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Environmental Correlates and Ecological Consequences for Long-Term Fish Assemblage Change in an Urbanising and Regulated River Basin

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ABSTRACT

Streams and rivers are increasingly threatened by intensifying land cover and land use (LCLU) change and streamflow alteration at a global scale. Stream fishes provide several ecosystem services and thus understanding fish responses to these anthropogenic changes benefits freshwater conservation and management. We compared historical survey data from 1956 to 1957 to replicated surveys conducted in 2023 to assess long-term changes in taxonomic and functional fish assemblage structure brought on by anthropogenic alterations in the Neches River Basin of Texas. We assessed components of temporal beta diversity to find the predominant form of assemblage change, nestedness or replacement, and related the predominant component to LCLU and streamflow change at whole basin and river mainstem extents. We then examined the relationship between temporal beta diversity and functional dispersion for traits related to fish stream size preference, substrate preference, and capacity to host mussels. Replacement was the primary form of temporal beta diversity at both spatial extents. At the basin extent, streamflow alteration was negatively correlated with replacement, while at the mainstem extent, urbanisation was positively correlated with replacement. Taxonomic replacement was positively correlated with functional dispersion change at high urbanisation levels but showed no relationship at low urbanisation levels or across a gradient of streamflow change. This study leverages rare long-term data to test for patterns in temporal beta diversity at taxonomic and functional levels rather than the more commonly used space-for-time substitutions and provides insight for management actions aimed at conserving stream fish assemblages in the face of LCLU and streamflow alterations.

1 | Introduction

Freshwater ecosystems are increasingly threatened by anthropogenic stressors brought on by intensifying land cover and land use (LCLU) change as well as stream impoundments (Reid et al. 2019). The conversion of forest cover into agriculture and urban areas is a major form of LCLU change globally. For example, from 2000 to 2020, nearly half of the global gross expansion in agriculture came from the removal of natural vegetation and developed land increased by 50% (Potapov et al. 2022). Studies have demonstrated that these alterations are detrimental to the hydrology, morphology and water quality of stream systems (Allan 2004; Walsh et al. 2005; Foufoula-Georgiou et al. 2015). Streams in urban watersheds are often

characterised by increased flash flooding, channel incision, bank erosion, scouring and pollutant loads, largely due to runoff from impervious surfaces; processes collectively known as the urban stream syndrome (Walsh et al. 2005). Meanwhile, agricultural streams are characterised by increased bank erosion, sediment deposition and nutrient inputs leached from fertilisers (Blann et al. 2009). These LCLU changes have occurred in concert with the construction of more than 4.4 million reservoirs (> 0.1 ha surface area) worldwide to impound flowing water for human uses (Lehner et al. 2024). These impoundments fragment stream habitats and homogenise flow regimes (Poff et al. 1997). This regulation of riverine landscapes is so prevalent that only 23% of the world's large rivers (> 1000 km) have unimpeded flow to the ocean (Grill et al. 2019).

The impacts of anthropogenic alterations to freshwater systems have cascading ecological consequences on the ecosystem and on other aquatic taxa. Both LCLU change and river regulation are linked to declines in fish populations and transformations of fish assemblages ultimately caused by habitat degradation and homogenisation (Poff et al. 1997; Allan 2004), habitat fragmentation (Grill et al. 2019), and filtering of pollutant-intolerant species (Walsh et al. 2005). Long-term taxonomic and functional shifts in riverine fish assemblages have been documented in river basins globally as a result of reservoir construction and land use changes, with common patterns being a reduction in both species diversity and habitat specialists (Quinn and Kwak 2003; Leitão et al. 2018; Gao et al. 2019). Because stream fishes support various ecological functions, biodiversity loss can reduce the resilience of rivers and streams to anthropogenic stressors (Holmlund and Hammer 1999). Due to their trophic position, fishes play a role in regulating food web dynamics by exerting top-down controls on lower consumers and primary producers, while also acting as a food source for other taxa such as reptiles, birds, and mammals (Power 1990). Additionally, fishes transport nutrients across spatial boundaries and increase nutrient availability through foraging, spawning, and migratory behaviour (Winemiller and Jepsen 1998). Freshwater mussels, which are vital for nutrient cycling and water quality (Vaughn 2018), require fishes as a host for a parasitic larval phase to complete their life cycle (Kat 1984). Because of this obligatory host relationship, fishes can influence the speciation, adaptation and distribution of freshwater mussels (Kat 1984; Schwalb et al. 2013). In response to drastic declines in mussel populations (Lopes-Lima et al. 2018; Haag 2019), research priorities aimed at promoting mussel conservation have emerged, including assessing fish host availability (i.e., populations) and contact probability (i.e., distributions) as well as impoundment impacts on fish movement (Ferreira-Rodríguez et al. 2019). Ultimately, understanding the impacts global change has on fish assemblages can inform mussel conservation efforts.

Studies assessing ecological responses to global change require careful consideration of the natural baseline used to measure change and the spatial scales at which change operates. Comparison of modern assemblage data to historical ecological baselines to assess long-term changes is a common practice for understanding ecosystem dynamics and guiding conservation and management decisions (Anderson et al. 1995; Harrel and Smith 2002; Bojková et al. 2014); however, identifying suitable baselines poses several challenges, particularly in freshwater systems. Despite the development of databases of biodiversity data at state, national and global levels, finding historical data that is useful for a replication study can be difficult to obtain due to missing metadata (e.g., sampling effort, gear type, inaccurate location, misidentified species, etc.), changes in site accessibility, as well as a general lack of data for a given system of interest (Fraser et al. 2020). Drawing accurate conclusions from comparisons to baselines also requires knowledge of the scales at which anthropogenic and natural drivers of assemblage organisation operate (Green et al. 2022). Detecting ecological responses to environmental changes in stream networks is often scale dependent (Allan 2004; McGarvey and Ward 2008; Perkin et al. 2019a) due to (1) longitudinal variation in physical conditions from headwaters to the mouths of rivers (Vannote et al. 1980), (2) impacts of both natural (i.e., tributary confluences, Benda et al. 2004) and anthropogenic (i.e., dams and reservoirs, Stanford and Ward 1983) discontinuity on physical conditions and fish assemblage composition and (3) the different dynamics, such as gross primary production, ecosystem respiration and hydrologic regime, present in streams of varying size order (Minshall et al. 1983; Rolls et al. 2018). Furthermore, tributaries in a basin often exhibit differences in species richness (Miranda et al. 2019), species composition (Gu et al. 2023), temporal fish assemblage change (Taylor et al. 1996) and ecological stability (Gu et al. 2023; Shen et al. 2024) compared to the mainstem river. Because of the great spatial variation present in stream systems, multiscale approaches are useful for detecting patterns that might otherwise be missed (Labbe and Fausch 2000; Perkin et al. 2019a).

Temporal beta diversity analysis offers insights into the mechanisms behind assemblage change and is increasingly applied to river systems (Tisseuil et al. 2012; Cook et al. 2018; Zbinden 2020; Bae and Kim 2024). Beta diversity is defined as the variation in species composition between local assemblages (i.e., at a given site) that share the same regional species pool (e.g., within the same river basin) (Whittaker 1972). This differentiation in local assemblage composition can arise from two possible mechanisms: nestedness and replacement (Harrison et al. 1992). Nestedness occurs when one assemblage represents a subset of species found in another larger assemblage either through species loss or species gain. Replacement occurs when one assemblage has species that differ from another assemblage of comparable species richness through species turnover. Partitioning beta diversity into contributions from nestedness and replacement offers insight into processes structuring the biodiversity of a given ecosystem (Baselga 2010). Although beta diversity is often applied to assess taxonomic change in assemblages along a spatial or environmental gradient (Whittaker 1960), the metric can also be used to assess assemblage change at the same site through time (herein referred to as temporal beta diversity) (Legendre and Gauthier 2014). If nestedness is the dominant form of species change where the historical assemblages are nested within contemporary assemblages, that would suggest assemblage change is being driven by species invasions (Gido et al. 2004). Alternatively, if nestedness is dominant and contemporary assemblages are nested within historical assemblages, then assemblage change has been the result of

species extirpation (Taylor and Warren 2001). Replacement as the dominant form would indicate that species change was primarily due to species turnover.

