Final Report

HISTORICAL CHANGES AND SEASONAL VARIATION IN FRESHWATER FISH ASSEMBLAGES OF THE NECHES AND UPPER SABINE RIVER BASINS

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by

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EXECUTIVE SUMMARY

Freshwater fish provide numerous ecosystem goods and services to people, such as provisioning services (food, recreational opportunities), information services (indicator species information), and cultural services (conservation values). Consequently, knowledge of fish species distributions and abundances, as well as information about how these have changed over time, is critical to natural resource management and stewardship. The work covered in this report advances the Texas Comptroller of Public Accounts Natural Resources Program mission to provide data for species status assessments by providing comprehensive evaluations of the freshwater stream fish abundances and distributions in the Neches River basin and upper Sabine River basin in east Texas. This report documents activities aimed at this goal based on three major tasks. Task 1 was to evaluate historical and contemporary fish distributions in each basin; Task 2 was to assess trends in fish assemblage change through time; Task 3 was to determine the most appropriate timing for fish surveys to inform long-term study designs. In total, this report has eight chapters that cover unique aspects of a large publicly available database detailing fish assemblage information collected from 286 surveys during 2023–2025.

Chapter I of this report provides background on the development of this study and how the remainder of chapters are structured around primary tasks.

Chapter II details the historical state of fish assemblages in large streams of the Neches River Basin, the development of repeated surveys 70 years after initial surveys, and an analysis of how fish assemblages changed as the river basin experienced flow alterations and urban development. Results suggest that few non-native species have invaded the Neches River basin; the largest changes in the fish assemblage occurred in areas nearest to urban development; the capacity of fish assemblages to provide ecosystem services such as hosting freshwater Unionid mussels has increased in urban areas.

Chapter III details the historical sate of fish assemblages in large rivers of the upper Sabine River Basin, the development and of repeated surveys 70 years after initial surveys, and an analysis of how fish assemblages changed as major reservoirs were constructed in the basin. Results suggest that few non-native species have invaded the upper Sabine River basin; the fish assemblage changed considerably at locations near to reservoirs but change attenuated with distance from reservoirs; fish assemblage change in the tailwaters of Lake Tawakoni was driven by loss of periodic, equilibrium, and opportunistic-periodic life history strategists as well as a loss of species that host freshwater mussels; fish assemblage change in the area immediately upstream of Toledo Bend Reservoir was driven by loss of opportunistic-periodic strategists and an increase in opportunistic strategists as well as an increase in fishes that host mussels.

Chapter IV details repeated seasonal surveys of fish assemblages in smaller streams in the Neches and Sabine basins to assess how different fish assemblages are between locations and seasons. Results reveal that local environmental variables unique to streams as well as regional variables unique to east Texas predict differences in fish assemblage structure across space; there was no evidence of differences in fish assemblage structure at the same locations when surveyed during different seasons; design of long-term studies in the future might consider summer low-flow periods for surveys to avoid challenges with high waters during other times of year and because no detectable difference in fish assemblage structure could be assigned to the season of surveys.

Chapter V details models used to assess changes in the distribution of 10 species of greatest conservation need (SGCN) between historical (1940-1999) and contemporary (2000-2025) periods. Results reveal that SGCN distributions were positively correlated with stream flow magnitude and stream size; SGCN distributions were negatively correlated with high proportions of managed forest and pasture/crop in watersheds; and SGCN cooccurrence with other species highlights the benefits of managing for these species to benefit other members of local fish assemblages.

Chapter VI details an assessment of the validity of the recently described Gumbo Darter and whether this species should be recognized and included on SGCN lists. Results reveal limited evidence for genotypic differences between Gumbo Darter and Mud Darter and ultimately point towards Gumbo Darter being synonymous with Mud Darter and therefore removed from SGCN lists.

Chapter VII details repeated surveys of the lower Neches River downstream of B.A. Steinhagen Reservoir (Dam B) between 1978-1980 and 2024. Results reveal a change in the fish assemblage across 112 river km between Dam B and a saltwater barrier near Beaumont, TX; assemblage changs were driven by decline among 8 species but increase among 3 species; and few non-native species have invaded the lower Neches River.

Chapter VIII details new surveys of small streams that drain directly into the upper Sabine River. The major contribution of this chapter is information on fish assemblage structure in streams that has not been surveyed in the past.

The final dataset generated from these chapters is deposited on FigShare (https://doi.org/10.6084/m9.figshare.31817077) and is freely available. In total, the database includes 137,823 individual fishes from 286 surveys. The deposited data includes metadata providing the details of the structure of the data. Specimens collected, sorted, and deposited into the Collection of Fishes in the Biodiversity Research and Teaching Collections at Texas A&M University are also freely available for loan (https://agrilife.org/tcwc/collections/ichthyology/).

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Cover photos show the Neches River at the State Highway 94 crossing circa 1954 (photo from Texas Game and Fish Commission) and 2023 (photo by Rebecca Mangold). We thank Bill Kirby and his team of biologists with the Sabine River Authority for providing logistical insight into the Sabine River Basin. We thank Terry Corbit, Jason Watson, and Brian Fife with Lower Neches Valley Authority for providing logistical support and insight into the Neches River Basin. We thank Whitny Howeth and Andrew Bennett with U.S. National Park Service for help with locating historical reports, permitting, and logistical support during field surveys. Many members of the Riverscape Ecology Laboratory, Montaña Aquatic Ecology Laboratory, and Conway Ichthyology Laboratory helped with this study. We appreciate project coordination by Lee Schoeck and Melissa Salmon with the Texas Comptroller of Public Accounts Natural Resources Program.

CHAPTER I: BACKGROUND AND STRUCTURE OF REPORT

Motivation for this study

Freshwater ecosystems in east Texas support high fish and mussel diversity compared to other regions in Texas. However, changes in land use associated with rapid urbanization, channelization, impoundments, and agriculture have impacted the species richness, abundance, and distribution of aquatic organisms in East Texas streams. Historical surveys of Texas freshwater fauna suggest a decrease in both regional and local species diversity. For example, previous fish surveys conducted by federal and Texas state agencies as well as other researchers, from sub-basins of the middle and lower Neches and lower Sabine Rivers, commonly reported freshwater species in East Texas that are now considered as species of greatest conservation need (SGCN) with state conservation ranks of S3 (i.e., imperiled in the state of Texas) and S4 (Apparently Secure) (TPWD 2012). Some of these SGCN include western creek chubsucker, blackspot shiner, Sabine shiner, and silverband shiner. In a document prepared by Bonner & Runyan (2007) using historical museum records of fishes in the lower Sabine River from 1948 to 2006, they reported the presence of western sand darter, silverband shiner and blackspot shiner in low abundance, but their surveys from 2006-2007 did not yield these species at all, suggesting a decline in population trends. In 2020, new cyprinids (e.g., the pallid shiner, the Mississippi silvery minnow, and the suckermouth minnow), catostomids (the spotted sucker), and percids (e.g., gumbo darter) inhabiting East Texas streams were added to the SGCN list (TPWD 2012, Birdsong et al. 2020a,b). Historical surveys (1950-1990s) reported these species in tributaries of the Neches-Angelina-Sabine rivers. However, recent surveys (SRA-TX 2007, Robertson et al. 2018, Montaña, unpublished data for 2017-2021) have occasionally yielded several of these species, but in much lower abundances. As freshwater habitats continue to degrade due to human-induced changes, new species are added to the SGCN list to avoid extirpations from their native ranges. Both Neches and Sabine rivers are within the Western Gulf Coast Plains (WGCP) ecoregion, a region that despite its rich freshwater biodiversity, is considered a hotspot for emerging human development, which can increase habitat fragmentation, alter flows, and alter stream substrates consequently affecting in-stream biota and spawning behavior of fishes. Given the rapid changes of the landscape in East Texas, a qualitative and quantitative assessment of the fish biodiversity is needed to fill information gaps concerning fish assemblages and their trends over time, imperiled species, relationships between species and their habitat conditions, and the distribution of fish species hosts of freshwater unionid mussels. This information is needed for delineating conservation and management plans, review list of species as SCGN, and for proper management of water resources and native fishes.

Inventory of the fish diversity in the Neches River and upper Sabine River watersheds will provide valuable information on the current status and spatial and temporal distribution of fish species throughout the watersheds. Likewise, results will contribute to the baseline fish assessments being conducted by the US Department of the Interior and US Geological Survey and TPWD in east Texas river systems. More research is needed to fill gaps to better understand species distributions, areas of occupancy, and relative abundance of fishes in the watersheds. These data are critical for updating NatureServe rankings and guiding future species listing decisions.

Objectives and tasks to be completed

Objective 1. – Historical and Contemporary Fish Distributions.

Our first objective was to review existing survey data for fish assemblages in the Neches River Basin and upper Sabine River basin to compile a dataset representing historical community surveys. We reviewed online databases and literature as well as historical reports of fishes collected from each basin. Based on the locations of previous collections, we conducted additional fields sampling to fill spatial gaps in coverage and repeat sampling at historical sites. Fish sampling methods followed standard protocols of mixtures of seining and backpack electrofishing as described in the Texas Commission on Environmental Quality standard sampling protocol that is also employed by the Texas Parks and Wildlife Department Inland Fisheries Division. Sampling of wadeable streams (i.e., <1 m depth) included a minimum of 900 seconds of electrofishing combined with 60 meters of seining with a 15-foot by 6-foot seine with 3/16-inch mesh. A minim of 10 hauls 10 m in length was conducted. Seining targeted deeper pools and runs, where backpack electrofishing is not as effective. For non-wadeable sites, boat-mounted electrofishing replaced backpack electrofishing. Physical vouchers for all species allowed under scientific permits were retained, and photo vouchers used for other specimens too large to fit in 1 gallon collection jars. Under this objective, we also assessed the habitat preferences, distribution, and taxonomic validity of the Gumbo darter (*Etheostoma thompsoni*), a species that was recognized as a distinct species only relatively recently (2012) and questions remain concerning the distribution of this species within east TX, and whether it is genetically distinct from the closely related Mud darter (*Etheostoma asprigene*). Specimens and genetic samples collected as part of our work in the Neches and Sabine basins, in combination with samples collected from other basins (in and outside of TX), allowed us to assess the taxonomic validity of Gumbo darter for the first time. This work contributes to our knowledge of SGCN in East TX, and provides data that will help with refinement of the number of species included on the SGCN list. Voucher specimens from this study were deposited in the Biodiversity Research and Teaching Collections at Texas A&M University where they are freely available for loan.

Objective 2. – Trend Analysis for Fish Assemblages and Species.

We assess assemblage-level (i.e., all fish species encountered) and species-level (i.e., individual species of interest) change in fish communities and species distributions in the Neches and upper Sabine river basins. Assemblage-level change focused on analyses of temporal beta diversity and understanding how changes in fish assemblages, if present, affected the capacity for fishes to serve as hosts to freshwater mussels. At the species level, we focused on changes in distributions of species of greatest conservation need (SGCN), many of which also serve as mussel hosts. These analyses collectively allowed for assessing trends in assemblages and species across the study area.

Objective 3. – Long-term Fish Monitoring Design.

Understanding the best methods and seasons to assess fish assemblage composition is a challenge in temperate freshwater systems because seasonal changes might affect both fish assemblage composition and the detectability of fishes in surveys. Historically, fish surveys were concentrated in the summer low flow season when stream access is most efficient. However, whether or not the same species are present in other seasons or if inference into fish assemblage structure changes with season is untested. We selected 15 sites assess temporal differences in sampling efficiency as a way of informing long-term sampling. These sites were sampled three times during each of two years (six surveys total) to assess temporal differences in fish assemblage and species occurrence using the same methods described in Objective 1. Seasonal surveys included fall (September-November), spring (March-May), and summer (June -August). We compared surveys using multivariate and rarefaction-based analyses to assess which time periods were most representative of the entire assemblage.

Overview of study components

This report consists of eight chapters, and the seven following this introductory chapter detail studies focused on addressing the objectives listed above.

Chapter II served as the Master of Science thesis for Rebecca Mangold in the Department of Ecology and Conservation Biology at Texas A&M University under the direction of Joshuah Perkin. This chapter is published in the journal Aquatic Conservation: Marine and Freshwater Ecosystems, 2025:35:e70240 (Mangold et al. 2025). This chapter addresses Objectives 1 and 2 by assessing the historical and contemporary fish assemblages of the Neches River Basin across gradients of land use change and streamflow alteration, including emphasis on how fish assemblage change relates to fishes serving as hosts to mussels.

Chapter III served as the Master of Science thesis for Johnathan Ellard in the Department of Ecology and Conservation Biology at Texas A&M University under the direction of Joshuah Perkin. This chapter has been submitted, revised, and resubmitted to the journal Scientific Reports. This chapter addresses Objectives 1 and 2 by assessing the historical and contemporary fish assemblages in the Sabine River prior to and following construction or large impoundments, including assessment of how fish assemblage change relates to fishes serving as hosts to mussels.

Chapter IV served as the Master of Science thesis for Annastasia Umstott in the Department of Biology at Stephen F. Austin State University under the direction of Carmen Montaña. This chapter has been submitted to the journal Freshwater Biology. This chapter addresses Objective 3 by conducting two years of seasonal surveys to assess how fish assemblage composition and beta diversity change with seasons and the related implications for long-term monitoring.

Chapter V served as the Master of Science thesis for Maggie Moses in the Department of Biology at Stephen F. Austin State University under the direction of Carmen Montaña. This chapter is formatted for submission to a peer-reviewed journal. This chapter addresses Objectives 1, 2, and 3 by fitting species distribution models to species of greatest conservation need and assessing how environmental determinants influenced fish assemblage structure across seasons.

Chapter VI served as the Master of Science thesis for Wesley Arand in the Department of Ecology and Conservation Biology at Texas A&M University under the direction of Kevin Conway. This chapter is formatted for submission to a peer-reviewed journal. This chapter addressed Objective 1 by evaluating the validity of Gumbo Darter as a species.

Chapter VII served as a project led by doctoral student Thomas Dodson in the Department of Ecology and Conservation Biology at Texas A&M University under the direction of Joshuah

Perkin. This chapter addressed Objective 1 and Objective 2 by assessing historical and contemporary fish assemblage structure in the Lower Neches River and analyzing long-term changes in fish assemblage composition.

Chapter VII served as a project led by Master of Science student Rebeccaa Mangold in the Department of Ecology and Conservation Biology at Texas A&M University under the direction of Joshuah Perkin. This chapter addresses Objective 1 by documenting the contemporary distribution of fishes at locations that were not historically surveyed.

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CHAPTER II: NECHES RIVER FISH ASSEMBLAGE

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, and Foufoula-Georgiou et al. 2015). Streams in urban watersheds are often characterized 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 characterized by increased bank erosion, sediment deposition, and nutrient inputs leached from fertilizers (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 homogenize flow regimes (Poff et al. 1997). This regulation of riverine landscapes is so prevalent that only 23% of the world's large rivers (>1,000 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 homogenization (Poff et al. 1997, Allan et al. 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 communities 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 behavior (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 community 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 community organization operate (Green et al. 2022). Detecting ecological responses to environmental changes in stream networks is often scale dependent (Allen 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 community 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 communities (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 community composition can arise from two possible mechanisms: nestedness and replacement (Harrison et al. 1992). Nestedness occurs when one community represents a subset of species found in another larger community either through species loss or species gain. Replacement occurs when one community has species that differ from another community 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 communities along a spatial or environmental gradient (Whittaker 1960), the metric can also be used to assess community 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 communities are nested within contemporary communities, that would suggest community change is being driven by species invasions (Gido et al. 2004). Alternatively, if nestedness is dominant and contemporary communities are nested within historical communities, then community 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 a community 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 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 analyzed community to prevent inflation by rare species (Laliberté and Legendre 2010). Multi-trait functional assessments are useful for understanding community 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 et al. 2010). Alternatively, a long-term study assessing the effects of improved water quality on fish communities in the Illinois River, USA found that taxonomic richness was positively related to functional diversity (Parker et al. 2018).

In this study, we compare historical data from 1956–1957 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, USA. 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 hypothesized 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 hypothesized 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 homogenization of functional traits in the community (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 community functional traits. Lastly, no relationship between ΔFDis and temporal beta diversity would suggest that the community 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 urbanization and streamflow alteration, taxonomic replacement would be associated with functional homogenization as environmental filtering removes specialist species (Figure 1c; Poff et al. 1997, Walsh et al. 2005).

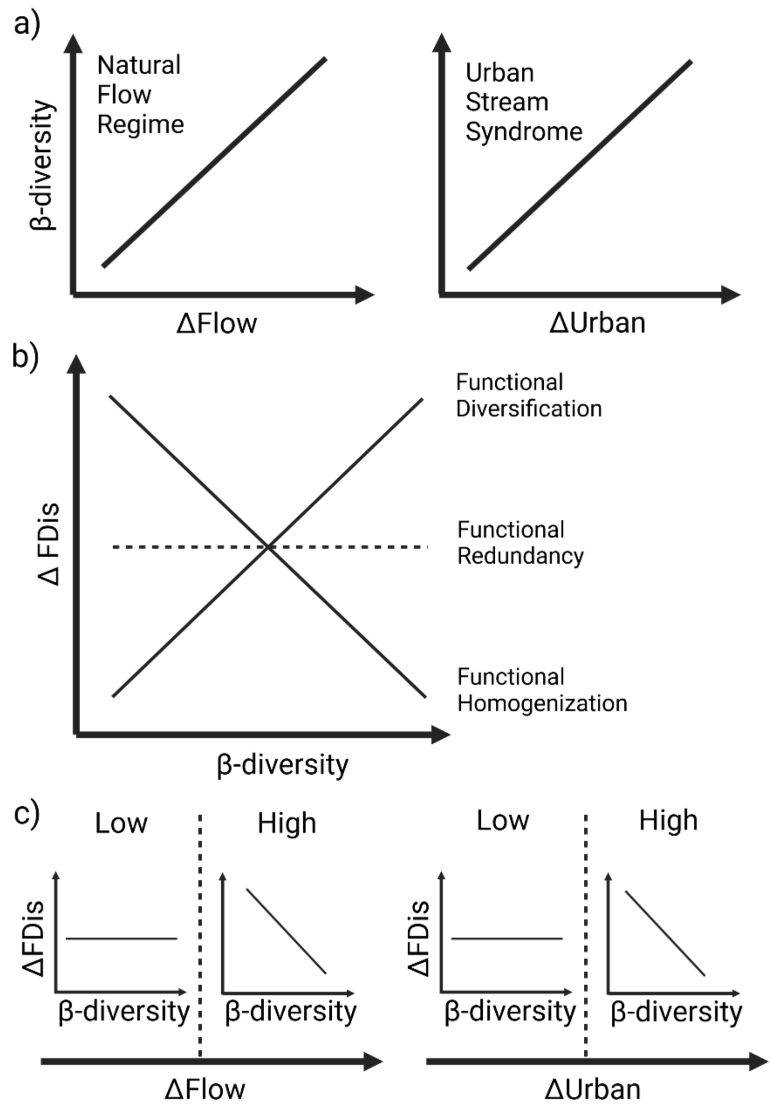

Figure 1. Conceptual diagram illustrating hypotheses tested in this study. (a) The Natural Flow Regime Paradigm (Poff et al. 1997) and the Urban Stream Syndrome (Welsh et al. 2005) predict greater beta diversity where flows are more altered (ΔFlow) and watersheds experience greater urbanization (ΔUrban). (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 urbanization.

Methods

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 km2 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 dekameters (dam3), and is located near the headwaters of the mainstem. Lake B.A. Steinhagen was completed in 1953, has a storage capacity of 85,430 dam3, 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 dam3 and is located about 40 river kilometers 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 upstream of Sam Rayburn Reservoir, and four sites along Pine Island Bayou (Figure 2c).

Fish Collections. – 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 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 4.6x1.8 m 4.8 mm mesh seine. Small fish were euthanized 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 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, 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).

Land Cover. – We collected LCLU data to represent the historical and contemporary periods. Historical land cover for the year 1957 was downloaded from the U.S. 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 National Hydrological Dataset (NHD) Plus High Resolution (U.S. Geological Survey 2018) for two reasons. First, this watershed boundary is a commonly chosen unit in assessing stream condition (Hain et al. 2018, Spiels et al. 2025) that represents a more localized 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). Secondly, use of network catchments would have produced nested land cover subsets, since sites are distributed longitudinally along the Neches River, Angelina River, and Pine Island Bayou. We then calculated the percentage change in LCLU classes in the watershed of each fish survey site using historical and contemporary raster data analyzed 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 urbanization in this study.

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 (Figure 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 (2004) 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 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 (Ford et al. 2014, Ford et al. 2016, Tarter 2019) and corresponding fish host data were derived from the Mussels of Texas Database (Randklev 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.

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) analyzed 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 (McCune and Grace 2002) 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 (βsor) from the Baselga family of beta diversity to calculate total temporal beta diversity, nestedness (βnes) and replacement (βsim) for each sampling location (Baselga 2010). βsor is presence/absence measure of beta diversity formulated as:

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

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 analyzed 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).

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 analyzed 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 homogenization 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 urbanization and streamflow alteration for each of the three traits (12 models total). Degrees of alteration for urbanization 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 urbanization (n=18) while sites with more than 2.2% increase in urban landcover were considered high urbanization (n=7). Sites with streamflow PCA distance less than 0.9 were considered low streamflow change (n=18) while sites with a stream flow 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).

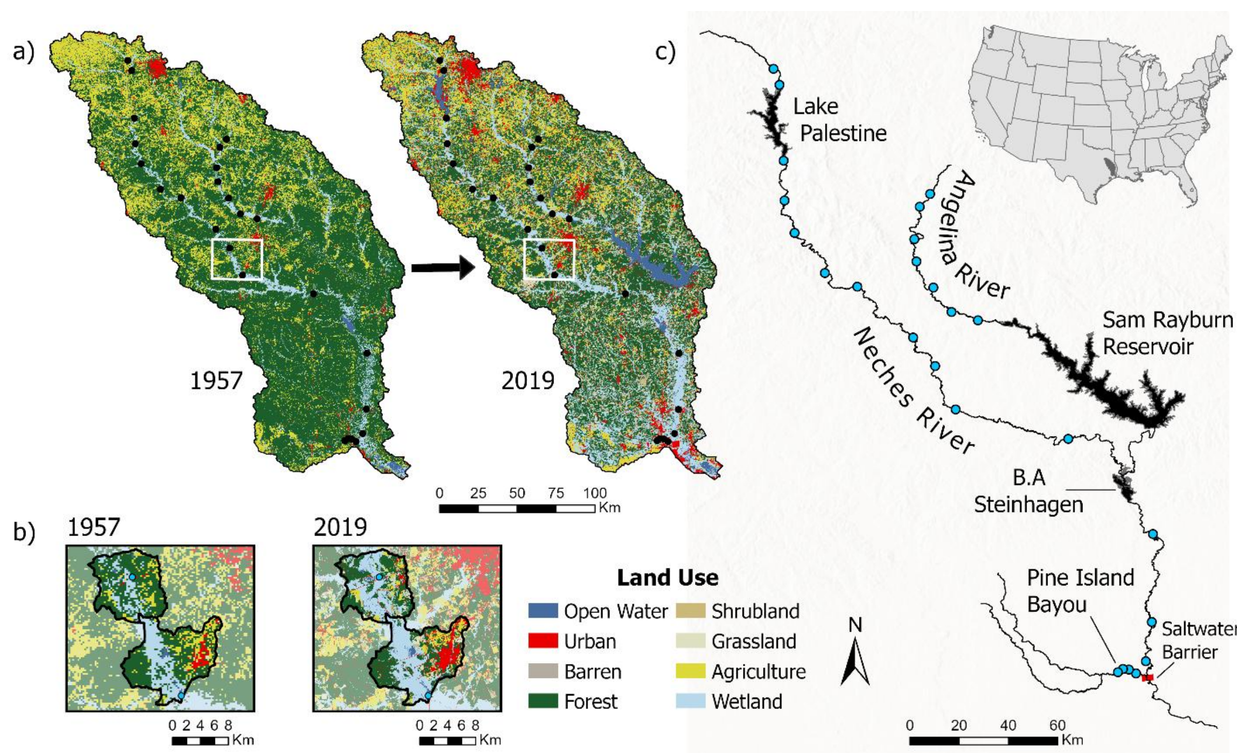

Figure 2. Study area illustrating a) Changes in landcover in the Neches River Basin from 1957 (Sohl et al. 2018) to 2019 (Dewitz and U.S. Geological Survey 2021) where black points indicate the sites sampled during the historical period (1956-1957) and revisited during the contemporary period (2023). (b) a zoomed in view of LCLU changes over time emphasizing 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).

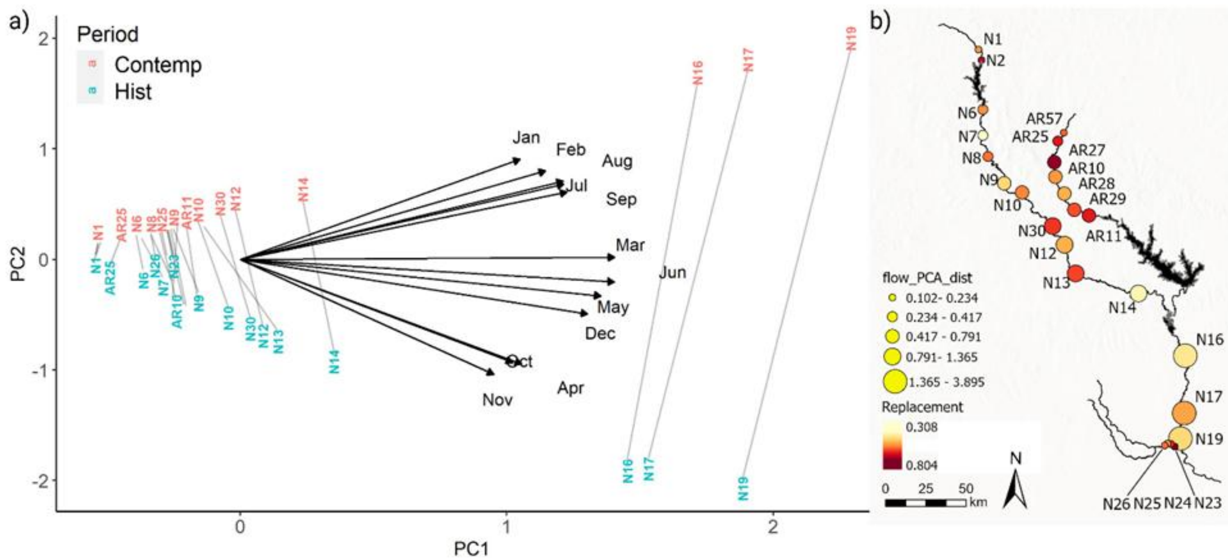

Figure 2.5. a) PCA of monthly streamflow estimates for the historical period (blue labels, Miller et al. 2018) and contemporary period (pink labels, McKay et al. 2012) where gray lines illustrate Euclidean distances between the historical and contemporary observation of each site. PC1 represents a gradient 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 color indicates temporal species replacement of the fish assemblage.

Results

Species Patterns. – 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).

Beta Diversity. – 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 Lepomis megalotis, *Notropis texanus, Micropterus salmoides, Hybopsis nuchalis, Etheostoma chlorosoma, Percina macrolepida, Ictalurus punctatus, Opsopoeodus emiliae,* and *Percina sciera* (Supplementary Table S3).

Linear relationships between replacement and anthropogenic alterations were scale-dependent (Table 2). 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 urbanization 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 (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).

Functional Diversity Relationships. – Relationships between taxonomic replacement and multi-trait ΔFDis at different degrees of anthropogenic alteration existed for urbanization 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 urbanization, 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 urbanization 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).

Table 1. Fish species used in taxonomic and functional diversity analysis listing number of mussel species hosted, stream size preference (Goldstein and Meador 2004), 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.

Common Name	**Species**	**# mussels hosted**	**Stream Size Preference**	**Substrate associations**	**Historical**		**Contemporary**	
					Basin	**Mainstem**	**Basin**	**Mainstem**
Engraulidae								
Bay Anchovy	*Anchoa mitchelli*	1	None	None	0/0	0/0	657/4	0/0
Clupeidae								
Gizzard Shad	*Dorosoma cepedianum*	5	Medium to Large Rivers	None	42/2	40/1	11/5	8/3
Threadfin Shad	*Dorosoma petenense*	0	Medium to Large Rivers	None	0/0	0/0	460/5	5/1
Cyprinidae								
Red Shiner	*Cyprinella lutrensis*	6	Range of sizes	Clay/Silt-Gravel	182/11	160/8	1699/18	1535/13
Blacktail Shiner	*Cyprinella venusta*	5	Creeks to Small Rivers	Sand-Cobble	559/19	471/12	1664/21	1280/12
Mississippi Silvery Minnow	*Hybognathus nuchalis*	0	Medium to Large Rivers	Muck-Gravel	7/2	7/2	693/8	693/8
Pallid Shiner	*Hybopsis amnis*	1	Medium to Large Rivers	Clay/Silt-Sand	215/4	198/3	774/14	511/6
Ribbon Shiner	*Lythrurus fumeus*	0	Creeks to Small Rivers	Muck-Sand	31/9	22/6	1957/23	347/12
Golden Shiner	*Notemigonus crysoleucas*	7	Medium to Large Rivers	None	65/5	23/3	4/1	4/1

Table 1. Continued

Common Name	Species	# mussels hosted	Stream Size Preference	Substrate associations	Historical		Contemporary	
					Basin	Mainstem	Basin	Mainstem
Blackspot Shiner	*Notropis atrocaudalis*	0	Creeks to Small Rivers	Muck-Gravel	67/5	63/4	0/0	0/0
Ghost Shiner	*Notropis buchanani*	0	Range of sizes	Sand-Gravel	143/10	113/8	288/8	255/5
Sabine Shiner	*Notropis sabinae*	0	Creeks to Small Rivers	Sand-Bedrock	300/11	300/11	96/8	89/5
Weed Shiner	*Notropis texanus*	2	Medium to Large Rivers	Sand-Cobble, Boulder-Bedrock	16/3	16/3	2736/22	1238/11
Mimic Shiner	*Notropis volucellus*	0	Range of sizes	Clay/Silt-Gravel	19/2	18/1	6/3	4/2
Pugnose Shiner	*Opsopoeodus emiliae*	0	Range of sizes	Gravel-Cobble	7/3	1/1	254/15	199/7
Suckermouth Minnow	*Phenacobius mirabilis*	0	Range of sizes	Muck-Cobble	0/0	0/0	11/7	5/3
Bullhead Minnow	*Pimephales vigilax*	2	Medium to Large Rivers	Gravel-Bedrock	235/15	177/8	2552/22	2338/13
Catostomidae								
Smallmouth Buffalo	*Ictiobus bubalus*	1	Large Rivers	none	16/3	16/3	0/0	0/0
Spotted Sucker	*Minytrema melanops*	0	Creeks to Small Rivers	Clay/Silt-Bedrock	0/0	0/0	124/10	111/6
Blacktail Redhorse	*Moxostoma poecilurum*	0	Range of sizes	Muck-Bedrock	1/1	1/1	15/4	13/3
Ictaluridae								
Channel Catfish	*Ictalurus punctatus*	13	Medium to Large Rivers	Sand-Boulder	0/0	0/0	60/12	42/8
Esocidae								
American Pickerel	*Esox americanus*	1	Range of sizes	none	12/5	11/4	7/1	7/1
Atherinopsidae								
Brook Silverside	*Labidesthes sicculus*	0	Creeks to Small Rivers	Muck-Bedrock	308/12	253/6	358/15	119/8
Inland Silverside	*Menidia beryllina*	0	Range of sizes	Sand	0/0	0/0	43/4	39/2

Table 1. Continued.

Common Name	Species	# mussels hosted	Stream Size Preference	Substrate associations	Historical		Contemporary	
					Basin	Mainstem	Basin	Mainstem
Fundulidae								
Golden Topminnow	*Fundulus chrysotus*	1	Creeks to Small Rivers	Muck-Clay/Silt	24/3	19/2	0/0	0/0
Blackstripe Topminnow	*Fundulus notatus*	2	Creeks	Muck-Cobble	209/17	184/10	431/24	294/14
Poeciliidae								
Western Mosquitofish	*Gambusia affinis*	4	Creeks	Muck_Cobble	1291/18	835/11	573/18	470/11
Centrarchidae								
Warmouth	*Lepomis gulosus*	7	Creeks	Muck-Clay/Silt	1/1	0/0	48/4	17/3
Bluegill	*Lepomis macrochirus*	13	Range of sizes	none	55/12	30/8	158/17	34/8
Longear Sunfish	*Lepomis megalotis*	10	Range of sizes	Sand-Cobble	1/1	1/1	369/24	291/14
Redear Sunfish	*Lepomis microlophus*	3	Creeks to Small Rivers	Muck-Sand	8/5	5/4	13/5	1/1
Redspotted Sunfish	*Lepomis miniatus*	1	Creeks to Small Rivers	Muck-Sand	31/11	18/7	6/4	3/3
Largemouth Bass	*Micropterus nigricans*	12	Range of sizes	Clay/Silt-Cobble	57/3	57/3	53/19	40/12
Spotted Bass	*Micropterus punctulatus*	6	Range of sizes	Muck-Sand	210/14	202/10	120/19	98/12
White Crappie	*Pomoxis annularis*	8	Range of sizes	Muck-Sand	51/2	1/1	98/11	89/6
Black Crappie	*Pomoxis nigromaculatus*	7	Range of sizes	Muck-Sand	25/4	10/3	16/6	9/3
Percidae								
Scaly Sand Darter	*Ammocrypta vivax*	0	Creeks to Small Rivers	Sand-Gravel	26/7	23/5	40/7	27/4
Bluntnose darter	*Etheostoma chlorosoma*	0	Creeks to Small Rivers	Muck-Sand	5/2	1/1	573/16	429/7

Slough Darter	*Etheostoma gracile*	0	Range of sizes	Muck-Clay/Silt	26/8	21/6	115/12	99/7
Harlequin Darter	*Etheostoma histrio*	0	Range of sizes	Muck-Clay/Silt, Gravel	0/0	0/0	8/3	7/2
Cypress Darter	*Etheostoma proeliare*	0	Range of sizes	none	0/0	0/0	68/5	67/4
Gumbo Darter	*Etheostoma thompsoni*	1	Range of sizes	Muck-Gravel	0/0	0/0	190/10	157/7
Bigscale Logperch	*Percina macrolepida*	0	Creeks to Small Rivers	Clay/Silt-Sand	1/1	0/0	40/8	40/8
Dusky Darter	*Percina sciera*	1	Creeks to Small Rivers	Gravel-Cobble	4/3	3/2	71/11	53/8
River Darter	*Percina shumardi*	0	Range of sizes	Gravel-Cobble	9/5	8/4	23/6	21/5

Table 2. 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.

Species	**IUCN rank**	**Texas Status**	**Basin Historical abund**	**Basin Contemp abund**	**Basin Average Contribution**	**p-value**	**Main Historical**	**Main Contemp**	**Main Average Contribution**	**p_value**	**Basin direction**	**Main Direction**
Ammocrypta vivax	LC	NL	0.0772	0.0549	0.0141	1	0.094	0.056	0.0147	0.99	–	–
Anchoa mitchelli	LC	NL	0.0000	0.0452	0.0069	**0.001**	0.000	0.000	0.0000	0.001	↑	–
Cyprinella lutrensis	LC	NL	0.1366	0.1942	0.0255	0.199	0.166	0.259	0.0225	0.083	–	–
Cyprinella venusta	LC	NL	0.2901	0.2352	0.0281	0.999	0.283	0.250	0.0192	0.997	–	–
Dorosoma cepedianum	LC	NL	0.0241	0.0386	0.0081	0.185	0.025	0.044	0.0087	0.266	–	–
Dorosoma petenense	LC	NL	0.0000	0.0547	0.0078	**0.001**	0.000	0.017	0.0024	**0.002**	↑	↑
Esox americanus	LC	NL	0.0510	0.0085	0.0076	1	0.074	0.015	0.0108	0.396	–	–
Etheostoma chlorosoma	LC	NL	0.0243	0.1480	[5]0.0209	**0.001**	0.016	0.116	[6]0.0149	**0.011**	↑	↑
Etheostoma gracile	LC	NL	0.0861	0.0914	0.0169	0.879	0.107	0.099	0.0167	1	–	–
Etheostoma histrio	LC	NL	0.0000	0.0187	0.0024	**0.001**	0.000	0.023	0.0028	**0.002**	↑	↑
Etheostoma proeliare	LC	NL	0.0000	0.0383	0.0051	**0.001**	0.000	0.056	0.0070	**0.002**	↑	↑
Etheostoma thompsoni	NE	SGCN	0.0000	0.0801	0.0109	**0.001**	0.000	0.098	0.0125	**0.001**	↑	↑
Fundulus chrysotus	LC	NL	0.0453	0.0000	0.0070	1	0.046	0.000	0.0064	0.993	–	–

Table 2 Continued.

Species	IUCN rank	Texas Status	Basin Historical abund	Basin Contemp abund	Basin Average Contribution	p-value	Main Historical	Main Contemp	Main Average Contribution	p_value	Basin direction	Main Direction
Fundulus notatus	LC	NL	0.2328	0.2255	0.0237	0.336	0.223	0.231	0.0184	0.173	–	–
Gambusia affinis	LC	NL	0.2641	0.1647	0.0298	0.73	0.254	0.177	0.0232	0.333	–	–
Hybognathus nuchalis	LC	SGCN	0.0192	0.0785	0.0118	**0.014**	0.034	0.140	[5]0.0182	**0.019**	↑	↑
Hybopsis amnis	LC	SGCN	0.0522	0.1365	[6]0.0201	**0.005**	0.070	0.101	0.0164	0.332	↑	–
Ictalurus punctatus	LC	NL	0.0000	0.0911	[8]0.0130	**0.001**	0.000	0.103	[8]0.0137	**0.002**	↑	↑
Ictiobus bubalus	LC	NL	0.0266	0.0000	0.0033	1	0.047	0.000	0.0058	0.258	–	–
Labidesthes sicculus	LC	NL	0.1581	0.1496	0.0252	1	0.128	0.136	0.0210	0.909	–	–
Lepomis gulosus	LC	NL	0.0104	0.0311	0.0053	0.109	0.000	0.037	0.0046	**0.002**	–	↑
Lepomis macrochirus	LC	NL	0.1439	0.1447	0.0226	0.793	0.159	0.106	0.0197	0.295	–	–
Lepomis megalotis	LC	NL	0.0094	0.2209	[2]0.0309	**0.001**	0.017	0.233	[1]0.0294	**0.001**	↑	↑
Lepomis microlophus	LC	NL	0.0501	0.0437	0.0111	1	0.070	0.014	0.0103	0.35	–	–
Lepomis miniatus	LC	NL	0.1270	0.0306	0.0186	0.105	0.128	0.041	0.0170	0.12	–	–
Lythrurus fumeus	LC	NL	0.1042	0.2514	[3]0.0287	**0.001**	0.112	0.199	0.0206	0.055	↑	–
Menidia beryllina	LC	NL	0.0000	0.0362	0.0053	**0.001**	0.000	0.040	0.0056	**0.001**	↑	↑
Micropterus punctulatus	LC	NL	0.1533	0.1578	0.0199	0.506	0.188	0.182	0.0157	0.553	–	–
Micropterus salmoides	LC	NL	0.0462	0.1442	0.0225	**0.001**	0.082	0.161	[4]0.0237	**0.006**	↑	↑
Minytrema melanops	LC	SGCN	0.0000	0.0774	0.0103	**0.001**	0.000	0.086	0.0107	**0.002**	↑	↑
Moxostoma poecilurum	LC	NL	0.0070	0.0285	0.0044	**0.05**	0.013	0.039	0.0059	0.103	↑	–
Notemigonus crysoleucas	LC	NL	0.0579	0.0079	0.0084	1	0.055	0.014	0.0082	0.936	–	–
Notropis atrocaudalis	LC	SGCN	0.0574	0.0000	0.0076	0.993	0.080	0.000	0.0104	0.152	–	–
Notropis buchanani	LC	NL	0.1198	0.0636	0.0181	0.994	0.165	0.069	0.0208	0.135	–	–
Notropis sabinae	LC	SGCN	0.1358	0.0721	0.0203	0.996	0.242	0.090	[2]0.0258	**0.028**	–	↓
Notropis texanus	LC	NL	0.0330	0.2493	[1]0.0327	**0.001**	0.059	0.207	[3]0.0243	**0.007**	↑	↑
Notropis volucellus	LC	NL	0.0205	0.0233	0.0055	0.463	0.018	0.029	0.0056	0.232	–	–

Table 2 Continued.

