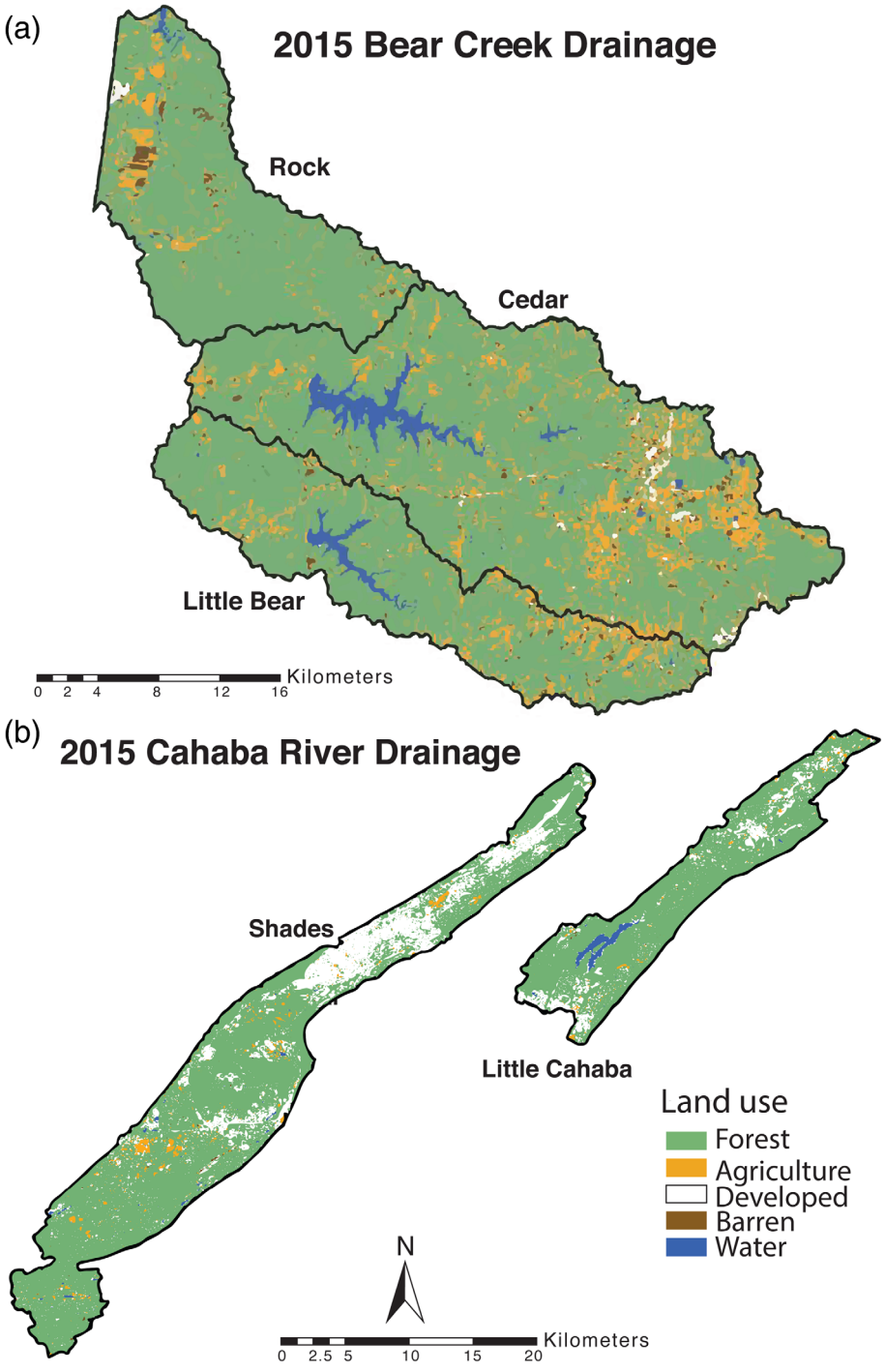

FIGURE 2 Bear Creek (a) and Cahaba River (b) drainage recent land use classifications results of Landsat 8 data using supervised maximum likelihood classifications. Outlined polygons represent each streams' watershed, with stream watersheds labeled outside of polygons. [Color figure can be viewed at wileyonlinelibrary.com]

associated with maximum discharge. Sizes of small adult crayfishes were positively associated with D50 and negatively associated with minimum discharge.