Species traits determine how organisms interact with their environment, making the functional diversity of an assemblage an important factor in ecosystem function and resilience (Petchey and Gaston 2006). To measure various aspects of this diversity, several metrics have been developed (Villéger, Mason, et al. 2008; Laliberté and Legendre 2010). One such metric, functional dispersion (FDis), measures the spread of species traits in multivariate space by calculating the mean distance of the species to a weighted centroid that shifts closer to more abundant species (Laliberté and Legendre 2010). This metric represents a robust measurement of functional diversity because it can be used on qualitative traits, and it accounts for relative abundance in the analysed assemblage to prevent inflation by rare species (Laliberté and Legendre 2010). Multi-trait functional assessments are useful for understanding assemblage response to anthropogenic changes (Mouillot et al. 2013), including how multiple changes to riverscapes affect stream fishes (Santee et al. 2024). Changes in taxonomic richness are often correlated with changes in functional diversity, with the direction of the relationship depending on the factors influencing the system. For example, habitat degradation from human activities in Terminos Lagoon, Mexico, resulted in a negative relationship between species richness and functional diversity, as habitat specialists declined and newly occurring species were functionally redundant with the species that remained (Villéger, Miranda, et al. 2010). Alternatively, a long-term study assessing the effects of improved water quality on fish assemblages in the Illinois River, United States, found that taxonomic richness was positively related to functional diversity (Parker et al. 2018).

In this study, we compare historical data from 1956 to 1957 to replicated sampling conducted in 2023 to assess long-term changes in taxonomic and functional fish assemblage structure brought on by anthropogenic alterations in the Neches River Basin of Texas, United States. We focus on two scales by manipulating the extent of observations included in the analysis; the basin extent included all sites in the study, and the mainstem extent included only sites on the mainstem Neches River. The first objective of this study was to assess temporal beta diversity from the historical to the contemporary period and determine the predominant form of species change, nestedness or replacement. We hypothesised that simultaneous population declines by some native species and population expansions by native and non-native species would contribute to temporal beta diversity being primarily driven by replacement (Anderson et al. 1995). The second objective of this study was to test for correlations between the predominant form of temporal beta diversity (identified in Objective 1) and environmental factors relating to urban landcover and streamflow alteration. We hypothesised that temporal beta diversity would increase as urban landcover in watersheds increased, as predicted by the urban stream syndrome concept (Walsh et al. 2005), and temporal beta diversity would be greatest for stream segments where flow regime alteration was greatest, as predicted by the natural flow regime paradigm (Poff et al. 1997; Figure 1a). The third and final objective of this study was to assess how the predominant component of temporal beta diversity (identified in Objective 1) was related to temporal changes in functional dispersion (ΔFDis) for functional traits associated with fish stream size preference, substrate associations, and mussel species hosted at locations with low and high levels of anthropogenic alteration. If ΔFDis is negatively correlated with temporal beta diversity (i.e., site-level contemporary functional dispersion becomes lower than historical functional dispersion as temporal beta diversity increases), then changes in species are associated with homogenisation of functional traits in the assemblage (Figure 1b). Alternatively, if ΔFDis is positively correlated with temporal beta diversity (i.e., site-level contemporary functional dispersion becomes higher than historical functional dispersion as temporal beta diversity increases), then change in species are associated with diversification of assemblage functional traits. Lastly, no relationship between ΔFDis and temporal beta diversity would suggest that the assemblage exhibits functional redundancy, meaning the functional traits of species are sufficiently similar among increasing or declining species (in the case of nestedness) or contemporary species replacing historical species (in the case of replacement) that no change in functional dispersion occurs through time. We predicted that at high degrees of urbanisation and streamflow alteration, taxonomic replacement would be associated with functional homogenisation as environmental filtering removes specialist species (Figure 1c; Poff et al. 1997; Walsh et al. 2005).

2 | Methods

2.1 | Study Area

This study focused on 25 stream reaches throughout the mainstem Neches River and two major tributaries, the Angelina River and Pine Island Bayou. The Neches River basin has a drainage area of 25,929 km^2 and spans the East Central Texas Plains, South Central Plains, and Western Gulf Coastal Plains ecoregions of east Texas (Benke and Cushing 2005). The basin has a mean annual precipitation of 136 cm, a mean annual air temperature of 19 °C, and land cover is dominated by mixed hardwood and southern pine forests (65%) with interspersed grassland (15%), agriculture (15%) and urban (5%) coverage (Benke and Cushing 2005, Figure 2a,b). The headwaters of the Neches River begin in Van Zandt County, and the river flows southeast for approximately 669 km before emptying into Sabine Lake and then the Gulf of Mexico (Texas Parks and Wildlife Department 1974). There are three major impoundments in the river basin, including Lake Palestine, B.A. Steinhagen (also known as Dam B), and Sam Rayburn (Figure 2c). Lake Palestine was completed in 1962, has a storage capacity of 453,073 cubic dekametres (dam^3) and is located near the headwaters of the mainstem. Lake B.A. Steinhagen was completed in 1953, has a storage capacity of 85,430 dam^3 and is located at the confluence of the Neches River and the Angelina River. Sam Rayburn Reservoir was completed in 1965, is the second largest reservoir in Texas with a storage capacity of 5,479,620 dam^3 and is located about 40 river kilometres upstream of the confluence between the Angelina River and the Neches River. Our study included 14 fish survey sites along the mainstem Neches River, including two sites upstream of Lake Palestine, nine sites between Lake Palestine and B.A. Steinhagen, and three downstream of B.A. Steinhagen. The remaining 11 fish survey sites were on tributary streams, including seven sites on the Angelina River