Species	IUCN rank	Texas Status	Basin Historical abund	Basin Contemp abund	Basin Average Contribution	p-value	Main Historical	Main Contemp	Main Average Contribution	p_value	Basin direction	Main Direction
Opsopoeodus emiliae	LC	NL	0.0312	0.1275	[7]0.0183	**0.002**	0.013	0.104	[9]0.0133	**0.006**	↑	↑
Percina macrolepida	LC	NL	0.0103	0.0600	0.0091	**0.002**	0.000	0.107	[7]0.0141	**0.001**	↑	↑
Percina sciera	LC	NL	0.0265	0.0811	[10]0.0120	**0.013**	0.029	0.101	[10]0.0132	**0.03**	↑	↑
Percina shumardi	LC	SGCN	0.0438	0.0429	0.0093	1	0.060	0.065	0.0115	0.917	–	–
Phenacobius mirabilis	LC	SGCN	0.0000	0.0473	0.0065	**0.001**	0.000	0.034	0.0042	**0.002**	↑	↑
Pimephales vigilax	LC	NL	0.2075	0.2370	0.0253	0.248	0.179	0.260	0.0225	0.087	–	–
Pomoxis annularis	LC	NL	0.0223	0.0835	[9]0.0129	**0.001**	0.013	0.083	0.0109	**0.006**	↑	↑
Pomoxis nigromaculatus	LC	NL	0.0439	0.0429	0.0102	0.995	0.055	0.034	0.0098	0.997	–	–

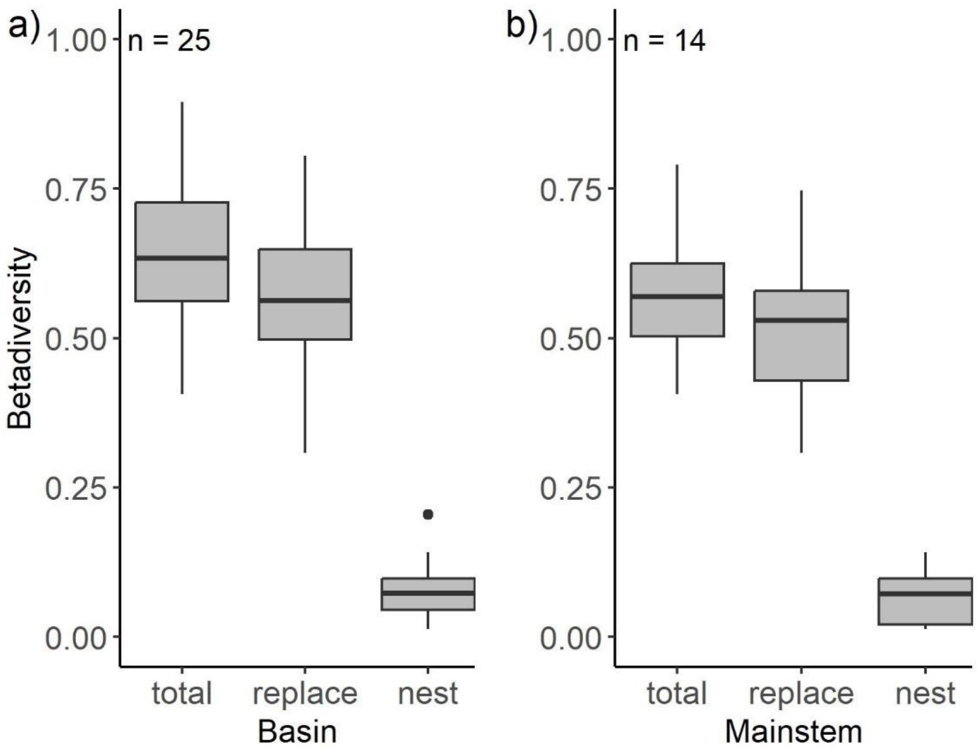

Figure 3. Boxplots of fish assemblage total beta diversity, replacement component (replace), and nestedness component (nest) showing replacement as the dominant form of taxonomic change from the historical (1956-1957) to contemporary (2023) periods at both the Basin (25 sampling sites) and Mainstem (14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

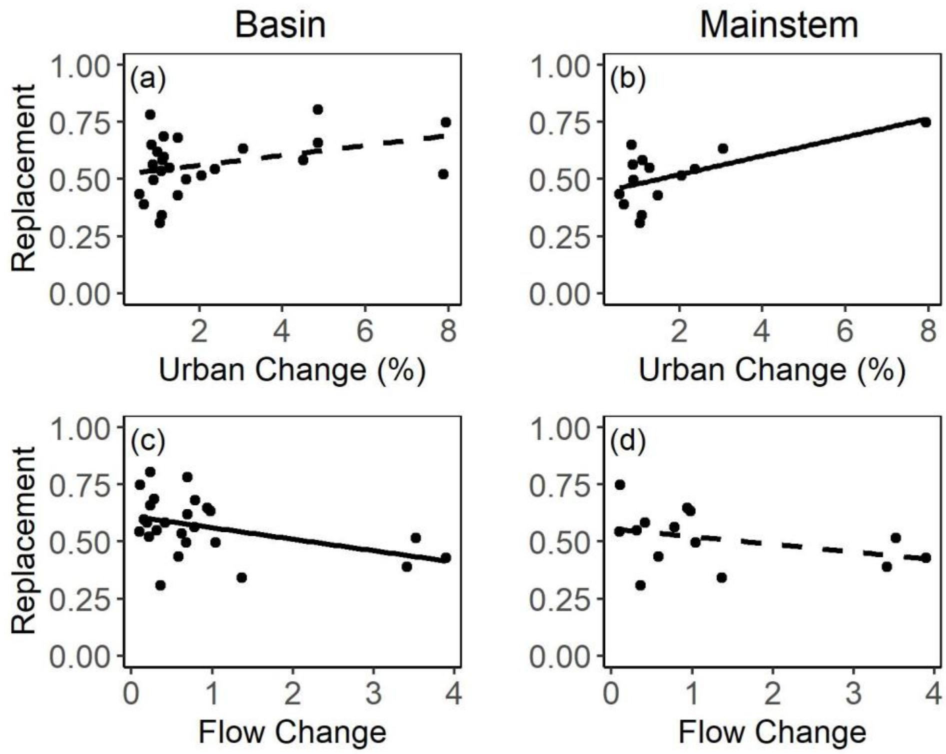

Figure 4. Linear regression models showing the replacement component of beta diversity as a function of percent of urban change in the watershed (a, b), streamflow change (c, d) at the Basin (n = 25, left column) and Mainstem (n = 14, right column) extents. Solid lines indicate significant relationships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

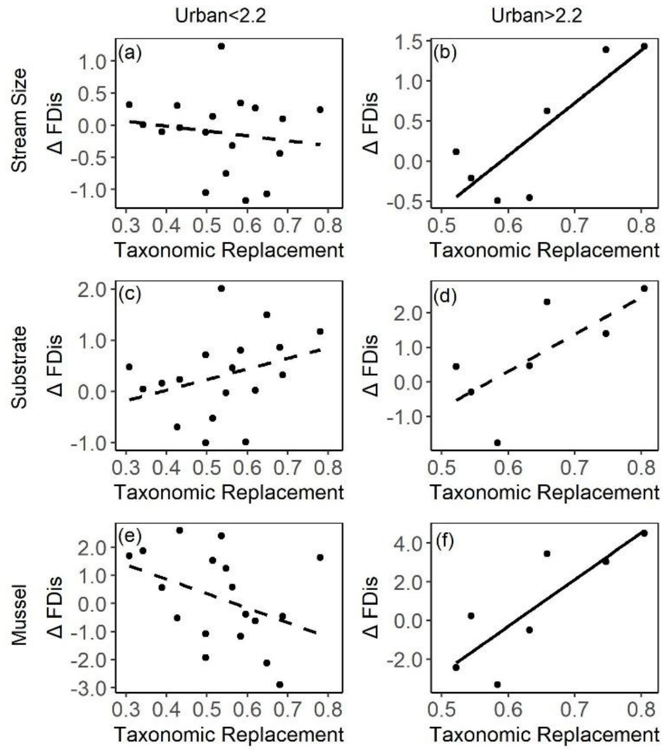

Figure 5. Linear regression models showing change in functional dispersion (FDis) as a function of taxonomic replacement at low (left column, less than 2.2%, n = 18) and high (right column, more than 2.2%, n = 7) degrees of urbanization for three functional traits: (a, b) Stream size preferences (Stream 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)

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 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 urbanization appeared to be dependent on spatial extent. Species replacement was highest at sites where urbanization 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 to 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 urbanization 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 urbanization 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 et al 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 communities in river systems (Poff et al 1997). We found that species replacement was greatest where temporal differences in monthly flow magnitudes was 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 1a) 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 1b). 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 1b). Thus, we hypothesize that when sites were sampled during the drought, fishes from small order tributaries in 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 recolonize 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 urbanization-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 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 urbanization over time were positively correlated with species replacement at the mainstem extent. We also found that at high degrees of urbanization, 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 Lepomis megalotis, Micropterus salmoides, and Ictalurus 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 favorable 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 urbanization 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 homogenization 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 2017).

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 urbanization and stream flow alteration. Our study found that increasing urbanization over time is associated with greater species replacement in the mainstem river. The negative effects of urbanization 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) 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 urbanization-driven fish assemblage shifts lead to a diversification of mussel host species. However, while mussel hosts tend to be generalist species that are tolerant to 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 urbanized 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 have been documented for both fish and mussels in which species richness increases with greater distance to reservoirs (Kinsolving and Bain 1993, Randklev et al 2016). Thus, a second management action supported by our results is the preservation of long, unfragmented reaches of large river that support both native mussels and fishes (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 (Saunder 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 urbanization 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 has 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 (Declaration B 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.

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 urbanization 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 urbanization and streamflow change, 2) sites with high degrees of urbanization 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 urbanization and streamflow change. The observed relationship between species replacement and mussel host functional dispersion at high urbanization 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 prioritized to ensure the long-term sustainability of fish populations. Future research should focus on integrating patterns of mussel distributions in urban areas, analyzing 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.

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CHAPTER III: SABINE RIVER FISH ASSEMBLAGE

Introduction

Flow regime alteration caused by dam construction and reservoir operation is a globally prevalent form of environmental disturbance that affects 77% freshwater riverine systems [1]. The natural flow regime paradigm posits that the natural dynamism of streamflow in rivers, measured by magnitude, frequency, duration, timing, and rate of change in flow, directly or indirectly regulates all ecological dynamics that support the native biodiversity of these ecosystems and its processes and services [2]. Consequently, alteration to natural flow regimes brought on by flow releases from reservoirs affects the ecology of rivers by altering aquatic habitat, water quality, energy sources, and biotic interactions [3]. Although dam construction and operation affect rivers in a variety of ways [4], the most apparent changes to the geomorphology of rivers and their aquatic communities occur near reservoirs, where "footprints" of dams are most notable and easily measured [5]. The tailwaters of dams with releases from their deep hypolimnetic zone can exclude native species [6, 7] and facilitate establishment of non-native species that require cooler water temperatures [8]. Conversely, reservoirs with releases from the shallow epilimnion can eliminate downstream cold-water habitats used by fishes [9]. With increasing hydrographic distance downstream from reservoirs, aquatic communities exhibit a longitudinal recovery gradient in which species occurrence and abundance return to natural baseline conditions [10, 11]. These downstream longitudinal recovery gradients can be leveraged to restore native fish assemblages when dam operations are managed to mimic key aspects of natural flow regime dynamics that occurred prior to flow regulation [12].

Reservoir construction can also affect aquatic organism communities in upstream directions by blocking the upstream passage of fluvial species and excluding those species from upstream lotic (flowing) habitats [13, 14]. In addition to this mechanism, species that naturally occur in river systems at low abundances, that are often generalist species and can thrive in slow moving water could experience population increases within lentic (non-flowing) habitats of reservoirs and then move upstream [15]. Likewise, fishes that can use streams but are stocked or introduced into reservoirs (i.e., facultative reservoir species) increase in abundance upstream of reservoirs, but there is a longitudinal decrease in occurrence of such species in an upstream direction [16, 17]. This pattern might be considered as a longitudinal recovery gradient in an upstream direction, brought on by transformation of lotic to lentic habitat within reservoirs coupled with fish movements out of reservoirs. Although there are negative ecological consequences associated with transforming habitats from lotic to lentic, the river-reservoir interface (RRI) defined as the zone of transition between a river system and a downstream reservoir can be used by native species. For example, in the Colorado River Basin of Texas, USA four RRIs had high native species diversity and were primarily inhabited by migratory and floodplain reproducing fish species [18]. Another study on the San Juan River and Lake Powell in Utah, USA revealed an increase in relative abundance of the imperiled Razorback Sucker (*Xyrauchen texanus*) in specific areas of the RRI [19]. These studies highlight the potential benefit of managing habitats within RRIs to mimic floodplain habitat and benefit native fishes.

Understanding, measuring, and addressing the ecological consequences of impoundment construction is a priority research area that might be advanced by considering spatial proximity to reservoirs and multiple measures of ecological change. Measuring ecological change caused by impoundment construction requires understanding ecological baselines [20], and such baselines are best developed through long-term research [5]. Although calls for long-term monitoring programs for fish assemblages are increasing, logistical challenges associated with such programs remain [21]. In the absence of comprehensive and continuous monitoring, snapshots of assemblage change developed using historical surveys coupled with repeated sampling might be the next best approach to assessing change [22]. Beta diversity is a measure of variation of species composition of assemblages among different sites [23]. Temporal beta diversity (taxonomic indices) provides a measure of ecological deviations from baselines to quantify temporal species assemblage change and has been applied widely in ecology [24, 25, 26], including for assessment of fish assemblage change [27, 28, 29]. This metric can attribute this change to differences in species richness (i.e., species loss or species addition), species nestedness (i.e., smaller subsetted groups of species rich sites or periods) or species replacement (i.e., a change of species present while maintaining the number of species; see review by Legendre [30]). When paired with information on reservoir proximity, hypothesized patterns in temporal beta diversity can be formulated. For example, under the premise of invasions by native facultative reservoir species (e.g., Falke & Gido [16]) or non-native species (e.g., Johnson et al. [31]), temporal nestedness might vary spatially such that historical assemblages nearest to reservoirs are nested subsets of contemporary assemblages after the addition of new species (Dam Invaders Hypothesis; Fig. 1a). Alternatively, the local extirpation of fluvial species near reservoirs (e.g., Edwards [6]) might contribute to contemporary assemblages near reservoirs representing a nested subset of historical assemblages (Proximity Extinctions Hypothesis; Fig. 1a). If both processes operate simultaneously, then a pattern of species replacement in proximity to reservoirs might emerge (Proximity Replacement Hypothesis; Fig. 1a). Knowledge of the beta diversity components driving assemblage change, and how it varies across a riverine landscape, can and should be incorporated into conservation and management actions aimed at maintaining biodiversity in regulated river systems [32, 33, 34].

Functional traits represent another constructive metric for measuring and managing the ecological consequences of impoundment construction. The trilateral continuum model of North American fish life history traits developed by Winemiller and Rose [35] provides a theoretical framework for predicting fish population responses to environmental change. The model defines three endpoint life history strategies (periodic, opportunistic, or equilibrium) based on functional traits (generation time, fecundity, juvenile survival). The model posits that opportunistic strategists (short-lived, low fecundity, low survival) persist in flashy, intermittent hydrologic regimes, periodic strategists (long-lived, highly fecund, low survival) persist in seasonal hydrologic regimes, and equilibrium strategists (long-lived, low fecundity, high survival) persist in stable hydrologic regimes. The model has been widely applied and its predictions generally supported in river systems affected by reservoir construction [33, 36, 37]. When paired with information on reservoir proximity, spatially explicit hypotheses for functional response to impoundment construction can be posed. Under the premise of increased equilibrium strategists in stable flow environments [36, 38], fishes employing this strategy might increase in abundance near reservoirs (Equilibrium Increase Hypothesis; Fig. 1b). Conversely, under the premise of opportunistic strategist decline when flows become increasingly stable [39, 40], fishes employing this strategy might decrease in abundance near reservoirs (Opportunistic Decrease Hypothesis; Fig. 1b). Periodic strategist response to impoundment construction might be more nuanced than other strategists given the benefit the RRI might confer to these strategists (e.g., Buckmeier et al. [18]). Consequently, periodic strategists might decline through time in areas immediately downstream of reservoirs where floodplain inundation is reduced or eliminated [41, 42] but might remain stable or increase through time near the RRI of downstream reservoirs

(Periodic RRI Hypothesis; Fig. 1b). Applying life history theory in the assessment of fish assemblage change through time and regarding spatial proximity to reservoirs can reveal the nature and causes of observed patterns, which then might be used in conservation and management of altered riverine ecosystems [35, 43].

Although functional traits related to life history provide insight into the mechanisms affecting fish population regulation, they provide limited insight into broader ecosystem-level consequences associated with fish assemblage change. Assessment of ecological functions provided by fishes, such as serving as hosts to freshwater mussels, can address this shortfall [44, 45]. Unionid freshwater mussels are highly threatened organisms that provide many ecosystem services [46, 47], but they rely on stream fishes to complete their early life history by parasitizing fish as they develop from glochidia into juvenile mussels [48]. This means that a change in fish assemblage structure has cascading ecosystem consequences that can be tracked using functional indices related to mussel hosting. Because fish can host more than one mussel species, mussel hosting may be measured as a multi-trait phenomenon. Laliberté and Legendre [49] developed a measure of multi-trait function diversity referred to as functional dispersion (F_{dis}) which uses a matrix of species traits to calculate a multidimensional distance from the centroid that is weighted by the relative abundance of each species and the presence or absence of a specific functional trait. In the context of fishes serving as mussel hosts, the matrix might be a fish species by mussel species matrix in which fishes known to host a mussel are assigned based on a binary value (0 = non-host; 1 = host). Then, the change in fish species occurrence and relative abundance can be used to track mussel host trait diversity where a decrease in F_{dis} through time would represent a loss in the capacity of the fish assemblage to host mussels, and an increase in F_{dis} would represent an increase in mussel host functional trait capacity. Freshwater mussels are known to colonize reservoir habitats, most likely through fish-based dispersal [50], thus consequent increases in host fish species richness, relative abundance, and hosting traits in proximity to reservoirs might augment mussel hosting functional diversity (Proximity Host Gain Hypothesis; Fig. 1c). In relation, Vaughn and Taylor [51] documented a longitudinal recovery gradient in mussel assemblage structure downstream of impoundments that mimicked the fish recovery gradient documented by Kinsolving and Bain [8]. Combes and Edds [52] found reduced mussel diversity immediately upstream of reservoirs. Though mussel declines are commonly confounded by multiple factors operating simultaneously [50], one hypothesis for their decline near reservoirs is the change in fish assemblages by declines in host fish species richness, relative abundance, and hosting trait availability near and within reservoirs (Proximity Host Loss Hypothesis; Fig. 1c). Tests of whether mussel host gain or loss has occurred near reservoirs will inform mussel conservation efforts in regulated rivers [48].

The goal of this study was to assess spatial patterns underpinning fish assemblage response to reservoir construction using historical and contemporary fish assemblage data from the mainstem of the upper Sabine River, Texas (USA) collected ~70 years apart. We addressed this goal by testing for longitudinal patterns in fish assemblage structure using taxonomic and functional trait indices before and after major reservoirs were constructed at the upstream (Lake Tawakoni) and downstream (Toledo Bend Reservoir) extents of the study area. First, we assessed the major form of temporal beta diversity for locations sampled prior to and following impoundment construction with known hydrographic distances from these impoundments. We tested the Dam Invaders, Proximity Extinction, and Proximity Replacement hypotheses by first testing for the dominant form of beta diversity using beta diversity decomposition and then testing for longitudinal patterns using generalized additive regression modelling. Second, we tested for change in the relative abundance of fish life history strategists near and away from reservoir locations. We tested the Equilibrium Increase, Opportunistic Decrease, and Periodic RRI hypotheses by calculating location-specific changes in relative abundances of life history strategists across a gradient of locations near and far away from reservoirs using generalized additive regression modelling. Finally, we tested for change in functional trait dispersion of fish mussel hosts across the riverscape prior to and following impoundment construction. We tested the Proximity Host Gain and Proximity Host Loss hypotheses using change in functional dispersion of fish host traits and generalized additive regression modelling. Testing these hypotheses across the complete longitudinal system provided a framework for assessing the taxonomic and functional responses by fish assemblages following reservoir construction. Our results can ultimately be used to guide conservation and management of biodiversity in regulated rivers around the world [53].

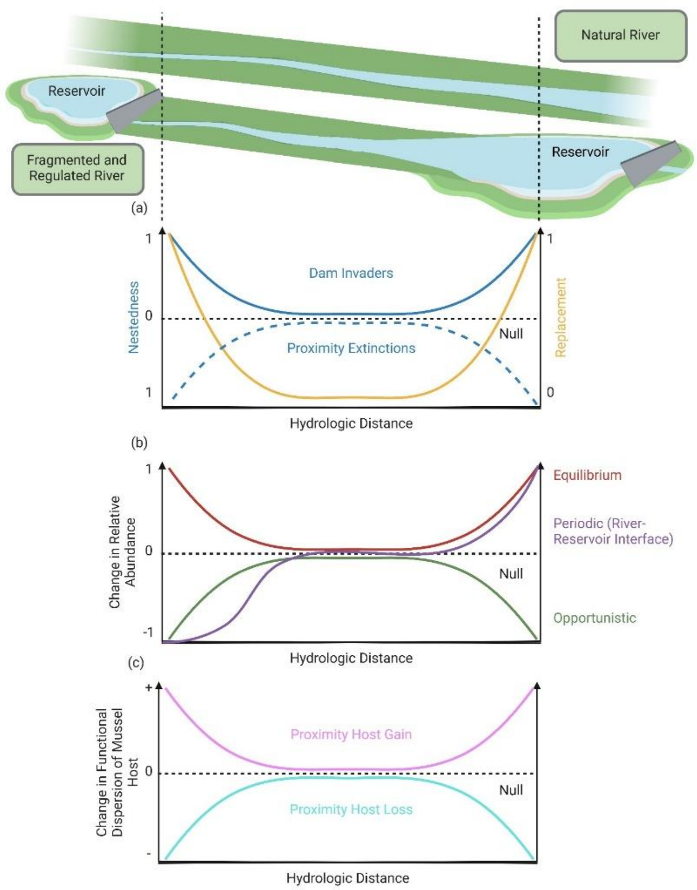

Figure 1. Conceptual diagram for hypotheses tested in this study. As rivers transition from natural to fragmented and regulated, longitudinal patterns in fish assemblage beta diversity, life history traits, and functional traits related to mussel hosting might emerge. (a) Near reservoirs beta diversity might emerge as historical assemblage structure being a nested subset of contemporary structure as new species invade (Dam Invader Hypothesis) or contemporary structure might be a nested subset of historical structure if extirpations occur near reservoirs (Proximity Extinctions Hypothesis); if both happen concurrently then replacement might occur near reservoirs (Proximity Replacement Hypothesis). (b) Relative abundance of three life history strategists might change through time such that equilibrium strategists increase near reservoirs,

opportunistic strategists decrease near reservoirs, or periodic strategists decrease downstream of reservoirs but increase in river-reservoir interfaces upstream of reservoirs. (c) Functional dispersion of fish serving as mussel hosts might increase (Proximity Host Gain Hypothesis) or decrease (Proximity Host Loss Hypothesis) near reservoirs. Created in BioRender.com.

Methods

Study area. – The study area encompasses the upper Sabine River of Texas, USA, from Lake Tawakoni (upstream extent) to Toledo Bend Reservoir (downstream extent) (Fig. 2). Lake Tawakoni was constructed in 1960, has a surface area of 153 km^2, and its tailwaters serve as the functional headwaters of the Sabine River [54]. Water storage in Lake Tawakoni is primarily for municipal, industrial, and irrigation purposes. Water releases are managed by two 0.5-m cast iron pipes controlled by sluice gates, though once the reservoir reaches an elevation of 437.5 feet (133.35 m) above mean sea level water passes over an ungated concrete spillway [54]. Toledo Bend Reservoir, which serves as part of the Texas-Louisiana border, was constructed in 1967 and has a surface area of 735 km^2 [54]. Toledo Bend Reservoir produces hydroelectric energy, provides flood control, and serves as a municipal and irrigation water supply reservoir. Water releases are managed by hydroelectric generators that track demand and spillway gates that generally open when water levels exceed 172.5 feet (52.5 m) above mean sea level. The total drainage area for the segment of river between both reservoirs is 18,591 km^2 and drains into the bottomland of the south-central plain ecoregions of Texas [54]. The entire basin has a humid subtropical climate with moderate rainfall throughout the year, averaging 1,270 mm annually [55, 56]. As of 2005, the average high of precipitation in Carthage, TX, was 131 mm in May, with an average low of 64 mm in August [55]. Additionally, severe droughts have impacted this system historically [55]. Upstream extents of the focal river segment have higher velocity of water flow in a narrower channel, while downstream extents form a wider channel with slower and deeper water in the vicinity of Toledo Bend Reservoir. The upper Sabine River mainstem has a median discharge of 3.7 m^3/s as of 2024 at USGS gage Sabine River near Mineola, TX (gage ID 08018500). Substrate and aquatic habitat vary throughout the basin, but are dominated by sandy substrate and woody debris, with some areas of rocky shoals.

Fish survey data. – The Texas Game and Fish Commission (TGFC) surveyed fishes throughout the upper Sabine River basin during 1954–1955 and we used the locations and methods of these surveys to guide contemporary surveys. The TGFC surveys are described in detail by Kemp [57] and were conducted prior to the impoundment of the river and the formation of what is now Lake Tawakoni and Toledo Bend Reservoir. Some of the historical survey locations were inundated by the construction of these reservoirs, and those locations were omitted from contemporary surveys because consistent gear types could not be used between time periods (i.e., water was too deep to seine). Other historical survey sites were small public ponds or lakes near the mainstem river that were typically sampled using gill nets, and we omitted these sites from analysis as well. Hoop net and rotenone collections were minimally used to target game species and composed ~0.5% of the total catch at unidentified sites. Hoop net and rotenone collections could not be separated from seining data but did not pose risk to comparative analyses because of data and site filtering, low catch from these methods, minimal use of the sampling methods, and the targeted game species being consistent across all sites. As a result, 28 of the original 59 locations visited by Kemp [57] were revisited as a part of this study. Mainstem Sabine River collections were made during summer months using seines and we replicated these collections during May-August 2023 using a combination of 4.6 m long by 1.8 m deep seines with 4.8 mm mesh (upstream locations with narrower channels) and 9.1 m long by 1.8 m deep seines with 6.4 mm mesh (downstream locations with broader channels). We targeted a length of 300 m at each site and conducted a minimum of 10 non-overlapping seine hauls. In both historical and contemporary surveys, all fishes small enough to fit into 3.8 L jars (i.e., <300 mm total length) were fixed in 10% formalin in the field, brought back to the laboratory, and transferred to 70% ethanol prior to identification and sorting. Specimens too large for preservation jars (i.e., >300 mm total length) were identified, photographed in the field, and released. Prior to fixation in formalin, specimens collected during contemporary surveys were euthanized with a lethal dose of clove oil and 95% ethanol following Texas A&M University Institutional Animal Care and Use Committee protocol 2023-0308. Field surveys were conducted under the approval of the Texas Parks and Wildlife Department through a Scientific Collection Permit (SPR-0218-068 issued to JSP). Specimens collected by Kemp [57] were cataloged in the Texas Natural History Collections at the University of Texas and can be accessed online [58], and those collected as part of the contemporary survey were deposited in the Collection of Fishes at the Texas A&M University Biodiversity Research and Teaching Collections (TCWC), under accession numbers TCWC 20808.01–20812.25, 20815.01–20820.31, 20834.01–20836.19, 20879.01–20885.19, and 20887.01–20893.21. We reviewed historical nomenclature and updated species names using the American Fisheries Society list of standardized names for North American fishes [59] to ensure consistent species designations across time periods. Historical and contemporary data were used to compile site-by-species matrices describing the abundance (i.e., number caught) for each species. Prior to analyses, we removed rare species that occurred in less than three collections for at least one of the time periods. This step was necessary because statistical tests for differences in occurrence between periods were intractable for species occurring in <3 collections.

Life history and mussel host trait classification. – All species in the historical and contemporary datasets were used to compile life history strategy (LHS) and mussel host trait data. Classifications into LHS categories were based on the theory presented by Winemiller and Rose [35] and previous designations by Hoeinghaus et al. [60] and Perkin et al. [37]. The six possible LHS trait classifications included: equilibrium (e), opportunistic (o), periodic (p), equilibrium-periodic (ep), opportunistic-equilibrium (oe), and opportunistic-periodic (op). Classifications of fishes into mussel host categories were based on a comprehensive list of 19 mussel species that occur in the basin [61]. We then compiled a list of all known fish hosts from both surveys that occur in the basin (n = 34 fishes) for each mussel species using reviews conducted by Ford & Oliver [62] and Sietman et al. [63]. We used these data to construct a mussel by fish species matrix in which suspected or confirmed fish hosts were coded as '1' for hosting or '0' for non-hosting for each mussel species.

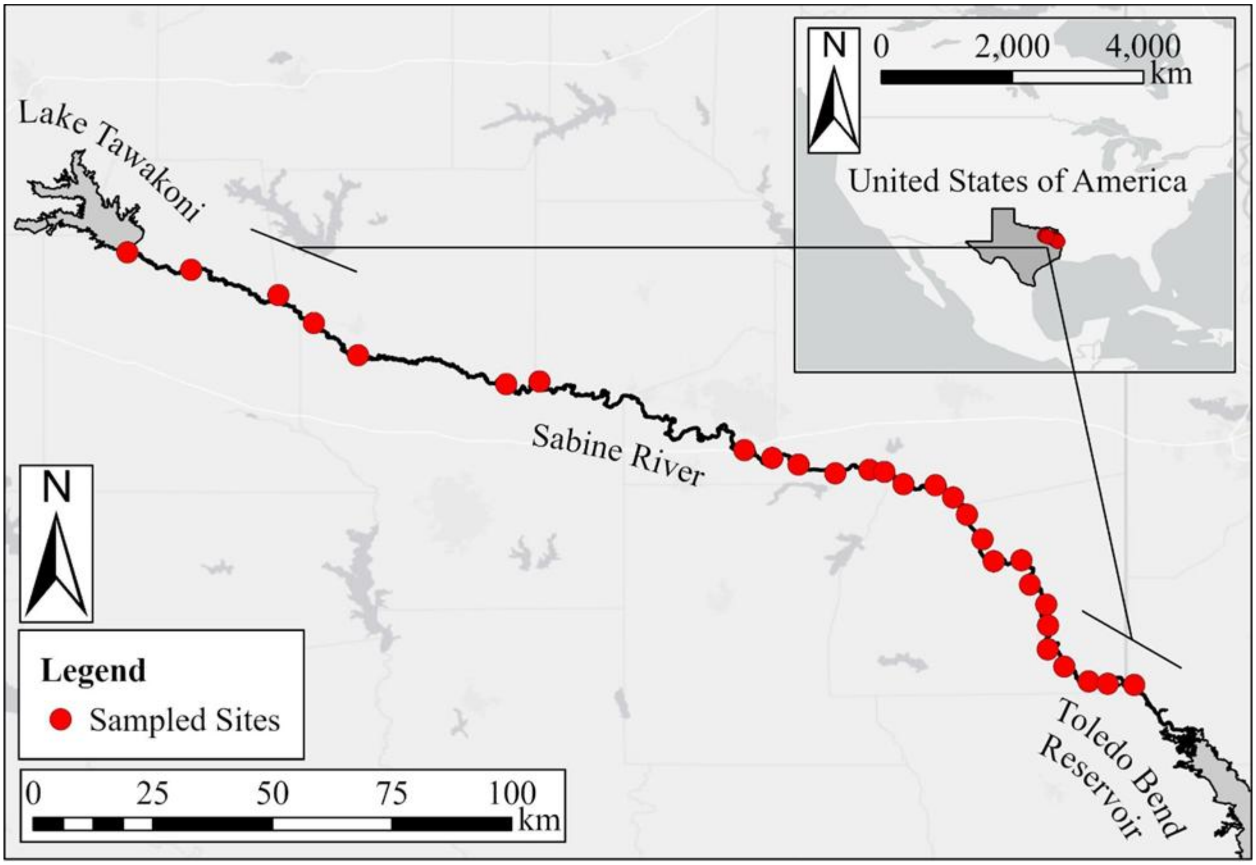

Figure 2. Map of the upper Sabine River, Texas (USA) showing locations of fish surveys sites (red points) sampled in 1954–1955 and 2023 between Lake Tawakoni (upstream extent; completed in 1960) and Toledo Bend Reservoir (downstream extent; completed in 1969).

Statistical analysis

Temporal beta diversity. – We quantified temporal beta diversity components (replacement versus nestedness) and tested for spatial variation in the prevailing form of temporal beta diversity (using Baselga Family indices – Nestedness and Replacement). Prior to analysis we used a fourth-root Hellinger transformation of species abundances to reduce the contributions of common versus rare species [64]. We then used the 'beta.div.comp' function from the 'adespatial' package in R to calculate the components of species replacement and species nestedness component using pairwise, site-specific contrasts between historical and contemporary periods [65]. This function provides proportional data describing the relative contributions of replacement and nestedness components to total beta diversity. We then used the dominant form of beta diversity (i.e., replacement; see Results section) to test spatial patterns in fish assemblage change through time. We fitted a generalized additive model (GAM) with replacement as the dependent variable and a smoothing function for the continuous measure of hydrographic distance (riverine km) starting at Lake Tawakoni dam and continuing downstream as the independent variable. A GAM structure was necessary because preliminary plotting illustrated a non-monotonic and non-linear relationship. We fit the model using a Gaussian error distribution using the 'gam' function from the 'mgcv' package in R [66]. To complement this temporal beta diversity analysis, a similarity percentage analysis (SIMPER) using the 'simper' function in the 'vegan' package in R [67] was conducted using a Hellinger transformation of species abundance to provide insight to the species contributing most to assemblage change. We also compiled the native/non-native status [68], the 2023 Texas Parks and Wildlife Department (TPWD) Species of Greatest Conservation Need (SGCN) state status [69], the International Union for Conservation of Nature (IUCN) Red List status [70], and the increase or decrease in species abundance over time for each species in our data set.

Fish life history strategies. – We assessed longitudinal change in relative abundances of life history strategies to gain insight into demographic processes that might drive assemblage change. We first calculated the relative abundances of each LHS class at each site during each period and then calculated the change in relative abundance through time. Using this metric, a positive value represents an increase in relative abundance of a LHS through time and a negative value represents a decrease. We then modelled longitudinal change using a non-linear GAM as described above. For this analysis, we included change in relative abundance as the dependent variable, a smoothing term for hydrographic distance downstream of Tawakoni Dam as the independent variable, and an additive term for LHS classification so that unique smoothers were fit to each classification. We assessed the significance of each smoothing term and created biplots for those that were significant ($\alpha = 0.05$).

Mussel hosts. – We assessed longitudinal changes in fish mussel host trait dispersion to determine if fish assemblage changes might be related to freshwater mussel declines. We first calculated the relative abundances of all mussel hosts present in the samples across all sites and time periods. We then paired these data with the mussel host trait matrix and used the 'Fdis' function from the 'FD' package in R to quantify the functional dispersion of mussel hosts at each of the 28 sites during the historical and contemporary periods [49, 71]. We calculated the difference in F_{dis} for each site between sampling snapshots, where a positive value represents an increase in mussel host trait dispersion and a negative value represents a decrease in mussel host trait dispersion. We then analyzed longitudinal change in mussel host trait dispersion using a GAM as described above. Due to F_{dis} relationship with hydrologic distance (see Results section), we used F_{dis} to test relationships with temporal species replacement (dominant form of beta diversity; see Results section) by upstream (i.e., 7 collection sites) and downstream (i.e., 21 collection sites) areas independently. For this test the upstream and downstream sites were determined by splitting the entire longitudinal distance of the study area in half. We fitted two linear models (LM) using the 'lm' function in the 'stats' package [72] for both upstream and downstream areas with F_{dis} as the dependent variable and temporal species replacement, taken from the temporal beta diversity analysis, as the independent variable. An LM structure was sufficient for both tests because all global validation model assumptions were met using the 'gvlma' function in the 'gvlma' package [73]. All analyses were conducted in R version 4.3.2 [69].

Results

Historical and contemporary collections. – In total, 139,781 fish specimens were included in the analyses (Supplementary Table S1). During the historical period, 82,885 individuals representing 12 families, 28 genera, and 49 species were recorded. The LHS classifications included 8 equilibrium (e), 6 equilibrium-periodic (ep), 6 opportunistic (o), 7 opportunistic-equilibrium (oe), 11 opportunistic-periodic (op), and 11 periodic (p) strategists. The percentage of fish present in the historical period that host at least one mussel species was 69.4% (34/49 species). During the contemporary period, 56,896 individuals representing 11 families, 25 genera, and 39 species were recorded. The LHS classifications included 6 e, 6 ep, 7 o, 5 oe, 9 op, and 6 p strategists. The percentage of fish present in the contemporary period that host at least one mussel species was 69.3% (27/39 species). Twelve species collected during the historical period were not collected during the contemporary period (Supplementary Table 2), and 2 species (Threadfin Shad *Dorosoma petenense* and Inland Silverside *Menidia beryllina*) were collected during the contemporary period but not the historical period.