4 | DISCUSSION

Stream characteristics differed between impounded and unimpounded streams and between sites up and downstream of impoundments; however, crayfish assemblage structure differences were detected in only unimpounded streams. Unlike similarities between stream characteristics of unimpounded stream sections, differences between stream characteristics of impounded stream sections disrupted the natural changes within crayfish assemblage structure along a stream continuum. In within-drainage comparisons, less aquatic vegetation and higher minimum temperatures, and top predator biomasses were associated with impounded streams, which Barnett et al. (2022) showed had a homogenized crayfish assemblage when compared to the unimpounded stream. In between-drainage comparisons, differences in minimum and maximum discharge, mean particle sizes,

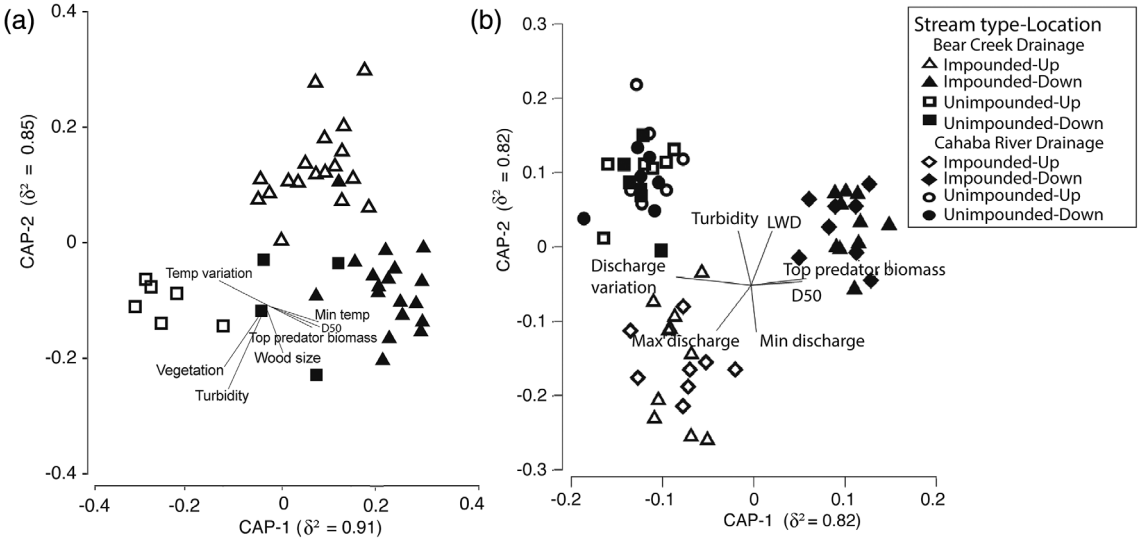

FIGURE 3 Canonical analysis of principal coordinates (CAP) ordination plots based on impounded and unimpounded stream characteristics for within- (a) and between-drainage (b) comparisons. Within-drainage comparisons assessed 2015 measurements of all study streams in the Bear Creek (BCD) Drainage. Between-drainage comparisons assessed 2016–2017 measurements of one impounded and one unimpounded stream in the BCD and Cahaba River drainages. 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 stream types. Up = upstream; Down = downstream; Temp variation = temperature variation; Vegetation = percent aquatic vegetation; Min temp = minimum water temperature; D50 = median particle size; LWD = number of large woody debris; Max discharge = maximum discharge; Min discharge = minimum discharge; Wood size = average size of woody debris; δ^2 = the size of the canonical correlation or strength of the association between the multivariate data and a priori groups.

TABLE 2 Means (SD) of stream characteristics that discriminated between up and downstream sections of impounded and unimpounded streams.