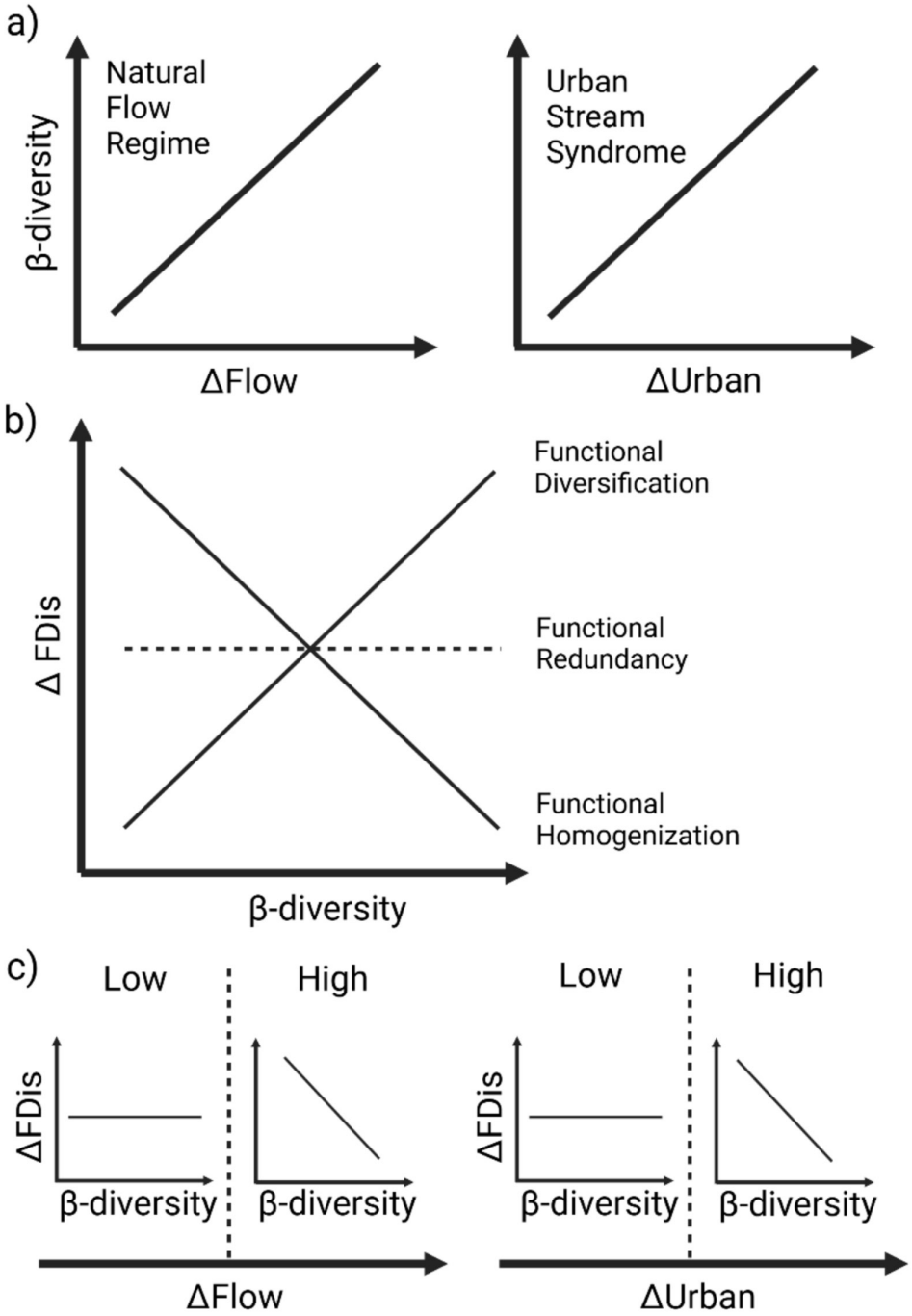

FIGURE 1 | Conceptual diagram illustrating hypotheses tested in this study. (a) The natural flow regime paradigm (Poff et al. 1997) and the urban stream syndrome (Welsh et al. 2005) predict greater beta diversity where flows are more altered (ΔFlow) and watersheds experience greater urbanisation (ΔUrban). (b) Possible relationships between beta diversity and change in functional trait dispersion (ΔFDis) and the associated ecological interpretations. (c) Expected relationships between beta diversity and ΔFDis at low and high degrees of flow alteration and urbanisation.

upstream of Sam Rayburn Reservoir, and four sites along Pine Island Bayou (Figure 2c).

2.2 | Fish Assemblages

We compared fish assemblage data collected from historical and contemporary survey periods. Historical fish assemblage data were compiled from two Texas Game and Fish Commission reports (Dorchester 1957a, 1958). The first report detailed fish collections from the Angelina River from June to August 1956, prior to the construction of Sam Rayburn Reservoir (Dorchester 1957a). The second report detailed fish collections from the Neches River mainstem from September 1956 and from May 1957, prior to the construction of Lake Palestine, as well as collections from Pine Island Bayou in April 1957 (Dorchester 1958). Dorchester (1958) surveyed each location twice and both collection events were combined into a single survey by adding the abundances of species between the two surveys (Potter et al. 2001). We repeated the surveys

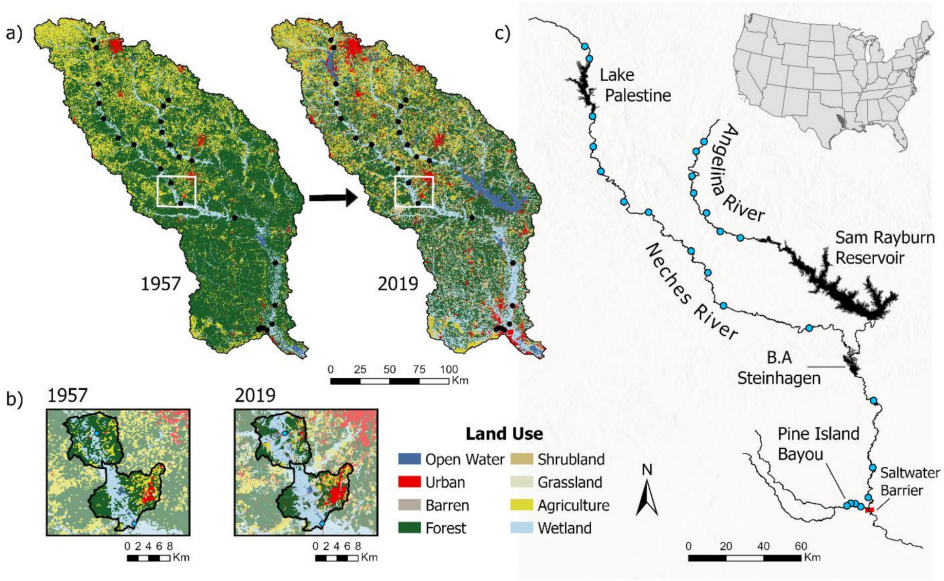

FIGURE 2 | Study area illustrating (a) changes in landcover in the Neches River Basin from 1957 (Sohl et al. 2018) to 2019 (Dewitz and U.S. Geological Survey 2021) where black points indicate the sites sampled during the historical period (1956–1957) and revisited during the contemporary period (2023). (b) A zoomed in view of LCLU changes over time emphasising the extents used to define land cover in the watershed for two sites near Nacogdoches, Texas, where blue points represent site locations and the black outlines show extent of the 12-digit HUC watershed associated with the site (extent of b is shown as white boxes in a). (c) Fish assemblage survey sites (blue points, $n = 25$) along stream segments (lines) in the mainstem Neches and the two tributaries (Angelina River, Pine Island Bayou). Major reservoirs in the basin include B. A. Steinhagen (constructed in 1953), Lake Palestine (1962), and Sam Rayburn Reservoir (1965), and permanent saltwater barrier is located on the lower Neches River mainstem (red box).

of Dorchester (1957a, 1958) from May to August of 2023 using identical survey locations and gear types. Reservoir construction resulted in some original survey sites being inundated by deep water; therefore, these locations were excluded from our study. At each site, we established a 300 m reach and pulled 10 seine hauls of 30 m length using a 4.6 × 1.8 m 4.8 mm mesh seine. Small fish were euthanised with a lethal dose of Eugenol (clove oil; 1 g/L) and preserved in 10% formalin, while fish too large to be physically vouchered were identified in the field, measured, photographed and released. Vouchered fish were brought back to the lab, transferred to 70% ethanol, identified using regional keys (Hubbs et al. 2008; Craig and Bonner 2019), and enumerated. All specimens collected as part of this study have been deposited within the Collection of Fishes at the TAMU Biodiversity Research and Teaching Collections, under accession numbers TCWC 20894.01–20851.16, 20671.01–20675.05, 20852.01–20902.21 and 20857.01–20673.21. Scientific names from the historical report were updated to their current senior synonyms for agreement with contemporary collections using Page et al. (2013).