Temporal beta diversity patterns. – Temporal beta diversity was primarily driven by species replacement. The proportion of temporal beta diversity attributable to replacement ranged 0.179 – 0.700 across all 28 sites, while the proportion attributable to nestedness ranged 0.002 – 0.193 (Fig. 3). Replacement beta diversity was not evenly distributed across the longitudinal gradient of the river. The GAM had a significant smoothing function for hydrographic distance ($F_{6.5, 7.5}$ = 9.9, P < 0.001) that explained 79.4% of deviance in replacement with an adjusted $R^2 = 0.73$. Species replacement was >0.50 just downstream of Tawakoni Dam but attenuated with downstream distance until just upstream of the impounded area of Toledo Bend Reservoir, where replacement sharply increased (Fig. 4). The SIMPER analysis revealed that 26 of 51 species contributions to assemblage dissimilarity between time periods were statistically significant. A total of 18 of these statistically significant contributions were associated with decreases in species average abundance, and the remaining 8 contributions were increases in species average abundance (Supplementary Table S2). The Western Sand Darter (*Ammocrypta clara*) is listed as a vulnerable species by the IUNC, designated a SGCN by TPWD, and is one of the 18 species whose abundances declined ($p < 0.001$) with zero catch in the contemporary survey. The Mississippi Silvery Minnow (*Hybognathus nuchalis*) is a SGCN in Texas and declined ($p < 0.001$) with zero catch in the contemporary survey. Other SGCN that declined in abundance are the Blackspot Shiner (*Notropis atrocaudalis*) ($p < 0.03$), Ironcolor Shiner (*Notropis chalybaeus*) ($p < 0.02$), and Sabine Shiner (*Notropis sabinae*) ($p < 0.001$), although the Sabine Shiner was the only one of these species present in the contemporary survey. In addition, there was significant decline of non-native Common Carp (*Cyprinus carpio*) ($p = 0.038$) and Red Breast Sunfish (*Lepomis auritus*) ($p < 0.001$) in the upper Sabine River, with zero catch in the contemporary survey (Supplementary Table S2). The species whose abundances increased with statistical significance were Gizzard Shad (*Dorosoma cepedianum*) ($p < 0.001$), Threadfin Shad ($p < 0.001$), Blue Catfish (*Ictalurus furcatus*) ($p = 0.041$), Channel Catfish (*Ictalurus punctatus*) ($p < 0.001$), Inland Silverside ($p < 0.001$), Spotted Bass (*Micropterus punctulatus*) ($p = 0.005$), Largemouth Bass (*Micropterus salmoides*) ($p < 0.001$), and Dusky Darter (*Percina sciera*) ($p = 0.016$).

Fish life history strategy patterns. – Change in relative abundance of life history strategists were not even across the river longitudinal gradient or among classifications. Equilibrium (e) and periodic (p) strategists were more abundant historically, whereas contemporary collections had relatively more opportunistic (o) strategists. The GAM fitted to the relationship between hydrographic distance and change in relative abundance of LHS groups revealed that 4 out of the 6 groups showed statistically significant longitudinal changes in relative abundance (Table 1). The full GAM had an adjusted $R^2 = 0.74$ and explained 76.3% of deviance in longitudinal change in LHS relative abundance. Equilibrium strategists declined by 10% just downstream of Lake Tawakoni Dam, but this decline attenuated with longitudinal distance downstream until just upstream of Toledo Bend Reservoir, where relative abundance increased by 2% (Fig. 5a). Opportunistic strategists increased by 30–60% in the vicinity of reservoirs but showed little change midway between the reservoirs (Fig. 5b). Periodic strategists declined by up to 10% just downstream of Lake Tawakoni, but this decline attenuated with longitudinal distance (Fig. 5c). Opportunistic-Periodic strategists declined by 50–75% near reservoirs but showed little change or an increase up to 40% in the middle segment of the river (Fig. 5d).

Mussel host trait dispersion . – A combination of functional trait dispersion gains and losses occurred for mussel host fishes. The GAM fitted to the relationship between hydrographic distance and change in functional trait dispersion had a significant smoothing term for distance ($F_{6.7, 7.7} = 9.15$, $p < 0.001$) and explained 78.3% of deviance in change in trait dispersion with an adjusted $R^2 = 0.71$. Mussel host trait dispersion declined most through time in the first 50 km downstream of Lake Tawakoni Dam but then showed longitudinal recovery and little change between 100 and 300 river km downstream (Fig. 6). Functional trait dispersion increased sharply in the 75 km upstream of Toledo Bend Reservoir. The LM fit to the relationship between temporal species replacement and F_{dis} for each independent upstream and downstream area was not statistically significant for the upstream area ($F_{1, 5} = 2.3$, $p = 0.19$) with an adjusted $R^2 = 0.17$ (Fig. 7a), but was significant in the downstream area ($F_{1, 19} = 10.59$, $p = 0.004$) with an adjusted $R^2 = 0.32$ (Fig. 7b).

Table 1. Summary statistics of a generalized additive model describing change in relative abundances of life history classification (LHC) groups between 1954–1956 and 2023 (dependent variable) and longitudinal distance (dist) from the dam at Lake Tawakoni (independent variable with a smoothing function) for the upper Sabine River, Texas, USA. The table give the LHS group (e = equilibrium, ep = equilibrium-periodic, o = opportunistic, oe = opportunistic-equilibrium, op = opportunistic-periodic, and p = periodic), effective degrees of freedom (eDf), reference degrees of freedom (Ref. Df), test statistic (F-value), and P-value (p-value) for smoothing terms fit to the effect of longitudinal distance.

LHC	eDf	Ref. Df	F-value	*p*-value
s(dist)*e	1.00	1.00	8.13	**0.004**
s(dist)*ep	1.00	1.00	0.89	0.346
s(dist)*o	5.89	6.96	23.10	**<0.001**
s(dist)*oe	1.00	1.00	0.13	0.724
s(dist)*op	7.57	8.45	35.48	**<0.001**
s(dist)*p	1.00	1.00	4.89	**0.029**

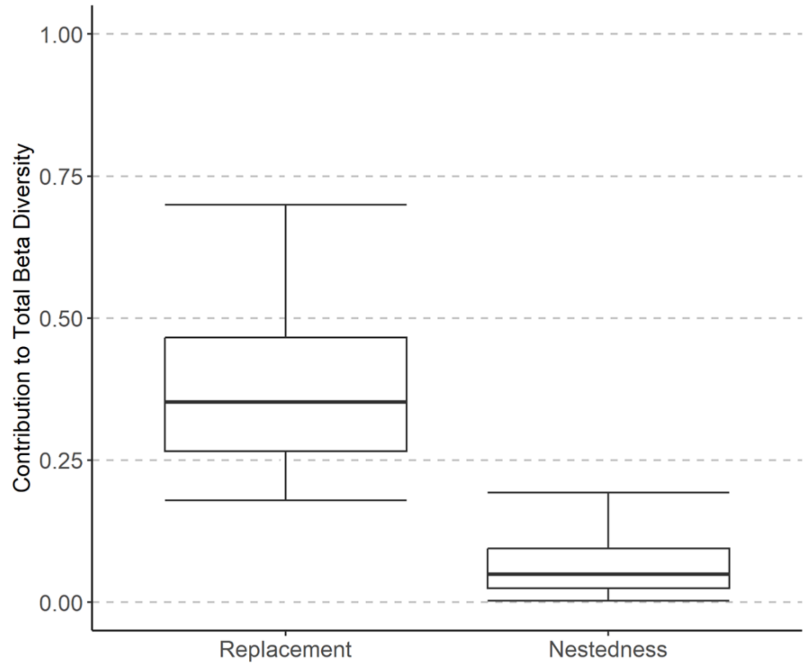

Figure 3. Box plots illustrating decomposition of temporal beta diversity into replacement and nestedness components for 28 fish assemblage sites surveyed in 1954–1955 and 2023 in the upper Sabine River, Texas, USA.

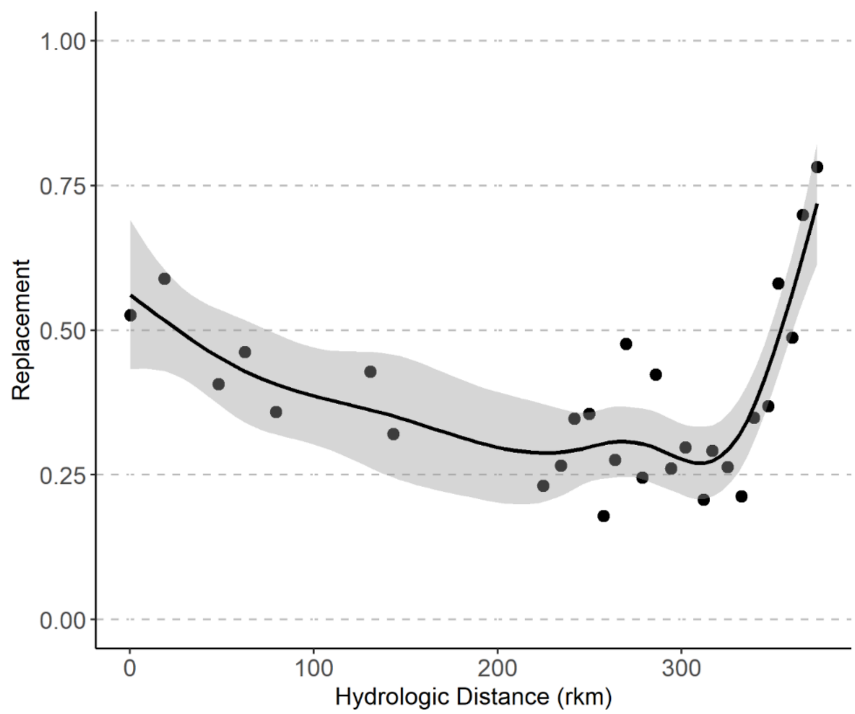

Figure 4. The longitudinal pattern of the contribution of species replacement to temporal beta diversity across 28 fish assemblage samples taken from the upper Sabine River, Texas, USA between Lake Tawakoni (upstream; distance = 0 km) and Toledo Bend Reservoir (downstream; distance = 373 km) in 1954–1955 and 2023. Black points represent sites, the solid line is a fitted generalized additive model, and the grey shaded area is the 95% confidence interval.

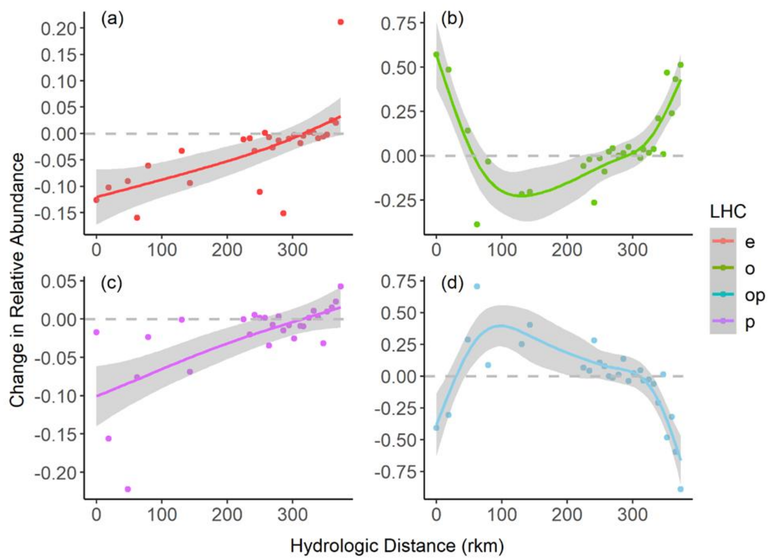

Figure 5. The change in relative abundance of life history classifications between 1954–1955 and 2023 as a function of longitudinal distance between Lake Tawakoni (upstream; distance = 0 km) and Toledo Bend Reservoir (downstream; distance = 373 km) in the upper Sabine River, Texas, USA. Multicolored points represent the sites that were sampled and the change in relative abundance (0 = no change, negative = decrease, positive = increase) for (a) equilibrium (e), (b) opportunistic (o), (c) periodic (p), and (d) opportunistic-periodic (op) strategists. Solid lines are fitted generalized additive models and grey shaded areas are 95% confidence intervals.

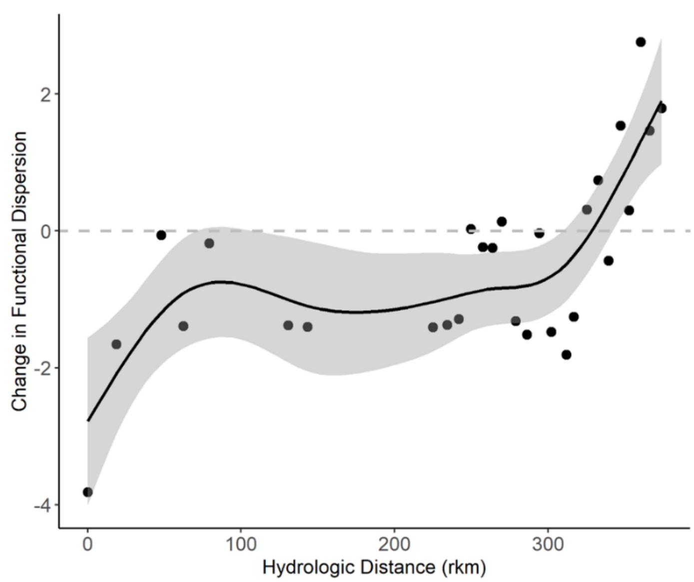

Figure 6. Change in fish assemblage mussel host functional trait dispersion between 1954–1955 and 2023 over the longitudinal distance between Lake Tawakoni (upstream; distance = 0 km) and Toledo Bend Reservoir (downstream; distance = 373 km) in the upper Sabine River, Texas, USA. The y-axis represents the increase (positive), decrease (negative), or lack of change (zero) in functional trait dispersion between sampling events. The black points are the 28 survey sites, the solid line is a fitted generalized additive model, and the shaded area is the 95% confidence interval.

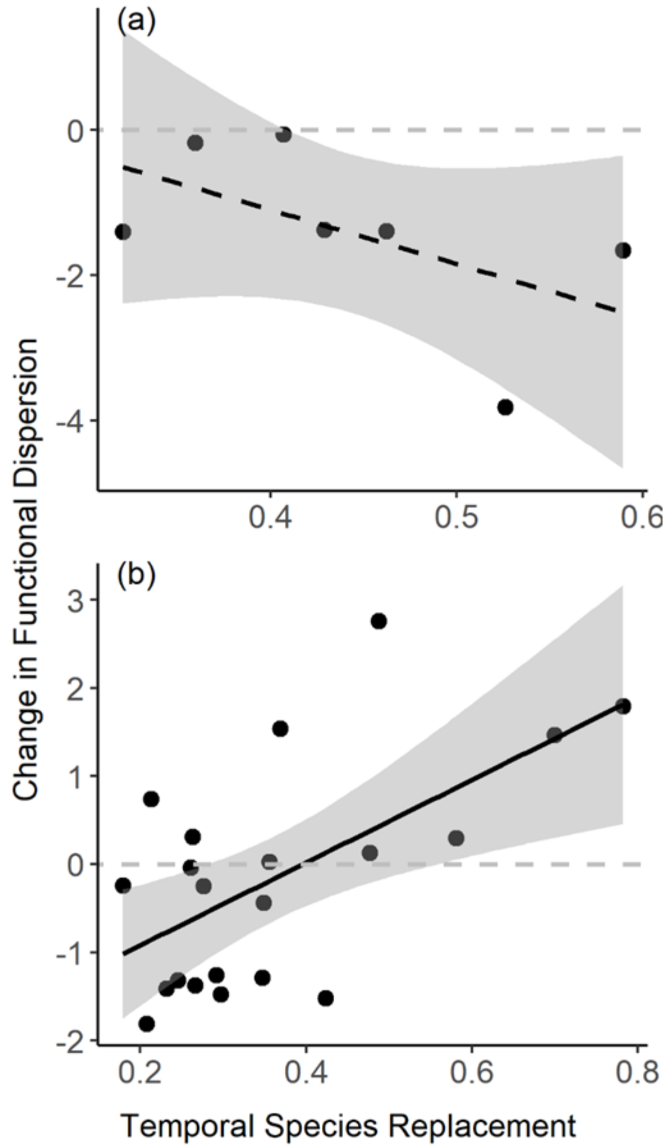

Figure 7. Change in mussel host functional trait dispersion as a function of temporal replacement of species between 1954–1955 and 2023 for each site in the (a) upstream area and (b) the downstream area between Lake Tawakoni and Toledo Bend Reservoir in the upper Sabine River, Texas, USA. The x-axis represents the species replacement metric for each site sampled. The y-axis represents the increase (positive), decrease (negative), or lack of change (zero) in functional trait dispersion between sampling events. The black points represent 28 sampling sites (n = 7 upstream; n = 21 downstream), black lines are linear model fits (solid = significant slope; dashed = insignificant slope), and grey areas are 95% confidence intervals.

Discussion

Longitudinal recovery gradients. – Our study advances the concept of longitudinal recovery gradients in which fish assemblages return to a natural baseline with increased distance from reservoirs. Our first hypothesis test revealed that fish assemblages changed through time near reservoirs and this change was not driven by simple species additions (i.e., Dam Invaders

Hypothesis not supported) or species losses (i.e., Proximity Extinctions Hypothesis not supported), but instead by both processes operating simultaneously to drive high levels of species replacement (i.e., Proximity Replacement Hypothesis supported). The high levels of species replacement near reservoirs attenuated with increased distance from reservoirs. Early work on this concept by Kinsolving and Bain [8] focused on fish assemblage surveys downstream of an existing reservoir and revealed an increase in relative abundance of fluvial specialists with increased distance up to 66 km downstream. A limitation of this previous work was that the endpoint of the recovery gradient was not determined, in part, because no surveys were conducted at greater distances from the reservoir (i.e., beyond 66 km) and because of lacking pre-impoundment baseline conditions. Our use of pre-impoundment baseline fish assemblage data coupled with temporal beta diversity metrics provided a method for estimating a recovery endpoint and determining whether it was reached. Our finding that the fish assemblage still experienced 25% turnover at 300 km downstream of the reservoir (i.e., five-times farther than Kinsolving and Bain [8]) suggests the scales at which fish assemblage respond to impoundments might be much broader than expected. We suspect the longitudinal recovery of the upper Sabine River fish assemblage might have continued if it were not for the effects of a second downstream impoundment whose effects were transmitted in an upstream direction. The known upstream effects of reservoirs on fish assemblages include expansion of lacustrine species upstream from the reservoir [15, 16], and we found evidence for this process in the area within 50 km upstream of Toledo Bend Reservoir. Based on earlier work, fish assemblages are altered by the downstream effects of Toledo Bend Reservoir for the remaining 250 km of river until the Sabine River enters the Gulf. Modern riverscapes represent highly fragmented and disconnected systems [74, 75], and our work provides insight into the spatial dimensions for ecological consequences framed within the context of historical baselines.

Life history strategies. – Our study documented strong responses by life history strategists to impoundment construction and advances previous spatial analyses (e.g., Mims & Olden [40]) by integrating spatiotemporal analysis (e.g., Perkin et al. [37]). Theory suggests that equilibrium strategists should benefit from flow stability created by reservoirs, while opportunistic and periodic strategists decline [35, 43]. We found that equilibrium and periodic strategists declined downstream of a reservoir where flows could be most regulated, but these declines were relatively minor compared to the replacement of species identified as opportunistic-periodic (intermediate) strategists by opportunistic strategists at locations near reservoirs. These results closely align with the Periodic RRI Hypothesis and the Opportunistic Decrease Hypothesis, though the latter is applied to intermediate strategists. Threadfin Shad and Inland Silverside are opportunistic strategists that were abundant contemporarily but not present in the historic survey. We suspect that deviations from expectations for environmental filtering (i.e., through streamflow alteration) of life history strategies based on theory were partially driven by either the increase in abundance of introduced opportunistic strategist (e.g., Threadfin Shad and Inland Silverside) in reservoirs [76, 77], or the proliferation of these potentially resident species after reservoir construction and subsequent expansion of optimal habitat [78]. Hubbs et al. [77] mentioned the widespread introduction of Threadfin Shad and Inland Silverside across Texas reservoirs, but little is known of the vectors of introduction by these habitat generalists within the literature [76, 79]. It is possible that the increase in opportunistic strategists near reservoirs is a result of minimally abundant historic resident species, such as Threadfin Shad and Inland Silverside, utilizing reservoir littoral and limnetic zones for preferred forage and spawning grounds after their construction [79]. Consequently, our results suggest that deviations from theoretical expectations derived from life history theory might be confounded by human introduction of populations in newly available physical habitat created by reservoir water [80].

Links between taxonomic and functional indices are important for understanding the mechanisms of assemblage change. In this study, changes in relative abundances of LHS groups showed patterns of longitudinal variation in the upper Sabine River. We predicted an increase in equilibrium strategist relative abundance near reservoirs [36, 38] but instead found that fishes employing this strategy declined in the tailwaters of the upstream impoundment and then gradually returned to baseline conditions 300 km downstream, thus displaying partial support for the Equilibrium Increase Hypothesis. This pattern was remarkably consistent with the response by periodic life history strategists. In the Sabine River system, equilibrium strategists provide parental care during and after nesting on substrates within littoral zones. Thus, stable flows facilitate successful nesting because there is low impact from flow pulses that scour nests and water level drawdowns that dewater shallow areas where the fish nests exist [36]. Our initial theoretical expectations were that flow releases from Lake Tawakoni were relatively less dynamic in comparison to larger hydropower dams with consistently managed releases (e.g., Toledo Bend Dam) [56]. Lake Tawakoni's primary means of flow releases are for conservation and flood releases from two 0.5 m diameter pipes, thus our expectation of relatively stable flows in the tailwaters of Lake Tawakoni [56]. However, the ungated spillway of Lake Tawakoni could contribute to flashier flows when the reservoir is at or near capacity and it is possible that this upstream area is more representative of a flashy lotic area because of dynamic flow releases from Lake Tawakoni. Water level drawdowns primarily impact the tailwaters of Lake Tawakoni and have less negative impact on the downstream reaches near Toledo Bend Reservoir, which could explain the longitudinal recovery gradient we see in equilibrium strategists [36]. Many Sabine River fishes that are periodic life history strategists spawn in floodplain habitats. Their abundance declines where lateral connectivity to floodplains is thwarted by reservoir operations that intercept high flow pulses that would otherwise inundate floodplains [81]. The magnitude and duration of floodplain inundation in the upper Sabine River have been negatively affected by Lake Tawakoni operations in the tailwaters below this dam [56, 82], and this may explain the apparent recovery of periodic life history strategists in the river's lower reaches. We suspect that other geomorphic changes related to instream habitats used by equilibrium strategists might also have occurred based on the reduced abundance of instream mussel assemblages in Lake Tawakoni's tailwaters compared to middle reaches of the river [56].

There was no support for the Opportunistic Decrease Hypothesis in relation to opportunistic strategists, and instead we found a pattern that was opposite to our expectations. However, findings for the intermediate strategy of opportunistic-periodic fishes did match our expectations regarding the Opportunistic Decrease Hypothesis. Fishes in the opportunistic-periodic group were native, stream-dwelling minnows (e.g., Ironcolor Shiner, Sabine Shiner, and Blacktail Shiner *Cyprinella venusta*). With regards to the endpoint opportunistic strategists, this group included some numerically dominant species, (e.g., Threadfin Shad and Inland Silverside) [16, 17, 78] that had been introduced or proliferated because of reservoir formation. Compared to opportunistic-periodic strategists, fish classified as opportunistic strategists have lower batch fecundities and shorter generation times that allow for reduced time to reproductive maturity and a greater potential for reproduction when stochastic flows do occur. Meador and Brown [83] found that 50% of declining fish species in eastern U.S. streams belonged to the intermediate opportunistic-periodic strategy and suggested this group exhibits strong habitat specialization and is sensitive to flow alterations. Our findings support this conclusion in the upper Sabine River. Opportunistic-periodic strategists revealed lower abundance in reaches where flows were most regulated (upstream) and habitats had been most altered (downstream river-reservoir interface). Finally, we found no evidence that periodic strategists increased in the downstream RRI, perhaps because our seining surveys were limited primarily to the flowing portions of the interface [18, 19], although this group was found to have contemporary abundance similar to the historical baseline in this area.

Fishes as mussel hosts. – Our results revealed that fish assemblage mussel hosting capacity declined in the tailwaters of the upstream reservoir but increased in the downstream RRI. Though our hypotheses were based on symmetrical host gain or loss at upstream and downstream extents of the riverscape, we instead found asymmetry in the temporal change in mussel hosting traits characterized by functional loss (Proximity Host Loss Hypothesis) in the upstream reach and functional gain (Proximity Host Gain Hypothesis) in the downstream reach. The increase of F_{dis} in the downstream reach of the river indicates a greater dispersion of mussel host traits present within the fish assemblage relative to the natural baseline [49, 71]. This mechanism might contribute to greater occurrence of certain mussel species in the reservoir [50]. However, a survey of mussel species in the upper Sabine River found the highest mussel richness and abundance at the midpoint of the river [56]. Interestingly, this was the same location where we found minimal change in fish assemblage structure. The best-fit model for mussel richness and abundance patterns was a quadratic model characterized by reduced mussels in the areas nearest to reservoirs [56]. This pattern closely matches previous longitudinal mussel surveys in other systems, notably longitudinal recovery of mussels with increased distance downstream [51] and upstream [52] from reservoirs. A major challenge in mussel conservation and management is to determine the relative effects of environmental factors versus changes in host fish abundance in regulating population abundance [51, 84]. Our work suggests that there was a decline of mussel hosting traits downstream from Lake Tawakoni, or a decrease in F_{dis}, where mussel assemblages are species poor and characterized by low abundance [56]. However, our results revealed an increase in the functional diversity of fish hosts in the downstream reach near the Toledo Bend RRI, where mussel assemblages are also species poor with low abundances. Consequently, there has been an increase in mussel hosting functional traits in the downstream extent of the riverscape compared to historical conditions because of species replacement; however, there is no evidence for a correlated (spatial) increase in mussel richness or abundance in the same area. These findings suggest that changes in mussel host availability may not be a significant driver of low mussel richness and abundance in the downstream reach of the Sabine River. Alternatively, if fishes that are opportunistic-periodic life history strategists are the principal hosts for mussel glochidia, then there is a strong correlation between temporal change in the distribution of these fishes (based on our results) and spatial declines in mussel richness and abundance [56].

Caveats and context. – Caveats and limitations should be considered when interpreting our results. First, our assessment of beta diversity was based on two surveys, each of limited duration. To yield reliable datasets, long-term surveys require standardized methods applied consistently by research teams that may turnover multiple times over decades [22, 85, 86]. At a minimum, two surveys can reveal impacts of environmental disturbances on community composition [86]. Unfortunately, multiple replicated surveys of the entire upper Sabine River fish assemblages are not available. The large spatial extent of the historical survey and difficulties associated with river accessibility in some reaches likely account for the lack of subsequent surveys [57]. Though based on comparison of just two time periods, our study revealed significant changes in fish assemblage structure using taxonomic and functional indices over a longitudinal gradient that experienced damming and flow regulation. Perkin et al. [37] conducted a similar study using two time periods in the lower Sabine River and found general support for life history theory predictions. However, no historical baseline data existed to support that study, and their analyses were based on immediate post-impoundment surveys and survey data collected 10 years later. A second limitation of our study was that the historical baseline data were collected during the 1950s under major drought conditions [57]. A growing number of studies have documented fish assemblage changes during drought periods, especially within fragmented riverscapes [87, 88, 89]. We could not separate effects of drought from effects of reservoirs (habitat fragmentation) on long-term change in fish assemblages of the upper Sabine River. In general, drought effects on fish assemblage composition have been found to be regional [90]. In contrast, the long-term changes in fish assemblage structure detected in this study were local and associated with distance from reservoirs. Finally, it should be noted our use of fish traits associated with hosting mussels in the upper Sabine River is dependent upon the reliability of expert opinions [61, 62, 63]. Future work refining the identities of fishes that host mussels will ultimately help to elucidate whether mussels and fish are equally (and independently) responding to altered habitats or if mussel declines are linked to changes in fish assemblages [91].

Conservation and management implications. – Multiple conservation actions and management interventions could address fish assemblage alterations in the Sabine River and other similarly affected rivers elsewhere. First, persistence of natural fish assemblage composition with increased distance from reservoirs is likely related to the channel lengths required for fishes to complete their life cycles [92, 93] as well as downstream attenuation of impacts to physicochemical processes that maintain fish habitat [74, 94]. A potentially critical conservation action is the preservation of long, undammed reaches [56, 95]. Second, although the data available for our study precluded comprehensive assessment of the mechanisms linking dam construction to fish assemblage alteration, streamflow regime management is an emerging conservation tool aimed at preserving biodiversity in regulated rivers. Natural flow regime mimicry has contributed to fish assemblage restoration in dam tailwaters where flow releases have the strongest geomorphological and ecological effects [12, 96]. Our synthesis of historical and contemporary data provides baseline information that could be used in the future to measure potential benefits of flow releases from Lake Tawakoni that mimic key components of the natural flow regime [97]. Third, the integrity of fish assemblages near upstream extents of reservoirs might be maintained through aquatic and riparian habitat management at river-reservoir interfaces. Buckmeier et al. [18] and Pennock et al. [19] suggested management of aquatic vegetation and shallow littoral zone habitats within RRIs might promote conservation of fluvial-dependent fish species in river systems affected by reservoirs. Although opportunistic-periodic strategists might not persist even in well managed RRI habitats, these areas could provide necessary feeding and spawning habitats for equilibrium and periodic strategists.

Conclusions. – Dam construction and stream impoundment affect most rivers on Earth [1] and understanding the societal and ecological consequences of these alterations can be challenging [98, 99]. This challenge is made more difficult by a lack of historical baseline data in most regions [100], meaning most assessments of ecological change use space-for-time substitutions based only on contemporary data [101]. This is true of longitudinal recovery gradients [Kinsolving and Bain], life history strategist responses [Mims and Olden], and fish-mussel interactions [102]. Another challenge is understanding the transferability of findings across river systems and contexts [103]. Our work addresses these challenges by leveraging rare baseline data to assess effects of impoundment construction on stream fishes by directly comparing pre- and post-construction settings. We find that the same concepts developed using only contemporary data are reflective of change when historical conditions are known. We also tested well-defined hypotheses based on previous works in other systems, thereby advancing the applicability of cross-system transferability of concepts and principles. Concerns over the effects of future dam and impoundment construction on riverine biodiversity require evidence-based understanding of the nature and direction of ecological consequences, and our work suggests lessons learned from the past can be applied in a prospective context to aid in balancing human development of rivers and the needs of natural ecosystems and their biota [104, 105].

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CHAPTER IV: SEASONAL DYNAMICS

Introduction

Multiple spatial and temporal scales influence the distribution of ecological communities (Levin 1992; Jackson et al. 2001; Vellend 2010). Across large scales (i.e., continental, regional), communities are structured by various ecological and biogeographic processes such as dispersal, speciation, drift, and extinction, which operate over longer temporal scales (Cornell and Lawton 1992; Jackson et al. 2001; Chase et al. 2005; Vellend 2016). At smaller scales (i.e., local), communities appear to be structured by environmental factors, resource productivity, and species interactions (e.g., competition, predation, mutualism; Ricklefs and Schluter 1993; Huston 1999; Vellend 2010, 2016), which can become pronounced in systems with strong seasonal dynamics. As a result, local community assembly invokes niche-based mechanisms (i.e., environmental and biological filtering; Diamond 1975; Mutshinda et al. 2009). Understanding the intricate relationships of these spatiotemporal scales and their complementary processes is critical for the implementation of effective management, conservation, and restoration practices.

Diversity partitioning measures (e.g., alpha, beta, and gamma) have provided valuable insights for researchers to understand the processes that govern local communities from regional species pools, and the accompanying changes in species composition (Gering and Crist 2002). Alpha diversity describes species richness of a local community, while gamma diversity is the total diversity in a region (Whittaker 1960). Both alpha and gamma diversity are connected through beta diversity (β-diversity), which describes the variation in species composition among local communities (Whittaker 1960; 1972). Analyzing β-diversity aids the prediction of shifts in species composition and the testing of hypotheses about the processes that influence and maintain biodiversity across space and time (Legendre and Cáceres 2013; Socolar et al. 2016). It has become the key to understanding many aspects influencing ecological communities such as environmental complexity, land use changes, and disturbances across multiple scales, from biogeographic to regional and local environmental gradients (Melo et al. 2009; Kessler et al. 2009; Anderson et al. 2010; Mori et al. 2018).

Partitioning β-diversity into species turnover/replacement (i.e., species gain and loss along spatial or temporal gradients; Legendre and Cáceres 2013) and nestedness (i.e., species richness differences between samples; Baselga 2010) can enhance our understanding of the processes that drive changes in species composition (Anderson et al. 2010; Legendre 2014), thereby providing a basis for designing, planning, and making decisions to inform biodiversity conservation (Socolar et al. 2016; Hill et al. 2017). Species turnover occurs as a consequence of environmental factors or spatial and historical constraints (Podani and Schmera 2011; Legendre and Cáceres 2013). Conversely, nestedness reflect subsets of a larger species pool, brought on by altitudinal gradients, barriers to dispersal, competition, colonization, extinction or human disturbances (Baselga 2012; Legendre 2014). Thus, these processes can act in communities independently or simultaneously (Baselga 2010). A meta-analysis conducted by Soininen et al. (2018) emphasized the importance of turnover and nestedness patterns across latitudinal gradients. Results from this meta-analysis suggested that increasing latitude was associated with a decrease in turnover and an opposing increase in nestedness across a wide range of taxa. Less attention has been placed on turnover and nestedness relationships along temporal gradients. Recent studies indicate that environmental changes such as climate fluctuations and habitat disturbances over time can influence nestedness and turnover patterns, affecting community composition (Tisseuil et al. 2012; Blowes et al. 2019). Therefore, there are implications for conservation strategies depending on the dominant underlying process. For example, high species turnover may indicate the need for conservation efforts across multiple sites, whereas a predominantly nested pattern would benefit in the prioritization of the most species-rich sites (Socolar et al. 2016).

While traditional measures of β-diversity primarily focus on taxonomic diversity, incorporating additional facets of diversity (such as functional and phylogenetic) has become increasingly common to provide a more comprehensive understanding of community dynamics (Swenson et al. 2012; Pool et al. 2014; Li et al. 2024). Together, these three facets of biodiversity may respond distinctly to ecological drivers across multiple spatial and temporal scales. For instance, taxonomic diversity treats species as independent and functional evolutionary equivalent units (Cadotte et al. 2011); while functional diversity reflects the diversity of species' niches through species-specific features (Mason et al. 2005), which can help capture the influences of organism's trait performance and ecosystem functions (Mouillot et al. 2007; Villéger et al. 2008; Montaña and Winemiller 2010; Bower and Winemiller 2019). On the other hand, phylogenetic diversity (i.e., evolutionary relationships among species) can help to elucidate evolutionary histories and biogeographic factors that shape community structure either through phylogenetic niche conservatism or phylogenetic overdispersion (Webb et al. 2002; Cavender-Bares et al. 2009).

Examining multiple facets of β-diversity can uncover distinct, or complementary, responses of taxonomic, functional, and phylogenetic diversity to environmental factors across regional and local scales. Generally, taxonomic β-diversity (TDβ) is shaped by the combined influences of broad-scale spatial processes and environmental filtering (Gianuca et al. 2017). In contrast, functional β-diversity (FDβ) has been found to be shaped by local environmental conditions, as these filters at finer spatial scales select species with traits suited to coexist at a given site (Peláez and Pavanelli 2019). Phylogenetic β-diversity (PDβ) on the other hand, may show spatial-scale dependence. At small to intermediate spatial scales, phylogenetic diversity may be explained by environmental conditions, owing to phylogenetic niche conservatism (i.e., tendency of organisms to retain their niche preferences over time) as a result of evolutionary constraints (Wiens 2004; Pavoine and Bonsall 2011). At larger scales, phylogenetic diversity may be strongly related to dispersal limitations caused by evolutionary processes (e.g., extinction, speciation) and historical factors (e.g., geological barriers) (Mouquet et al. 2012; Bower and Winemiller 2019). Thus, the combination of these three approaches have been used to disentangle patterns of biodiversity and their underlying ecological drivers (Strecker et al. 2011; Pool et al. 2014; Yang et al. 2024).

Aquatic ecosystems in Texas are characterized by a rich biodiversity, which includes a diverse range of freshwater and marine organisms (Buzan 1997). Freshwater fishes have distinct distributional patterns across the state, with a trend of higher diversity observed from a west to east gradient (Hubbs 1957). The Neches and Sabine River basins in East Texas support extensive floodplain networks and complex flow regimes, making them among the most freshwater species-rich basins in the region (Hubbs et al. 1991). Given the mosaic of aquatic habitats and complex stream networks, these river basins provide an excellent natural platform for exploring regional and local scale β-diversity patterns and drivers. Regional land use practices throughout these basins are dominated by forests, agriculture and increasing urbanization. Local stream conditions comprise greater flow regime heterogeneity and fish diversity compared to more western basins (e.g., Brazos and Trinity River) (Swanson 2022). Yet despite this high fish diversity, shifts in local species diversity and abundance in East Texas have been observed in the last decades (Anderson et al. 1995). Species of cyprinids, catostomids, and percids that once were considered stable in East Texas are now listed as Species of Greatest Conservation Need (SGCN) because of anthropogenic activities impacting their habitats (Moriarty and Winemiller 1997, Williams and Bonner 2006). The continued degradation of freshwater habitats due to human-induced changes poses a growing threat to native fish assemblages, highlighting the need for conservation efforts to prevent further extirpation of species from their native ranges.

In this study, we aimed to investigate the relationships among β-diversity facets (i.e., TDβ, FDβ, and PDβ; Figure 1.1) and their respective components (i.e., turnover, nestedness) to understand patterns of structure and assembly of stream fish assemblages in the Neches and Sabine River basins in East Texas. To accomplish this goal, we examined how a temporal gradient (i.e., seasonality) and spatial (i.e., regional and local) environmental variables influenced the three β-diversity facets (Figure 1.1a). Given their geographic proximity, both situated primarily in the Piney Woods ecoregion and sharing hydrological characteristics, we hypothesized (H1) that the TDβ, FDβ, and PDβ would exhibit similar responses in both river basins and across seasons (Figure 1.1a — d). In agreement with other studies of fish assemblages in tropical and temperate systems (López-Delgado et al. 2020; Zbinden et al. 2022), we hypothesized that 2) TDβ would be higher than FDβ and PDβ and driven by turnover (Figure 1.1b). Turnover has been identified as the dominant component structuring taxonomic β-diversity in various taxa, a likely result of environmental and spatial filtering (Soininen et al. 2018). On the other hand, the FDβ of temperate assemblages (e.g., fish, benthic invertebrates, benthic algae) has been more influenced by nestedness, as low-trait diversity assemblages tended to be subsets of high trait-diversity assemblages (Toussaint et al. 2016; Heino & Tolonen 2017; Wu et al. 2021). we also hypothesized (H3) that TDβ and PDβ would be strongly correlated (Figure 1.1c), as previously documented in stream assemblages in tropical and temperate systems (Branco et al. 2020; Xia et al. 2023). Additionally, FDβ and PDβ were hypothesized to be correlated, as complementary trait and phylogenetic underdispersion in stream fishes across the United States is thought to be due to phylogenetic niche conservatism (Bower and Winemiller 2019). 4) Lastly, we hypothesized (H4) that regional variables (e.g., land cover) would influence TDβ and PDβ of fish assemblages across all seasons, while FDβ would be shaped by both regional and local environmental variables (Figure 1.1d). Across stream fish assemblages in East Texas river basins, regional variables such as land uses were found to influence taxonomic diversity (Swanson 2023), while regional and local-scale variables (e.g., hydrological) were important to the functional-trait structure stream fishes in Texas (Pease et al. 2015).