	Impounded		Unimpounded	
Stream characteristics	**Upstream**	**Downstream**	**Upstream**	**Downstream**
Within-drainage comparisons				
Minimum water temperature (°C)	7.3 (1.36)	11.4 (1.57)	6.0 (2.07)	8.9 (4.27)
Temperature variation	21.3 (4.10)	15.0 (3.69)	23.0 (5.06)	24.8 (6.67)
D50	36.4 (23.1)	350.3 (679.8)	66.5 (35.9)	18.3 (5.1)
Aquatic vegetation (%)	9.3 (5.7)	15.4 (9.7)	15.7 (13.0)	32.0 (5.0)
Wood size (mm)	33.2 (21.5)	49.8 (25.3)	28.4 (27.1)	86.8 (37.3)
Turbidity (NTU)	10.0 (3.0)	16.1 (7.4)	16.6 (7.2)	14.1 (6.3)
Top predator biomass (g)	158.3 (207.5)	247.7 (221.4)	4.9 (8.0)	21.2 (25.3)
Between-drainage comparisons				
D50	42.3 (59.4)	363.5 (664.3)	51.2 (49.4)	20.9 (12.3)
Large woody debris (*N*)	5 (6)	8 (7)	6 (7)	12 (6)
Turbidity	7.5 (6.4)	7.8 (3.0)	13.6 (9.17)	12.4 (7.8)
Maximum discharge (m^3/s)	391.91 (499.73)	21.17 (18.83)	62.14 (131.48)	356.00 (421.13)
Minimum discharge (m^3/s)	1.04 (1.52)	0.22 (0.09)	0.04 (0.05)	0.16 (0.20)
Discharge variation	198.81 (33.78)	130.00 (59.45)	229.32 (55.74)	223.22 (58.42)
Top predator biomass (g)	77.2 (103.5)	309.4 (326.8)	28.2 (43.9)	32.2 (78.5)

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. D50 = median particle size (mm). Temperature variation = coefficients of variation for spring and fall water temperatures. All other stream characteristic definitions in Appendix S4.

TABLE 3 Total crayfish density (crayfish/100 m^2) in upstream (up) and downstream (down) sections of impounded and unimpounded streams for within-drainage (W-D) and between-drainage (B-D) comparisons in the Bear Creek and Cahaba River drainages, Alabama, United States.

	Drainage		Impounded				Unimpounded		
W-D	Bear Creek	Crayfish	Cedar-up	Cedar-down	Little Bear-up	Little Bear-down	Rock-up	Rock-down	Total
		Faxonius validus	0.0392	0.0246	0.0768	0.0624	0.5223	0.0162	**0.7416**
		Faxonius erichsonianus	0.0367	0.0163	0.0498	0.0205	0.0346	0.0440	**0.2019**
		*Cambarus striatus**	0.0002	0.0000	0.0018	0.0003	0.0731	0.0077	**0.0832**
		*Faxonius compressus**	0.0000	0.0000	0.0000	0.0024	0.0000	0.0239	**0.0263**
		Faxonius etnieri	0.0000	0.0000	0.0000	0.0000	0.0000	0.0031	**0.0031**
		*Lacunicambarus dalyae**	0.0000	0.0000	0.0004	0.0004	0.0000	0.0023	**0.0031**
Total			**0.0762**	**0.0409**	**0.1288**	**0.0860**	**0.6300**	**0.0972**	1.0591
B-D	Bear Creek								
		Faxonius validus			0.1101	0.0348	0.3804	0.0177	**0.5431**
		Faxonius erichsonianus			0.0576	0.0546	0.0123	0.0610	**0.1855**
		*Cambarus striatus**			0.0070	0.0000	0.0610	0.0077	**0.0757**
		*Faxonius compressus**			0.0000	0.0090	0.0000	0.0471	**0.0560**
		Faxonius etneiri			0.0000	0.0000	0.0000	0.0040	**0.0040**
		*Lacunicambarus dalyae**			0.0000	0.0004	0.0000	0.0100	**0.0104**
		Procambarus hayi			0.0000	0.0007	0.0000	0.0000	**0.0007**
Total					**0.1747**	**0.0995**	**0.4537**	**0.1475**	0.8754
	Cahaba River				Little Cahaba-up	Little Cahaba-down	Shades-up	Shades-down	
		Faxonius virilis			0.0153	0.0048	0.0034	0.0028	**0.0263**
		Faxonius erichsonianus			0.0030	0.0025	0.0019	0.0058	**0.0133**
		Cambarus coosae			0.0001	0.0010	0.0000	0.0000	**0.0011**
		Procambarus clarkii			0.0007	0.0000	0.0000	0.0004	**0.0011**
		*Cambarus striatus**			0.0002	0.0003	0.0000	0.0021	**0.0026**
		*Procambarus acutus**			0.0005	0.0000	0.0000	0.0000	**0.0005**
		Faxonius spinosus			0.0001	0.0000	0.0000	0.0000	**0.0001**
		*Cambarus acanthura**			0.0000	0.0000	0.0000	0.0001	**0.0001**
Total					**0.0200**	**0.0086**	**0.0053**	**0.0111**	0.0450