2.3 | Land Cover

We collected LCLU data to represent the historical and contemporary periods. Historical land cover for the year 1957 was downloaded from the US Geological Survey (USGS) Forecasting Scenarios of Land-use Change model (Sohl et al. 2018). These data were derived by the USGS using land cover trends combined with supplementary data from the Census of Agriculture, historical housing density data, and regional wetlands. Contemporary land cover for the year 2019 was obtained from the National Land Cover Database (NLCD; Dewitz and U.S. Geological Survey 2021). We defined the watershed of each survey site using 12-digit Hydrological Unit Codes from the National Hydrological Dataset (NHD) Plus High Resolution (U.S. Geological Survey 2018). This watershed boundary is a commonly chosen unit in assessing stream condition (Hain et al. 2018; Spieles et al. 2025) that represents a more localised watershed where stronger correlations between urban land cover and fish assemblage variation are observed compared to the network catchment (i.e., total area of upstream land) (Perkin et al. 2019b). We then calculated the percentage change in LCLU classes in the watershed of each fish survey site using historical and contemporary raster data analysed using the 'Tabulate Area' tool in ArcGIS Pro (version 3.2). We defined three LCLU classes for assessment of change, including agriculture (hay/pasture and cropland), forest (deciduous forest, mixed forest and evergreen forest) and urban (low, medium and high intensity development). Preliminary analyses showed that the urban LCLU class was the only one that correlated with temporal beta diversity (Supplementary Table S1), and thus we focus only on urbanisation in this study.

2.4 | Streamflow Alteration Metrics

Monthly stream discharge datasets were obtained for each month of 1957 and 2023 and joined to the NHD Version 2 stream segments corresponding to each site in ArcGIS Pro. We used estimates of natural stream discharge (i.e., streamflow expected to occur without anthropogenic alteration to the hydrologic system) for the historical period and flow estimates adjusted by streamflow gage observations for the contemporary

period. Estimates of historical natural monthly stream discharge for the year 1957 were modeled by Miller et al. (2018) using predictor variables related to temperature, precipitation, runoff, and physical watershed characteristics. For the contemporary period, we used the Extended Runoff Unit Method table from the NHD Version 2 (McKay et al. 2012) to assign monthly gage adjusted runoff values averaged for 1971–2000. We performed a principal components analysis (PCA) of the monthly streamflow using the 'rda' function from the 'vegan' package in R and extracted the Euclidean distance between the historical and contemporary observation of each site to represent overall changes in stream discharge (Supplementary Figure S1).

2.5 | Trait Data

We used functional traits of fishes to assess the ecological consequences of anthropogenic alterations. Trait data were collected for fish stream size preference and substrate associations, as changes in these traits would reflect the impact that land use and reservoirs have on the hydrology and morphology of rivers (Stanford and Ward 1983; Walsh et al. 2005). We also collected trait data on mussel species that use fish as a host to assess how fish assemblage change might impact the mussel populations in the basin (Supplementary Table S2). All traits were binary variables where species were assigned a value of 1 if the trait was present and a value of 0 if the trait was absent. Stream size preference data were from Goldstein and Meador (2005) and included five mutually exclusive categories: creeks (1–3 m wide), creeks to small rivers (> 3–15 m), medium to large rivers (> 15 m), large rivers (> 50 m) and a range of sizes (associated with 3 or more stream sizes). Data on substrate associations were from the FishTraits database (Frimpong and Angermeier 2009) and included seven categories: muck, clay/silt, sand, gravel, cobble, boulder, and bedrock. A checklist of mussel species in the Neches River mainstem, Angelina River and Pine Island Bayou was compiled from a review of several studies (N. B. Ford et al. 2014; D. F. Ford et al. 2016; Tarter 2019) and corresponding fish host data were derived from the Mussels of Texas Database (Randklev, Robertson, et al. 2023) and the Freshwater Mussel Host Database (Douglass et al. 2017). Unlike stream size preference, substrate association traits and mussel species hosted were not mutually exclusive categories, so fish species were often assigned to one or more substrate classes or mussel species.

2.6 | Statistical Analysis

2.6.1 | Taxonomic Beta Diversity

We conducted a series of regression-based analyses at the basin and mainstem extents to assess relationships between temporal beta diversity measured at the taxonomic resolution and anthropogenic alterations to the riverscape. The basin extent included all sites from the Neches River, Angelina River, and Pine Island Bayou ($n = 25$) analysed collectively, while the mainstem extent included only sites on the mainstem Neches River ($n = 14$). Prior to analysis, we removed species present in < 10% of sites during both the historical and contemporary periods and applied a fourth-root Hellinger transformation to fish abundances (Legendre and Gallagher 2001). We then calculated temporal beta diversity between historical and contemporary time periods for each site using the 'beta.div.comp' function of the 'adespatial' package in R (Dray et al. 2023). We used the Sørensen pairwise dissimilarity index (β_{sor}) from the Baselga family of beta diversity to calculate total temporal beta diversity, nestedness (β_{nes}) and replacement (β_{sim}) for each sampling location (Baselga 2010). β_{sor} is a presence/absence measure of beta diversity formulated as:

$$\beta_{sor} = \beta_{sim} + \beta_{nes} \equiv \frac{b+c}{2a+b+c} = \frac{b}{a+b} + \left(\frac{c-b}{2a+b+c}\right)\left(\frac{a}{b+a}\right)$$

where a is the number of shared species between sites, b is the number of species unique to the poorer site, and c is the number of species unique to the richer site. We used boxplots to illustrate the dominate form of beta diversity across all sampling locations at the basin and mainstem extents. We then performed a similarity percentage analysis (SIMPER) using the 'simper' function of the 'vegan' package (Oksanen et al. 2022) to determine which species were driving the changes in assemblage structure over time. Finally, we analysed the relationships between the dominant form of beta diversity (dependent variable) and changes in stream discharge (pairwise distances from PCA), and urban change in watershed (%) as predictor variables. We fit independent linear models to each relationship for each extent (four models total) to test hypotheses related to alteration-specific and scale-specific anthropogenic changes to the riverscape. We fit models and assessed the significance of slopes ($\alpha = 0.05$) using the 'lm' function from the 'stats' package (R Core Team 2022).

2.6.2 | Functional Diversity

We assessed changes in functional traits over time to assess ecological consequences for taxonomic beta diversity. We used three classes of functional traits (stream size preference, substrate associations, and mussel species hosted) to test for changes in functional dispersion through time. Prior to analysis, species abundance data were converted from absolute abundance to relative abundance. We calculated FDis for each of the three trait classes using the 'dbFD' function of the 'FD' package (Laliberté et al. 2014). We analysed trait classes independently to improve interpretation of directional changes from the historical to contemporary periods. For example, a decrease in FDis for a given trait would represent homogenisation over time, while an increase in FDis would represent higher trait evenness or trait diversification over time. We used linear regression with site-level changes in FDis over time (i.e., delta FDis) as the response variable and temporal beta diversity as the predictor variable to test for patterns at high and low degrees of urbanisation and streamflow alteration for each of the three traits (12 models total). Degrees of alteration for urbanisation and streamflow change were assigned high and low classifications using the head/tail breaks algorithm, which finds groupings for data with a heavy-tailed distribution (Jiang 2013). Sites with less than 2.2% increase in urban landcover in the watershed were considered low

urbanisation ($n = 18$), while sites with more than 2.2% increase in urban landcover were considered high urbanisation ($n = 7$). Sites with streamflow PCA distance less than 0.9 were considered low streamflow change ($n = 18$), while sites with a streamflow PCA distance greater than 0.9 were considered high streamflow change ($n = 7$). Because of sample size constraints, this analysis of functional diversity and taxonomic replacement relationships was conducted only at the basin extent. All analyses were conducted using R version 4.2.2 (R Core Team 2022).