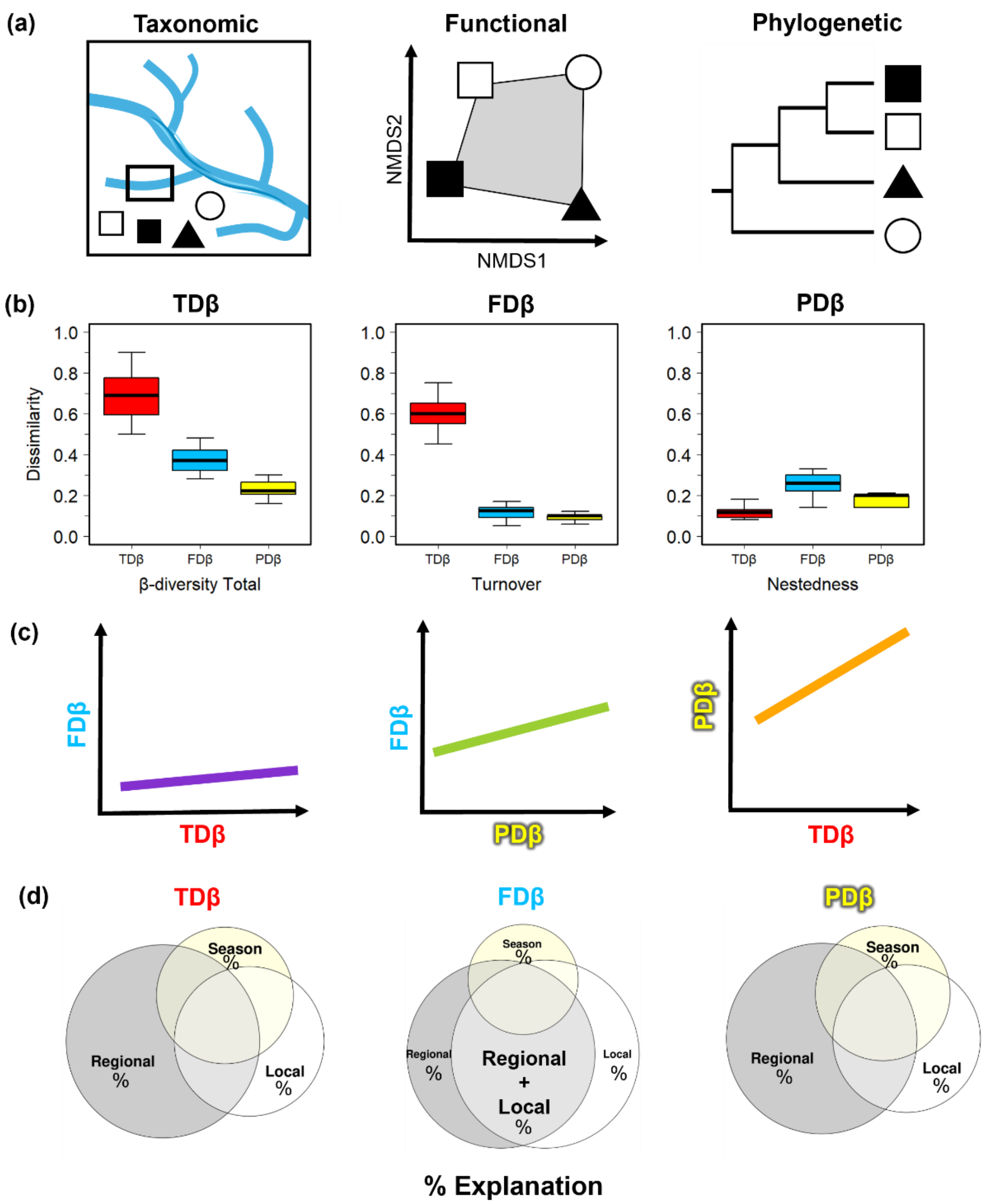


Figure 1.1. (a) Visual illustrations of fish assemblage data, two-dimensional functional space, and phylogenetic tree data. Hypothesis testing (b — d): H1 (b), TDβ turnover expected to be higher than FDβ and PDβ turnover. H2 (c), TDβ and PDβ expected to be correlated. H3 (d), regional variables would predominantly influence TDβ and PDβ, while FDβ would be driven by both regional and local variables.

Methods

Study Area and Sampling Sites. – The Neches and Sabine River basins in East Texas, are mainly situated in the South-Central Plains ecoregion, also referred to as the "Piney Woods" (Figure 1.2). Pine forests, bottomland hardwood forests, and agriculture dominate the landscape, with industrial activities being more prevalent in the upper and lower reaches. The hydrology of this region is defined by highly dendritic and slow-moving stream networks, which receive the highest average annual rainfall in the state (> 1,500 mm).

The Neches River basin is entirely within Texas and drains an area of approximately 26,000 square kilometers. Neches River headwaters are located in Van Zandt County and continues approximately 670 kilometers (416 miles) southeast to Sabine Lake that drains into the Gulf of Mexico. Many river and stream segments throughout the Neches River basin have been recognized as ecologically significant due to their exceptional freshwater wetland habitats, diverse aquatic life, high water quality, and riparian conservation areas (NPS 2010; TPWD 2017b). The river is impounded by two major reservoirs: Lake Palestine and B.A. Steinhagen Lake. A major tributary of the Neches River is the Angelina River, which originates in Rusk County and flows approximately 191 kilometers (119 miles) before joining the Neches River upstream of B.A. Steinhagen Lake. The Angelina River is also impounded to form Sam Rayburn Reservoir, the second largest reservoir in the state. Two national forests are found in the Neches River basin: Davy Crockett National Forest, bordered on the northeast by the Neches River mainstem, and Angelina National Forest on the north and south shores of Sam Rayburn Reservoir.

The Sabine River basin constitutes part of the state boundary with Louisiana, encompassing about 15,700 square kilometers in Texas. Two forks of the upper Sabine River are located within the Blackland Prairies ecoregion in Collin County and Hunt County. The mainstem of the Sabine River then flows southeast for 580 kilometers (360 miles) through the Piney Woods and finally to its confluence with the Neches River at Sabine Lake. Two large reservoirs have been constructed on the river mainstem: Lake Tawakoni in the upper reaches and Toledo Bend Reservoir. Toledo Bend Reservoir is the largest reservoir in Texas (185,000 acres or 750 km2) and the Southern United States (TPWD). Sabine National Forest is the easternmost of the four national forests in Texas and forms part of the boundary between Texas and Louisiana along with Toledo Bend Reservoir. Additionally, land uses throughout the river basin include agriculture and recreation, with heavy industrialization in the upper and lower basin areas due to surrounding metropolitan areas (SRA-TX 2024).

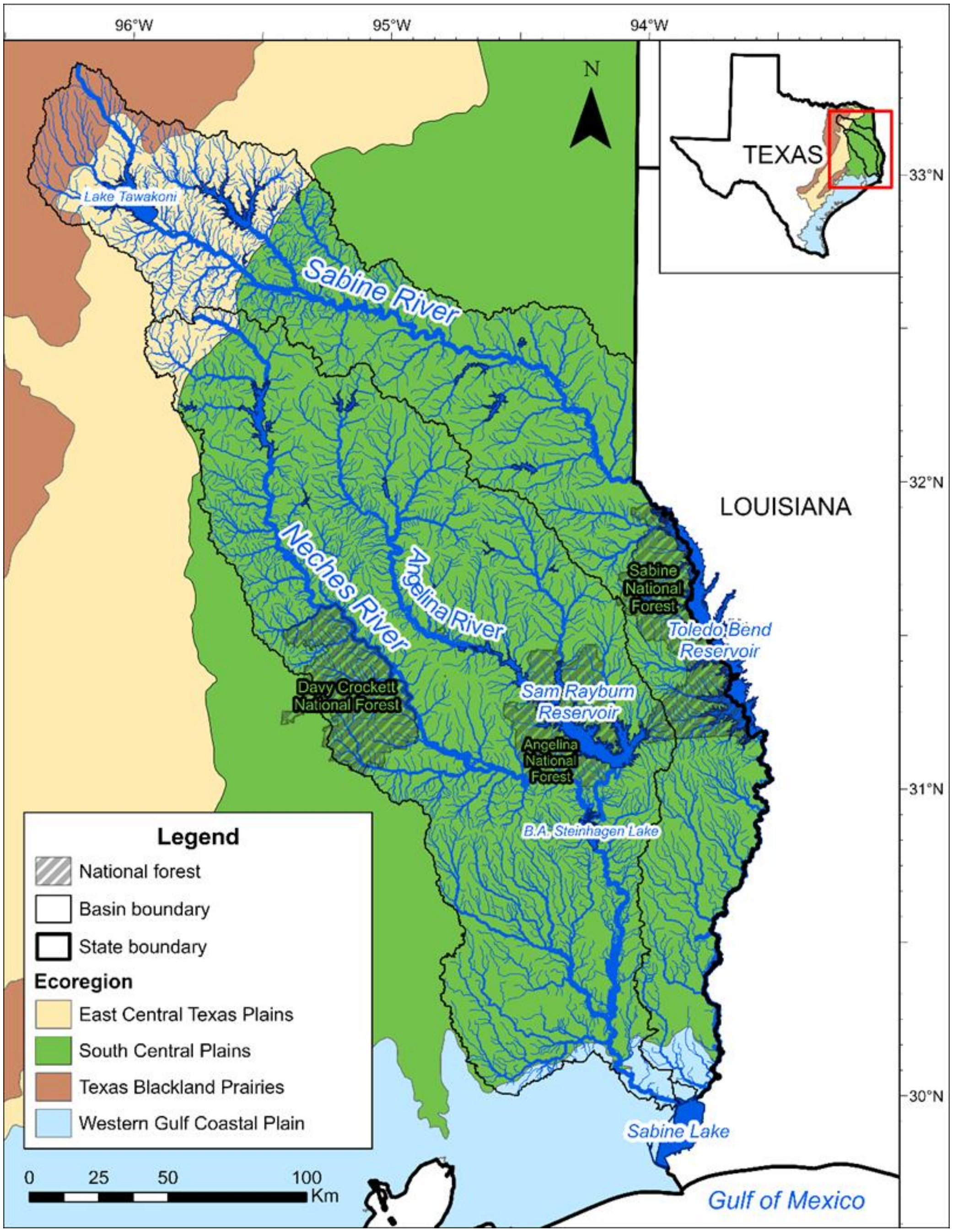


Figure 1.2. Map depicting the Neches River basin and Sabine River basin in the South-Central Plains ecoregion, East Texas.

Standardized surveys of habitat and fish assemblages were conducted at 60 stream sites across three seasons in the Neches River basin (n = 30) and Sabine River basin (n = 30) from June 2023 to May 2024 (Figure 1.3; Table 1.1). Seasonal surveying periods were defined as follows: summer (June–August 2023), autumn (September–November 2023), and spring (March–May 2024). A total of 60 sites were surveyed during the summer of 2023 (30 sites in each river basin). Due to unfavorable weather conditions and logistical challenges, 45 sites were surveyed in the autumn of 2023 (Neches: 24 sites, Sabine: 21 sites) and 48 sites in the spring of 2024 (Neches:

27 sites, Sabine: 21 sites). Although surveys were also conducted during winter (December–February), they were excluded from analysis due to uneven surveying effort between basins and across the other three seasons (Neches: 11 sites, Sabine: 5 sites). All sites were located within the Piney Woods ecological region and classified as 1st, 2nd, or 3rd order streams (USGS 2019). Sites were chosen based on historical fish assemblage surveys conducted by multiple researchers from the 1990s (McCullough 1994; Kelly 1995; LaMont 1998; Geeslin 2001), to contemporary surveys completed between 2020 and 2021 by the Montaña Aquatic Ecology Lab at Stephen F. Austin State University (Swanson 2023).

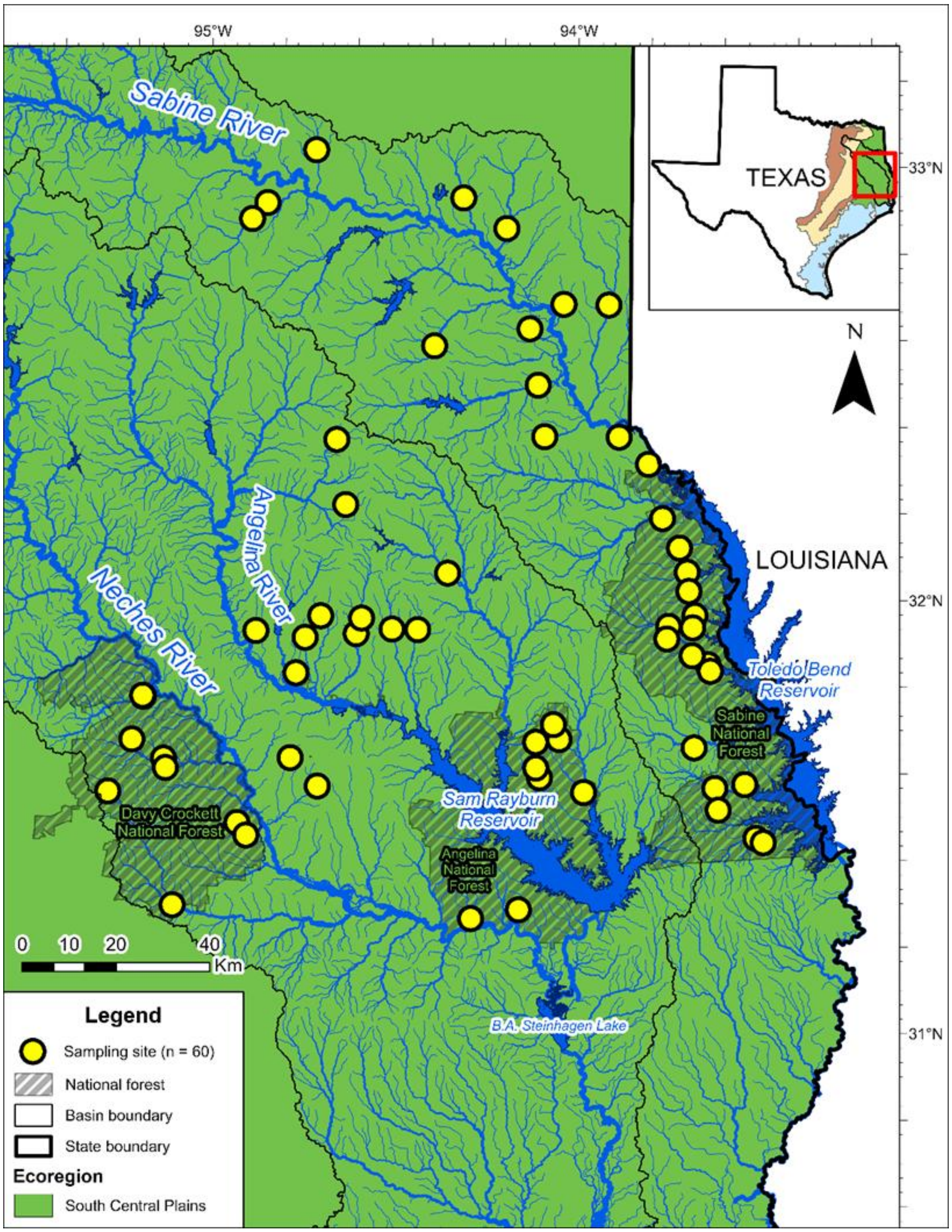


Figure 1.3. Map depicting the sampling sites in the Neches and Sabine River basins, Texas.

Table 1.1. List of sampling sites surveyed in the Neches and Sabine River basins, Texas.

#	Site	River Basin	County	Latitude	Longitude
1	Turkey Creek	Neches	San Augustine	31.3945	-94.1948
2	Lick Creek	Neches	San Augustine	31.4232	-94.2080
3	Running Branch	Neches	San Augustine	31.3887	-94.2470
4	Boykin Creek	Neches	Jasper	31.0661	-94.2816
5	Graham Creek	Neches	Angelina	31.0481	-94.3880
6	Hickory Creek	Neches	Houston	31.4658	-95.1294
7	Walnut Creek	Neches	Houston	31.4678	-95.1308
8	Lee Creek	Neches	Houston	31.3831	-95.1529
9	Hackberry Creek	Neches	Trinity	31.2263	-94.9143
10	Sandy Creek DCNF	Neches	Trinity	31.2025	-94.8939
11	Piney Creek	Neches	Trinity	31.0659	-95.0559
12	Naconiche Creek	Neches	Nacogdoches	31.7121	-94.4497
13	Banita Creek	Neches	Nacogdoches	31.5933	-94.6536
14	La Nana Creek	Neches	Nacogdoches	31.6233	-94.6420
15	Beech Creek	Neches	Nacogdoches	31.8412	-94.6815
16	Tuscosso Creek	Neches	Nacogdoches	31.6026	-94.5155
17	Carrizo Bayou	Neches	Nacogdoches	31.6031	-94.5729
18	Ham Creek	Neches	Rusk	31.9662	-94.7037
19	Sandy Creek ANF	Neches	San Augustine	31.2931	-94.1387
20	Harvey Creek	Neches	San Augustine	31.3207	-94.2378
21	Scott Creek	Neches	San Augustine	31.3393	-94.2463
22	Hurricane Creek	Neches	Angelina	31.2990	-94.7355
23	Jack Creek	Neches	Angelina	31.3528	-94.7974
24	Hager Creek	Neches	Houston	31.3475	-95.0816
25	Cochino Bayou	Neches	Houston	31.3294	-95.0767
26	Lynch Creek	Neches	Houston	31.2823	-95.2047
27	Bonaldo Creek	Neches	Nacogdoches	31.5161	-94.7876
28	Alazan Bayou	Neches	Nacogdoches	31.5848	-94.7681
29	Mill Creek	Neches	Nacogdoches	31.6267	-94.7340
30	Legg Creek	Neches	Nacogdoches	31.5962	-94.8790
31	Murvaul Creek	Sabine	Panola	32.0759	-94.2506

Table 1.1. Continued.

#	Site	River Basin	County	Latitude	Longitude
32	Socagee Creek	Sabine	Panola	32.2316	-94.0925
33	Morris Creek	Sabine	Shelby	31.9774	-94.0667
34	McFaddin Creek	Sabine	Panola	31.9768	-94.2345
35	Styles Creek	Sabine	Shelby	31.9258	-93.9997
36	Carroll Creek	Sabine	Shelby	31.8216	-93.9671
37	Brawley Creek	Sabine	Shelby	31.7650	-93.9282
38	Siepe Bayou	Sabine	Shelby	31.7186	-93.9103
39	Blue Bayou South	Sabine	Shelby	31.6820	-93.9059
40	Mill Creek	Sabine	Panola	32.2318	-94.1944
41	Respass Creek	Sabine	Panola	32.1840	-94.2706
42	Grace Creek	Sabine	Gregg	32.5225	-94.7600
43	Peavine Creek	Sabine	Gregg	32.4195	-94.8688
44	Rabbit Creek	Sabine	Gregg	32.3884	-94.9029
45	Potters Creek	Sabine	Harrison	32.4343	-94.4244
46	Eightmile Creek	Sabine	Harrison	32.3764	-94.3258
47	Irons Bayou	Sabine	Harrison	32.1491	-94.4859
48	Brittain Creek	Sabine	Shelby	31.6356	-93.8920
49	Martinez Bayou	Sabine	Shelby	31.6119	-93.8969
50	Indian Creek off 2261	Sabine	Shelby	31.6142	-93.9510
51	Bourghs Creek	Sabine	Sabine	31.5414	-93.8618
52	Reeves Creek	Sabine	Sabine	31.5288	-93.8565
53	Colorow Creek	Sabine	Sabine	31.5582	-93.8976
54	Buckley Creek	Sabine	Shelby	31.5901	-93.9549
55	Indian Creek off 944	Sabine	Sabine	31.3109	-93.7775
56	Housen Bayou	Sabine	Sabine	31.3032	-93.8443
57	Tebo Creek	Sabine	Sabine	31.3809	-93.8915
58	Big Sandy Creek	Sabine	Sabine	31.2077	-93.7518
59	Walnut Creek	Sabine	Sabine	31.2614	-93.8367
60	South Prong Creek	Sabine	Sabine	31.1993	-93.7350

Local and Regional Environmental Data Collection. – Local habitat assessment was conducted at every stream site following methods modified from the Texas Commission on Environmental Quality monitoring procedures (TCEQ 2014; Table 1.2). At each stream site, surveys began ~ 20 meters upstream from the closest access point (e.g., bridge or trail). Five transects were placed within the stream reach, each ~ 30 meters upstream from one another, to complete 150-meters (Figure 1.4). Local in situ water quality variables such as dissolved oxygen (mg/L), temperature (^{0}C), specific conductance (µS/cm), and pH were measured at the 1st and 5th transects, using a

YSI Pro 2030 meter and Apera Instruments AI316 probe. Wetted channel width (m) and active channel width (i.e., width of the channel [m] between riparian vegetation lines) were measured with a Keson Model OTR50M tape measure at every 30 meters transect. Turbidity (NTU) and left and right bank angle (degrees [º]) were also measured at all transects using the Apera Instruments TN400 Turbidity meter and eOUTIL IP65 inclinometer. Substrate composition was visually estimated using the following categories: bedrock, large boulder (> 45 cm), boulder (> 25 - 45 cm), cobble (> 6 – 25 cm), gravel (> 2 mm – 6 cm), sand (0.06 – 2 mm), mud/silt (< 0.06 - 0.002 mm), clay (< 0.002 mm) and detritus). Water depth (m) was measured using a depth pole, water velocity (m/s) with a Marsh McBirney Model 2021D portable flow meter, and canopy cover (%) with using a Forestry Supplies Model-C spherical crown densiometer. These variables, along with substrate type, were recorded at five equidistant points across the width of the stream at each transect. Undercut bank (%), algae (%), woody debris (%), and macrophytes (%) were visually estimated visually within a 3-meter range, upstream and downstream of each transect. When flows and connectivity allowed for accurate water velocity readings, total discharge (m3/s) was measured at a representative transect within the stream reach. To estimate total water discharge, the depth (m) and water velocity (m/s) readings were measured at 10 equidistant points across the width of the stream at 0.6 of the depth. The distance between these points was determined by multiplying the stream width by 0.1, and depth and water velocity readings were recorded at the middle of each section (Figure 1.5). The values of depth, velocity, and distance between points were multiplied for each point, and the total discharge was obtained by summing the values from all 10 points (TCEQ 2014).

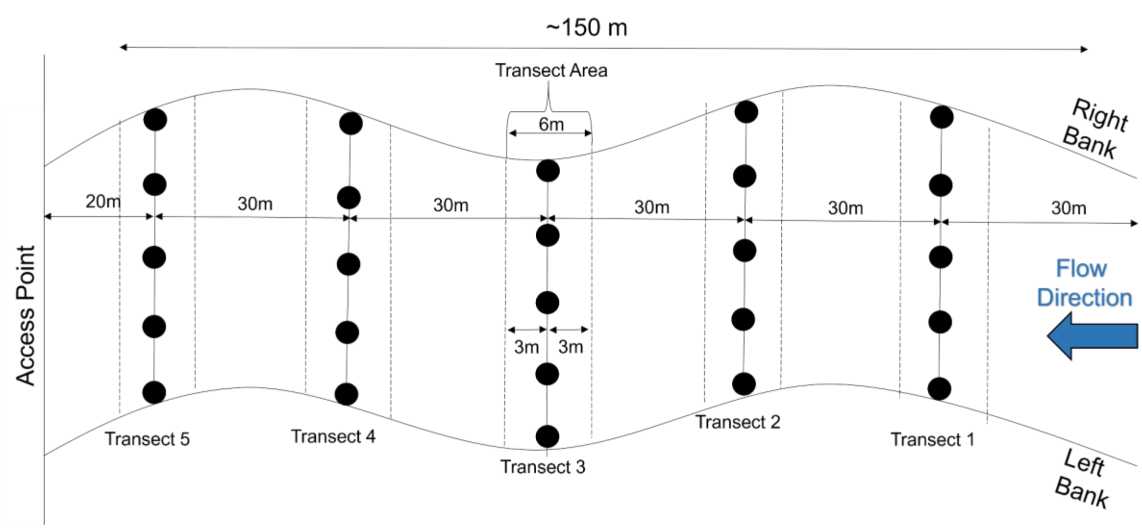


Figure 1.1. Schematic layout of the stream reach and five transects in a stream site. Black circles represent a point where environmental variables were measured within each transect. The blue arrow indicates the direction of flow. Modified from TCEQ (2014).

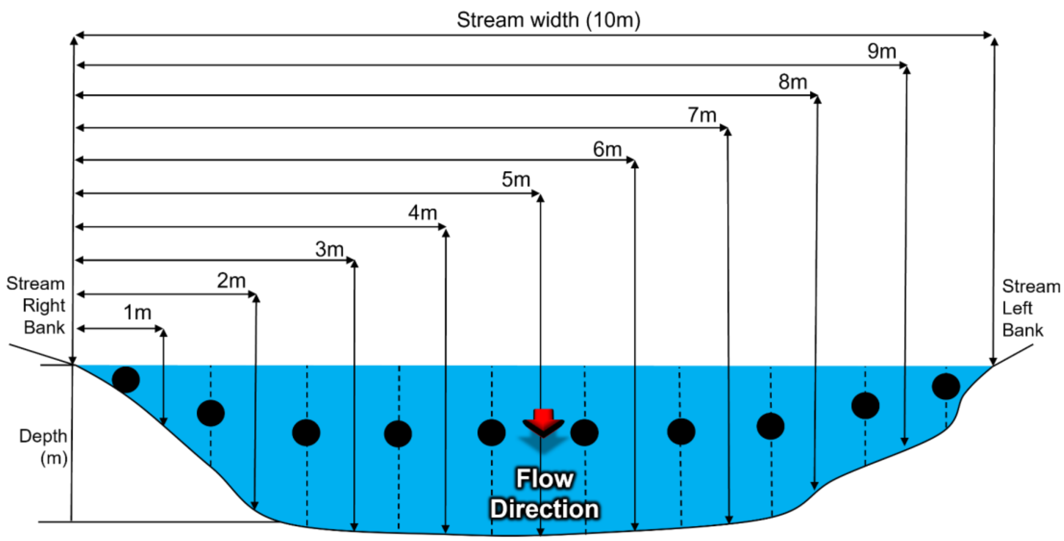
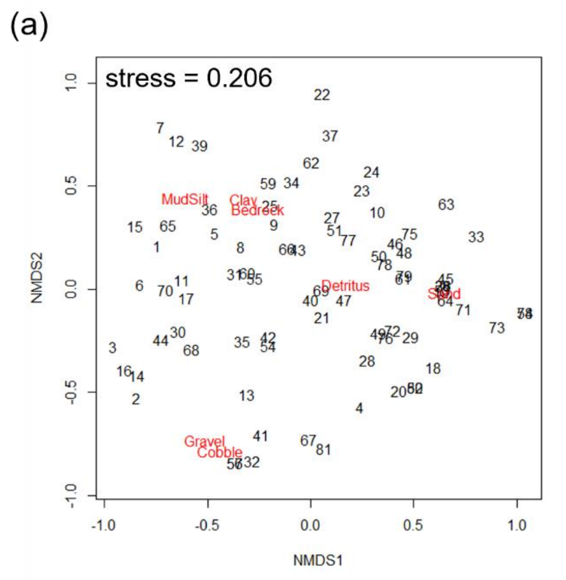


Figure 1.2. Hypothetical layout for measuring stream discharge of a stream with a 10-meter wetted- width. Black circles represent a point where depth and velocity were measured. The red arrow indicates the direction of the stream flow. Modified from Dingman 2015.

Table 1.2. Local-scale environmental variables (n = 18) measured at various transects for each sampling site the Neches and Sabine River basins.

Category	Measurement	Description
Stream morphology	Wetted Width (m)	Perpendicular width of the stream from waters edge too waters edge
Stream morphology	Channel Width (m)	Perpendicular width of the stream from where the water typically stays within (measurements at base/edge of small riparian plants and grasses)
Stream morphology	Left angle (°)	Angle of the embankment at the water's edge for river left
Stream morphology	Right angle (°)	Angle of the embankment at the water's edge for river right
Hydrology	Depth (m)	Depth in meters at river left of transect (total of 5-point estimates in transect)
Hydrology	Velocity (m/s)	Velocity of water flow in meters per second at river left of transect (total of 5-point estimates in transect)
Hydrology	Discharge (cms)	Discharge of the water at the site in cubic meters per second (measured at one representative transect)
Riparian	Canopy Opening	Coverage of canopy over the water, when facing upstream (total of 5-point estimates in transect)
Instream habitat	Substrate (class)	Identity of majority substrate class (total of 5-point estimates in transect)
Instream habitat	Undercut (%)	Percent of undercut present within the transect width (i.e. 3 meters upstream and downstream from center line of transect)
Instream habitat	Algae (%)	Percent of algae present within the transect width (i.e. 3 meters upstream and downstream from center line of transect)
Instream habitat	Woody (%)	Percent of woody debris present within the transect width (i.e. 3 meters upstream and downstream from the center line of transect)
Instream habitat	Macrophytes (%)	Percent of macrophytes present within the transect width (i.e. 3 meters upstream and downstream from center line of transect)
Water chemistry	DO (mg/L)	Dissolved oxygen in milligrams per litre (measured at 1st and 5th transects)
Water chemistry	Temp (°C)	Temperature in degrees Celsius (measured at 1st and 5th transects)
Water chemistry	Cond. (µs/cm)	Conductivity in MicroSiemens per centimeter (measured at 1st and 5th transects)
Water chemistry	pH	Potential of hydrogen (measured at 1st and 5th transects)
Water chemistry	Turbidity (NTU)	Turbidity in Nephelometric Turbidity Unit

The mean values for all continuous variables across all five transects were z-score standardized to mean 0 and standard deviation of 1 to account for different units of measurement (Becker et al. 1988). Substrate data were recorded as proportions out of 100. To reduce the dimensionality of this instream variable, a nonmetric multidimensional scaling (NMDS) analysis was conducted using the "metaMDS" function in the *vegan* package in R (Oksanen et al. 2019; Figure 1.6). The NMDS utilized Bray Curtis dissimilarity, with no auto transformations applied, and two constrained axes (k = 2). The resulting axes (NMDS axes 1 and 2) were extracted and retained as local variables in subsequent analyses.



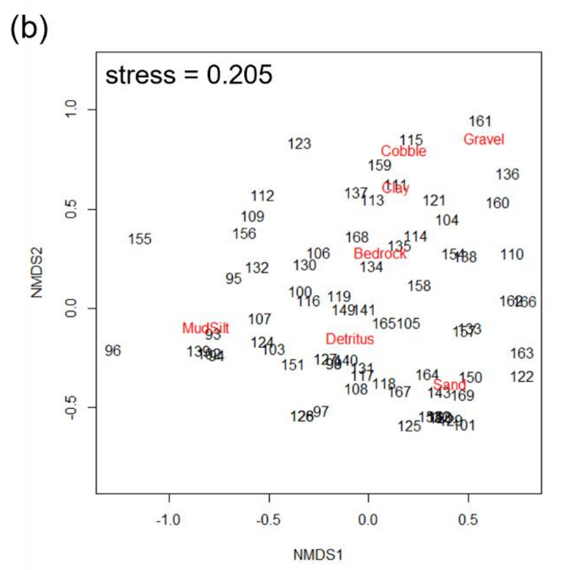


Figure 1.3. Non-metric multidimensional scaling (NMDS) of substrate composition based on Bray Curtis dissimilarity of all sites, across three surveying seasons, in the Neches (a) and Sabine River basins (b). Each number represents a sampling site.

Several regional environmental variables were generated from a 10-m digital elevation model (DEM), using National Elevation Dataset (NED) raster files (USGS 2013; Table 1.3). These include flow accumulation (m2), elevation (m), and slope (m). Precipitation in millimeters per month (Wang et al. 2016) was accumulated across the entire study period (June 2023 – May 2024). Stream order and indices of stream fragmentation caused by dams (Cooper et al. 2022) were joined to each stream reach code of the National Hydrography Dataset (NHD) Plus Version 2 (USGS 2019). NMDS analyses were performed on the stream fragmentation indices, to reduce their dimensionality (Figure 1.7), using the “metaMDS” function. Environmental variables were z-score standardized prior to analysis and two dimensions specified (k = 2). Auto-transformations were disabled, and Euclidean distance was used as the dissimilarity metric. The resulting two NMDS axes were utilized as regional environmental variables for further analysis. Watershed area (km^2) was also gathered for each drainage area from the NHD. Land cover expressed as percentages was extracted for each drainage area from the U.S. Geological Survey Annual National Land Cover Database (NLCD) raster dataset (Brown et al. 2023). A total of 15 categories of land cover are represented in the NLCD dataset. This study aggregated land cover classes into broader categories for analysis including developed areas (i.e., open space, low intensity, medium intensity, and high intensity) which were grouped into a single “Developed” land cover variable. Forest type (i.e., deciduous, evergreen, and mixed forest) were combined into “Forest” variable. Similarly, agricultural land uses, including pasture and cultivated crops were combined to “Agriculture” land cover. Woody wetlands and emergent herbaceous wetlands were consolidated to a single “Wetlands” category. Therefore, a total of eight land cover types were included in analyses (i.e., Open Water, Developed, Barren, Forest, Shrub, Grassland, Agriculture, Wetlands; Table 1.3).

Table 1.3. Regional-scale environmental variables (n = 15) generated by a digital elevation model (DEM) or extracted from online databases.

Category	Measurement	Description	Source
Hydrology	Precipitation (mm/month)	Mean precipitation in millimeters per month ranging from June 2023 – May 2024	PERSIANN (Precipitation Estimation from Remotely Sensed Information using Artificial Neural Networks; Wang et al. 2016)
Hydrology	Flow accumulation (km^2)	Total area in kilometers squared of upstream pixels from a site using 10m resolution DEM	3D Elevation Program 1-Meter (USGS 2019)
Channel morphology	Elevation (m)	Mean elevation in meters at each site using 10m resolution DEM	3D Elevation Program 1-Meter (USGS 2019)
Channel morphology	Slope (m)	Mean slope in meters at each site using 10m resolution DEM	3D Elevation Program 1-Meter (USGS 2019)
Channel morphology	Watershed area (km^2)	Total area in kilometers squared contained in the watershed associated with a site	NHDPlus (National Hydrography Dataset Plus) version 2 (USGS 2019)
Channel morphology	Stream order	Position of stream in the hierarchy of river networks	NHDPlus (National Hydrography Dataset Plus) version 2 (USGS 2019)
Land cover	Fragmentation	Indices of habitat fragmentation caused by dams	Dam metrics representing stream fragmentation and flow alteration for the conterminous United States linked to the NHDPLUSV2 (Cooper & Infante 2022)
Land cover	Open water (%)	% of catchment area classified as open water land cover (NLCD 2023 class 11)	National Land Cover Database (NLCD; Brown et al. 2023)
Land cover	Developed (%)	% of catchment area classified as developed land use (NLCD 2023 classes 21+22+23+24)	National Land Cover Database (NLCD; Brown et al. 2023)
Land cover	Barren (%)	% of catchment area classified as barren land cover (NLCD 2023 class 31)	National Land Cover Database (NLCD; Brown et al. 2023)

Land cover	Forest (%)	% of catchment area classified as forest land cover (NLCD 2023 classes 41+42+43)	National Land Cover Database (NLCD; Brown et al. 2023)
Land cover	Shrub (%)	% of catchment area classified as shrub/scrub land cover (NLCD 2023 class 52)	National Land Cover Database (NLCD; Brown et al. 2023)
Land cover	Grassland (%)	% of catchment area classified as grassland/herbaceous land cover (NLCD 2023 class 71)	National Land Cover Database (NLCD; Brown et al. 2023)
Land cover	Agriculture (%)	% of catchment area classified as agricultural land cover (NLCD 2023 classes 81+82)	National Land Cover Database (NLCD; Brown et al. 2023)
Land cover	Wetlands (%)	% of catchment area classified as wetland land cover (NLCD 2023 classes 90+95)	National Land Cover Database (NLCD; Brown et al. 2023)

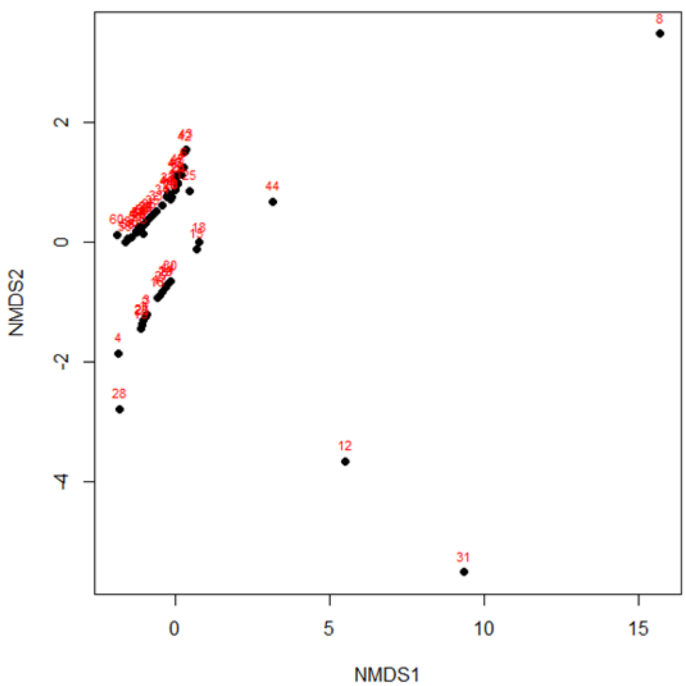


Figure 1.4. Non-metric multidimensional scaling (NMDS) of habitat fragmentation caused by dams, based on Euclidean distance, of all sampling sites in the Neches and Sabine River basins. Numbers in red represent sites.

Biotic Data Collection. – Following the local data collection at each sampling site, fish assemblage surveys were conducted throughout the 150-meter stream reach. A Halltech HT2000B Backpack Electrofisher was employed in the upstream direction for a minimum of 900 seconds of active shocking. Following electrofishing, a minimum of 10 non-overlapping seine hauls, using a 3 m long x 1.5 m deep x 4 mm mesh seine, were performed in the upstream direction, to target deeper pools and runs where backpack electrofishing is not as effective or possible. All available habitats were surveyed by the two collection methods. All fishes captured at these sites were placed in aerated buckets according to gear type, buckets were filled with water from the stream, and a portable aerator. Larger-bodied fish were counted, identified to the species taxonomic level and later released into the stream. According to gear type, the remaining fishes were anesthetized with clove oil and preserved in a labeled jar containing 10% formalin and transported to the Montaña Aquatic Ecology Lab at Stephen F. Austin State University where they were sorted, identified, and quantified.

Functional and Phylogenetic Trait Data Collection. – A dataset of 17 functional traits for all fish species recorded in this study was compiled from the FishTraits database (Frimpong & Angermeier 2009). The dataset included nine trophic ecology traits based on adult feeding habits: benthic feeding, surface feeding, consumption of algae, macrophytes, detritus, aquatic and terrestrial invertebrates, fish (piscivory), blood (e.g., parasitic lampreys), and eggs. Each species was assigned to a binary value for each trait. For example, a value of 0 indicated absence and 1 indicated presence. The remaining variables associated with life history strategies included: maximum total length, age at maturity, longevity, fecundity, spawning frequency, spawning season length, and minimum and maximum temperature tolerance. These traits were selected based on previous studies that utilized similar traits related to size, life histories, and feeding ecology to assess functional fish diversity (Pool et al. 2014; Zbinden et al. 2022). The dimensionality of this functional trait dataset was reduced using NMDS based on Gower distances calculated from standardized trait data (mean = 0, standard deviation = 1). NMDS was constrained to four axes, as this number is limited by the number of species (n) minus one (n-1). A minimum of five species was required for functional diversity analyses to ensure meaningful ordination, therefore sites with fewer than five species were removed. NMDS was performed using the "metaMDS" function, with no transformations applied, 1,000 random starts, and four constrained axes (Figure 1.8). The species scores, which reflect the position of each species in the reduced multidimensional space, were extracted for subsequent functional β-diversity analyses.