Note: * = habitat specialist (i.e., species that are secondary burrowers that use the stream riparian zones or that typically use specific microhabitats [i.e., rocky riffles]).

and amount of LWD were associated with impounded stream crayfish assemblages, which were also homogenized (Barnett et al., 2022). Additionally, turbidity, woody debris, substrate particle size, and top predator fish biomass differed between up and downstream sections of impounded and unimpounded streams in within- and between-drainage assessments. Yet, top predator fish biomass was the only variable that was also correlated with crayfish assemblages in both within- and between-drainage assessments, with lower crayfish densities at sites with higher top predator fish biomass. Stream characteristics correlated with crayfish assemblages may have differed between within- and between-drainage comparisons because the discharge variable was only used in between-drainage comparisons. Nonetheless, these results indicate that stream characteristics associated with crayfishes may vary depending on physiographic region and species present.

This is the first study to relate biotic and abiotic variables associated with relatively large dams to crayfish assemblage structure. In Mississippi, small impounded streams had narrower, deeper channels (smaller width to depth [W:D] ratios) compared to unimpounded streams, and this was associated with crayfish catch per unit effort and species presence (Adams, 2013). In the current study, W:D ratios did not differ between impounded and unimpounded streams or between stream sections. Differences between these studies may be due to the finer substrates and erodible soils in the Northern Hilly Gulf Coastal Plain ecoregion sampled by Adams (2013) compared to the Southeastern Plains and Southwestern Appalachians ecoregions

we sampled. Similar to Adams (2013), water quality parameters did not differ between impounded and unimpounded stream sections (except turbidity, which was not measured by Adams, 2013). Because we measured water quality only when we sampled crayfishes and water quality can vary widely within seasons, we could not evaluate long-term effects on water quality caused by impoundments.

TABLE 4 Distance-based linear model results of stream characteristics that best explained within- and between-drainage crayfish assemblage structure.

Model	R^2	N	Pseudo-F	RVI
Within-drainage	0.29	5		
Vegetation			5.76**	1.00
Total top predator biomass			5.29**	0.60
Minimum temperature			4.32**	0.80
Temperature variation			2.04	0.40
Between-drainage	0.29	6		
D50			6.09**	1.00
Maximum discharge			5.32**	1.00
Large woody debris			3.78*	0.83
Minimum discharge			2.60*	0.83
Flashiness			1.34	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; * = $p \leq 0.05$; ** = $p \leq 0.01$; RVI = relative variable importance (variables with RVI of 1.00 were included in all of the best models); D50 = median particle size.