3 | Results

3.1 | Taxonomic and Beta Diversity

In total, 22,354 specimens representing 73 species were collected, including 4,677 (30 genera, 53 species) in the historical period and 17,677 (34 genera, 57 species) in the contemporary period. Prior to removal of rare species that occurred in < 3 collections, 37 species (31 after rare removal) were found in both periods, 16 species (4 after rare removal) were found only in the historical period, and 20 species (10 after rare removal) were found only in the contemporary period (Supplementary Table S2). Notable species that were caught in the contemporary collections but were removed from analysis due to rarity included Blue Sucker, *Cycleptus elongatus*, and Western Sand Darter, *Ammocrypta clara*, which are both listed as species of greatest conservation need (SGCN; i.e., species with low or declining populations in need of conservation action) in Texas (Birdsong et al. 2020). Temporal beta diversity was driven primarily by replacement rather than nestedness at both the basin (Figure 3a) and mainstem extents (Figure 3b). Contributions of replacement to total beta diversity ranged 0.308–0.805 across all 25 sites, and contributions of nestedness ranged 0.013–0.205.

Assemblage change through time was largely attributed to species increases at both the basin and mainstem extent (Supplementary Table S3). At the basin extent, all species with a significant ($p < 0.05$) contribution to assemblage change through time were species that experienced increases, with *Notropis texanus*, *Lepomis megalotis*, *Lythurus fumeus*, *Micropterus salmoides*, *Etheostoma chlorosoma*, *Hybopsis amnis*, *Opsopoeodus emiliae*, *Ictalurus punctatus*, *Pomoxis annularis* and *Percina sciera* as the greatest contributors to assemblage differences (Supplementary Table S3). At the mainstem extent, *Notropis sabinae*, listed as a SGCN in Texas, was the second greatest contributor to assemblage change over time and the only species that experienced a decrease. Among the species with a significant contribution to assemblage change over time due to abundance increases, the largest contributors were *L. megalotis*, *N. texanus*, *M. salmoides*, *Hybopsis nuchalis*, *E. chlorosoma*, *Percina macrolepida*, *I. punctatus*, *O. emiliae* and *P. sciera* (Supplementary Table S3).

Linear relationships between replacement and anthropogenic alterations were scale-dependent. There was no relationship between increasing urban land use and species replacement at the basin extent (Replacement = 0.0217*(Δurban) + 0.517, $p = 0.076$, Figure 4a), but replacement correlated positively with increasing urbanisation at the mainstem extent (Replacement = 0.0409*(Δurban) + 0.439, $p = 0.016$, Figure 4b). Replacement was negatively correlated with change in stream discharge at the basin extent

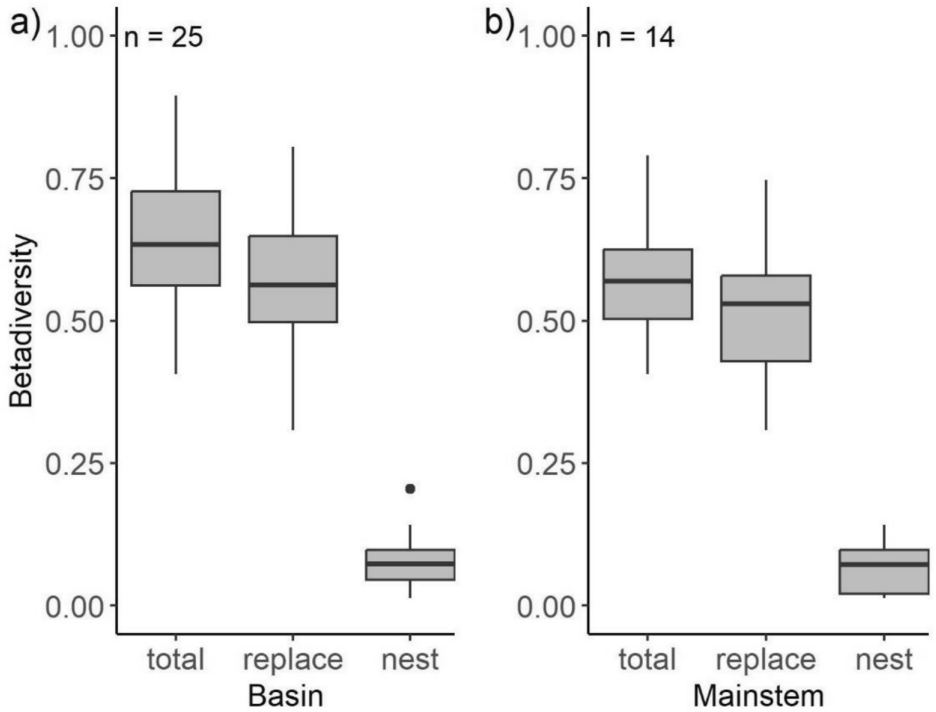

FIGURE 3 | Boxplots of fish assemblage total beta diversity, replacement component (replace), and nestedness component (nest) showing replacement as the dominant form of taxonomic change from the historical (1956–1957) to contemporary (2023) periods at both the Basin (25 sampling sites) and Mainstem (14 sampling sites) extents of the Neches River Basin, Texas, United States.

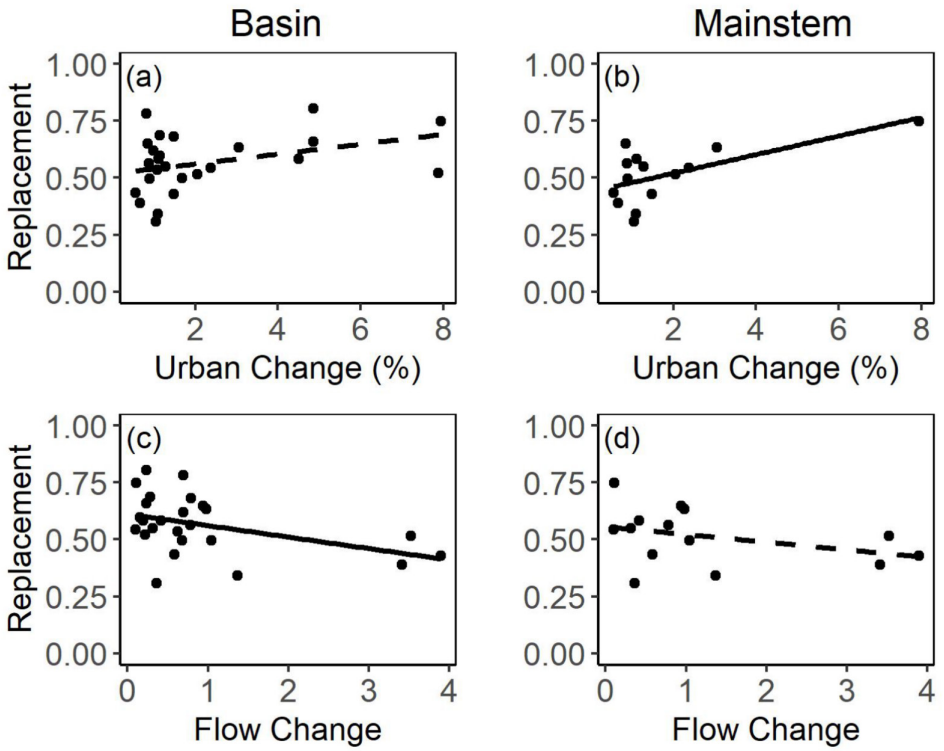

FIGURE 4 | Linear regression models showing the replacement component of beta diversity as a function of percent of urban change in the watershed (a,b), streamflow change (c,d) at the Basin ($n = 25$, left column) and Mainstem ($n = 14$, right column) extents. Solid lines indicate significant relationships while insignificant relationships are represented by dashed lines.