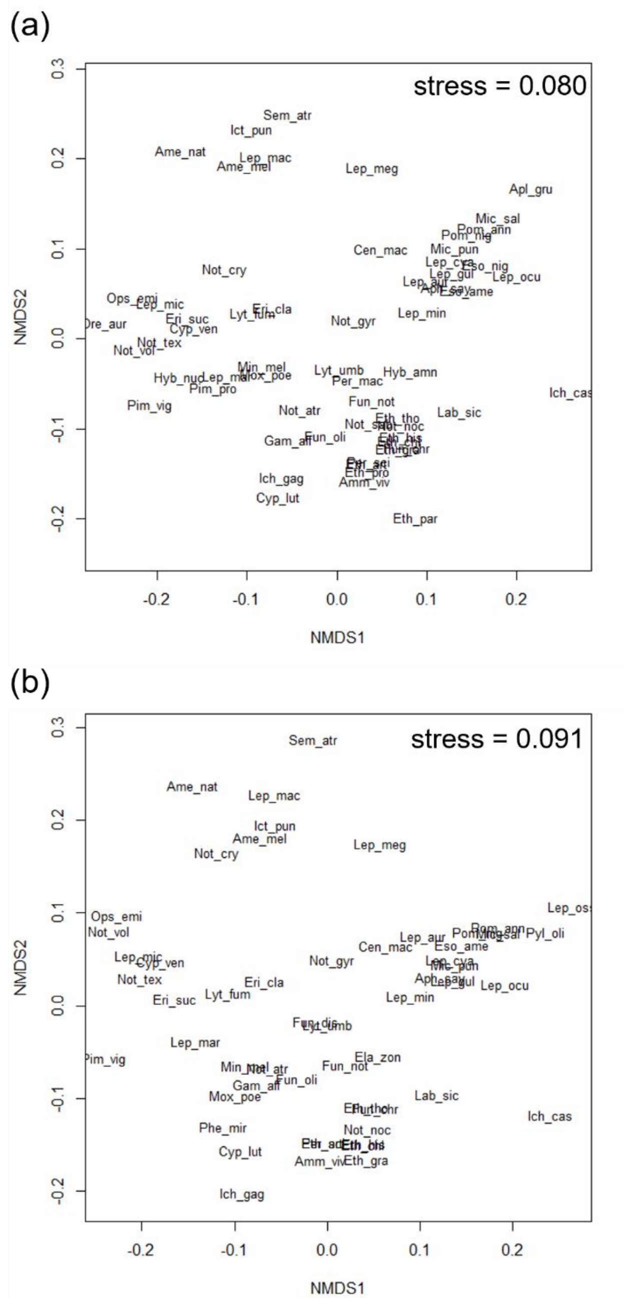


Figure 1.5. Non-metric multidimensional scaling (NMDS) of species traits, based on Gower distances, in three seasons of sampling in the Neches (a) and Sabine River basins (b). Species names reflect their position in NMDS ordination space of trait composition.

A time-calibrated phylogenetic tree that included the fish species in this study was generated using the “Build a Timetree” function on timetree.org (Kumar et al. 2022).
For species that were not represented in the TimeTree database, their position in the tree was assigned to their closest taxonomic relatives that were represented (Figure 1.9). For example, the two species that were not represented in the database, Western Creek Chubsucker *Erimyzon claviformis* and Gumbo Darter *Etheostoma thompsoni*, their positions were assigned to Creek

Chubsucker *Erimyzon oblongus* and Mud Darter *Etheostoma asprigene*, respectively, based on previously published literature (Suttkus et al., 2012; Hunt et al. 2021).

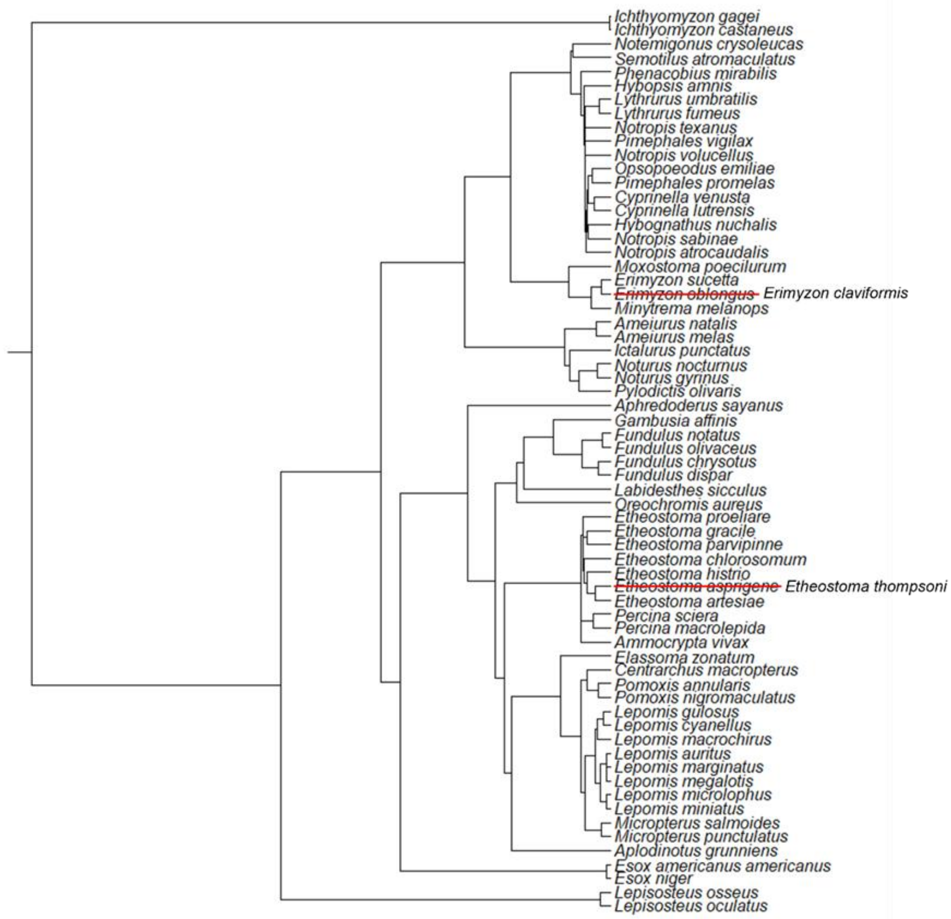


Figure 1.6. Time-calibrated phylogenetic tree of fish species recorded in the Neches and Sabine River basins, used to calculate phylogenetic β-diversity. Species crossed with red lines (i.e., *Erimyzon sucetta* and *Etheostoma asprigene*) had their positions replaced with their closest taxonomic relatives recorded in this study (i.e., *Erimyzon claviformis* and *Ethestoma thompsoni*).

Statistical Analyses. – The goal of this study was to elucidate the spatial and temporal scale effects on multiple β-diversity facets of stream fish communities. Statistical analyses were conducted separately for each river basin (i.e., Neches and Sabine), across three distinct seasons (i.e., summer, autumn, and spring), and over an aggregated annual scale. To account for the unequal surveying effort across the three seasons and mitigate surveying bias, interpolation (i.e., rarefaction) and extrapolation curves were constructed for each river basin using the "iNEXT" function of the *iNEXT* package (Hsieh et al. 206). These curves assessed species accumulation based on incidence data (order q = 0; Hill 1973), and projected species richness estimates, with the number of sites doubled (Chao et al. 2014). Confidence intervals of 95% and based on 1000 randomizations were used to evaluate significant differences in species richness among seasons. Multiple facets of β-diversity were calculated and decomposed into total β-diversity and its additive components of turnover and nestedness using the Sørensen dissimilarity index. First, pairwise TDβ was calculated for species incidence data for each sampling site, using the

"beta.pair" function of the *betapart* package (Baselga et al. 2021). The same β-diversity decomposition was calculated for FDβ on the species score data, using "functional.beta.pair" function of the same package. The decomposition of PDβ was calculated based on the relative species branch lengths from the time-calibrated phylogenetic tree, using "phylo.beta.pair" function. Additionally, a permutational analysis of multivariate dispersion (PERMDISP; Anderson et al. 2006) was performed using the "betadisper" function of the *vegan* package to test whether the average distances of assemblages to group multivariate centroids among β-diversity facets were significantly different ($p < 0.05$). Significant differences revealed by PERMDISP indicate that a particular β-diversity component exhibits greater variability and heterogeneity among sites, thus reflecting higher β-diversity (Anderson et al. 2006).
The relationships among the total TDβ, FDβ, and PDβ dissimilarity matrices were assessed using partial Mantel tests, with 999 permutations. The Mantel correlation coefficient (r), which ranges from −1 to 1, indicates the strength and direction of the relationship, with values near either extreme suggesting a strong positive ($r = 1$) or negative ($r = -1$) correlation. Pairwise comparisons were performed for all combinations of dissimilarity matrices using the "mantel.rtest" function from the ade4 package (Dray et al. 2007), and $p \leq 0.05$ to indicate statistical significance.

Variation partitioning was used to examine the relative contributions of regional, local, and seasonal environmental variables, on each β-diversity matrix of each river basin on the annual scale, using distance-based redundancy analysis (db-RDA) framework. Unlike traditional redundancy analysis (RDA), which relies on Euclidean distances (i.e., straight-line distance between points), db-RDA allows for the use of other distance measures such as Bray-Curtis or Sørensen distance (Legendre and Anderson 1999). First, three matrices based on the explanatory variables: a site by regional variables matrix, site by local variables matrix, and a time matrix based on the season of sampling were created. For each total β-diversity matrix (i.e., TDβ, FDβ, PDβ), regional and local explanatory variables that exhibited significant multicollinearity (variance inflation factor, VIF ≥ 5) were individually removed using the "vifstep" function of the *usdm* package (Naimi et al. 2014). Second, prior to conducting db-RDA, the remaining non-collinear variables were then screened using a forward selection process to prevent overestimation of the explained variance (Blanchet et al. 2008). This forward selection process was performed using the "forward.sel" function of the *adespatial* package, based on 9999 permutations, and $p \leq 0.05$ to indicate statistical significance. The final regional and local variables that were retained through forward selection were then used as explanatory variables in separate db-RDAs to assess their relationship with the total β-diversity matrices. This was performed using the dbrda" function (McArdle & Anderson 2001) in the *vegan* package. To assess the relative contribution of seasonality to each β-diversity facet, sampling season identity (i.e., summer, autumn, spring) was used to construct a temporal distance matrix using a principal coordinates of neighbor matrices (PCNM). The resulting eigenvectors were extracted and used as the singular temporal variable for all variation partitioning models (Borcard and Legendre 2002). Following the creation of the three explanatory matrices, variance partitioning was conducted on the total TDβ, FDβ, and PDβ for each river basin using the "varpart" function of the *vegan* package. The significance of unique contributions of regional, local, and seasonal variables to total β-diversity were assessed using the "anova" function of the *vegan* package at a significance level of $p < 0.05$.

Results

Fish Assemblage Diversity, Composition, and Distribution. – A total of 23,646 individuals were recorded from the Neches and Sabine River basins and were contained in 65 fish species (Neches = 60 species, Sabine = 55 species) from 35 genera and 17 families across three seasons of surveys (Table 1.4). Across three seasons, summer had the highest species richness with 60 species (Neches = 52 species, Sabine = 51 species), followed by autumn with 52 species (Neches = 46 species, Sabine = 44 species), and spring with 50 species (Neches = 49 species, Sabine = 43 species). Despite differences in species richness across seasons, 95% confidence intervals of all seasons exhibited overlap in both river basins, suggesting that species richness was not significantly different (Figure 1.10).

The average species richness at the annual scale in the Neches River basin and Sabine River basin was comparable with 13 species and 14 species, respectively. Fish assemblages were dominated by species in the family Leuciscidae (15 species), followed by Centrarchidae (13 species). Leucisicids of nine genera comprised 32.28% of the total sample and Centrarchids of the genus *Lepomis* (i.e., sunfishes) made up 23.67%. Western Mosquitofish *Gambusia affinis* was the most abundant species, comprising 22.31% of the total sample.

There were ten species unique to the Neches River basin including Freshwater Drum *Aplodinotus grunniens*, Mississippi silvery minnow *Hybognathus nuchalis*, Pallid Shiner *Hybopsis amnis*, Sabine Shiner *Notropis sabinae*, Fathead Minnow *Pimephales promelas*, Chain Pickerel *Esox niger*, Goldstripe Darter *Etheostoma parvipinne*, Cypress Darter *Etheostoma proeliare*, Bigscale Logperch *Percina macrolepida*, and Blue Tilapia *Oreochromis aureus*, while five species were unique to the Sabine River basin including, Longnose Gar *Lepisosteus osseus*, Suckermouth Minnow *Phenacobius mirabilis*, Flathead Catfish *Pylodictus olivaris*, Starhead Topminnow *Fundulus dispar*, and Banded Pygmy Sunfish *Elassoma zonatum*.

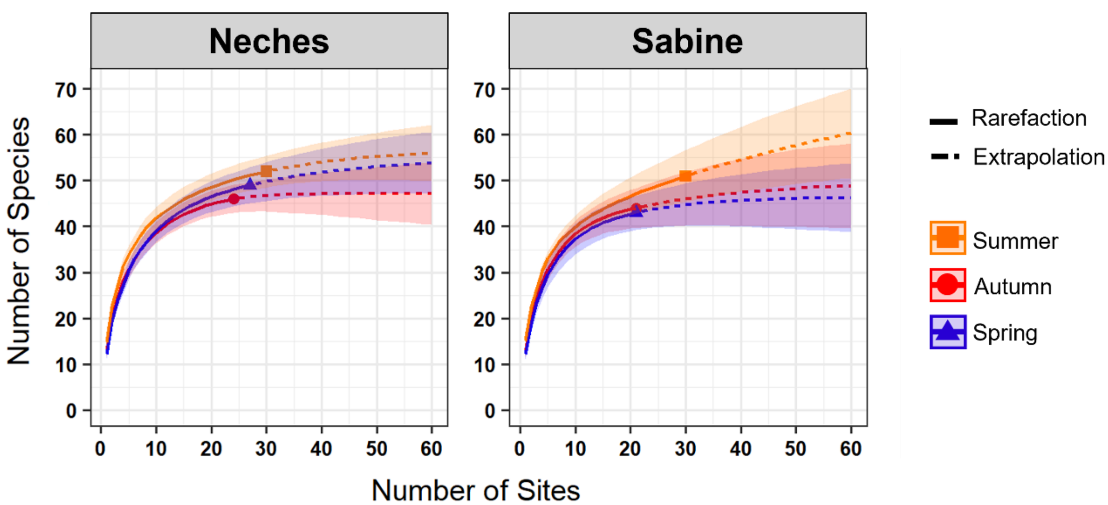


Figure 1.7. Rarefaction curves for the Neches (left) and Sabine (right) River basins, estimating fish species richness across three seasons (summer, autumn, spring). Symbols represent sampling season: orange for summer, red for autumn, and blue for spring. Solid lines depict observed richness, dashed lines show extrapolated species richness estimates, and shaded areas represent 95% confidence intervals, based on 1000 randomizations. The overlapping confidence intervals indicate no significant differences in species richness across seasons in either river basin.

Table 1.4. List of fish species collected from the Neches and Sabine River basins, Texas, across three seasons throughout 2023-2024. Species are listed based on taxonomic group.

				River Basin	
Order	**Family**	**Scientific Name**	**Common Name**	**Neches**	**Sabine**
Petromyzontidae	Petromyzontidae	*Ichthyomyzon castaneus*	Chestnut Lamprey	2	22
Petromyzontidae	Petromyzontidae	*Ichthyomyzon gagei*	Southern Brook Lamprey	16	36
Lepisosteiformes	Lepisosteidae	*Lepisosteus oculatus*	Spotted Gar	2	2
Lepisosteiformes	Lepisosteidae	*Lepisosteus osseus*	Longnose Gar	0	1
Cypriniformes	Cyprinidae	*Notemigonus crysoleucas*	Golden Shiner	59	77
Cypriniformes	Leuciscidae	*Cyprinella lutrensis*	Red Shiner	23	85
Cypriniformes	Leuciscidae	*Cyprinella venusta*	Blacktail Shiner	1352	294
Cypriniformes	Leuciscidae	*Hybopsis amnis*	Pallid Shiner	9	0
Cypriniformes	Leuciscidae	*Hybognathus nuchalis*	Mississippi Silvery Minnow	71	0
Cypriniformes	Leuciscidae	*Lythrurus fumeus*	Ribbon Shiner	915	712
Cypriniformes	Leuciscidae	*Lythrurus umbratilis*	Redfin Shiner	392	1744
Cypriniformes	Leuciscidae	*Notropis atrocaudalis*	Blackspot Shiner	402	227
Cypriniformes	Leuciscidae	*Notropis sabinae*	Sabine Shiner	107	0
Cypriniformes	Leuciscidae	*Notropis texanus*	Weed Shiner	317	252
Cypriniformes	Leuciscidae	*Notropis volucellus*	Mimic Shiner	12	2
Cypriniformes	Leuciscidae	*Opsopoeodus emiliae*	Pugnose Minnow	32	99
Cypriniformes	Leuciscidae	*Phenacobius mirabilis*	Suckermouth Minnow	0	2
Cypriniformes	Leuciscidae	*Pimephales promelas*	Fathead Minnow	1	0
Cypriniformes	Leuciscidae	*Pimephales vigilax*	Bullhead Minnow	206	145
Cypriniformes	Leuciscidae	*Semotilus atromaculatus*	Creek Chub	116	115
Cypriniformes	Catostomidae	*Erimyzon claviformis*	Western Creek Chubsucker	16	7
Cypriniformes	Catostomidae	*Erimyzon sucetta*	Creek Chubsucker	141	41
Cypriniformes	Catostomidae	*Minytrema melanops*	Spotted Sucker	72	30

Table 1.4. Continued.

Order	Family	Scientific Name	Common Name	River Basin	
				Neches	**Sabine**
Cypriniformes	Catostomidae	*Moxostoma poecilurum*	Blacktail Redhorse	33	19
Siluriformes	Ictaluridae	*Amerius melas*	Black Bullhead	38	17
Siluriformes	Ictaluridae	*Amerius natalis*	Yellow Bullhead	111	168
Siluriformes	Ictaluridae	*Ictalurus punctatus*	Channel Catfish	8	5
Siluriformes	Ictaluridae	*Noturus gyrinus*	Tadpole Madtom	5	3
Siluriformes	Ictaluridae	*Noturus nocturnus*	Freckled Madtom	75	37
Siluriformes	Ictaluridae	*Pylodictus olivaris*	Flathead Catfish	0	1
Esociformes	Esocidae	*Esox americanus*	Redfin Pickerel	32	30
Esociformes	Esocidae	*Esox niger*	Chain Pickerel	1	0
Percopsiformes	Aphredoderidae	*Aphredoderus sayanus*	Pirate Perch	210	341
Atheriniformes	Atherinidae	*Labidesthes sicculus*	Brook Silverside	3	53
Poeciliidae	Poeciliidae	*Gambusia affinis*	Western Mosquitofish	3330	1945
Cyprinodontiformes	Fundulidae	*Fundulus chrysotus*	Golden Topminnow	2	3
Cyprinodontiformes	Fundulidae	*Fundulus dispar*	Starhead Minnow	0	1
Cyprinodontiformes	Fundulidae	*Fundulus notatus*	Blackstriped Topminnow	1328	47
Cyprinodontiformes	Fundulidae	*Fundulus olivaceus*	Blackspotted Topminnow	95	791
Perciformes	Centrarchidae	*Centrarchus macropterus*	Flier	4	14
Perciformes	Centrarchidae	*Micropterus punctulatus*	Spotted Bass	64	35
Perciformes	Centrarchidae	*Micropterus nigricans*	Largemouth Bass	65	80
Perciformes	Centrarchidae	*Lepomis auritus*	Redbreast Sunfish	85	38
Perciformes	Centrarchidae	*Lepomis cyanellus*	Green Sunfish	117	212
Perciformes	Centrarchidae	*Lepomis gulosus*	Warmouth	121	158
Perciformes	Centrarchidae	*Lepomis macrochirus*	Bluegill	561	403
Perciformes	Centrarchidae	*Lepomis marginatus*	Dollar Sunfish	13	55

Table 1.4. Continued.

Order	Family	Scientific Name	Common Name	River Basin	
				Neches	**Sabine**
Perciformes	Centrarchidae	*Lepomis megalotis*	Longear Sunfish	1427	2000
Perciformes	Centrarchidae	*Lepomis microlophus*	Redear Sunfish	25	39
Perciformes	Centrarchidae	*Lepomis miniatus*	Redspotted Sunfish	153	148
Perciformes	Centrarchidae	*Pomoxis annularis*	White Crappie	3	10
Perciformes	Centrarchidae	Pomoxis nigromaculatus	Black Crappie	3	2
Perciformes	Percidae	*Ammocrypta vivax*	Scaly Sand Darter	12	15
Perciformes	Percidae	Etheostoma artesiae	Redspot Darter	38	96
Perciformes	Percidae	Etheostoma chlorosoma	Bluntnose Darter	195	97
Perciformes	Percidae	Etheostoma gracile	Slough Darter	175	124
Perciformes	Percidae	*Etheostoma histrio*	Harlequin Darter	4	1
Perciformes	Percidae	*Etheostoma parvippine*	Goldstripe Darter	12	0
Perciformes	Percidae	*Etheostoma proeliare*	Cypress Darter	3	0
Perciformes	Percidae	*Etheostoma thompsoni*	Gumbo Darter	24	1
Perciformes	Percidae	*Percina macroplepida*	Bigscale Logperch	3	0
Perciformes	Percidae	*Percina sciera*	Dusky Darter	64	53
Perciformes	Sciaenidae	*Aplodinotus grunniens*	Freshwater Drum	1	0
Perciformes	Elassomatidae	*Elassoma zonatum*	Banded Pygmy Sunfish	0	4
Cichliformes	Cichlidae	*Oreochromis aureus*	Blue Tilapia	1	0

Temporal Scale Analysis of β-Diversity Facets
a) Annual Scale

At the annual scale, total stream fish β-diversity and its turnover and nestedness components varied across the three facets in both the Neches and Sabine River basins (Figure 1.11). In the Neches, average total β-diversity values were TDβ = 0.57, FDβ = 0.55, and PDβ = 0.25. PERMDISP analyses indicated no significant differences between TDβ and FDβ ($p = 0.92$; Figure 1.11a), but both were significantly greater than PDβ ($p < 0.001$). Turnover primarily contributed to TDβ and was higher than both FDβ and PDβ turnover ($p < 0.001$; Figure 1.11b). In contrast, nestedness contributed more to FDβ than to TDβ or PDβ ($p < 0.001$; Figure 1.11c), with no differences between TDβ and PDβ nestedness ($p = 0.12$). Similar patterns were observed in the Sabine, where average total β-diversity values were TDβ = 0.54, FDβ = 0.56, and PDβ = 0.24. Again, TDβ and FDβ did not significantly differ ($p = 0.99$; Figure 1.11d) and were both higher than PDβ ($p < 0.001$; Figure 1.11d). Turnover dominated TDβ and was higher than both FDβ and PDβ turnover components ($p < 0.001$; Figure 1.11e). Nestedness was greater in FDβ compared to both TDβ and PDβ ($p < 0.001$; Figure 1.11f), with no differences between TDβ and PDβ nestedness ($p = 0.97$).

All total β-diversity facets were significantly correlated in both river basins (Figure 1.12). In the Neches, Mantel tests revealed a strong correlation between TDβ — PDβ ($r = 0.675$, $p = 0.001$; Figure 1.12c), followed by TDβ — FDβ ($r = 0.593$, $p = 0.001$; Figure 1.12a), and weak correlations were found between FDβ — PDβ ($r = 0.426$, $p = 0.001$; Figure 1.12b). Similar patterns were revealed by Mantel tests in the Sabine, where TDβ — PDβ were strongly correlated ($r = 0.616$, $p = 0.001$; Figure 1.12f), followed by TDβ — FDβ ($r = 0.523$, $p = 0.001$; Figure 1.12a), and FDβ — PDβ ($r = 0.321$, $p = 0.001$; Figure 1.12e).

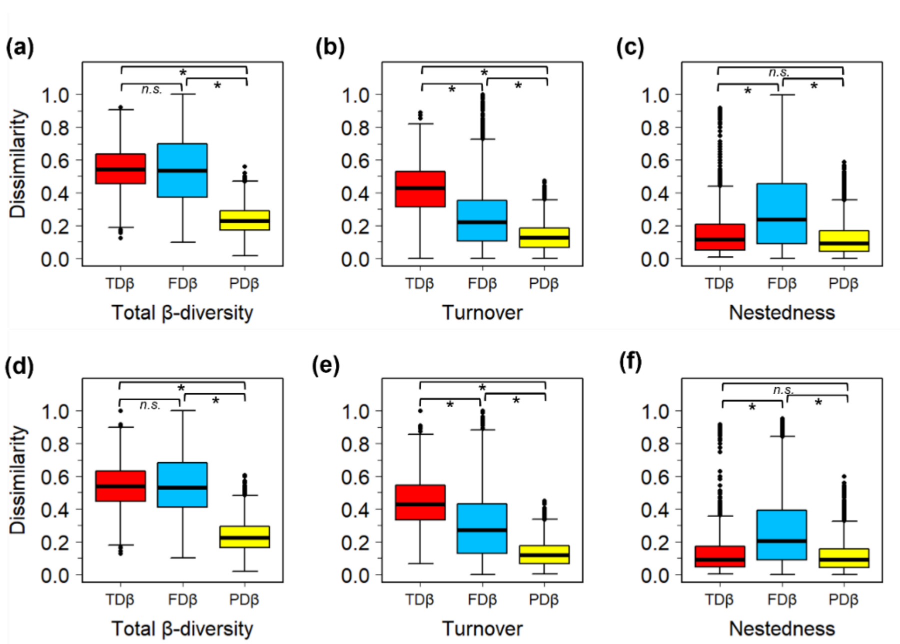


Figure 1.8. Boxplots of β-diversity facets, TDβ, FDβ, and PDβ of fish assemblages in the Neches (a — c) and Sabine (d — f) River basins on the annual scale, partitioned into total β-diversity, turnover, and nestedness components. Stars indicate statistical significance ($p < 0.05$) and *n.s.* indicates a non-significant relationship between β-diversity components.

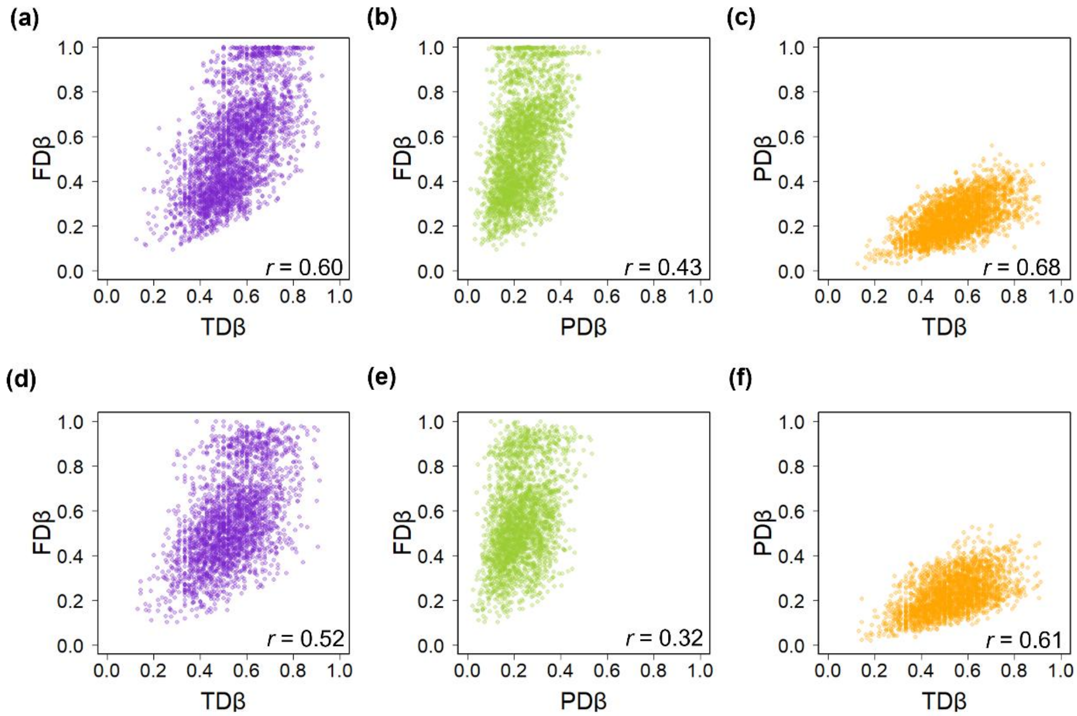


Figure 1.9. Correlations of total β-diversity facets (TDβ, FDβ, and PDβ) of fish assemblages in the Neches (a — c) and Sabine (d — f) River basins on the annual scale. Correlation coefficients (r) are shown for each total β-diversity relationship. All relationships were significant, $p < 0.05$.

b) Seasonal Scale

At the seasonal scale, differences among total β-diversity facets (TDβ, FDβ, PDβ) and their components turnover and nestedness were observed in both the Neches and Sabine River basins (Table 1.5, 1.6). In all seasons, total TDβ and FDβ were not significantly different from one another ($p > 0.05$), whereas total TDβ and FDβ were significantly higher than PDβ. The turnover component of all β-diversity facets was different in all seasons ($p = 0.001$; Table 1.6), with TDβ exhibiting higher turnover, followed by FDβ, and finally PDβ (Table 1.5). Furthermore, FDβ nestedness was higher than both TDβ and PDβ nestedness (Table 1.5, 1.6), while TDβ and PDβ nestedness were not significantly different ($p > 0.05$). When testing for differences in total β-diversity, turnover, and nestedness components across seasons, no statistical differences were observed between any β-diversity facet and in either basin ($p > 0.05$; Table 1.7).

Correlations among total β-diversity facets were significant in both river basins (Table 1.8), except for two relationships observed in the Sabine River basin: TDβ — FDβ relationship in the summer season ($r = 0.487$) and FDβ — PDβ relationship in spring ($r = 0.184$). In the Neches, strong correlations were observed between PDβ — TDβ in summer ($r = 0.710$) and autumn ($r = 0.682$), while TDβ — FDβ were strongly correlated in spring ($r = 0.664$, Figure 1.11g). Similarly, in the Sabine, PDβ — TDβ showed strong correlations in summer ($r = 0.642$) and autumn ($r = 0.667$), whereas TDβ — FDβ were strongly correlated in spring ($r = 0.579$). Across both river basins, FDβ — PDβ exhibited weak correlations in all seasons (Table 1.8)

Table 1.5. Descriptive statistics of TDβ, FDβ, and PDβ of stream fish assemblages in the Neches and Sabine River basins, partitioned into total β-diversity, turnover (Turn), and nestedness (Nest) components during summer, autumn, and spring. Values represent mean and standard deviation.

Basin	**Facet**	**Summer**	**Autumn**	**Spring**
Neches	Total TDβ	0.545 (±0.122)	0.553 (±0.134)	0.602 (±0.168)
	TDβ Turn	0.421 (±0.132)	0.422 (±0.150)	0.458 (±0.184)
	TDβ Nest	0.138 (±0.128)	0.142 (±0.115)	0.191 (±0.194)
	Total FDβ	0.482 (±0.202)	0.565 (±0.229)	0.621 (±0.212)
	FDβ Turn	0.226 (±0.162)	0.247 (±0.223)	0.267 (±0.210)
	FDβ Nest	0.256 (±0.225)	0.320 (±0.242)	0.356 (±0.279)
	Total PDβ	0.231 (±0.086)	0.242 (±0.095)	0.258 (±0.093)
	PDβ Turn	0.132 (±0.076)	0.126 (±0.093)	0.136 (±0.079)
	PDβ Nest	0.101 (±0.093)	0.118 (±0.091)	0.131 (±0.112)
Sabine	Total TDβ	0.504 (±0.125)	0.575 (±0.158)	0.543 (±0.125)
	TDβ Turn	0.381 (±0.152)	0.460 (±0.169)	0.463 (±0.147)
	TDβ Nest	0.139 (±0.114)	0.166 (±0.225)	0.085 (±0.063)
	Total FDβ	0.506 (±0.209)	0.563 (±0.183)	0.595 (±0.192)
	FDβ Turn	0.218 (±0.175)	0.315 (±0.179)	0.365 (±0.200)
	FDβ Nest	0.292 (±0.236)	0.250 (±0.199)	0.229 (±0.195)
	Total PDβ	0.207 (±0.072)	0.264 (±0.115)	0.225 (±0.084)
	PDβ Turn	0.119 (±0.076)	0.141 (±0.089)	0.124 (±0.058)
	PDβ Nest	0.090 (±0.072)	0.135 (±0.123)	0.101 (±0.072)

Table 1.6. Summary of permutational analysis of multivariate dispersion (PERMDISP) testing differences between β-diversity facets (TDβ, FDβ, PDβ) and their components within each season (summer, autumn, spring), in the Neches and Sabine River basins. Statistical significance ($p < 0.05$) is indicated with a star (*).

Basin	Season and Component	FDβ — TDβ	PDβ — FDβ	TDβ — PDβ
Neches	Summer total β-diversity	0.334	*0.001	*0.001
	Summer β-diversity turnover	*0.001	*0.002	*0.001
	Summer β-diversity nestedness	*0.005	*0.001	0.834
	Autumn total β-diversity	0.98	*0.001	*0.001
	Autumn β-diversity turnover	*0.009	*0.011	*0.001
	Autumn β-diversity nestedness	*0.005	*0.001	0.856
	Spring total β-diversity	0.54	*0.001	*0.001
	Spring β-diversity turnover	*0.002	*0.001	*0.001
	Spring β-diversity nestedness	*0.001	*0.001	0.753
Sabine	Summer total β-diversity	0.97	*0.001	*0.001
	Summer β-diversity turnover	*0.001	*0.001	*0.001
	Summer β-diversity nestedness	*0.001	*0.001	0.51
	Autumn total β-diversity	0.957	*0.001	*0.001
	Autumn β-diversity turnover	*0.014	*0.001	*0.001
	Autumn β-diversity nestedness	*0.001	*0.002	0.965
	Spring total β-diversity	0.553	*0.001	*0.001
	Spring β-diversity turnover	*0.048	*0.001	*0.001
	Spring β-diversity nestedness	*0.003	*0.012	0.867

Table 1.7. Summary of permutational analysis of multivariate dispersion (PERMDISP) testing the seasonal differences (summer, autumn, spring) in total β-diversity, turnover, and nestedness components across the three β-diversity facets (TDβ, FDβ, and PDβ), in the Neches and Sabine River basins. Seasonal comparisons did not exhibit statistical significance at $p > 0.05$.

Basin	β-diversity component	Summer — Autumn	Autumn — Spring	Spring — Summer
Neches	Total TDβ	0.776	0.975	0.645
	TDβ turnover	0.983	0.993	0.957
	TDβ nestedness	0.84	0.657	0.327
	Total FDβ	0.373	0.981	0.281
	FDβ turnover	0.603	0.911	0.361
	FDβ nestedness	0.232	0.927	0.411
	Total PDβ	0.746	0.857	0.423
	PDβ turnover	0.723	0.635	0.989
	PDβ nestedness	0.204	0.992	0.164
Sabine	Total TDβ	0.513	0.894	0.789
	TDβ turnover	0.832	0.489	0.206
	TDβ nestedness	0.999	0.498	0.483
	Total FDβ	0.995	0.931	0.893
	FDβ turnover	0.601	0.874	0.319
	FDβ nestedness	0.351	0.999	0.344
	Total PDβ	0.958	0.965	0.855
	PDβ turnover	0.955	0.999	0.947
	PDβ nestedness	0.75	0.987	0.75

Table 1.8. Correlation coefficients (r) between total β-diversity (TDβ — FDβ), (FDβ — PDβ), and (PDβ — TDβ) of stream fishes in the Neches and Sabine River basins. Statistical significance ($p < 0.05$) is indicated with a start (*).

Basin	Season	TDβ — FDβ	FDβ — PDβ	PDβ — TDβ
Neches	Summer	*0.607	*0.571	*0.710
	Autumn	*0.623	*0.434	*0.682
	Spring	*0.664	*0.233	*0.632
Sabine	Summer	0.487	*0.348	*0.642
	Autumn	*0.511	*0.402	*0.667
	Spring	*0.579	0.184	*0.508

Variation Partitioning of β-Diversity Facets. – The forward selection process identified different environmental variables at regional and local scales significantly ($p < 0.05$) influencing each total β-diversity facet uniquely, in each river basin (Table 1.10). These variables retained in each db-RDA encompassed a broad range of aspects related to land cover type, climatic factors, indices of fragmentation caused by dams, physical stream characteristics, instream habitat, and water chemistry. For example, the forward selection process retained eight regional (e.g., agricultural, barren, and wetland land cover types, stream order, fragmentation, slope, watershed area, and precipitation) and six local variables (e.g., wetted width, pH, substrate type, discharge, depth, and macrophytes) that appeared important to the TDβ in the Neches. Additionally, four regional (e.g., wetland land cover, stream order, fragmentation, and precipitation) and two local (e.g., wetted width and discharge) variables explained the FDβ. Finally, five regional (e.g., agricultural and wetland land cover types, stream order, fragmentation, precipitation) and six local variables (e.g., conductivity, dissolved oxygen, pH, wetted width, canopy cover, depth) appeared important to PDβ (Table 1.10).

Fewer regional and local variables were retained in the db-RDAs of the Sabine River basin (Table 1.10). For example, four regional (e.g., stream order, wetland and agricultural land cover types, and elevation) and four local variables (e.g., wetted width, substrate, woody debris, and flow) were retained for explaining the TDβ. Two regional (e.g., developed land cover and stream order) and only one local (e.g., depth) variable explained FDβ, and three regional (e.g., stream order, elevation, and agricultural land cover) and two local variables (e.g., wetted width and substrate) influenced PDβ (Table 1.10).

Table 1.9. Local and regional environmental variables, retained in the forward selection process for β-diversity facets (TDβ, FDβ, and PDβ) in stream fish assemblages of the Neches and Sabine River basins. The variables are arranged in the order in which they were retained. AdjR2Cum (cumulative R-square), F, and p-values are shown. All db-RDAs were significant (p-value < 0.05).