Fish predation can significantly reduce crayfish abundances (Englund, 1999; Mather & Stein, 1993; Nystrom et al., 2006). In the current study, top predator fish (bass and catfish) biomasses were higher in impounded than unimpounded streams and higher downstream than upstream of impoundments, which correlated with decreased relative densities of crayfishes. Fishes are gape-limited predators, with larger fish able to consume larger prey. Additionally, predator fishes are often more abundant in impounded streams due to their relatively high tolerances of altered conditions and their stocking as game fishes (Phillips & Johnston, 2004; Taylor et al., 2001), with crayfishes being the primary food sources for many game fishes (Dorn & Mittlebach, 1999). Recreational impoundments are often stocked and managed for larger game fishes (Michaletz & Dillard, 1999), which can impact entire stream systems, depending on the ability of fishes to disperse up and downstream of dams (Ruhr, 1956; Winston et al., 1991).

In seasonally variable environments, stream biota evolved under dynamic hydrographs. Stabilization of natural flow and temperature regimes by dams can drastically impact key life history events of stream fauna. Crayfish mating, spawning, foraging, and growth are all linked to water temperatures and flows (Barnett et al., 2017; Lowery, 1988; Mead, 2008). The new environment created by a stabilized flow and temperature regime can also impact crayfish assemblage structure, with a decrease in habitat specialists, and increase in habitat generalist and invasive species (Bunn & Arthington, 2002; Light, 2003), creating more homogenized stream assemblages (Rahel, 2002). In the current study, stream temperatures and flow variations were correlated with crayfish assemblage structures. For

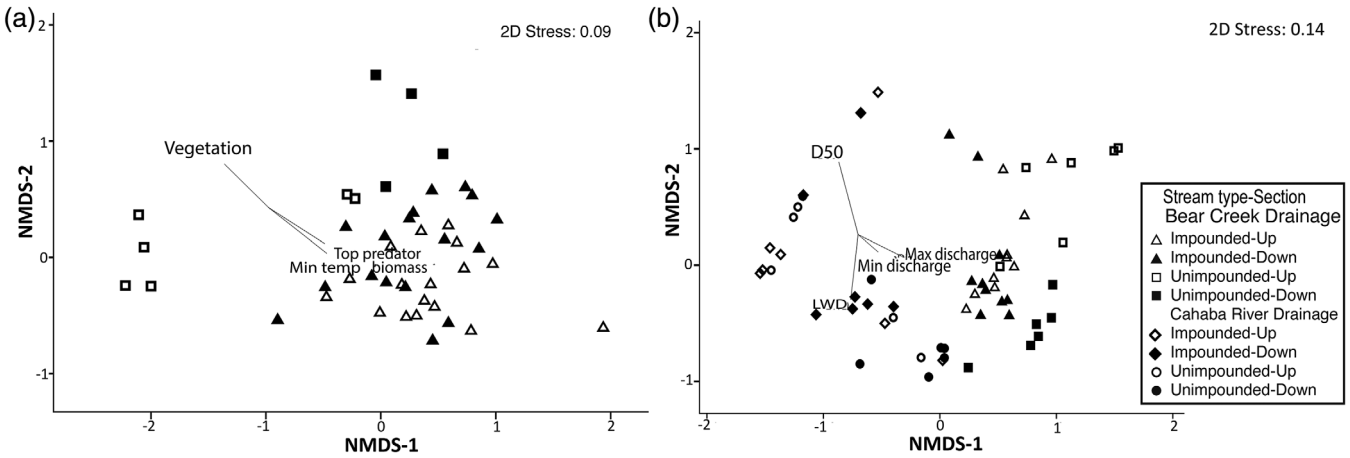

FIGURE 4 Assemblage structure ordinations (NMDS) based on crayfish relative densities for within- (a) and between-drainage (b) comparisons. Within-drainage comparisons assessed all study streams in the Bear Creek (BCD) Drainage. Between-drainage comparisons assessed one impounded and one unimpounded stream in the BCD and Cahaba River drainages. Symbols represent sites from each stream (a) or stream type (b) and location within streams (up or downstream). Some symbols overlap. Stream characteristics that discriminated between impounded and unimpounded streams and were strongly correlated with the ordination (see stream characteristic results) are overlayed. Stream characteristic vectors show the relative association and magnitude of correlation for each variable. Up = upstream; Down = downstream; Vegetation = percent aquatic vegetation; Min temp = minimum water temperature; D50 = median particle size; LWD = number of large woody debris; Max discharge = maximum discharge; Min discharge = minimum discharge.