TABLE 1 | Results of the simple linear regressions testing for correlations between taxonomic species replacement and change in functional dispersion for forms and intensities of anthropogenic alteration for mussel species hosted (mussel hosting), stream size preference (stream size) and substrate association (substrate preference) traits. For urbanisation, low alteration was defined as sites with $< 2.2\%$ increase in the watershed ($n = 18$) and high alteration was defined as sites with $\geq 2.2\%$ increase in the watershed ($n = 7$). For streamflow change, low alteration was defined as sites with a PCA distance < 0.9 while high alteration was defined as sites with a PCA distance ≥ 0.9. Linear model intercepts, slopes, coefficient of determination (R^2) and slope significance (p value) are given for each model; bolded values indicate significant results.

Trait	Alteration	Intensity	Intercept	Slope	R^2	p
Mussel hosting	Urbanisation	Low	0.541	−0.030	0.156	0.105
Mussel hosting	Urbanisation	High	**0.622**	**0.029**	**0.693**	**0.020**
Mussel hosting	Streamflow change	Low	0.589	0.009	0.031	0.481
Mussel hosting	Streamflow change	High	0.486	−0.046	0.386	0.137
Stream size	Urbanisation	Low	0.532	−0.033	0.025	0.532
Stream size	Urbanisation	High	**0.605**	**0.106**	**0.697**	**0.019**
Stream size	Streamflow change	Low	0.589	0.058	0.131	0.140
Stream size	Streamflow change	High	0.458	−0.189	0.550	0.056
Substrate preference	Urbanisation	Low	0.521	0.049	0.102	0.196
Substrate preference	Urbanisation	High	0.605	0.049	0.527	0.065
Substrate preference	Streamflow change	Low	0.571	0.046	0.186	0.074
Substrate preference	Streamflow change	High	0.471	0.093	0.356	0.157

(Replacement = −0.0502*(Δflow) + 0.611, $p = 0.0347$, Figure 4c) but not the mainstem extent (Replacement = −0.0338*(Δflow) + 0.556, $p = 0.203$, Figure 4d).

3.2 | Functional Diversity Relationships

Relationships between taxonomic replacement and multi-trait ΔFDis at different degrees of anthropogenic alteration existed for urbanisation but not flow regime alteration. No relationships between taxonomic replacement and change in functional dispersion across stream size, substrate preference, and mussel hosting traits were identified for streamflow alteration regardless of its intensity (Table 1). Taxonomic replacement ranged 0.3–0.8 among sites experiencing low intensity urbanisation, but replacement was not predictive of changes in trait functional dispersion for fish stream size preferences (Figure 5a), substrate associations (Figure 5c), nor mussel hosting (Figure 5e). A positive correlation between taxonomic replacement and ΔFDis was evident among sites experiencing high intensity urbanisation for stream size preference (Figure 5b) and mussel species hosted (Figure 5f), but the positive slope for substrate association was not significantly different from zero (Figure 5d).

4 | Discussion

This study demonstrates that long-term anthropogenic alterations to river watersheds affect stream fish assemblages at different spatial scales and highlights the potential ecological consequences of assemblage change. Decomposition of beta diversity into its components of nestedness and replacement can be used to identify the primary form of assemblage change following environmental change (Legendre 2014). Previous studies have linked spatial beta diversity to environmental change (Dala-Corte et al. 2019) or associated components of beta diversity to alteration gradients over short timelines (Camara et al. 2023). We found that over a ~70-year period

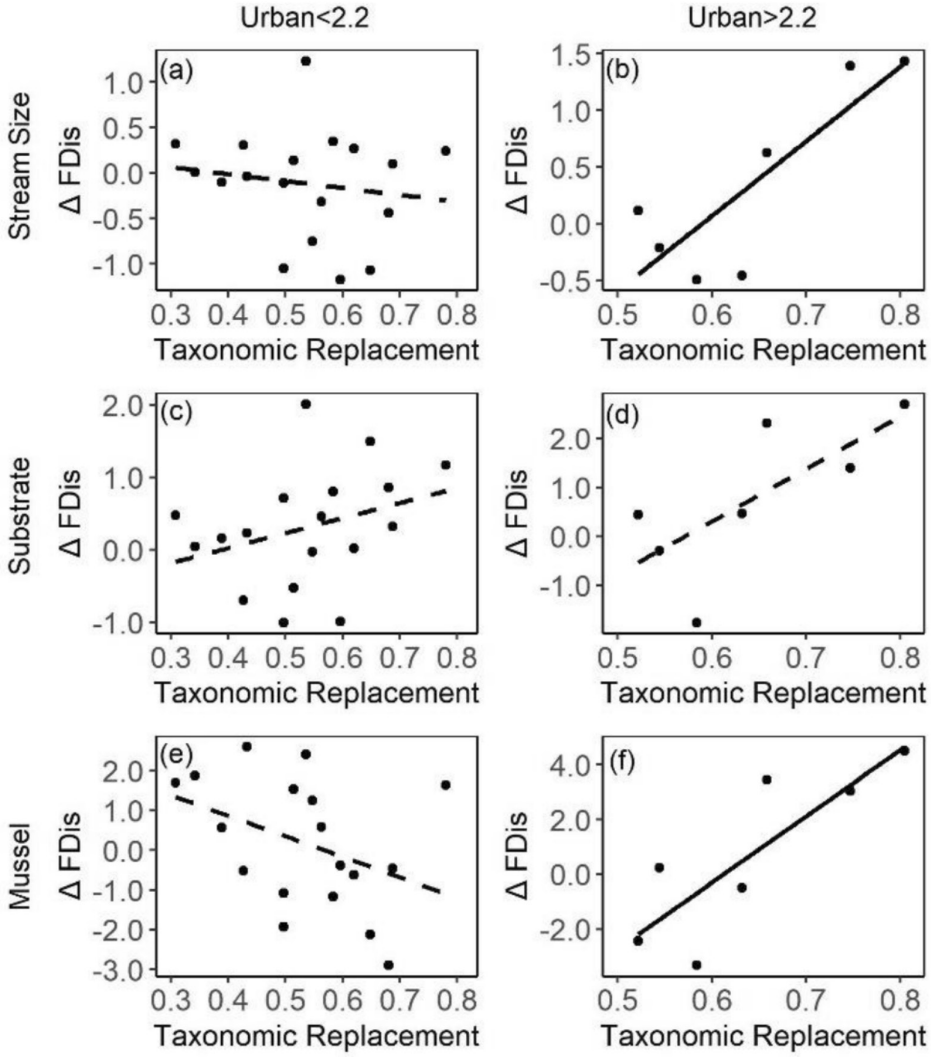

FIGURE 5 | Linear regression models showing change in functional dispersion (FDis) as a function of taxonomic replacement at low (left column, less than 2.2%, $n = 18$) and high (right column, more than 2.2%, $n = 7$) degrees of urbanisation for three functional traits: (a,b) stream size preferences (stream size), (c,d) substrate associations (substrate) and (e,f) mussel species hosted (mussel). Solid black lines indicate statistically significant relationships while dashed black lines indicate nonsignificant relationships (see Table 1 for regression model results).

species replacement was the predominant form of temporal beta diversity in the basin, providing support for our first hypothesis. Relationships between species replacement and flow alteration or urbanisation appeared to be dependent on spatial extent. Species replacement was highest at sites where urbanisation was greatest at the mainstem extent, but no relationship was observed at the basin extent. Likewise, replacement was highest at sites with the least streamflow change at the basin extent, but no relationship at the mainstem extent. These findings provide partial support for our second hypothesis that assemblage change would be positively correlated with anthropogenic alteration as predicted by the Urban Stream Syndrome (Walsh et al. 2005) and the Natural Flow Regime Paradigm (Poff et al. 1997). Our third hypothesis was also partially supported by our results. We found that there was no relationship between taxonomic replacement and ΔFDis at low levels of anthropogenic alteration, which was in line with our expectations. However, at high levels of urbanisation, we found a positive relationship between taxonomic replacement and ΔFDis for two traits (stream size preference and mussels species hosted), which was counter to our expectation of a negative relationship. Finally, we found no relationship between taxonomic replacement and ΔFDis at high levels of streamflow alteration for any fish traits. Our findings show that streamflow alteration and urbanisation elicited different responses from stream fish assemblages in both the magnitude and direction of response.