Neches River Basin							
Total TDβ							
Regional factor	*AdjR2Cum*	*F*	*p-value*	*Local factor*	*AdjR2Cum*	*F*	*p-value*
Barren	0.071	7.010	< 0.001	Wetted width	0.088	8.737	< 0.001
Order	0.128	6.142	< 0.001	pH	0.123	4.125	0.003
NMDS2 (fragmentation)	0.167	4.687	0.002	NMDS2 (substrate)	0.160	4.486	0.003
Slope	0.191	3.270	0.011	Discharge	0.186	3.386	0.007
Watershed area	0.217	3.542	0.005	Depth	0.203	2.608	0.019
Precipitation	0.241	3.372	0.007	Macrophyte	0.218	2.484	0.033
Agriculture	0.271	4.085	0.003				
Wetland	0.296	3.602	0.008				
Total FDβ							
Wetland	0.061	5.966	0.007	Wetted width	0.123	11.665	< 0.001
Stream order	0.113	5.343	0.008	Discharge	0.150	3.396	0.037
NMDS2 (fragmentation)	0.147	3.965	0.254				
Precipitation	0.215	7.330	0.002				
Total PDβ							
Barren	0.164	16.668	< 0.001	Conductivity	0.049	5.098	0.005
Developed	0.192	3.775	0.012	Dissolved oxygen	0.086	4.256	0.004
Stream order	0.213	3.092	0.018	Wetted width	0.123	4.245	0.003
NMDS2 (fragmentation)	0.232	2.850	0.028	Canopy cover	0.139	2.453	0.046
Precipitation	0.261	4.060	0.005	Depth	0.155	2.427	0.047
				pH	0.171	2.467	0.04
Sabine River Basin							
Total TDβ							
Regional factor	*AdjR2Cum*	*F*	*p-value*	*Local factor*	*AdjR2Cum*	*F*	*p-value*
Stream order	0.108	9.621	< 0.001	Wetted width	0.068	6.140	< 0.001
Wetland	0.141	3.653	0.003	NMDS2 (substrate)	0.095	3.160	0.007
Agriculture	0.162	2.757	0.015	Woody debris	0.112	2.320	0.032
Elevation	0.186	2.989	0.010	Flow	0.134	2.714	0.017
Total FDβ							
Developed	0.048	4.547	0.017	Depth	0.066	5.930	0.005
Stream order	0.075	3.000	0.038				
Total PDβ							
Stream order	0.030	3.174	0.018	Wetted width	0.047	4.482	0.005
Elevation	0.051	2.587	0.047	NMDS2 (substrate)	0.079	3.473	0.016
Agriculture	0.079	3.057	0.030				

All variation partitioning models were significant ($p < 0.05$) for all total β-diversity facets in the Neches and Sabine River basins (Figure 1.15). The seasonal variable did not make any notable contribution, both individually and in combination with regional and local variables. Individually, regional and local factors had relatively similar contributions to TDβ (regional 0.126, local 0.119; Figure 1.15a), while their combined effects were slightly higher in the Neches (0.182; Figure 1.15a). This same pattern was observed for FDβ and PDβ, though the combined contributions were comparably higher (0.352, Figure 1.15b, c). On the other hand, the individual contributions of regional and local variables in the Sabine were more prevalent for FDβ and PDβ (Figure 1.15e, f). This was especially pronounced for FDβ where regional variables and local variables (0.209 and 0.219, respectively) made greater contributions than when combined (0.098, Figure 1.15e).

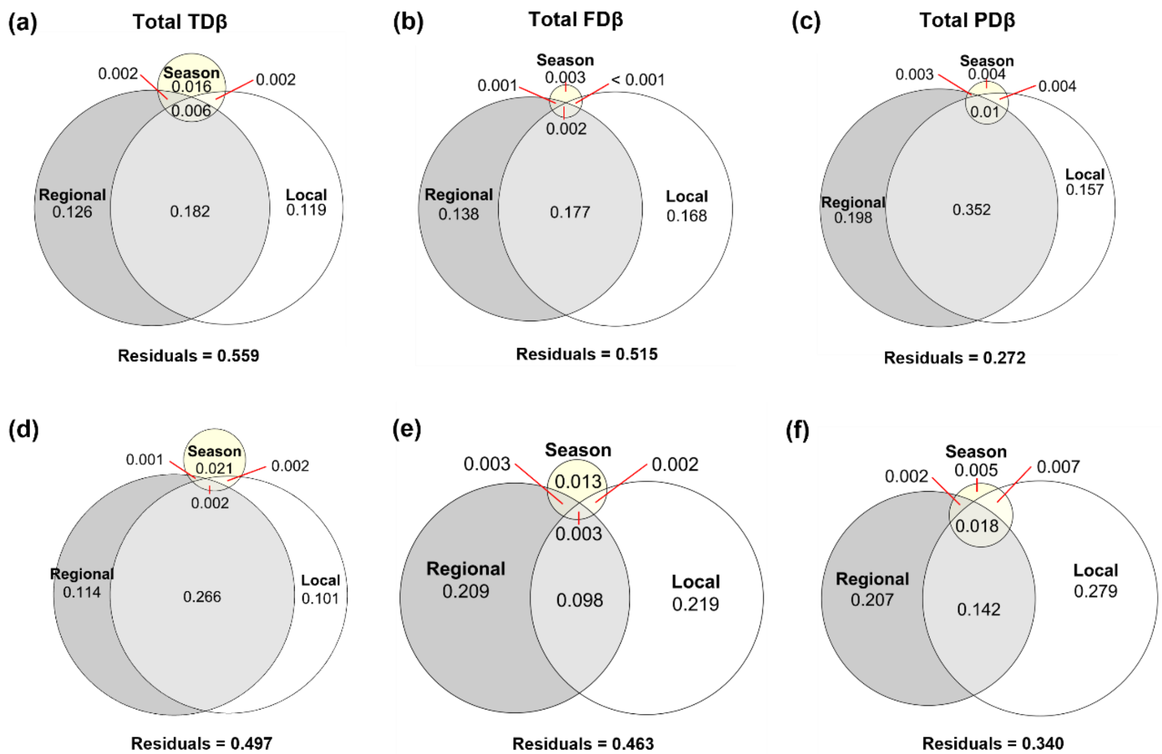


Figure 1.10. Euler diagrams depicting the relative contributions of regional, local, and seasonal variables to the total TDβ (a, d), FDβ (b, e), and PDβ (c, f) of stream fish communities in the Neches (a — c) and Sabine (d — f) River basins. All models were significant ($p < 0.05$).

Discussion

Streams within the Neches and Sabine River basins in East Texas support some of the most diverse freshwater fish assemblages in the state, influenced by similar ecological processes, evolutionary histories, and environmental factors. To disentangle the dissimilarity of taxonomic, functional, and phylogenetic diversities (i.e., β-diversity; TDβ, FDβ, PDβ, respectively), we assessed variations among facets at the annual scale, within seasons (i.e., summer, autumn, spring) and within individual facets (TDβ, FDβ, PDβ) across seasons. Surveys of fish assemblages in both river basins indicate that individual β-diversity facets and their turnover and nestedness components remain consistent in all seasons (H1 supported). However, differences among β-diversity facets and their components were observed at the annual scale and within seasons. Total TDβ was not greater than total FDβ, and driven by turnover, though the total β-diversity of both facets were higher than total PDβ at the annual and seasonal scale (H2 partly supported). FDβ nestedness was greater than the nestedness of TDβ and PDβ facets. Strong correlations between total TDβ — PDβ and TDβ — FDβ were found in the Neches and Sabine basins, while weak correlations between FDβ — PDβ were observed (H3 partly supported).

Lastly, the combination of both regional and local variables (e.g., land cover, hydrology, climate, geomorphology) influenced the total TDβ, FDβ, and PDβ of fish assemblages in the Neches basin (H3 mostly not supported). A similar combination of regional and local variables explained the total TDβ in the Sabine basin, while individual effects of regional and local variables (e.g., land uses, geomorphology) shaped the FDβ and PDβ facets (H3 not supported).

Annual Patterns of β-Diversity Facets

Studies of β-diversity and its components have provided insights into understanding the drivers of biodiversity across multiple spatial and temporal scales (Baselga et al. 2010; Socolar et al. 2016; Soininen et al. 2017). In this study, TDβ was hypothesized as having greater total β-diversity and driven by turnover processes. At the annual scale, this process did emerge as the dominant component shaping TDβ fish assemblages in the Neches and Sabine River basins and likely reflects the complex and highly dendritic structure that characterizes the hydrology in East Texas, regardless of the effects from seasonality. Most river networks are predominantly composed of headwater streams (i.e., 1st and 2nd order) which are known to contain greater environmental heterogeneity and greater isolation compared to downstream stream reaches (Benda et al. 2004). Furthermore, species richness in these headwater streams are often lower, yet they tend to exhibit greater dissimilarity in terms of species composition (Finn et al. 2011) that can result in varied patterns of TDβ and FDβ (Zbinden et al. 2022). Contrary to the original hypothesis, total FDβ was not lower than total TDβ. This high FDβ may highlight the unique traits that many species in East Texas possess. For instance, the Neches and Sabine basins contained unique species from several families including, Lepisosteidae, Leuciscidae (formerly family Cyprinidae), Ictaluridae, Fundulidae, and Centrarchidae that are taxonomically and functionally diverse. However, the nestedness component of FDβ in both basins was higher than the other β-diversity facets and contributed similarly as turnover. Assemblages that exhibit higher FDβ nestedness, may indicate the persistence of functionally redundant species (i.e., multiple species perform similar ecological roles or functions; Walker 1992) which results in nested subsets of species traits. Although TDβ and FDβ were not different at the annual scale, each facet captured distinct aspects of species composition and presence of both functionally unique and redundant species. Assessing the total PDβ of assemblages in East Texas also offers valuable insights as low PDβ likely reflects the close evolutionary relationships and shared biogeographic histories of fishes in the Piney Woods ecoregion (Hubbs 1957), which ultimately reduces phylogenetic dissimilarity. In this study, 17 fish families were recorded, but three families (i.e., Leuciscidae, Centrarchidae, and Percidae) accounted for over half of the total species richness, with leuciscids comprising about a quarter of all species observed. This pattern is consistent at broader spatial scales, as two fish families (i.e., Leuciscidae and Centrarchidae) appear to contain the greatest proportion of species richness (Anderson et al. 1995; Pease et al. 2011). Furthermore, the family Leuciscidae contains widespread and diverse fishes, but it has been largely resolved as monophyletic (Schönhuth et al. 2018).

Significant correlations between β-diversity facets suggest that they provide complementary insights into assemblage structure and assembly processes. Fish assemblages in the Neches and Sabine basins exhibited strong relationships between total TDβ — PDβ and total TDβ — FDβ. Supporting the second hypothesis, TDβ may be strongly correlated to PDβ due to hydrological barriers (e.g., stream divides) that would have historically restricted species dispersal and shaped both species composition and evolutionary relationships (Hubbs et al. 1957). Likewise, significant correlations between TDβ — FDβ may reflect the joint effects of dispersal limitation and environmental filtering, as barriers to dispersal constrain the regional species pool, while local environmental conditions filter which functional traits persist (Weiher and Keddy 1995; Cavender-Bares et al. 2006). Functional traits related to trophic ecology (i.e., diet composition), and life history traits (e.g., body length, fecundity, spawning season) may respond to selection pressures imposed by the environment over time. For example, these same functional traits have been positively associated with increased taxonomic diversity in North American freshwater fish assemblages (Pool et al. 2016). On the other hand, the weak correlations observed between FDβ — PDβ highlights distinct aspects of community structure and assembly. Although fish assemblages in East Texas streams exhibit variations in their functional traits, they are composed of species with closely shared evolutionary lineages. This decoupling suggests that functional differences among communities are not strongly constrained by phylogenetic relatedness. In other words, closely related species often occupy different functional roles, a pattern that does not suggest phylogenetic niche conservatism, as initially hypothesized.

Seasonal Patterns of β-Diversity Facets

Within the same season, differences in the total β-diversity of all facets and their components revealed the same patterns of significance as observed on the annual scale. In summer, autumn, and spring, TDβ was not different from FDβ. Additionally, the turnover component was highest for TDβ, followed by FDβ, and PDβ, while nestedness was highest for FDβ in all seasons. These consistent variations in β-diversity, observed in all seasons, suggest that the effects of seasonality similarly structure fish assemblages in East Texas streams. Furthermore, comparisons of individual β-diversity facets across seasons (e.g., TDβ in summer vs. TDβ in autumn) also revealed no significant differences, supporting seasonality as a factor that similarly structures the β-diversity in this region. Texas, for example, has a humid subtropical climate and is characterized by relatively mild winters, and the absence of pronounced seasonal fluctuations in temperature and flow (Matthews 1998; Perkin et al. 2015). The lack of strong seasonal fluctuations in East Texas likely limits the influence of seasonality on assemblage structure. Significant correlations between total β-diversity facets were observed across seasons. Similar to the annual scale, there were strong correlations between TDβ — PDβ and TDβ — FDβ in all seasons, while correlations between FDβ — PDβ were significant but weak. The consistency of these relationships across temporal scales suggests that the same ecological processes shape the TDβ, FDβ, PDβ in the Neches and Sabine basins, irrespective of seasonal shifts.

Environmental Drivers Explaining β-Diversity Facets

Variance partitioning analyses offered additional insights into the relative contributions of regional, local, and seasonal factors on β-diversity facets of stream fish assemblages in East Texas. Notably, seasonality did not appear to be important to any β-diversity facet in either river basin. In contrast to temperate regions, aquatic ecosystems in tropical regions exhibit remarkable seasonality, leading to extreme changes in the hydrology of their river systems (Willis et al. 2005; Syvitski et al. 2014). Though Texas encompasses a wide range of climates, from arid to subtropical, East Texas does not experience the pronounced seasonal hydrological shifts characteristic of tropical systems, which may explain the limited influence of seasonality on β-diversity facets in the Neches and Sabine basins. During surveys in summer and autumn of 2023, Texas was experiencing drought, with several stream sites losing connectivity or drying out completely. Therefore, the effects of seasonality on fish assemblages may have been further reduced. Even during drought years, annual precipitation records over a 30-year period showed that rainfall remained within 25% of the average, suggesting a limited impact of drought related effects (Carr 1967).

The combined contributions of regional and local factors to the TDβ and PDβ of fish assemblages in the Neches basin may reflect interactions between processes operating at different spatial scales. Regional-scale factors such as land cover, climate, and physical characteristics can drive successive changes to local instream habitats through a spatially nested hierarchy (Frissell et al. 1986). Ecoregions in Texas, defined by relative homogeneity of biotic and abiotic components (e.g., type, quality, and quantity of environmental resources) of both terrestrial and aquatic systems (Griffith et al. 2007), may reflect this hierarchical structure. Within these ecoregions, local stream habitat variables (e.g., substrate, wetted width, discharge) vary in response to underlying regional influences (e.g., precipitation, land uses), and as a result, both regional and local factors have been significantly correlated with fish assemblage composition in Texas streams (Pease et al. 2011). The influence of interacting regional and local variables, particularly on the β-diversity of freshwater fishes, has also been observed in both tropical and temperate systems (Zbinden and Matthews 2017; López-Delgado et al. 2020; Zbinden et al. 2022; Lima et al. 2024). For example, a study of stream fish communities in a tributary of the Yangtze River in China, found that both regional (e.g., land use) and local factors, (e.g., water chemistry, hydrological variables) influenced the TDβ and PDβ across wet and dry seasons (Xia et al. 2023). On the other hand, variation of FDβ in the Neches was partitioned relatively evenly among individual regional and local factors and their combined contributions, suggesting that a complex interplay of biotic factors across multiple scales shape fish assemblage structure in these local streams. These findings support studies in both tropical and temperate freshwater systems which highlight the roles of larger and local-scale factors on the functional diversity of freshwater fish assemblages (Hoeinghaus et al. 2007; Pool et al. 2010; Pease et al. 2012; Walsh et al. 2022).

The total TDβ, FDβ, and PDβ in the Sabine basin were explained by fewer regional and local variables (e.g., stream order, land cover type, stream hydrology and morphology) compared to the Neches (e.g., land cover type, fragmentation, substrate type, precipitation, water chemistry, stream hydrology and morphology), perhaps suggesting a lower degree of environmental variability. Specifically, the total TDβ in Sabine stream fish assemblages responded similarly to the combination of regional and local variables as in the Neches. However, indices of fragmentation, slope, climatic factors, and water chemistry parameters that were important environmental predictors in the Neches, were not retained for the Sabine. Moreover, the lower residuals (i.e., unexplained variation) of the TDβ model further support this assumption of lower variability, as fewer factors accounted for more of the observed variation. In contrast to TDβ, patterns of FDβ and PDβ in the Sabine River basin were driven by the individual contributions of regional and local factors. Land cover types that are anthropogenic in origin (i.e., developed or agricultural) influenced the FDβ and PDβ in the Sabine River basin. The impacts of anthropogenic land uses on various facets of β-diversity of fish assemblages have been well-documented (Dala-Corte et al. 2019; Roa-Fuentes et al. 2019; Zbinden et al. 2022; Yang et al. 2024). Stream order was an important variable in every β-diversity partitioning model of the Neches and Sabine basins. Longitudinal patterns of species richness are known to be related to stream order (Harrel et al. 1967; Vannote et al. 1980), and the relevance of stream order to TDβ has been observed in streams in Oklahoma (Zbinden and Matthews 2017). While the imposed numerical classification of stream order itself has limited importance to fish (Matthews 1998), local-scale instream variables that were retained across all models (i.e., wetted width, depth, substrate type) are known to be influenced by the upstream-downstream gradient (Vannote et al. 1980; Schlosser 1991).

Overall, my findings highlight the diversity of stream fish assemblages in the Neches and Sabine River basins. Analyzing the β-diversity of these assemblages provide valuable insights into the opposing turnover and nestedness processes that govern their taxonomic, functional, and phylogenetic organization and structure across space and time. The significant relationships between these β-diversity facets demonstrated the complementary nature of using an integrated approach to study diversity patterns. In addition, identifying the environmental drivers that explain β-diversity patterns is a major goal of ecologists, especially for the purpose of conservation. An intricate and intertwined relationship of regional and local factors were revealed for each β-diversity facet. The identification of influential environmental drivers further emphasizes the need for a holistic approach to conservation and management, especially in diverse ecosystems.

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CHAPTER V: DISTRIBUTIONS OF SPECIES OF GREATEST CONSERVATION NEED

Introduction

Freshwater ecosystems are among the most biologically diverse environments in the world, supporting 9.5% of described species (Strayer & Dudgeon, 2010), despite covering only 0.8% of the Earth's surface (Dudgeon et al., 2006). This astounding diversity is influenced by several key ecological factors including habitat heterogeneity, isolation of freshwater ecosystems, and species trait adaptations (Smith et al., 2002; 2010; Hering et al., 2012; Val et. al., 2022; Ouellet et al., 2022; Waldman & Quinn, 2022). High habitat heterogeneity (i.e., variation in habitat structures and resource availability over time and space; Shade et al., 2008) can provide more available niche space, leading to an increase in biodiversity within that area (Kerr &Packer, 1997; Hering et al., 2012; Faghihinia et al., 2021). Additionally, isolation of freshwater systems can promote evolutionary processes, such as speciation, which further promotes biodiversity (Smith et al., 2002; 2010; Leprieur et al., 2009; Val et. al., 2022). Finally, many species have developed a wide variety of traits and adaptations (e.g., morphological, physiological, and behavioral) that allow them to utilize both freshwater and marine environments which further contribute to freshwater's high biodiversity (Flitcroft et al., 2019; Ouellet et al., 2022; Waldman & Quinn, 2022). Despite their ecological importance, freshwater ecosystems are under severe threat due to increased anthropogenic activities, resulting in alteration of freshwater systems and their fauna (Richter et al., 1997; Dudgeon et al., 2006; Jelks et al., 2008; Strayer & Dudgeon, 2010).

Threats to freshwater ecosystems are influenced by anthropogenic stressors such as overexploitation, water pollution, habitat fragmentation, flow modification, and invasive species (Richter et al., 1997; Dudgeon et al., 2006; 2010; Utz et al., 2010). Urban development and structural barriers (e.g., dams, reservoirs, and culverts) can further exacerbate these pressures by degrading in stream conditions and limiting the movement and reproduction of fish (Warren et al., 2000; Perkin et al., 2019) consequently altering fish assemblages (Scott, 2006; Jelks et al., 2008, Cooper et al., 2017). The prospective loss of species biodiversity is of great concern, as it reflects potential mounting environmental pressures and broader ecosystem changes (Dudgeon et al., 2006; Jelks et al., 2008). Monitoring shifts in species distributions is therefore critical for detecting environmental variables influencing species decline and guiding targeted conservation efforts, especially with ongoing anthropogenic stressors that continue to degrade aquatic ecosystems worldwide (Hering et al., 2012; Waldman & Quinn, 2022).

In North America, of the 1,213 freshwater fish species known, 39 species and 18 subspecies are considered extinct, reflecting a concerning trend of increasing extinction rates that started around the 1950s (Burkhead, 2012; Birdsong et al., 2021). The Southeastern United States, in particular, is known for its high diversity of freshwater fishes and endemic species (Warren et al., 2000; Jelks et al., 2008). This diversity is influenced by the region's high habitat heterogeneity, isolation of river systems, warm climate, and generally high rainfall (Mulholland et al., 1997, Val et. al., 2022). These conditions help to create a rich, diverse species pool in this southeastern region. However, the freshwater fish species found in this region are among the most at risk in the United States, with an increasing number being listed as imperiled (Warren et al., 2000; Walsh et al., 2011; Elkins et al., 2019).

Freshwater ecosystems in Texas, situated on the western edge of the Southeastern biodiversity hotspot, are experiencing significant alterations, including groundwater extraction, river fragmentation, water quality degradation, and the introduction of non-native species

(Birdsong et al., 2021). In Texas, there are 191 identified species of native freshwater fish, of which 76 are considered Species of Greatest Conservation Need (SGCN, species that are rare and/or may be experiencing population declines and require further study), and 5 species are likely extinct (Cohen et al., 2018; Birdsong et al., 2020; 2021). The Headwater Catfish *Ictalurus lupus* was listed as a species of special concern in Texas due to population declines which have been attributed to agricultural irrigation practices and the introduction of the non-native Channel Catfish *Ictalurus punctatus* (Parker et. al*.,* 2021; Williams et al., 1989). Likewise, the Prairie Chub *Macrhybopsis australis*, a species endemic to the Red River drainage, in Texas and Oklahoma, has been impacted by increased water extraction, flow modification, and habitat fragmentation (Steffensmeier et al., 2023). Both species have experienced extirpation from portions of their historical ranges, emphasizing the widespread impact of anthropogenic disturbances, and the increased need for conservation efforts to maintain freshwater fish biodiversity in Texas (Parker et. al*.,* 2021; Steffensmeier et al., 2023).

In the eastern part of the state, the Neches, Sabine, and Cypress River basins are home to over 100 fish species (Hendrickson & Cohen, 2022). Despite extensive historical surveys, there is a lack of comprehensive studies focusing on the current distribution and ecological requirements (i.e., both biotic and abiotic requirements) of fish species of conservation concerns (Cohen et al., 2018; Robertson et al., 2017; 18; Birdsong et al., 2020; 21). Several species within three families Leuciscidae (formerly Cyprinidae), Catostomidae, and Percidae that were historically considered stable in east Texas streams (Moriarty & Winemiller, 1997; Williams & Bonner, 2006; Bart, 2008) are now listed as SGCN. As in many other areas of Texas, east Texas has been identified as a hotspot for anthropogenic development (TPWD, 2012). Therefore, given the consequences of anthropogenic influences on freshwater ecosystems and large number of freshwater fish species being listed as SGCN, it is important to gain a comprehensive understanding of the regional and local variables that are influencing the distribution and occurrences of these SGCN in east Texas.

Understanding the current distribution and ecological requirements of imperiled species is an important step in implementing conservation management plans (Groves et al., 2002). In response to the growing need to accurately map species distributions and predict species occurrences, ecologists are increasingly using methodologies such as ecological niche models (ENMs) which have shown impressive predictive power (Phillips et al., 2006; 2008; Lira-Noriega et al., 2020). These niche-based models apply the theoretical principles of niche theory (i.e., species realized niche is determined by various environmental factors, Hutchinson, 1957) to make predictions of species distributions. The models use species occurrences (i.e., occurrence records with latitude and longitude coordinates) and environmental variables to assess areas where the species is occurring to predict suitable habitat where the species may be found, based on similarity of environmental conditions in those predicted areas (Warren & Seifert, 2011; Escobar et al., 2018; Lira-Noriega et al., 2020). Ecological niche models are now a widely used tool, with applications ranging from invasive species management (Vander Zanden & Olden, 2008) to conservation planning (Peterson, 2003; Allen et al., 2022). Although many early applications focused on terrestrial taxa, EMNs have also been effectively used in aquatic ecosystems, to assess populations of fish (Domínguez-Domínguez et al., 2006; Morris & Ball, 2006; Williams et al., 2013; Perkin et al., 2019; Allen et al., 2022), mussels (Williams et al., 2013; Walters et al., 2017; Laszlo et al., 2022), and crayfish (Daniela Ghia et al., 2013). Laszlo et al. (2022) performed EMNs to predict habitat suitability for two state-threated mussel species, *Fusconaia askewi* and *F. lananensis* in east Texas. Their models predicted areas that would be highly suitable, resulting in the discovery of five new records of mussels in the region (Laszlo et al., 2022).

When examining species distributions, it is important to consider the spatial scale of study, since regional and local factors can reveal different ecological processes (Vellend, 2016). Regional processes provide valuable insights into broad-scale suitability of habitat and are typically examined through abiotic factors such as climate, hydrology (e.g., drainage area, river basins, and long-term flow patterns), land use, and geology (Angermeier & Winston, 1998; Jackson et al., 2001; Matamoros et al., 2016). For example, Abell et al. (2008) provided insight into global patterns of freshwater fish species richness and endemism across different regions of the world using ecoregions from around the world. Bouska et al. (2015) examined regional processes by performing species distribution models for fourteen warm water fish species native to the central United States and found that climate variables were important for all species, but other factors such as land uses still were important.

While these regional analyses provide a broad understanding of species habitat suitability, analysis of local environmental variables provides better insights into both abiotic and biotic factors which influence local population dynamics, species structure, and occurrence. For instance, species life history traits act as ecological filters that shape community structure and influence species distributions (Pratt & Lauer, 2013; Li et al., 2020). Local interspecific interactions among fishes can lead to alterations in abundance, sex ratio, growth, diet, and habitat use (Crow et al., 2010; Montaña & Winemiller, 2010). A study by Wang (2022) investigated species co-occurrence patterns of fishes in the in the Yellow River estuary in China on a monthly basis to assess whether there were species that commonly occurred together (i.e., aggregated) or never or rarely occurred (i.e., segregated). While no significant overall patterns were observed, some significant species co-occurrence pairs were observed in different months indicating the importance of seasonal dynamics in shaping community structure. Pratt and Lauer (2013) found that five congeneric darter species co-occurring in the White River and Whitewater River watersheds in Indiana segregated within the streams based on microhabitat features such as flow velocity and substrate size, with each species exhibiting distinct preferences. In tropical rivers where communities are constantly reshuffled due to seasonal variations in water levels, species co-occurrence appear to respond to habitat type and hydrological phases (Echeverría & Rodríguez, 2017). Therefore, several factors might act together to influence the occurrence of species in their habitats as well as their biotic interactions.

In this study, we assessed environmental factors at the regional and local scales that may explain the distribution of ten imperiled fish species in the families of Leuciscidae (formerly Cyprinidae), Catostomidae, and Percidae within the streams of the Neches, Sabine, and Cypress River basins in east Texas. we utilized both historical records and contemporary surveys to perform ecological niche models using Maxent to address the following questions: (1) What regional abiotic variables are important in predicting the habitat suitability for the occurrence and distribution of the focal SGCN in historical and contemporary time periods? (2) Has predicted habitat suitability changed over time; and if so, are these changes explaining the distribution and occurrence of the targeted species? Changes in land use type (e.g., urbanization, agriculture, forested), precipitation patterns, and stream order have shown associations with the distribution of several imperiled fishes in east Texas streams (Kleinsasser et al., 2004; Swanson, 2022). Therefore, we hypothesize that variables associated with land cover and hydrology will be important predictors for species distributions and habitat suitability across the three river basins in east Texas.

In addition to assessing regional factors, local environmental variables collected during 2023–2025 surveys were used to evaluate local factors influencing species occurrences within these basins across three seasons to address the following questions: (1) what local abiotic variables are important for predicting the occurrence of the focal SGCN? (2) what species co-occurrence patterns are influencing focal species occurrence and distributions. We hypothesized that instream characteristics (e.g., substrate diversity) and hydrological variables (e.g., water flow and depth) will be important abiotic factors explaining species occurrence within streams. Many of the focal species in this study, particularly those in the families of Leuciscidae (shiners), and Percidae (darters) are fluvial specialists that rely on specific flow and substrate conditions for survival and reproduction (Bestgen et al., 1999; William & Bonner, 2006; Bean et al., 2010; Taylor & Peterson, 2015). Therefore, we predict that in stream reaches with consistent flow and substrate diversity, particularly sand or gravel, fluvial specialists will be commonly found. we also predict that species co-occurrence within these stream reaches will be filtered by specific stream variables (e.g., substate, flow, depth), so that species that share similar habitat requirements will be aggregated together (Thompson et al., 2018; Cordero & Jackson, 2021).

Table 1. List of imperiled species examined in this study. In Texas, the current conservation status and listed rank, as well as the major river basin(s) where each species is located is provided. S2 – Imperiled, S3- Vulnerable, S4- Apparently Secure, SNR- Unranked, NL- Not listed, T- State Threatened (Hendrickson & Cohen, 2022; Texas Parks and Wildlife Department, 2024).

Common Name	Scientific Name	Family	State Conservation Status	State/Federal	River Basin
Blackspot Shiner	*Notropis atrocaudalis*	Leuciscidae	S3	NL/NL	Neches, Sabine, Cypress
Ironcolor Shiner	*Notropis chalybaeus*	Leuciscidae	S3	NL/NL	Neches, Sabine, Cypress
Sabine Shiner	*Notropis sabinae*	Leuciscidae	S3	NL/NL	Neches, Sabine
Silverband Shiner	*Notropis shumardi*	Leuciscidae	S4	NL/NL	Neches, Sabine, Cypress
Suckermouth Minnow	*Phenacobius mirabilis*	Leuciscidae	S4	NL/NL	Neches, Sabine
Western Sand Darter	*Ammocrypta clara*	Percidae	S3	NL/NL	Neches, Sabine
Orangebelly Darter	*Etheostoma radiosum*	Percidae	S3	NL/NL	Neches, Sabine
Gumbo Darter	*Etheostoma thompsoni*	Percidae	SNR	NL/NL	Neches, Sabine
Spotted Sucker	*Minytrema melanops*	Catostomidae	S3	NL/NL	Neches, Sabine, Cypress
Western Creek Chubsucker	*Erimyzon claviformis*	Catostomidae	S2S3	T/NL	Neches, Sabine, Cypress

Methods

The Neches River, Sabine River, and Cypress River have historically supported a diverse aquatic fauna, including many of the Species of Greatest Conservation Need (SGCN) within this study (Table 1). These three basins are located in the most eastern part of Texas, specifically in the South-Central Plains ecoregion, also referred to as the "Piney Woods" (Figure 1). The Neches River basin is located entirely in Texas and contains the East Central Texas Plains, South Central Plains, and Western Gulf Coastal Plains ecoregions (Griffith et al., 2007). The basin drains an area of approximately 26,000 square kilometers and consists of two major rivers, the Neches River and the Angelina River. The Neches River begins in Van Zandt County southeast of Dallas and flows approximately 670 km until it reaches Sabine Lake, where it then continues to the Gulf of Mexico. The Neches River is impounded and contains two major reservoirs, Lake Palestine, and Bismark Adair (B.A.) Steinhagen Lake. The Angelina River is a tributary of the Neches River that begins in Rusk County, Texas, and flows approximately 191 km until its confluences with the Neches River upstream of B.A. Steinhagen Lake (USACOE, 2012b). The Angelina River is also impounded and forms the second largest reservoir in the state, the Sam Rayburn Reservoir. The Neches River basin includes many state owned wildlife management areas, national forests (Davy Crockett National Forest and Angelina National Forest), and the Big Thicket National Preserve. Areas within this river basin have been nominated as ecologically significant and were recognized as riparian conservation areas (Clark, 2010; TPWD, 2017; Robertson et al., 2018).

The Sabine River Basin is part of the state boundary with Louisiana and is situated between the Neches and the Cypress River Basins (Figure 1). The basin includes the same three ecoregions as the Neches River basin and an additional ecoregion, the Texas Blackland Prairies. While the basin is also shared with Louisiana, Texas encompasses approximately 76 percent of the total area of the basin draining an area of about 15,700 square kilometers. The portion of the Sabine River located in Texas begins in Hunt County, and flows ~ 265.5 km to the Texas Louisiana border and drains ~12,551 square kilometers into the largest reservoir in Texas, Toledo Bend Reservoir. The Sabine River then continues to flow into Sabine Lake which then continues into the Gulf of Mexico. The Sabine National Forest, a protected area within the Sabine River basin is located along the Toledo Bend Reservoir then extends into the Neches River basin. The land within this basin is used for mineral production, silviculture, agriculture, and manufacturing (USACOE, 2012c; SRA, 2018).

The Cypress River basin is one of the smallest basins in Texas, encompassing approximately 7,283 square kilometers (Figure 1). The basin consists of several major streams including Big Cypress Bayou, Black Cypress Bayou, and Little Cypress Creek. The main stream of the basin, Big Cypress Creek, begins in eastern Hopkins County, Texas, and flows ~ 97 km before transitioning into Big Cypress Bayou downstream of the impoundment that creates the Lake O' the Pines, one of eight reservoirs found within the basin. Big Cypress Bayou then flows ~ 66 km before reaching Caddo Lake, the largest natural Lake in Texas, which is shared with Louisiana. In this area the basin contains the Caddo Lake National Refuge (USACOE, 2012a; Braun & Moring, 2013; Robertson et al., 2016). In the basin, Black Cypress Bayou a tributary to Big Cypress Bayou was nominated as a least impacted reference stream candidate by the Texas Commission on Environmental Quality (TCEQ, 2005). The water quality in the basin tends to be low in dissolved oxygen due to a combination of high organic inputs and low flows (TCEQ, 2002; Robertson et al., 2016). The main ecoregions within this basin are only the East Central Texas Plains and the South-Central Plains (Figure 1), which appear influenced by human activities associated with paper and steel manufacturing, livestock production, and oil and gas production.

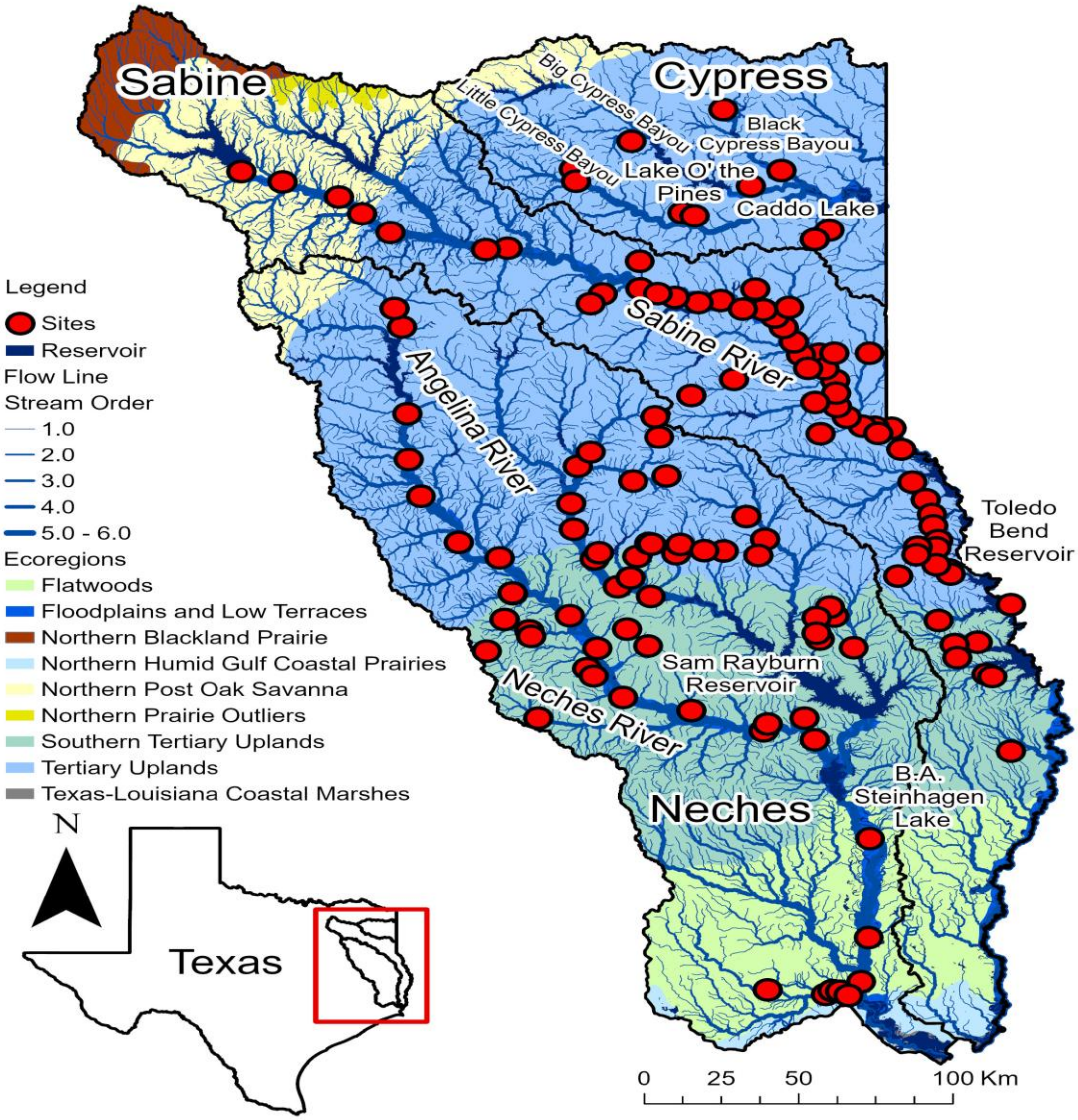

Figure 1. Map depicting the major ecoregions and location of sampling sites (N = 135) within the Neches River, Sabine River, and Cypress River Basins in east Texas.

Species Distributional Data Collection. – Occurrence data for the ten focal species were collected from various online databases, including the Fishes of Texas Project (FoTX), Texas A&M University Biodiversity Research and Teaching Collections (BRTC), Texas Parks and Wildlife Department Inland Fisheries Survey Reports, and Global Biodiversity Information Facility (GBIF). These sources were identified through a comprehensive review of peer-reviewed and gray literature (i.e., non-peer-reviewed sources). Presence data for each species were extracted from these sources, focusing on occurrence records within the Neches River, Sabine River, and Cypress River basins in east Texas. Additionally, contemporary field surveys were conducted from Summer (June) 2023 through Spring (May) 2025, excluding winter, and were integrated with other data sources for use in the ecological niche models. A total of 81 stream sites and 54 mainstem sites were surveyed across the three river basins (Figure 1), where several Species of Greatest Conservation Need (SGCN), including the focal species, have been reported. Seasonal sampling was designated as follows: Summer (June–August), Fall (September–November), and Spring (March–May). During this time, 62 sites were sampled in the Neches River basin, 63 sites in the Sabine River basin, and 10 sites in the Cypress River basin. Once compiled, the occurrence points for each species were categorized into historical and contemporary datasets. The specific range of years used for historical and contemporary datasets was determined based on the majority of occurrence records available for each species for that time period. A detailed breakdown of these time frames for each species is provided in Table 2. All presence points were assigned spatial locations using latitude and longitude coordinates and saved in CSV format. These occurrence points were then converted from geographic coordinates (latitude and longitude) to the Universal Transverse Mercator (UTM) Zone 15N projection in R to align with the coordinate system of the environmental layers from ArcGIS Pro (version 3.0). The cleaned occurrence dataset and environmental layers were then input into an R script to run Maxent software (version 3.4.4; Phillips et al., 2022) for developing ecological niche models for each focal species.