TABLE 5 Linear models of crayfish assemblage relationships with stream characteristics (listed in order of increasing *p* values) that discriminated between impounded and unimpounded streams.

Comparison	Dependent variables	Explanatory variables	Estimate	*F*	*p*	*M-R²*	*C-R²*
W-D	Juvenile relative density	Top predator biomass	−0.104	8.03	<0.01	0.39	0.48
		Aquatic vegetation	0.528	9.07	0.05		
		Minimum temperature	−1.243	2.76	0.10		
		Turbidity	0.622	2.42	0.13		
		Temperature variation	−1.000	1.54	0.22		
		Wood size	−0.138	0.57	0.46		
		D50	0.065	0.33	0.57		
	Adult relative density	Top predator biomass	−0.083	16.30	< 0.01	0.55	0.55
		Aquatic vegetation	0.248	5.50	0.02		
		Minimum temperature	−0.990	5.44	0.02		
		Turbidity	−0.429	3.69	0.06		
		D50	0.084	1.90	0.18		
		Wood size	0.097	1.02	0.32		
		Temperature variation	−0.138	0.09	0.76		
	Small crayfish size	Aquatic vegetation	−0.060	4.39	0.05	0.20	0.44
		Minimum temperature	−0.166	2.49	0.13		
		Wood size	−0.043	2.00	0.18		
		Temperature variation	−0.065	1.80	0.20		
		Turbidity	0.039	1.48	0.24		
		Top predator biomass	0.006	0.78	0.39		
		D50	0.003	0.14	0.72		
B-D	Juvenile relative density	Turbidity	0.873	11.42	< 0.01	0.53	0.55
		Discharge variation	1.016	3.69	0.06		
		Top predator biomass	−0.072	3.07	0.09		
		D50	−0.191	2.06	0.16		
		LWD	−0.226	1.32	0.26		
		Maximum discharge	−0.039	0.11	0.74		
		Minimum discharge	−0.107	0.07	0.80		
	Adult relative density	Top predator biomass	−0.056	4.31	0.04	0.24	0.34
		Maximum discharge	0.146	3.96	0.05		
		Discharge variation	−0.269	1.38	0.24		
		Turbidity	−0.120	0.71	0.40		
		D50	−0.022	0.11	0.75		
		Minimum discharge	−0.090	0.08	0.78		
		LWD	−0.015	0.02	0.89		
	Small crayfish size	D50	0.058	8.99	< 0.01	0.34	0.51
		Minimum discharge	−0.090	4.18	0.05		
		Top predator biomass	0.272	3.14	0.09		
		Maximum discharge	−0.040	1.96	0.18		
		Turbidity	−0.146	1.83	0.19		
		LWD	−0.065	1.07	0.31		
		Discharge variation	0.227	0.36	0.55		

Note: Explanatory variables are ordered by decreasing *F*-value. M-R^2 = marginal R^2; C-R^2 = conditional R^2; W-D = within-drainage comparison (assessing all sites in the Bear Creek (BCD) Drainage); B-D = between-drainage comparison (assessing one impounded and one unimpounded stream in the BCD and Cahaba River drainage); Small crayfish size = 25th percentile of adult postorbital carapace lengths. Other abbreviations as listed in Figure 3.

example, *Cambarus striatus*, a species that seasonally occupies streams when not residing in streambank or floodplain burrows (Bouchard, 1978), was rarely collected in BCD impounded streams, where flow regimes were more stable and flooding (i.e., stream-floodplain connectivity) likely reduced. Additionally, the most abundant crayfishes collected within flowing sections of BCD impounded streams were also the most abundant crayfishes collected from guts of fishes within impoundments (Barnett et al., 2022), indicating that these crayfish species were habitat generalists adapted to both lentic and lotic conditions.