The predominant form of temporal fish assemblage change observed in the basin was replacement rather than nestedness. The high degree of replacement suggests that abiotic conditions might have changed over time, leading to compositional shifts through environmental filtering (Zbinden and Matthews 2017). However, the low nestedness values suggest that, despite these abiotic changes, the diversity of available niches remained stable (Legendre 2014). Assemblage change driven by replacement suggests there has been concurrent expansions of some species distributions and contractions in other species distributions throughout the Neches River Basin. Our SIMPER analysis found that assemblage change was largely from species increases, a result that is more consistent with nestedness than with replacement. This apparent discrepancy is a result of the different scales at which the temporal beta diversity analysis and the SIMPER analysis were performed. Scale is composed of two components: extent, defined as the overall spatial area, and grain (also referred to as resolution), defined as the smallest unit of observation (Wiens 1989). Different scales of analysis often impact the observed ecological responses to LCLU (Allan 2004; Perkin et al. 2019a) and streamflow variation (McGarvey and Ward 2008), including analyses of beta diversity (Dala-Corte et al. 2019). In this study, we intentionally changed the extent (i.e., number of sites included) while holding grain (i.e., site-level assemblage abundance data) constant to uncover different relationships with anthropogenic alteration at the basin versus mainstem extents. This approach allowed inference on where changes in fish assemblages might be most strongly tied to environmental change. For example, the significant relationship between urban change and fish assemblage replacement at the mainstem extent but not the basin extent may indicate that other environmental variables have a greater impact on species turnover in the tributaries. Alternatively, the SIMPER analysis changes both the extent (i.e., performed at basin and mainstem extent) as well as the grain (i.e., pooled the fish abundance data of all sites included in extent) to identify species that contributed most to overall assemblage change between the historical and contemporary period. Thus, the SIMPER analysis provides information on species occurrence and abundance across the basin, a coarse index of change, while temporal beta diversity provides information on site-level differences in relative abundance at multiple extents (Perkin et al. 2019a).

Fluctuations in streamflow components (i.e., magnitude, frequency, duration, timing and rate of change) play a vital role in shaping fish assemblages in river systems (Poff et al. 1997). We found that species replacement was greatest where temporal differences in monthly flow magnitudes were least, which did not support our second hypothesis that streamflow change would be positively correlated with the predominant form of temporal beta diversity. One explanation for this unexpected result is the specific environmental context of the historical collections. In this study, streamflow changes were associated with increasing discharge magnitude (Supplementary Figure S1a) due to prolonged, intense drought conditions in the historical period (Dorchester 1957b) as opposed to decreasing discharge magnitude that is commonly found in systems following increased regulation by impoundments (Graf 2006). The degree of streamflow increases mirrored a gradient of increasing stream size. The sites that experienced the greatest increase in streamflow and the least taxonomic species replacement were located on the downstream-most segments of the Neches River where stream size is greatest and there are few but large tributary streams (Supplementary Figure S1b). Conversely, the sites with smaller increases in streamflow but more species replacement were mostly located in the upper parts of the basin where stream size is smaller and there is high connectivity with small tributary streams (Supplementary Figure S1b). Thus, we hypothesise that when sites were sampled during the drought, fishes from small-order tributaries in the upper part of the basin that are more susceptible to complete drying might have used the Neches and the Angelina for refuge habitat (Magoulick and Kobza 2003). When the drought conditions passed, these fishes might have moved to recolonise the tributaries, and the fish assemblage reverted to pre-drought conditions, resulting in the greatest species replacement we observed. We found that there was no relationship between species replacement and functional diversity change at varying degrees of streamflow alteration, which suggests that fish assemblages at those locations exhibited functional redundancy in regard to species replacement due to flow change. That is, the contemporary species that replaced historically present species exhibit the same stream size, substrate, and mussel host traits regardless of differences in flow magnitudes. Inferences about species replacement, functional diversity and streamflow alteration only represent patterns at a coarse level of information for only one component of streamflow (i.e., magnitude) due to limited overlap of streamflow gages and sampled reaches. It is possible that different relationships with species replacement could be found if finer-resolution streamflow data were available. Despite the coarse level of analysis, flow magnitude is the component

of streamflow most frequently investigated in understanding ecological responses to streamflow alteration (Poff and Zimmerman 2010) and affects several aspects of fish assemblage structure. For example, flow magnitude is correlated with fish species richness (Xenopoulos and Lodge 2006), and alterations in flow magnitudes could act as a filter for species with specific flow requirements (McManamay and Frimpong 2015). Thus, incorporation of streamflow analysis at even coarse scales can be informative to stream fish ecology.

Urban development within watersheds, even at relatively low intensities, can contribute to declines in stream fishes (Allan 2004). The urban stream syndrome posits that increased runoff associated with impervious surfaces causes frequent disturbances, resulting in fewer sensitive species and more disturbance-tolerant species (Walsh et al. 2005). Studies have found that this pattern of urbanisation-driven sensitive species decline and disturbance-tolerant species increases may occur without a reduction of species richness in some river basins (Walsh et al. 2005). Furthermore, Wenger, Mason, et al. (2008) found that several fish species exhibited a threshold response to urban landcover near streams where urban landcover comprising just 2–4% of a 1.5 km radius adjacent to the stream resulted in dramatic declines in species occurrence. In support of this, we found that small increases (2.2–8%) in urbanisation over time were positively correlated with species replacement at the mainstem extent. We also found that at high degrees of urbanisation, species replacement was associated with functional diversification for stream size preference and mussels hosted traits. Because functional dispersion is weighted by abundance, this result may be due to shifts toward fish assemblages composed of evenly abundant generalist species rather than assemblages with a higher number of rare, specialist species. Stefani et al. (2020) found a similar result in which shifts in common generalist species were responsible for long-term increases in functional dispersion in small streams in Northern Italy. Furthermore, fish species that are hosts to the most mussel species in the Neches River basin are generalists like *L. megalotis*, *M. salmoides* and *I. punctatus*, which were also some of the species that contributed most to fish assemblage change at the basin level. We predicted that species replacement would be facilitated in part by non-native species introductions; however, all fish species included in our analysis were native species. This suggests that in the Neches River Basin, fish assemblage changes over time are a result of concomitant expansions and contractions of native species ranges and abundances. This finding is consistent with Scott and Helfman (2001), who found that disturbance from LCLU changes can create favourable habitat conditions for native generalist species that are present but rare pre-alteration to increase in abundance post-alteration. Scott and Helfman (2001) also pointed out that expansion of native, generalist species begins in larger streams and then progresses to smaller tributaries. Our finding of a relationship between urbanisation and fish assemblage replacement in the mainstem but not the entire basin (including tributaries) supports the notion that the Neches River Basin might be at a midpoint in the homogenisation process where native species are responding but widespread non-native invasions have not yet occurred (Scott and Helfman 2001). It is also worth noting that spatial configuration of urban land as well as other land covers along with their extents within a watershed may also be a significant influence on freshwater biodiversity within that watershed (King et al. 2005; Arantes et al. 2018).