Table 2. List of focal fish species and the time periods for the data that was used in Maxent analysis for each time period.

Common Name	Historical Occurrence	Contemporary Occurrence
Blackspot Shiner	1970-1995	2005-2025
Ironcolor Shiner	1972-1994	2003-2024
Sabine Shiner	1970-1995	2005-2025
Silverband Shiner	1974-1995	2000-2014
Suckermouth Minnow	1970-1995	2006-2024
Western Sand Darter	1970-1993	2000-2023
Orangebelly Darter	1940-1986	N/A
Gumbo Darter	1970-1995	2005-2024
Spotted Sucker	1970-1995	2006-2025
Western Creek Chubsucker	1971-1995	2007-2025

Local Environmental Data Collection. – We conducted seasonal surveys for stream conditions and water quality to examine how local variables could be used to predict our focal fish species. At each stream site, the sampling started approximately 20 meters upstream from the closest access point. A total stream reach of about 150 meters was established for each site, and within the stream reach, five transects of approximately 30 meters were delineated (Figure 2). The Texas Commission on Environmental Quality (TCEQ) standard protocols for sampling wadable streams (TCEQ, 2014) was used, consisting of measurements of instream channel characteristics, stream morphology, and riparian characteristics were taken along each transect (Table 3). Environmental data were recorded in a spreadsheet that was linked to the fish assemblage data by unique site identifiers. At each transect, the following environmental variables were collected: turbidity (NTU), wetted channel width [i.e., width of water (m)], active channel width (i.e., width of the channel (m) between riparian vegetation lines), left and right bank angle (degrees [º]), substrate composition, water velocity (m/s), depth (m) and canopy cover (%). Substrate composition was delineated as bedrock, large boulder (>45 cm), boulder (>25-45 cm), cobble (>6-25 cm), gravel (>2 mm-6 cm), sand (0.06-2 mm), mud/silt (<0.06-0.002 mm), detritus or clay (0.002 mm). The substrate composition, depth (m), water velocity (m/s), and canopy cover (%) were measured at five equidistant points across the width of the stream from bank to bank, at all transects. Additionally, habitat variables which include undercut bank (%), algae (%), woody debris (%), and macrophytes (%) were estimated visually and by touch within a 3-meter range, upstream and downstream, of the five equidistant measurements from bank to bank at each transect. At transects one and five, water quality parameters of dissolved oxygen (mg/L), temperature (ºC), specific conductance (µS/cm), and pH were collected. Finally, total discharge (m^3/sec) was measured when there was a representative transect within the stream reach. In this case, the depth (m) and water velocity (m/s) readings were taken at 10 equidistant points across the width of the stream. The distance between these points was determined by multiplying the stream width by 0.1. Discharge was then calculated by multiplying the depth, velocity, and distance between points, and then summing the values from all 10 points together. All of the parameters were measured as part of the habitat assessment and entered into a Microsoft Excel spreadsheet and all of the pseudo replicated measurements were averaged for each site for statistical analysis.

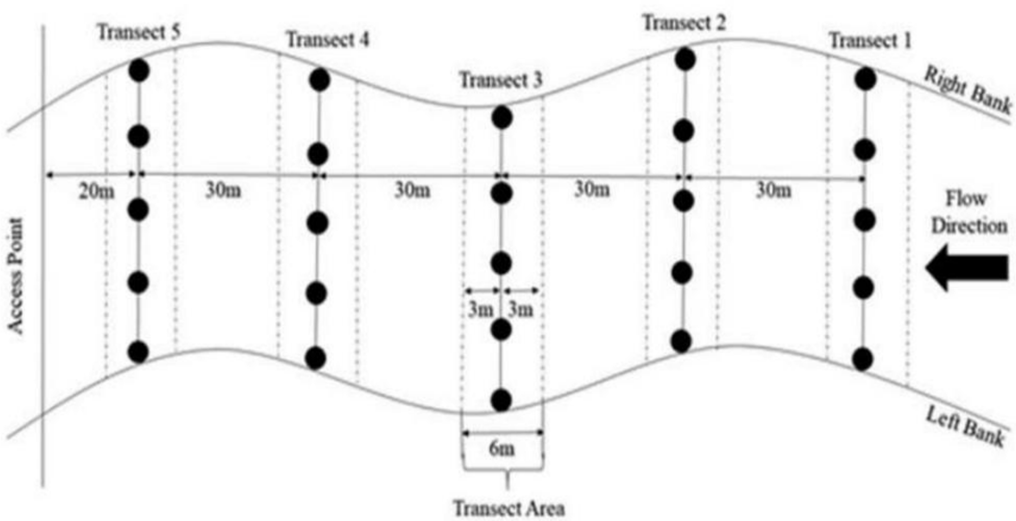

Figure 2. Visual layout of transects for each site. Black points represent the point where environmental variables will be collected. Black arrows represent flow direction. Modified from TCEQ (2014).

Table 3. Local-scale environmental variables (n = 18) measured at various transects for each sampling site the Neches, Sabine, and Cypress River basins.

Category	Measurement	Description
Stream morphology	Wetted Channel Width (m)	Perpendicular width of the stream from waters edge too waters edge
Stream morphology	Channel Width (m)	Perpendicular width of the stream from where the water typically stays within (measurements at base/edge of small riparian plants and grasses)
Stream morphology	Left angle (°)	Angle of the embankment at the water's edge for river left
Stream morphology	Right angle (°)	Angle of the embankment at the water's edge for river right
Hydrology	Depth (m)	Depth in meters at river left of transect (total of 5-point estimates in transect)
Hydrology	Velocity (m/s)	Velocity of water flow in meters per second at river left of transect (total of 5-point estimates in transect)
Hydrology	Discharge (cms)	Discharge of the water at the site in cubic meters per second (measured at one representative transect)
Riparian	Canopy Opening	Coverage of canopy over the water, when facing upstream (total of 5-point estimates in transect)
Water chemistry	DO (mg/L)	Dissolved oxygen in milligrams per liter (measured at 1st and 5th transects)
Water chemistry	Temp (°C)	Temperature in degrees Celsius (measured at 1st and 5th transects)
Water chemistry	Cond. (µs/cm)	Conductivity in Micro Siemens per centimeter (measured at 1st and 5th transects)

Table 3. Continued.

Category	Measurement	Description
Instream habitat	Macrophytes (%)	Percent of macrophytes present within the transect width (i.e., 3 meters upstream and downstream from center line of transect)
Instream habitat	Substrate (class)	Identity of majority substrate class (total of 5-point estimates in transect)
Instream habitat	Undercut (%)	Percent of undercut present within the transect width (i.e., 3 meters upstream and downstream from center line of transect)
Instream habitat	Algae (%)	Percent of algae present within the transect width (i.e., 3 meters upstream and downstream from center line of transect)
Instream habitat	Woody (%)	Percent of woody debris present within the transect width (i.e., 3 meters upstream and downstream from the center line of transect)

Fish Data Collection. – Fish surveys were conducted seasonally, from Summer 2023 to Spring 2025. A backpack electrofisher unit (Halltech HT2000B Electrofisher) was used in the upstream direction for a minimum of 900 active shocking seconds. Following electrofishing, a minimum of 10 non-overlapping seine hauls, using a 3 m long x 1.5 m deep x 4 mm mesh seine, was performed in the upstream direction. These two collection methods allowed more habitat types to be sampled in order to have a good representation of the fish assemblage from each study site. Fish collected were placed in buckets containing a portable aerator, and filled with water from the stream, then separated according to gear type (electrofishing vs. seine). Larger fish were identified to the species taxonomic level, counted, measured (total body length, mm), and then released back into the stream. The remaining fish were anesthetized (according to gear type) with clove oil and preserved in a labeled jar containing 10% formalin and transported to the Aquatic Ecology laboratory at Stephen F. Austin State University for analysis.

In the lab, preserved fish were separated by sampling method, identified to their lowest taxonomic level of species using taxonomic keys, counted, and measured (e.g., total length) using a metric ruler. The specimens were then transferred to 70% ethanol for long-term storage at the Texas A&M Biodiversity Research and Teaching Collection. The fish counts were then entered into an excel spreadsheet for each species, by each site, for each season for statistical analysis.

Regional Environmental Data Collection. – Regional environmental data associated with stream hydrology, land cover, and climate were gathered from multiple online sources to be used in the Maxent software to help predict species distribution across river basins and time periods. These datasets provided key environmental variables related to hydrology, land cover, and climate within the study area. Hydrographic variables were primarily derived from the National Hydrography Dataset Plus Version 2 (NHDPlusV2; Vector Processing Units 12a and 11a), obtained from the United States Geological Survey (USGS) and the U.S. Environmental Protection Agency (EPA). Major river basin boundary information was used for the study area (i.e., Neches, Sabine, and Cypress) from the Texas Water Development Board (TWDB).

Hydrographic variables extracted from NHDPlusV2 included stream order (Strahler 1957), slope, drainage area (Km^2), and estimates of flow (Q0001C). Riparian buffer zones were delineated using data available within NHDPlusV2. Land cover data were obtained from the Multi-Resolution Land Characteristics (MRLC) Consortium and used to assess land use patterns across the study area. Land cover classifications included categories such as forest types, shrubland, grassland, pasture, varying degrees of developed areas, and wetlands. For all species, a land use raster from 1985 was chosen to represent the midpoint of the historical occurrence records, while a 2015 land use raster was selected as the midpoint of the contemporary occurrence records, accommodating the varying availability of data across species (Table 2). Joint land cover types, such as "developed low," "developed high," or "forest deciduous," “Forest Mixed” were combined into single raster for broader categories like "developed" or "forest" to ensure consistency in the analysis (Table 4). Climatic variables, including mean annual temperature and precipitation, were obtained from the PRISM Climate Data repository, developed by the Northwest Alliance for Computational Science and Engineering, with historical data derived from the NHDPlusV2 dataset (1971–2000), which incorporates PRISM data no longer available independently outside of NHDPlusV2 (Table 4). These high-resolution raster datasets provided spatially explicit climate data across the study region, enabling the incorporation of climatic influences on species distributions. For the contemporary period, the latest PRISM 30-year normals rasters (1991–2020) were used to align with the temporal scope of the historical data. The years of climatic data were selected to correspond with the respective land cover datasets for each species and time period. All data were processed and managed in ArcGIS Pro 3.0.0, with further refinement conducted for Maxent, as detailed in the Maxent section below.

Table 4. Regional-scale environmental variables (n = 13) generated by a digital elevation model (DEM) or extracted from online databases.

Category	Measurement	Description	Source
Hydrology	Precipitation (mm/Annual)	Historical: Mean precipitation in millimeters * 100. Originally derived from the PRISM normals cover the period 1972-2000. Contemporary: baseline datasets describing average annual conditions over the most recent three full decades. The current PRISM normals cover the period 1991-2020.	National Hydrological Dataset (NHDPlusV2) USGS and PRISM Group at Oregon State University
Hydrology	Flow (cfs)	Flow with Reference Gage Regression applied to Q0001B (cfs)	National Hydrological Dataset (NHDPlusV2) USGS
Channel Morphology	Catchment Area (Km^2)	Feature area in square kilometers	National Hydrological Dataset (NHDPlusV2) USGS
Channel Morphology	Stream order	Position of stream in the hierarchy of river networks	NHDPlus (National Hydrography Dataset Plus) version 2 (USGS 2019)
Channel Morphology	Slope	Slope of flowline (meters/meters) based on smoothed elevations; a value of -9998 means that no slope value is available.	National Hydrological Dataset (NHDPlusV2) USGS

Table 4. Continued.

Category	Measurement	Description	Source
Land cover	Barren (%)	% of catchment area classified as barren land cover (NLCD 2023 class 31)	National Land Cover Database (NLCD; Brown et al., 2023)
Land cover	Open water (%)	% of catchment area classified as open water land cover (NLCD 2023 class 11)	National Land Cover Database (NLCD; Brown et al., 2023)
Land cover	Forest (%)	% of catchment area classified as forest land cover (NLCD 2023 classes 41+42+43)	National Land Cover Database (NLCD; Brown et al., 2023)
Land cover	Developed (%)	% of catchment area classified as developed land use (NLCD 2023 classes 21+22+23+24)	National Land Cover Database (NLCD; Brown et al., 2023)
Land cover	Shrub (%)	% of catchment area classified as shrub/scrub land cover (NLCD 2023 class 52)	National Land Cover Database (NLCD; Brown et al., 2023)
Land cover	Grassland (%)	% of catchment area classified as grassland/herbaceous land cover (NLCD 2023 class 71)	National Land Cover Database (NLCD; Brown et al., 2023)
Land cover	Agriculture (%)	% of catchment area classified as agricultural land cover (NLCD 2023 classes 81+82)	National Land Cover Database (NLCD; Brown et al., 2023)
Land cover	Wetlands (%)	% of catchment area classified as wetland land cover (NLCD 2023 classes 90+95)	National Land Cover Database (NLCD; Brown et al., 2023)

Maxent Modelling. – We used Maxent models to examine regional environmental variables that may explain the distribution of the focal species in the Neches, Sabine, and Cypress rivers basins in east Texas between historical and contemporary time periods. In order to do this, species occurrence and environmental data for all species were standardized for compatibility with Maxent 3.4.4 (Phillips et al., 2022) using tools within ArcGIS Pro 3.0.0; and an R script used for this analysis was adapted from Banta (2025) (University of Texas at Tyler), obtained via his Patreon account (https://www.patreon.com/joshbanta, accessed March 2025). Species occurrence data (Table 2) were processed as described in the *Species Distributional Data Collection* section. All presence points were assigned with spatial locations using latitude and longitude coordinates and saved in CSV format. These occurrence points were then converted from geographic coordinates (latitude and longitude) to the UTM Zone 15N projection in R to align with the coordinate system of the environmental layers from ArcGIS Pro (version 3.0), and duplicates were removed. For species found across all three basins (Sabine, Neches, and Cypress), stream flowlines were merged from the NHDPlusV2 dataset and reprojected to match the coordinate system (EPSG:26915). The occurrence points were then converted to a simple features (sf) object in R and snapped to the nearest stream flowline using the st_nearest_feature() and st_nearest_points() functions. Points snapping more than 100 meters from a flowline were excluded to ensure spatial accuracy. These spatially aligned points were retained for modeling.

Regional environmental data as detailed in the *Regional Environmental Data Collection* section were compiled and imported into ArcGIS Pro as raster files or shapefiles. Shapefile inputs were converted to raster using the *Feature to Raster* tool, and all rasters were reprojected to UTM Zone 15N using the *Project Raster* tool with a consistent cell size to standardize resolution. Historical environmental data included streamflow, precipitation (from NHDPlusV2, 1971–2000, based on PRISM), and 1985 NLCD land cover as the midpoint for occurrence records, while contemporary data utilized the 1991–2020 PRISM dataset and 2015 NLCD land cover. Joint land cover types (e.g., developed low and developed high) were combined into single rasters for broader categories like "developed" or "forest." These rasters were similarly mosaicked and aligned to a reference layer with a consistent extent, resolution, and coordinate system (UTM Zone 15N) using bilinear resampling for continuous variables and nearest-neighbor resampling for categorical variables like stream order. These layers were then converted to ASCII format for use in Maxent 3.4.4 (Phillips et al., 2022). Environmental layers corresponding to the same time period as the occurrence data (e.g., 1985 land cover for historical, 2015 for contemporary) were selected and activated, alongside time-independent variables like stream order. When species were found only in the Neches and Sabine basins, then the Cypress region layers were excluded. Environmental variables were classified as categorical (e.g., stream order) or continuous (e.g., streamflow, precipitation, land cover percentages) based on their nature. Flowlines were cropped to the extent of the land cover rasters and buffered by 100 meters to create polygons. Land cover percentages within these buffered zones were calculated using the “exact_extract()” function from the *exactextractr* package, converting binary land cover data into percentage values for each category (e.g., percentage of open water, developed land). Missing values in the percentage data were replaced with zeros, and the percentages were rasterized back onto the environmental stack using the mean function, ensuring spatial consistency. The final predictor stack, combining streamflow, precipitation, stream order, and land cover percentages, was saved for modeling.

To prepare the predictor variables for Maxent modeling, missing values in non-percentage layers were filled using a 5x5 focal window with the mean for continuous variables and the mode for categorical variables like stream order. Variance Inflation Factor (VIF) analysis was conducted using the “vifcor()” function from the *usdm* package, with a correlation threshold of 0.7, to remove collinear continuous variables. Variables with zero variance or all missing values at occurrence points were also excluded. Stream order was designated as a categorical variable, and its levels were set based on unique values (e.g., StreamOrder_1, StreamOrder_2; to correspond with Steam Order classifications). The refined predictor stack was saved for use in Maxent. At this point, occurrence points with missing predictor values were identified and filtered out using the “extract()” function, with plots generated to visualize occurrence points over each predictor layer for quality control. If all points were missing values, the process was halted; otherwise, the cleaned occurrence dataset was retained.

After cleaning the predictor variables and occurrence points, the Maxent software was primed using an initial model with *autofeature* selection and random seed, confirming usable occurrence points after filtering those with missing predictor values. A bias file was created using kernel density estimation (KDE) or uniform sampling if KDE failed (i.e., due to deficient occurrence points), and background points (up to 10,000) were generated, weighted by the bias file or uniformly, with NA values removed. Model tuning was conducted with the "ENMevaluate()" function from the *ENMeval* package, applying random k-fold partitioning (10 folds) if 50 or more occurrence points were available, or jackknife partitioning otherwise. This tested feature class combinations (Linear, Linear and Quadratic, Hinge, Linear, Quadratic, and Product, and Linear, Quadratic, Hinge, Product, and Threshold) and regularization multipliers (1 to 5 in 0.5 increments), selecting the best model based on the lowest delta AICc or highest average test AUC (with tie-breaking for simpler models). The fivefold cross-validation approach (Elith et al., 2011; Daniel et al., 2017) was then applied, with models evaluated based on Area Under the Curve (AUC) values of 0.75 or higher, a threshold used in prior studies as an indicator of a useful model (Dunithan, 2012; McCusker et al., 2014; Daniel et al., 2017). Jackknife plots, generated to identify the most influential environmental predictors, were used to further refine the model (Phillips, 2017).

After training and evaluating the model, thresholds were set to classify suitable areas for predicting species' occurrence, adjusted based on sample sizes and tailored to each focal species (McCusker et al., 2014). The final Maxent model was executed with up to five cross-validation replicates, enforcing tuned feature classes (e.g., linear, quadratic, hinge) and settings like response curves, jackknife tests, and random seed. Predictions were averaged across replicates to produce habitat suitability maps for each species, visualized with a custom color palette (21 breaks from 0 to 1), and overlaid with occurrence points, saved as TIFF and ASCII files. Model performance metrics, training and test AUC, AUC difference, correlation coefficient (COR), Kappa, and True Skill Statistic (TSS) were calculated per replicate using confusion matrices based on the maximum sensitivity plus specificity threshold, averaged, and saved. These outputs were interpreted to assess the environmental factors influencing each species' distribution. Following model training, evaluation, and thresholding, non-essential environmental variables were iteratively removed and models re-run until AUC values no longer improved for each species and time period.

Enhanced response curves were generated for each final model using the species_*_*_only.dat files produced by Maxent, processed with *ggplot2* and *dplyr*. For each predictor variable, response data were averaged across replicates, and 95% confidence intervals were calculated. Stream order, as a categorical variable, was plotted as a bar graph with error bars, while continuous variables (e.g., streamflow, precipitation, land cover percentages) were plotted as curves with confidence ribbons. Plots were customized with descriptive labels (e.g., "Streamflow (m^3/s)," "Developed Land (%)") and a consistent cloglog scale (0 to 1). A combined faceted plot of all response curves was also created, ensuring consistent formatting and scales. All plots were saved as PNG files in the plot's directory, averaged across the number of replicates for robust interpretation. The same methodology was applied to contemporary data, adapting the process for the 1991–2020 PRISM dataset and 2015 NLCD land cover data as midpoints for occurrence records, with adjustments for species-specific geographic ranges. All spatial data processing, modeling, and visualization were performed in R using packages such as *terra, sf, raster, exactextractr, dismo, ENMeval, ggplot2,* and *dplyr*. Then all maps were imported into ArcGIS Pro for further visualization, including the addition of basin boundaries, reservoir layers, and final color adjustments.

Maxent Species Richness Maps. – Maxent model outputs, consisting of habitat suitability rasters (predmaxavg.asc) and results files (maxentResults.csv), were retrieved from species-specific directories for nine contemporary and ten historical fish species. Habitat suitability rasters were loaded for each species, with the coordinate reference system set to NAD 1983 UTM Zone 15N. A binary threshold was determined using the mean Maximum Test Sensitivity Plus Specificity Cloglog value from the Maxent results, defaulting to 0.5 if unavailable. Rasters were aligned to a reference raster using bilinear resampling to ensure consistent spatial properties. Binary rasters were generated by applying species-specific thresholds, and species richness was calculated by summing these binary rasters for each period (historical: 10 species; contemporary: 9 species). Richness maps were smoothed using a 3x3 focal mean filter, rounded, and masked to exclude areas with no data. Richness maps were categorized into five classes (0, 1, 2–4, 5–7, and 8–9 or 8–10 species) with distinct colors. Maps were saved as TIFF and as ASCII files. These ASCII files were then imported into ArcGIS Pro for further visualization, including the addition of basin boundaries, reservoir layers, and final color adjustments. The analysis was conducted in R using the *terra, fields, sf*, and *stars* packages for geospatial processing.

Maxent Time Period Comparison. – The final Maxent model for each species and time period were stored in separate subfolders within a base directory. Subfolders contained predictive raster files (predmaxavg.asc) and model performance metrics (maxentResults.csv and metrics_table.csv). Historical and contemporary subfolders were specified for each species. The Orangebelly Darter lacked contemporary data and thus excluded from comparative analyses. All rasters were projected in the Universal Transverse Mercator (UTM) Zone 15N coordinate reference system. For each species with both historical and contemporary data, predictive rasters were loaded using the *raster* package (version 3.6-26). Contemporary rasters were cropped and resampled to align with historical rasters using bilinear interpolation to ensure consistent spatial extents and resolutions. Unsmoothed difference maps were generated by subtracting historical predicted probability rasters from contemporary ones. These difference maps were saved as ASCII files (difference_map_unsmoothed.asc) in species-specific output directories. Thresholds for converting continuous probability rasters to binary suitability maps were extracted from maxentResults.csv files. The primary threshold used was the "Maximum test sensitivity plus specificity Cloglog threshold," with the "Maximum training sensitivity plus specificity logistic threshold" as a fallback if the primary was unavailable. If neither threshold was found or the file was inaccessible, a default threshold of 0.5 was applied. Model performance was assessed using the Area Under the Curve (AUC) of the Receiver Operating Characteristic, extracted from metrics_table.csv. Mean AUC and standard deviation were calculated, excluding any "averages" row to avoid bias. If AUC data were missing or invalid, NA values were recorded.

Binary suitability maps were created by applying the extracted thresholds to unsmoothed historical and contemporary rasters. Significant habitat changes were identified by comparing binary maps, where differences indicated areas with changed suitability status. These significant difference maps were saved as ASCII files (significant_differences_unsmoothed.asc). The proportion of significant cells was calculated as the percentage of total valid cells exhibiting differences. All maps were imported into ArcGIS Pro for further visualization.

In order to test for significant differences between historical and contemporary predicted probabilities, paired Wilcoxon signed-rank tests were conducted on unsmoothed raster values using the *stats* package (version 4.3.2). Non-NA values from aligned rasters were compared, and p-values were reported to determine significance ($p < 0.05$). Results, including AUC statistics, thresholds, p-values, and percentage of significant area, were saved in text files (model_comparison_results.txt) for each species.

Local Patterns of Species Distribution and Occurrences. **–** A non-metric multidimensional scaling (NMDS) analysis, based on the species abundances was used to visualize differences in species composition across the Neches, Sabine, and Cypress River basins in east Texas. Analyses were performed at both the mainstem and stream scales, with stream analyses further separated by season (Spring, Summer, Fall); all mainstem and stream datasets were analyzed separately. The similarity matrices were calculated using the Bray-Curtis Similarity Index (Bray & Curtis 1957). The species abundance data was Hellinger transformed prior to being used in the ordination analysis to better approximate a normal distribution for the data. After performing the NMDS, a pairwise permutational multivariate analysis of variance (PERMANOVA) was performed using 10000 permutations. Each NMDS was conducted using the *vegan* package (Oksanen et al., 2022). The pairwise PERMANOVA were performed using the "adonis2" function from the *vegan* package (Oksanen et al., 2022) and the *ggplot2* package was used for additional visualization. Additionally, a similarity percentage analysis (SIMPER) and indicator species analysis (IndVal) were performed using the vegan package (Oksanen et al., 2022) to identify species contributing to variations in the fish community composition across basins and seasons.

A Redundancy Analysis (RDA) based on Euclidean distances was conducted to examine the relationships between focal fish species (Table 1) and local environmental variables including habitat (i.e., Undercut, Algae, Woody Debris, Macrophyte Cover, and Canopy Cover), hydrological (i.e., Depth, Discharge, Wetted Width, Channel Width, Slope, and Flow), and water quality parameters (i.e., Dissolved Oxygen [DO], Temperature, Conductivity, Turbidity, and pH), and substrate characteristics (e.g., Bedrock, Cobble, Gravel, Sand, Mud/Silt, Detritus, Clay, Boulder). Analyses were performed at both the mainstem and stream scales, with stream analyses further separated by season (Spring, Summer, Fall); all mainstem and stream datasets were analyzed separately.

All analyses were performed in R version 4.2.2 (R Development Core Team 2022), primarily using the *vegan* package (Oksanen et al., 2022) for ordination, *usdm* (Naimi et al., 2014) for multicollinearity diagnostics, and additional packages including *dplyr* (Wickham et al., 2019), *tibble*, *GGally*, *ggplot2* (Wickham, 2016), *ggfortify*, *factoextra, fundiversity, FD, rstatix, ggpubr, gridExtra,* and *car* (Fox, 2019) for data manipulation, visualization, and diagnostic procedures. Prior to conducting RDA, species abundance data were Hellinger-transformed to reduce the influence of dominant species and improve linear relationships with environmental gradients.

The RDA was conducted on two primary matrices: a site × environmental variables matrix and a site × Hellinger-transformed species abundance matrix. Species counts were aggregated by site and cast into wide format. Environmental variables were converted to numeric where necessary, with invalid or non-numeric entries (e.g., "#VALUE!", "N/A", "") replaced with NAs. Variables with >10% missing data were excluded, and any rows with remaining NAs were removed. Continuous environmental variables were normalized using $\log(x + 1)$ transformation.

Multicollinearity among predictors was assessed using the *vifstep* function from the *usdm* package, applying a threshold of 5 to iteratively remove highly collinear variables until all retained predictors exhibited acceptable VIF values (e.g., all values were close to the same number such as all 1.5 instead of some values at 1.5 and another value at 4.3).

The significance of the overall RDA models, canonical axes, and individual predictors was evaluated using 1000-permutation ANOVA tests via the "anova" function. Forward selection of predictors was conducted using the "ordistep" function, defaulting to all VIF-filtered variables if stepwise selection failed. Adjusted R^2 values were calculated using the "RsquareAdj" function from *vegan*.

Ordination plots were produced using scaling 2 (i.e., show relationship among environmental variables and species rather than among sites) to visualize relationships among focal species and environmental gradients, with focal species highlighted using distinct colors. Correlation matrices between focal species and environmental variables were computed with *cor* and visualized using *corrplot*. All results and visual outputs were saved by dataset (e.g., "Mainstem", "Stream_Spring") to the desktop directory.

Random forest models (RFMs) were used to identify the most important environmental variables predicting the presence of six focal species across the Neches, Sabine, and Cypress River basins (Figure 21-24). The analyses were performed in R (version 4.2.2, R Development Core Team 2022) using the *randomForest* package (Liaw and Wiener 2002) for model fitting, *usdm* (Naimi et al., 2014) for variance inflation factor (VIF) analysis, *performanceEstimation* (Torgo, 2014) for SMOTE, and *ggplot2* (Wickham 2016), *ggpubr* (Kassambala, 2020), and other packages for data processing and visualization. Fish presence/absence data and environmental variables were sourced from a combined dataset of mainstem and stream surveys, and focal species that had at least 8 occurrences combined between the mainstem and stream datasets. The Blackspot Shiner, Sabine Shiner, Suckermouth Minnow, Gumbo Darter, Spotted Sucker, and Western Creek Chubsucker) were the only species that met the conditions for the analysis.

Predictors included 25 environmental variables: stream depth (mm), dissolved oxygen (mg/L), water temperature (°C), streamflow (cfs), conductivity (µS/cm), pH, turbidity (NTU), canopy cover (%), algal cover (%), macroinvertebrate density, woody debris (%), undercut banks (%), wetted width (m), channel width (m), stream slope (%), substrate composition (bedrock, cobble, gravel, sand, mud/silt, detritus, clay, boulder, all in %), habitat type (e.g., mainstem or stream), and stream order. VIF analysis was performed with a threshold of 3 to exclude collinear variables. The Synthetic Minority Oversampling Technique (SMOTE) was applied to address class imbalance, doubling the minority class (present) and sampling twice as many majority class (absent) instances.

For each species, a random forest model was fitted with 500 trees, using an optimized number of predictors sampled at each split (`mtry`), determined via the "tuneRF" function with a step factor of 1.1 and 100 trees for tuning. Variable importance was assessed using the mean decrease in Gini impurity, and partial dependence plots (PDPs) were generated to visualize the relationship between each predictor and the probability of occurrence for each species. Models were evaluated using out-of-bag (OOB) error rates. A combined variable importance plot across all species was created to compare predictor importance, with predictors ordered by their average mean decrease in Gini. All outputs, including model summaries, OOB error plots, correlation matrices, and diagnostic logs, were saved in the working directory.

Species co-occurrence analyses using probabilistic models (Veech, 2013) were conducted to examine associations (aggregated, segregated, or random) of focal imperiled fish species with other species in the community. Species incidence matrices were created using presence/absence data derived from fish counts collected at multiple sites across seasons from Summer 2023 to Spring 2025, as described in the methods. Data were analyzed annually and by season to assess temporal variation in co-occurrence patterns. For the annual analysis, presence data were aggregated across seasons by assigning presence (1) to a species at a site if it was recorded in any season. The analysis was performed in R (version 4.2.2, R Development Core Team 2022) using the *cooccur* package (Griffith et al., 2016) for co-occurrence analysis, and additional packages including *dplyr* and *stringr* (Wickham et al., 2019), *tidyr* (Wickham & Girlich 2024), ggplot2 (Wickham, 2016), *corrplot* (Wei & Simko, 2021), were used for data manipulation, visualization, and diagnostics.

Fish count data were converted to presence/absence (1/0) based on counts > 0, with missing or non-numeric counts set to 0. Site codes were validated to ensure a consistent format (numeric prefix followed by "S", "SP", or "F" for Summer, Spring, or Fall), and seasons were extracted from site codes. Species with no presences annually or in a given season, were excluded from the respective matrices. Co-occurrence probabilities were calculated for each species pair using Veech's probabilistic model, which computes exact probabilities of observing a given number of co-occurrences under a null hypothesis of independent distributions, based on a hypergeometric distribution. Species pairs with p-values < 0.05 for greater (`p_gt`) or fewer (`p_lt`) co-occurrences than expected were considered significantly positive (aggregated) or negative (segregated), respectively.

Associations were analyzed for seven focal species combined between the mainstem and stream datasets. Effect sizes were calculated as the difference between observed and expected co-occurrences. Results were visualized using bar plots of significant effect sizes for each focal species by season, combined bar plots across seasons, pair profile plots showing the number of positive associations per species. A grouped bar plot was generated for each season to show the percentage of significant positive and negative associations for focal species compared to the assemblage-wide average. Outputs, including co-occurrence probabilities, effect sizes, significant pairs, focal species summaries, and bar number mappings, were saved as CSV, TXT, PNG, and PDF files in season- and species-specific directories (e.g., "Pair_Profiles", species-specific folders).

Results

Fish Assemblage Diversity, Composition, and Distribution. – A total of 28,059 individual fish were recorded from streams of the Neches, Sabine, and Cypress River basins across three sampling seasons, from summer 2023 through spring 2025 (Appendix S2). These individuals represented 76 species, with 50 species recorded in the Cypress, 62 for the Neches, and 59 for the Sabine. Sampling in the mainstem during the summer of 2023, resulted in 75,438 individuals, across 72 species (Neches = 63 species; Sabine = 55 species. The most abundant species captured in streams was Western Mosquitofish *Gambusia affinis*, with 5,550 total individuals comprising 19.78% of the total catch, followed by the Longear Sunfish *Lepomis megalotis* (4,130 individuals; 14.72%). The dominant species in the mainstem included Red Shiner *Cyprinella lutrensis* (35,723 individuals; 47.35%) and Bullhead Minnow *Pimephales vigilax* (9,644 individuals; 12.78%).

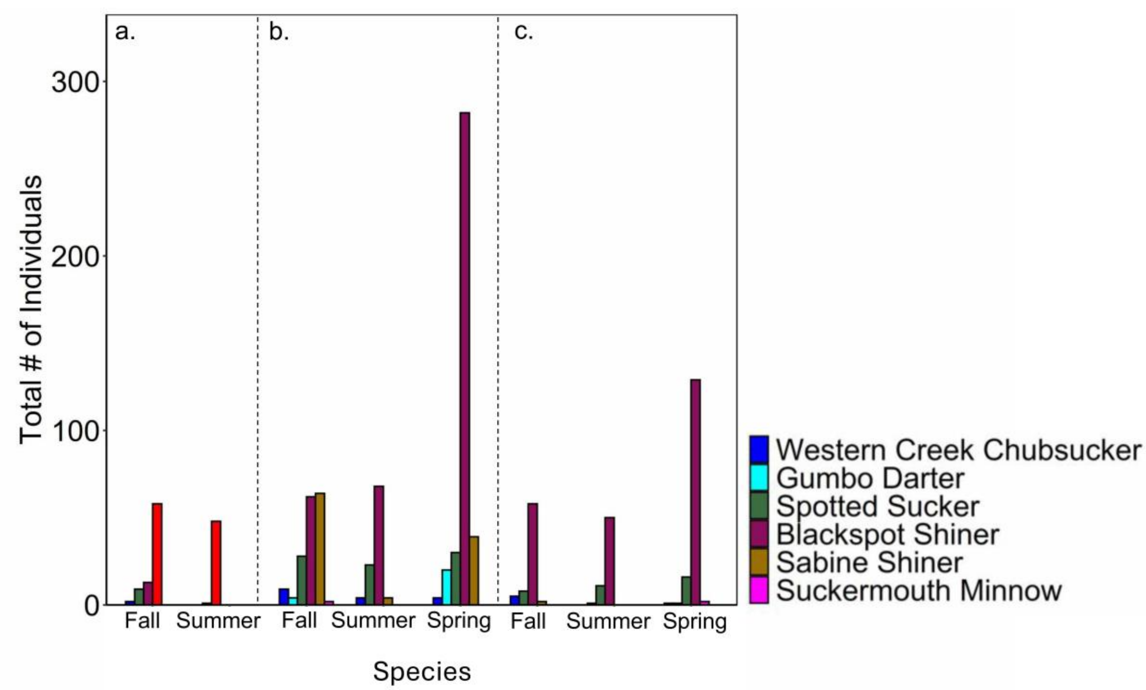

Figure 3. Total number of focal imperiled species collected by river basin (a) Cypress (b) Neches, and (c) Sabine and by season (i.e., Fall, Spring, and Summer) at stream sampling sites from Summer 2023 through Spring 2025.

In this study, seven of the ten focal species were collected in the stream surveys: Western Creek Chubsucker (n = 27; 0.01%), Gumbo Darter (n = 25; 0.09%), Spotted Sucker (n = 125; 0.4%), Blackspot Shiner (n = 662; 2.4%), Ironcolor Shiner (n = 106; 0.4%), Sabine Shiner (n = 109; 0.4%), and Suckermouth Minnow (n = 4; 0.01%) (Figure 3). Collectively, these SGCN species accounted for 1,058 individuals, or approximately 3.8% of the total stream catch (Figure 3). While in the mainstem summer, five of the ten focal species were collected including, Western Sand Darter (n = 9; 0.01%), Gumbo

Darter (n = 214; 0.3%), Spotted Sucker (n = 133; 0.2%), Sabine Shiner (n = 542; 0.718%), and Suckermouth Minnow (n = 11; 0.015%; Figure 4). Notably, the Western Sand Darter was detected only in mainstem sites, while the Ironcolor Shiner and Western Creek Chubsucker were only reported in stream habitats (Figure 4).

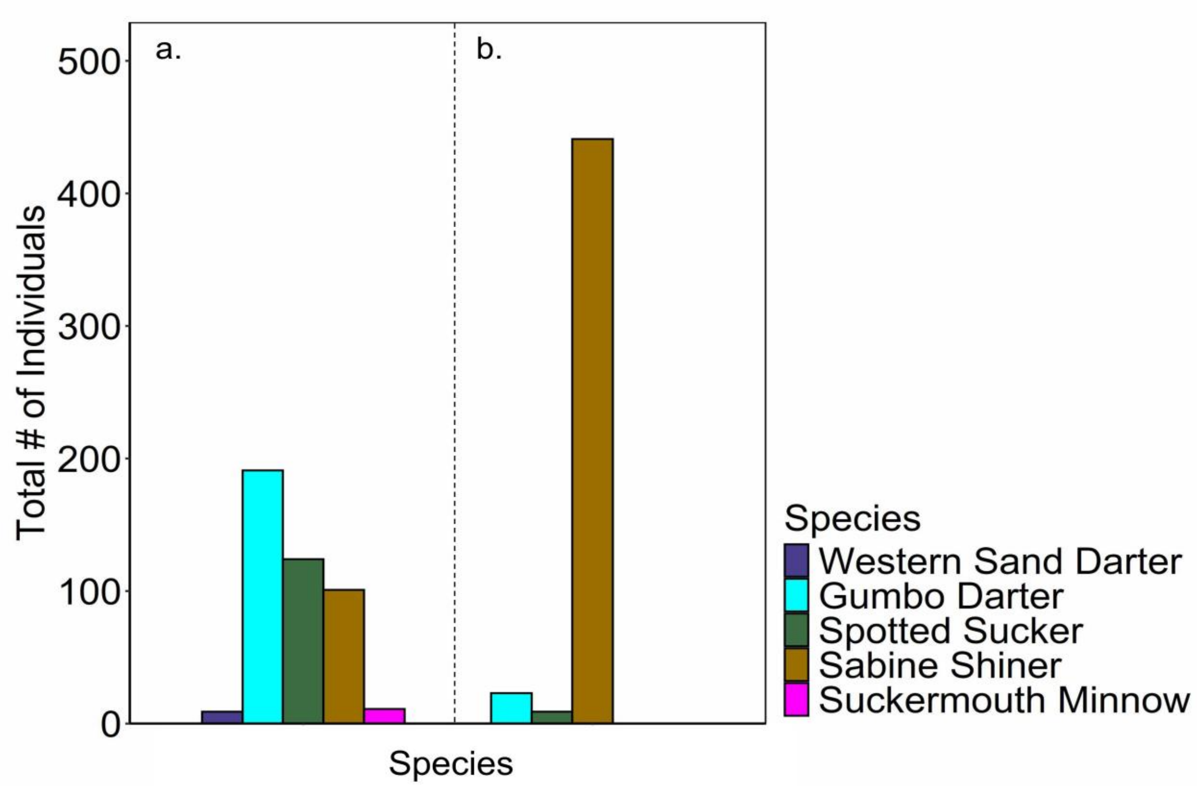

Figure 4. Total number of individuals collected in the mainstem of the two river basins (a) Neches and (b) Sabine at mainstem stream during summer 2023.