Habitat complexity is one of the most important factors influencing the assemblage structure and health of stream communities (Angermeier & Karr, 1984; Smith et al., 2014). Reducing habitat complexity may decrease the availability of suitable microhabitats for habitat specialists and limit predation refugia. Barnett et al. (2022) reported few or no habitat specialists in impounded compared to unimpounded streams. Using their data, we found that small crayfishes (juveniles and adults) were less abundant in sites with less vegetation and smaller substrates, conditions more common in impounded streams. Larger crayfishes are less susceptible to predation and better able to secure and retain shelter than smaller crayfishes (Nakata & Goshima, 2003; Rahel & Stein, 1988); therefore, reducing stream habitat complexity puts smaller crayfishes at a disproportionally greater predation risk. For example, a habitat specialist (*Faxonius compressus*) that was 62% shorter than other species and commonly found in shallow, gravelly riffles (Bouchard, 1972) was abundant in unimpounded but not impounded streams in the BCD (Barnett et al., 2022). The low abundance of this species from impounded streams could have been due to a lack of suitable habitat and/or elimination by predation. Predation may also cause smaller crayfishes to alter their habitat use. Juveniles were less abundant at sites with clearer water, and better visibility may increase predation pressure on crayfishes.

Floodplain land use is intimately connected with stream water quality and habitat structure (Rahel, 2002; Scott & Helfman, 2001). The CRD was more urbanized than the BCD, which had more agriculture. In the CRD, only adult crayfish relative densities and sizes varied between impounded and unimpounded streams, whereas in the BCD, assemblage structure, adult and juvenile crayfish relative densities, and adult crayfish sizes differed (Barnett et al., 2022). Similar to dam-induced stream changes (Baxter, 1977; Ward, 1976), urbanization can exacerbate fine sediment loads leading to less interstitial space, decreased aquatic vegetation, and an increase in large piscivorous fish abundance (Slawski et al., 2008; Wang et al., 2001). Because urbanization and impoundments can create similar stream changes, they may lead to similar biotic communities, making it difficult to tease out impoundment effects in the CRD. Additionally, *F. virilis*, an invasive species, was the most abundant crayfish throughout CRD streams, which may create additional stressors for native crayfishes, including outcompeting natives for food and shelter (Weis, 2010). Future research assessing the synergistic effects of impoundments, urbanization, and invasive species is needed.

Unimpounded streams were not perfect controls for impounded streams. In addition to the dams and impoundments themselves, in both drainages, impounded streams had higher maximum and minimum flows upstream of impoundments than we observed in unimpounded streams. Nevertheless, during summer months, stream drying and isolated pools occurred in upstream sections of impounded and unimpounded streams, and upstream sections also had similar species present. Additionally, we sampled a shorter distance along the unimpounded stream than impounded streams in the BCD. 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 detected between crayfish assemblages in downstream sections may not be due to the geographic distances sampled.

Unlike for unimpounded streams, stream characteristics differed between up and downstream sections of impounded streams. Water temperature and flow regimes were more stable, habitats more complex, and predator fish biomass higher downstream of impoundments relative to upstream. Those differences correlated with crayfish assemblage differences, including lower densities and larger-bodied species at more stable and less complex sites. Stream characteristic differences in impounded streams also disrupted the natural changes within crayfish assemblage structure along a stream continuum, with homogenized crayfish assemblages detected in impounded streams (Barnett et al., 2022). Stream characteristics explained much of the density, size, and assemblage structure variation (20–55%) within crayfish communities. Differences in results between drainages may be a consequence of impoundment effects interacting with other factors— including land use, physiographic setting, predator fish biomass, and invasive species— to alter crayfish assemblages. This observational study begins to tease apart the effects of impoundments on crayfish assemblages, but future experimental studies are needed to further disentangle effects of the impoundment, environment, and biota on crayfishes. Experimental studies could shine light on the effect size and direction of change caused to crayfish assemblages. As with other stream faunal assemblages, dam-induced changes to stream characteristics were correlated with differences in crayfish assemblage structure, with potentially cascading effects in trophic dynamics, organic matter processing, and nutrient fluxes.

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DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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