Our findings help inform freshwater fish conservation both specifically for the Neches River Basin and generally for regulated river systems. Despite the alteration that has occurred in the basin over time, we found that SGCN species like Blue Sucker and Western Sand Darter are persisting in some sections of the river. This finding shows that although many historical species are rare and declining now, there are opportunities to restore their populations through conservation and management efforts targeting reduced impacts from urbanisation and stream flow alteration. Our study found that increasing urbanisation over time is associated with greater species replacement in the mainstem river. The negative effects of urbanisation on river systems have primarily been attributed to increased stormwater runoff (Walsh et al. 2005); thus, a first management action might be implementing infrastructure that increases stormwater infiltration (e.g., infiltration trenches, permeable pavement) and harvesting (e.g., green roofs, rainwater tanks, wetlands), which represents an effective method to reduce alterations to stream hydrology and morphology (Askarizadeh et al. 2015). Stormwater runoff control measures may be especially helpful in basins like the Neches that experience consistent precipitation throughout the year (Benke and Cushing 2005), as urban development produces greater alteration to flow regime components compared to basins with large but infrequent precipitation events (Booth et al. 2016). Our study found that taxonomic species replacement at sites with high urban change was correlated with greater mussel host functional dispersion. This suggests that urbanisation-driven fish assemblage shifts lead to a diversification of mussel host species. However, while mussel hosts tend to be generalist species that are tolerant of poor water quality found in urban streams, mussel populations themselves are often highly sensitive to pollution (Gangloff et al. 2009) and may not persist in highly urbanised ecosystems. This highlights the importance of enhancing mussel habitat in less developed areas where environmental conditions are more suitable for long-term population viability. Evidence of longitudinal recovery gradients has been documented for both fish and mussels in which species richness increases with greater distance to reservoirs (Kinsolving and Bain 1993; Randklev, Ford, et al. 2016). Thus, a second management action supported by our results is the preservation of long, unfragmented reaches of large rivers that support both native mussels and fishes (D. F. Ford et al. 2016). Much of the lower Neches River basin lies within the Big Thicket National Preserve where riparian corridors remain intact, and this preserve serves as a form of freshwater protected area (Saunders et al. 2002). Thus, a third management action might include maintaining or reestablishing similar corridors in other portions of the basin which might help to offset the effects of urbanisation within those watersheds (Fischer et al. 2010).

Findings on streamflow change and species replacement were contrary to normal expectations due to the basin's historical drought but still highlight the significant impact that deviations in streamflow magnitude have on structuring fish assemblages. Streamflow magnitude has been shown to be a predominant factor in fish diversity (Xenopoulos and Lodge 2006), yet water shortages in rivers are becoming more prevalent through human

population growth and climate change (Brown et al. 2019). In recent decades, interest has emerged concerning restoring riverine ecosystems by managing dam releases to mimic key components of the natural flow regime (Richter and Thomas 2007). This is achieved by determining environmental flows (e-flows), that is, the timing and quantity of water flows that are necessary to sustain aquatic biota (Brisbane Declaration 2007). This requires comprehensive community data for different aquatic taxa downstream of the impoundments that might be managed to support e-flow requirements. For example, the Brazos River Basin and Bay Expert Science Team developed e-flow recommendations for the Brazos River in part by accounting for the distribution, abundance trends, and life history requirements of fishes throughout the river (Brazos BBEST 2012). These recommendations were then validated by Perkin et al. (2023) who found that the shoal chub, a fluvial specialist sensitive to streamflow alterations, had the highest recruitment in years where most streamflow targets were met, while recruitment steadily declined in years that met less than half of the streamflow targets. The lower Neches River is included in the Sustainable Rivers Program (SRP), a nationwide project that seeks to implement environmental flow strategies at U.S. Army Corps of Engineer (USACE) infrastructure. Though we did not detect Shoal Chub in the lower Neches River (where the species is reported; Pizano-Torres et al. 2017), our data are useful for identifying other flow-sensitive species (e.g., Sabine Shiner; Williams and Bonner 2006) that might be used to guide e-flow management as a part of the SRP.

5 | Conclusions

The direct and indirect effects of human alterations to terrestrial landscapes and aquatic riverscapes represent primary threats to aquatic biodiversity (Reid et al. 2019). Our study demonstrates long-term changes to fish assemblages that correlated with urbanisation and streamflow change across multiple spatial extents and reveals the ecological consequences of taxonomic changes driven by these alterations. We found that (1) fish assemblage change was likely driven by urbanisation and streamflow change, (2) sites with high degrees of urbanisation experienced functional diversification in stream size preference and mussel host traits as taxonomic replacement increased and (3) historical drought conditions played a primary role in shaping fish responses to streamflow. These findings highlight the importance of stream management, such as stormwater management, expansion of riparian corridors, and the application of environmental flows, for mitigating the effects of alteration from urbanisation and streamflow change. The observed relationship between species replacement and mussel host functional dispersion at high urbanisation levels suggests potential opportunities and challenges for mussel conservation efforts. Given the impact of streamflow magnitude on fish assemblages, the development and assessment of e-flows should be prioritised to ensure the long-term sustainability of fish populations. Future research should focus on integrating patterns of mussel distributions in urban areas, analysing the potential impact of spatial configuration of urban land—in addition to the total urban land—on mussel host distributions within a watershed, and finer resolution streamflow data to better inform the relationships identified in this study.

Ethics Statement

All sampling and preservation were conducted according to approved Texas A&M Institutional Animal Care and Use Committee protocols (AUP 2023-0308).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors confirm that the data supporting the findings of this study is available within the article and its supplementary materials.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Linear regression results from preliminary analysis assessing the correlation between different land cover types and temporal beta diversity. **Table S2:** Fish species used in taxonomic and functional diversity analysis listing number of mussel species hosted, stream size preference (Goldstein and Meador 2005), range of substrate associations (Frimpong and Angermeier 2009), as well as the number of individuals caught/number of sites present at the basin and mainstem extent for both the Historical and Contemporary period. **Table S3:** Results of similarity percentage analysis for all species included in analysis at both the basin and mainstem extents. Table gives the species name, International Union for Conservation of Nature (IUCN) rank status (LC = least concerned, NE = not evaluated), Texas conservation status (NL = not listed, SGCN = species of greatest conservation need), as well as the historical and contemporary proportion of abundance, contribution of species to change over time, p value, and direction of change (↑ = increase over time, ↓ = decrease over time, – = no change) for both basin and mainstem extents. Superscripts show the order of the top 10 average contributions to species change for species with significant increases or decreases at both the basin and mainstem extent. **Figure 1:** (a) PCA of monthly streamflow estimates for the historical period (blue labels, Miller et al. 2018) and contemporary period (pink labels, McKay et al. 2012) where grey lines illustrate Euclidean distances between the historical and contemporary observation of each site. PC1 represents a gradient of stream size with smaller stream reaches on the left and larger stream reaches moving toward the right. PC2 represents a temporal gradient. (b) Map of sites where size of points represents Euclidean distances from monthly streamflow change and colour indicates temporal species replacement of the fish assemblage. **Data S1:** Supplementary information.