Environmental Predictors of Imperiled Species Distribution in east Texas Streams
A. Regional Environmental Predictors: Ecological Niche Models' Performances

Ecological niche models based on regional variables using Maxent demonstrated good performance for most focal species across both historical and contemporary time periods, with final model AUC values exceeding 0.70 for the majority of species (Table 5). Exceptions included the historical model for the Orangebelly Darter, which had a mean AUC of 0.67 ± 0.24, and the Western Creek Chubsucker, which had a historical AUC of 0.62 ± 0.15. A contemporary model for the Orangebelly Darter could not be generated due to insufficient occurrence data. Wilcoxon signed-rank tests comparing the historical and contemporary model outputs were statistically significant for all species (Table 5). The percentage of predicted suitable habitats that differed between time periods varied across species, with the Western Creek Chubsucker exhibiting the largest difference (52.96%), followed by the Blackspot Shiner at (39.78%) and the Silverband Shiner (35.12%).

Table 5. Summary of the most important environmental variables during historical and contemporary periods from the Maxent models predicting imperiled species.

Species	***Model***	***Variable***	***Permutation Importance (%)***	***AUC***	***% Significant Area (Threshold, Unsmoothed)***	***Wilcoxon Test***
Blackspot Shiner *Notropis atrocaudalis*	Historical	Stream Order	33.4	0.72 ±	39.78%	p < 0.01
	N = 76	% Pasture_Crops	22.4	0.04		
		Catchment Area	16.7			
		Streamflow (cfs)	14.3			
		Slope	11.1			
	Contemporary	Slope	38.2	0.7 ±		
	N = 103	Streamflow (cfs)	17.2	0.03		
		% Open Water	13.7			
		% Woody Wetlands	8.1			
		% Pasture_Crops	7.8			
Ironcolor Shiner *Notropis chalybaeus*	Historical	Stream Order	48.2	0.9 ±	19.72%	p < 0.01
	N = 37	Streamflow (cfs)	41.3	0.06		
		Slope	7.7			
		% Shrub_Scrub	1.5			
		Developed %	1.4			
	Contemporary	Streamflow (cfs)	89.7	0.77 ±		
	N = 8	Slope	7.1	0.1		
		% Forest	3.2			

Table 5. Continued.

Species	*Model*	*Variable*	*Permutation Importance (%)*	*AUC*	*% Significant Area (Threshold, Unsmoothed)*	*Wilcoxon Test*
Sabine Shiner *Notropis sabinae*	Historical	Stream Order	81.1	0.91 ±	2.81%	p < 0.01
	N = 104	% Forest	5.7	0.03		
		% Woody Wetlands	4.1			
		Catchment Area	3.1			
		% Shrub_Scrub	2.8			
	Contemporary	Streamflow (cfs)	80.4	0.92 ±		
	N =65	Stream Order	7.4	0.08		
		% Developed	3.9			
		% Woody Wetlands	3.4			
		% Emergent Herbaceous Wetlands	1.7			
Silverband Shiner *Notropis shumardi*	Historical	Streamflow (cfs)	54.8	0.93 ±	35.12%	p < 0.01
	N =6	Catchment Area	23.8	0.05		
		Slope	20.6			
		% Pasture_Crops	0.8			
	Contemporary	Streamflow (cfs)	80	0.71 ±		
	N = 8	% Forest	20	0.18		

Table 5. Continued.

Species	*Model*	*Variable*	*Permutation Importance (%)*	*AUC*	*% Significant Area (Threshold, Unsmoothed)*	*Wilcoxon Test*
Suckermouth Minnow *Phenacobius mirabilis*	Historical	Stream Order	84.8	0.88 ±	7.11%	$p < 0.01$
	N = 29	Streamflow (cfs)	11.5	0.07		
		Shrub_Scrub %	1.3			
		Slope	1.1			
		Woody Wetlands %	0.8			
	Contemporary	Forest %	44.8	0.89 ±		
	N = 12	Stream Order	29.6	0.08		
		Pasture_Crops %	23.9			
		Slope	1.7			
		Streamflow (cfs)	0			
Gumbo Darter *Etheostoma thompsoni*	Historical	Forest %	64.5	0.94 ±	8.67%	$p < 0.01$
	N = 27	Stream Order	35.5	0.03		
		Streamflow (cfs)	0			
	Contemporary	Streamflow (cfs)	75.6	0.86 ±		
	N = 24	Stream Order	24.4	0.1		

Table 5. Continued.

Species	*Model*	*Variable*	*Permutation Importance (%)*	*AUC*	*% Significant Area (Threshold, Unsmoothed)*	*Wilcoxon Test*
Western Sand Darter *Ammyocrypta clara*	Historical	Stream order	71.2	0.96 ±	3.02%	$p < 0.01$
	N = 17	% Forest	10.5	0.04		
		% Barren	4.4			
		% Pasture_Crops	4.4			
		Catchment Area	2.9			
	Contemporary	Streamflow (cfs)	95.9	0.98 ±		
	N = 4	Precipitation	4.1	0.018		
		Stream Order	0			
Orangebelly Darter *Etheostoma radiosum*	Historical	Stream order	79.4	0.67 ±	NA	NA
	N = 4	% Developed	20.6	0.24		
		Catchment area	0.0			
		Streamflow	0.0			
	Contemporary	N/A	N/A	N/A	N/A	N/A

Table 5. Continued.

Species	*Model*	*Variable*	*Permutation Importance (%)*	*AUC*	*% Significant Area (Threshold, Unsmoothed)*	*Wilcoxon Test*
Spotted Sucker *Minytrema melanops*	Historical	Stream Order	63.8	0.80 ±	11.44%	$p < 0.01$
	$N = 90$	%Woody Wetlands	23.1	0.07		
		Precipitation	5.7			
		Streamflow (cfs)	3.2			
		% Developed	1.3			
	Contemporary	Stream Order	60.1	0.78 ±		$p < 0.01$
	$N = 90$	Streamflow (cfs)	24.8	0.01		
		% Woody Wetlands	13.7			
		% Pasture_Crops	1.4			
Western Creek Chubsucker *Erimyzon claviformis*	Historical	Streamflow (cfs)	47.7	0.62 ±	52.96 %	$p < 0.01$
	$N = 28$	% Grassland	40.4	0.15		
		Stream Order	11.9			
	Contemporary	% Open Water	20.7	0.73 ±		
	$N = 37$	% Pasture_Crops	19.9	0.07		
		Streamflow (cfs)	19.5			
		Slope	17.0			
		% Forest	13.4			

Evaluation of Shared Environmental Predictors Among Species and Time Periods

Among the fourteen regional variables included in the model, streamflow and stream order were the most consistent predictor variables for most species in both time periods. During the historical period streamflow was a predictor variable for all 10 species (Figure 5); while in the contemporary period 9 of the 10 species appeared to be predicted by streamflow (Figure 6), with historical species likely to occur at flows > 2000 cfs. Stream order was a predictor for 9 of 10 historical models and 6 of 10 contemporary models (Figure 7), with most species likely occurring in stream orders > 3. Though there were some exceptions, the Orangebelly Darter had highest probability of occurrence in stream order 2 during the historical period. Slope also contributed frequently to the models, being a good predictor for 7 species in the historical period and for 6 species in the contemporary period (Figure 8). Percent pasture/crops and percent forest cover were important predictors for at least 5 of the 10 species across one or both time periods (Figures 9–10). Three additional land cover variables—percent grassland, percent developed land, and catchment area (km^2)—were important for at least 5 species, but only during the historical period (Figures 11–12).

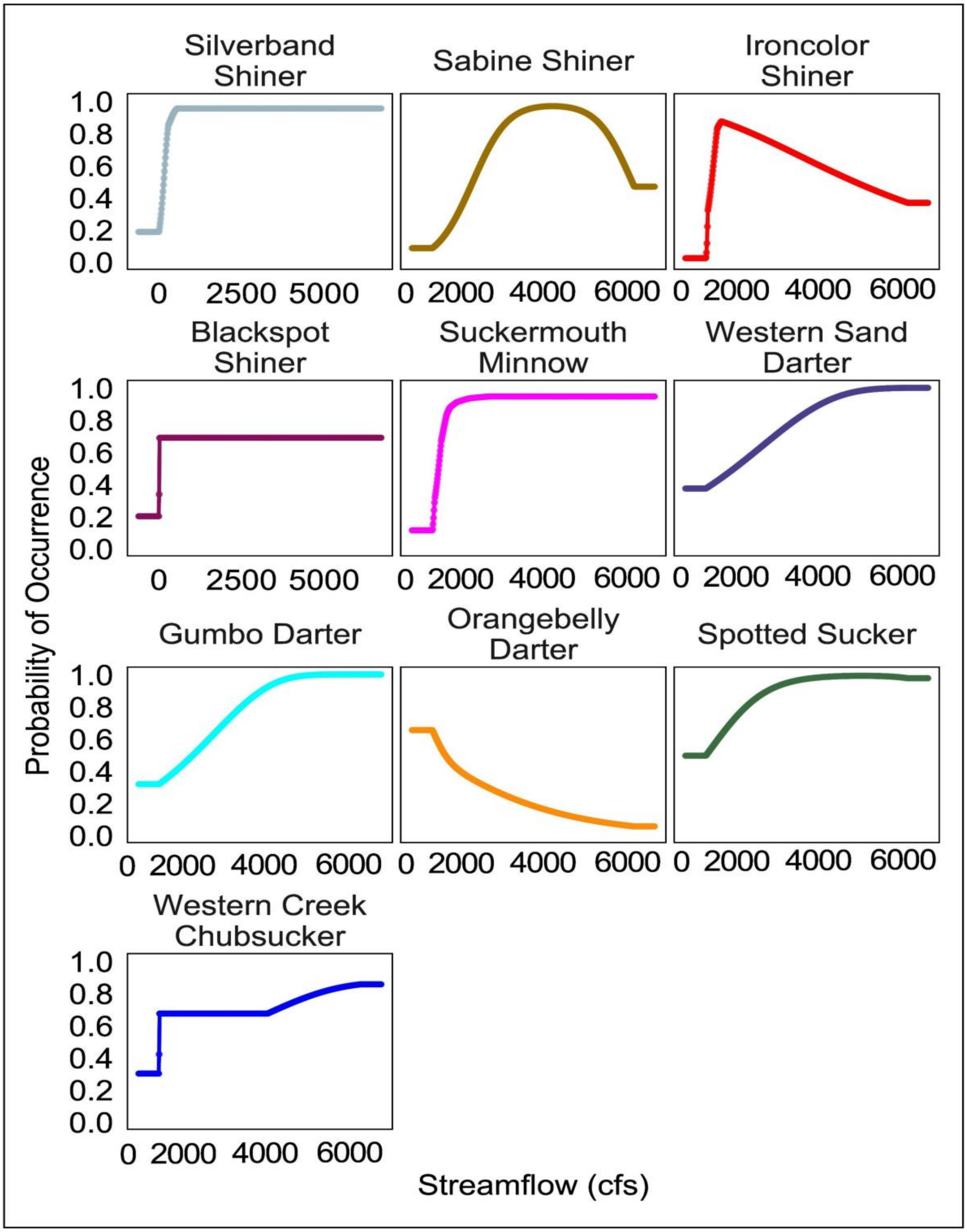

Figure 5. Model response curves showing the probability of occurrence of the focal fish species based on stream flow across streams in the Neches, Sabine, and Cypress River basins during the historical period (1940–1999).

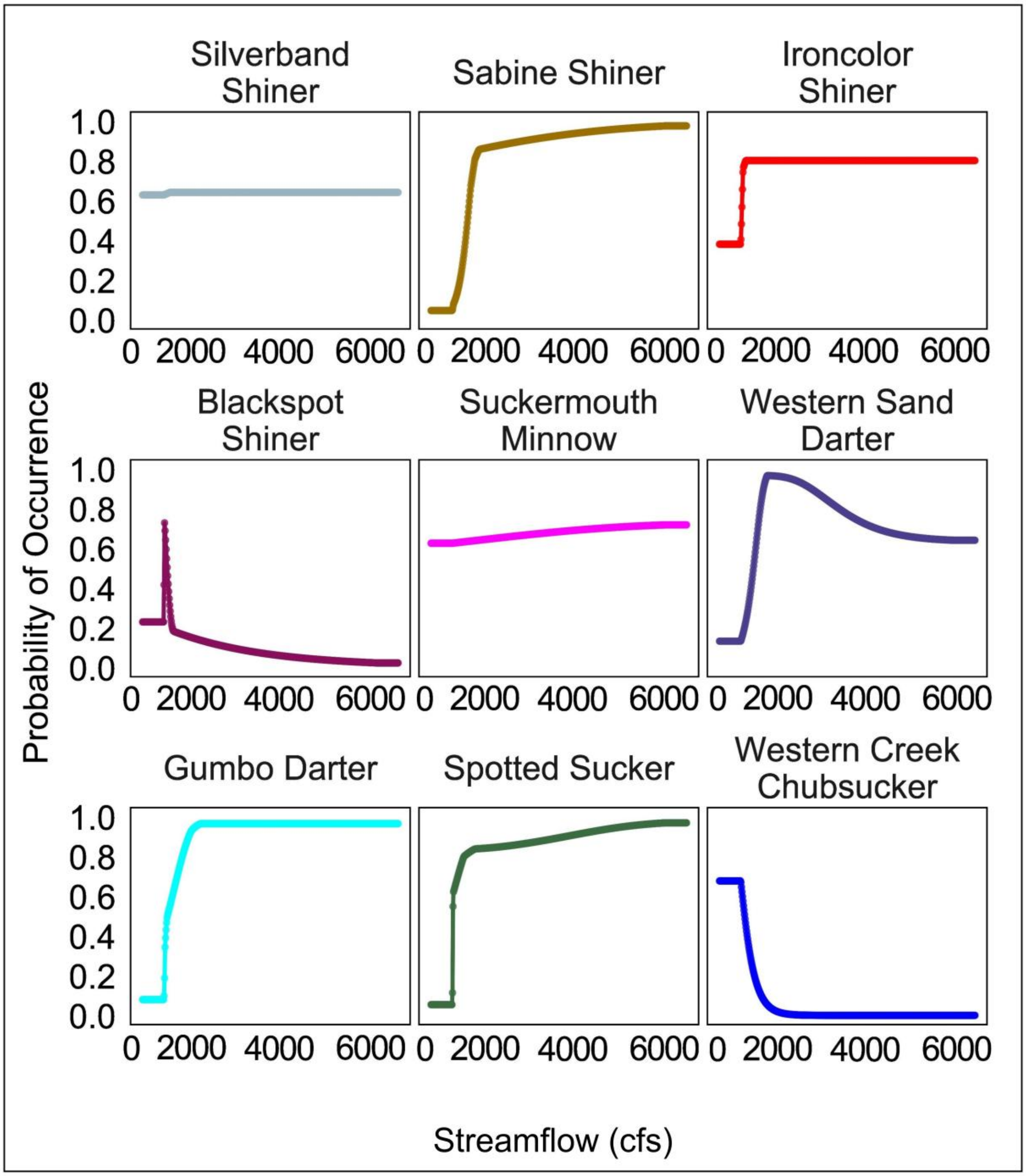

Figure 6. Model response curves showing the probability of occurrence of the focal fish species based on stream flow across streams in the Neches, Sabine, and Cypress River basins during the contemporary period (2000–2025).

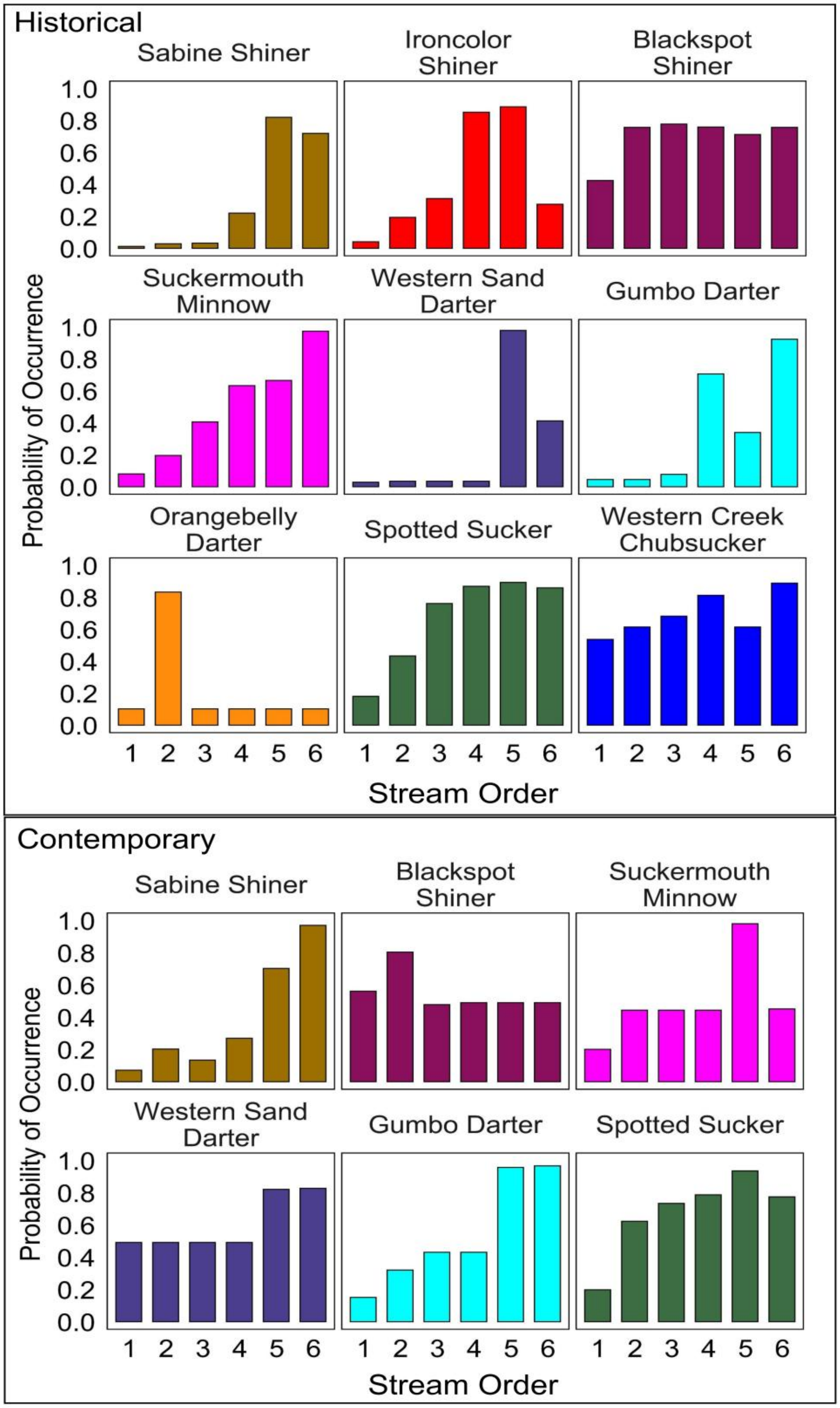

Figure 7. Model response curves showing the probability of occurrence of the focal fish species based on stream order across streams in the Neches, Sabine, and Cypress River basins during the historical (1940–1999) and contemporary (2000–2025) periods.

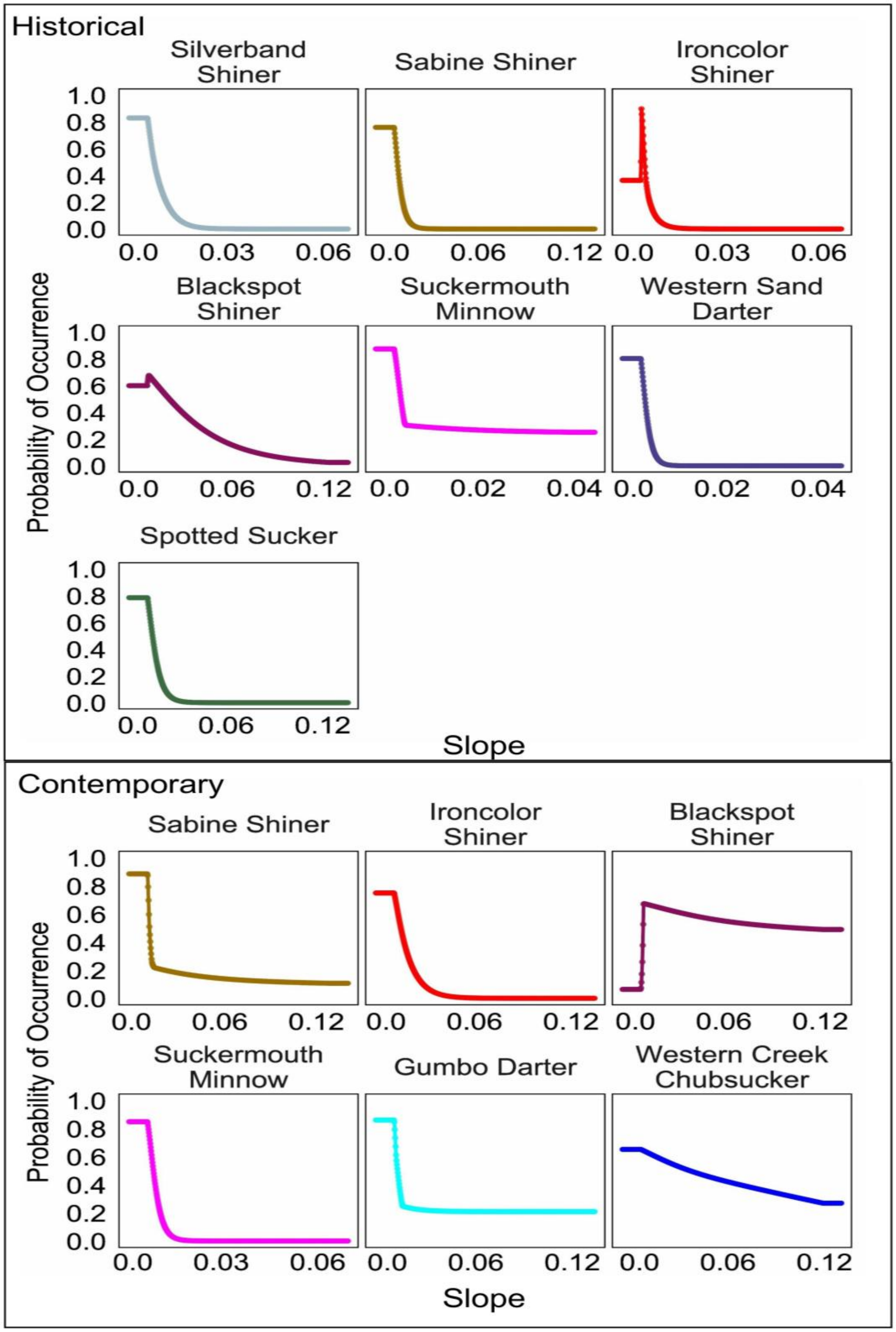

Figure 8. Model response curves showing the probability of occurrence of the focal fish species based on slope across streams in the Neches, Sabine, and Cypress River basins during the historical (1940–1999) and contemporary (2000–2025) periods.

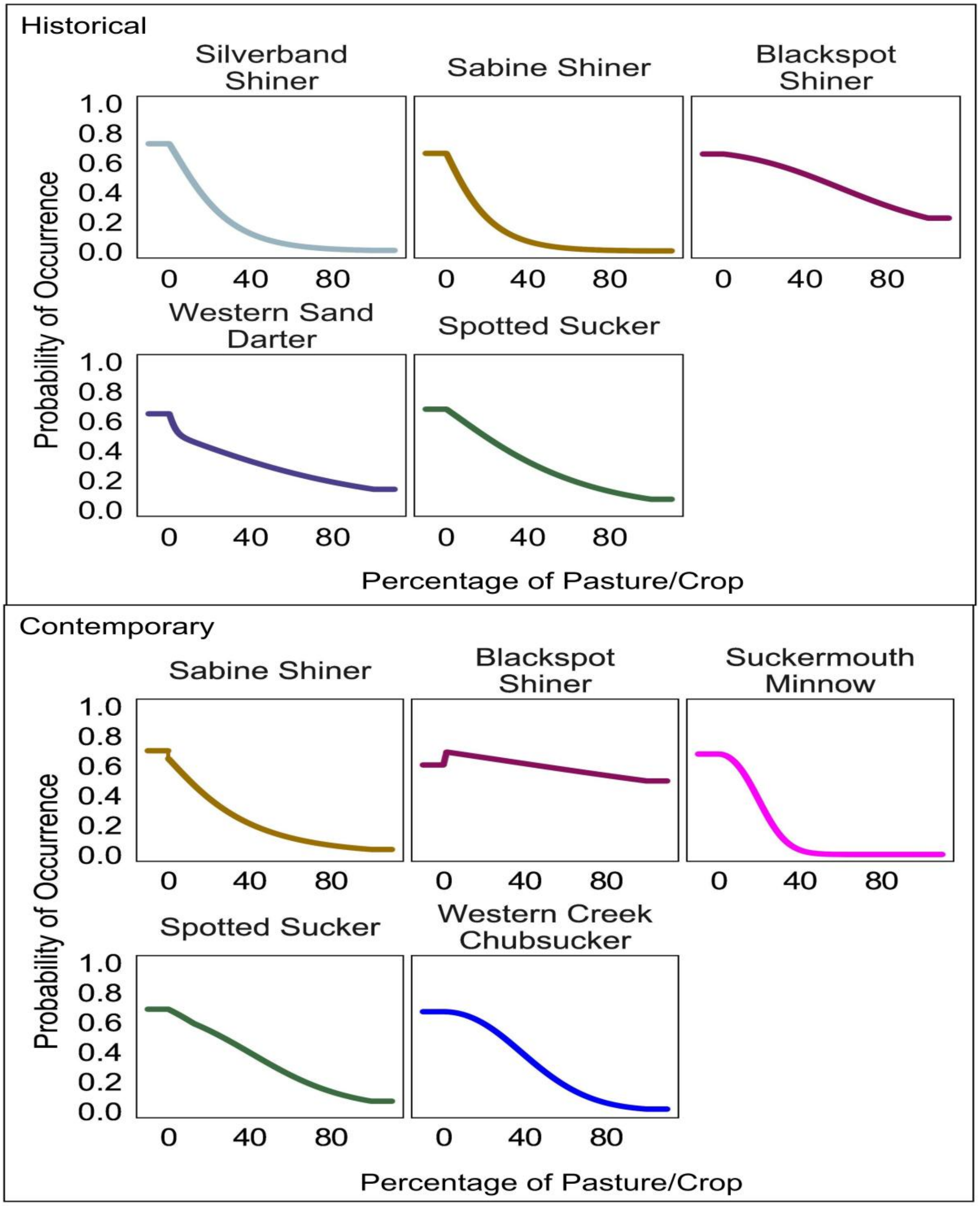

Figure 9. Model response curves showing the probability of occurrence of the focal fish species based on percentage of pasture/crop land cover across streams in the Neches, Sabine, and Cypress River basins during the historical (1940–1999) and contemporary (2000–2025) periods.

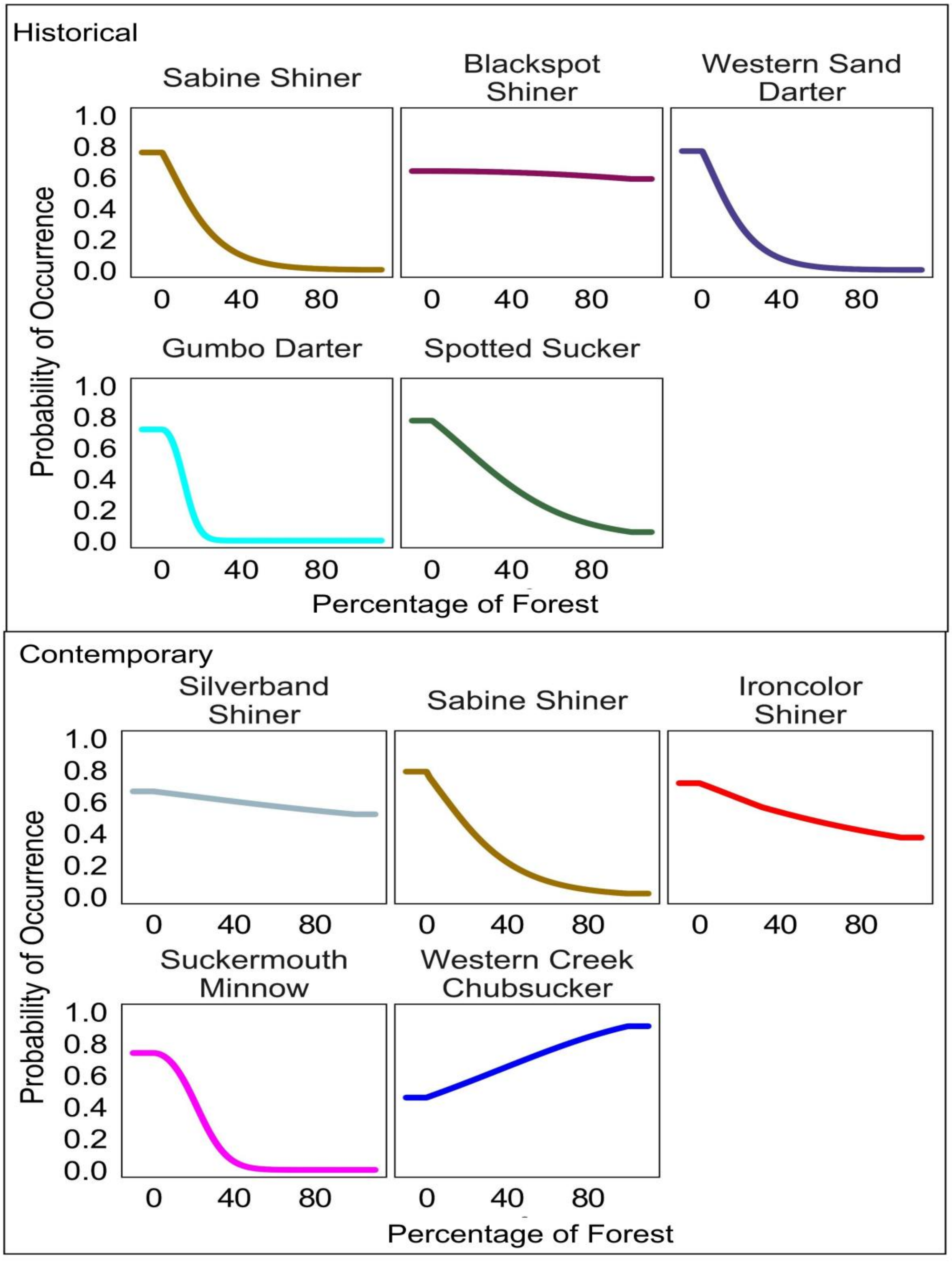

Figure 10. Model response curves showing the probability of occurrence of the focal fish species based on percentage of forest land cover across streams in the Neches, Sabine, and Cypress River basins during the historical (1940–1999) and contemporary (2000–2025) periods.

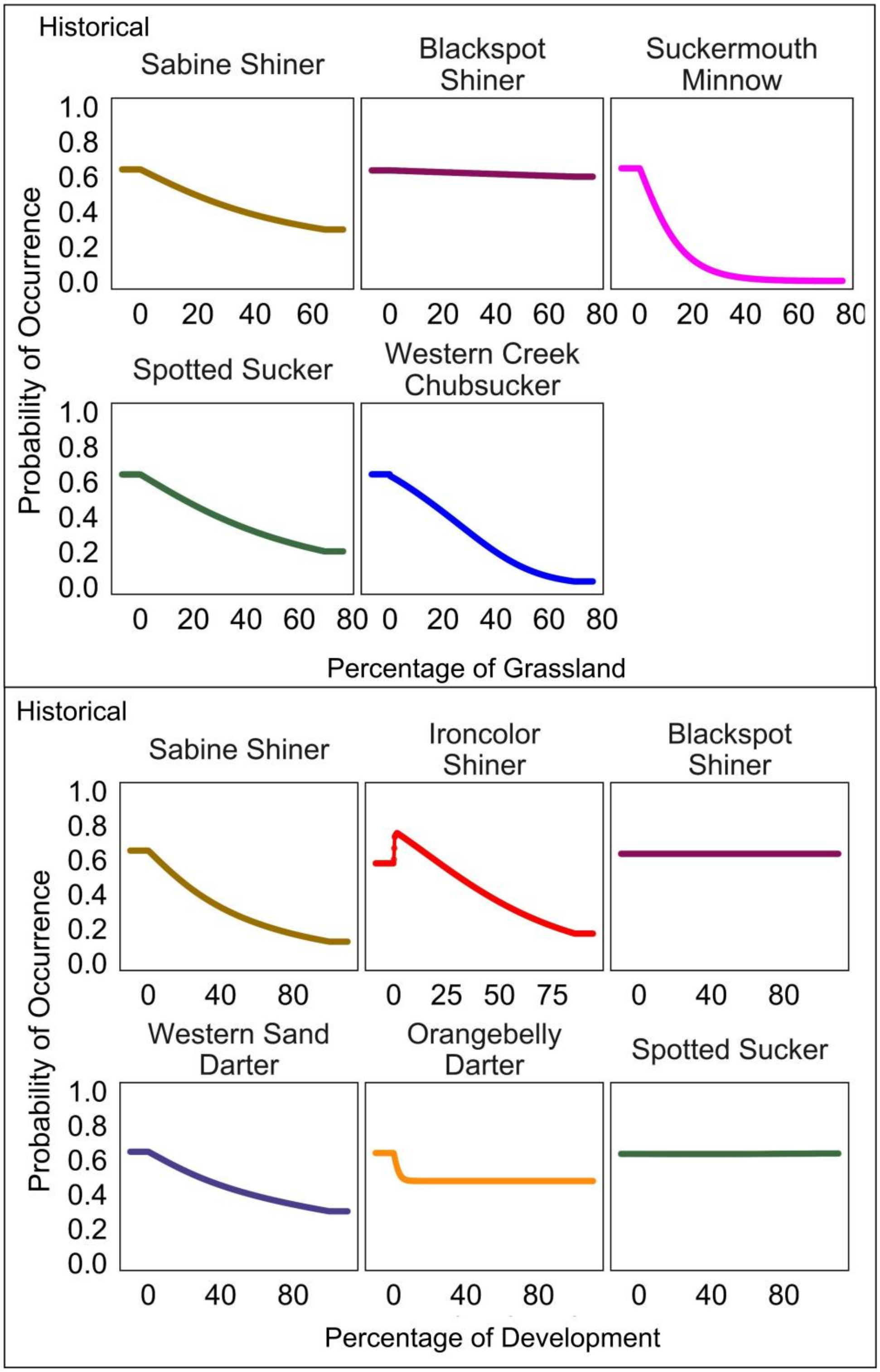

Figure 11. Model response curves showing the probability of occurrence of the focal fish species based on percent grassland (top) and percent developed land (bottom) across streams in the Neches, Sabine, and Cypress River basins during the historical (1940–1999) period.

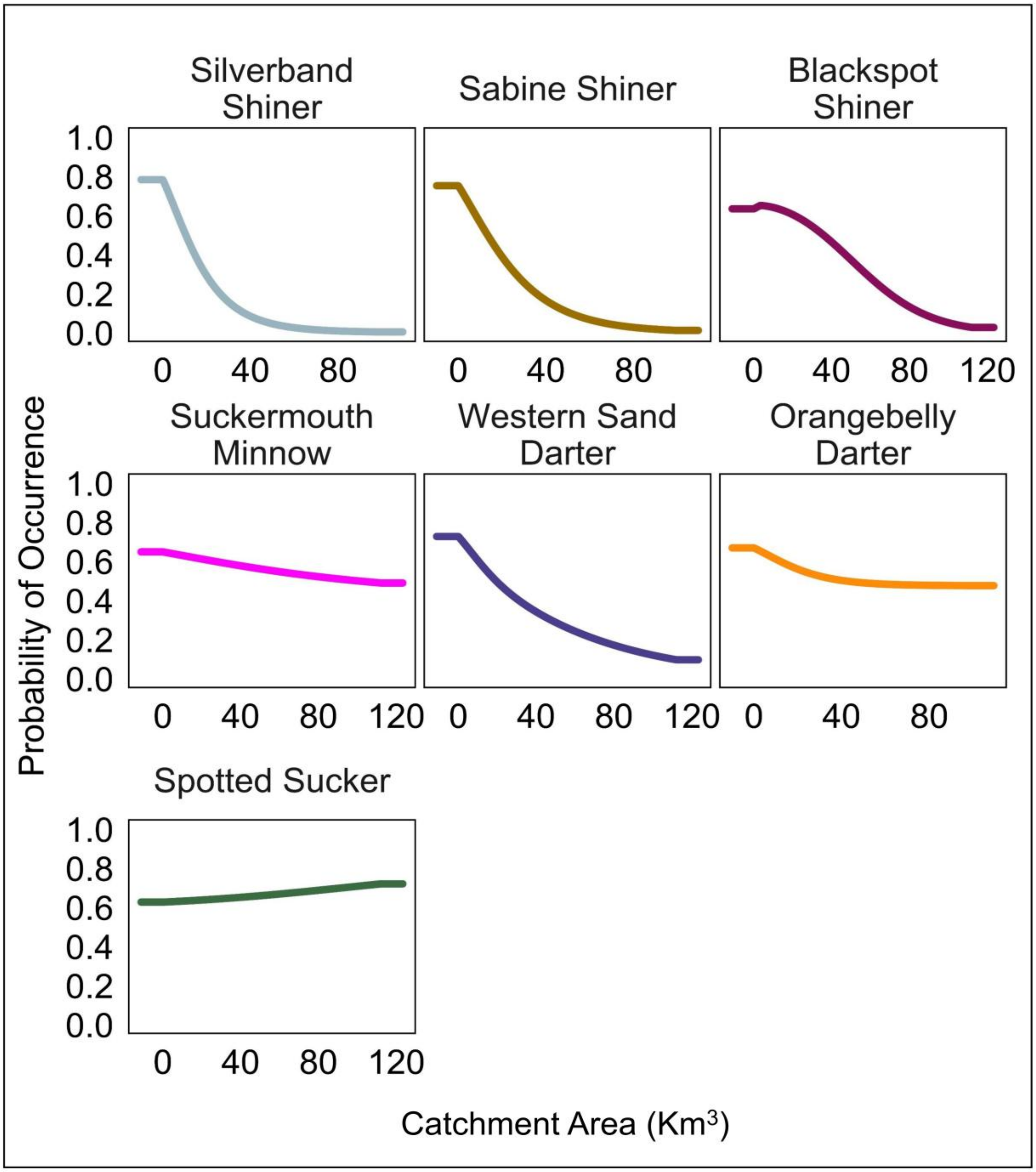

Figure 12. Model response curves showing the probability of occurrence of the focal fish species based on catchment area (km²) across streams in the Neches, Sabine, and Cypress River basins during the historical period (1940–1999).

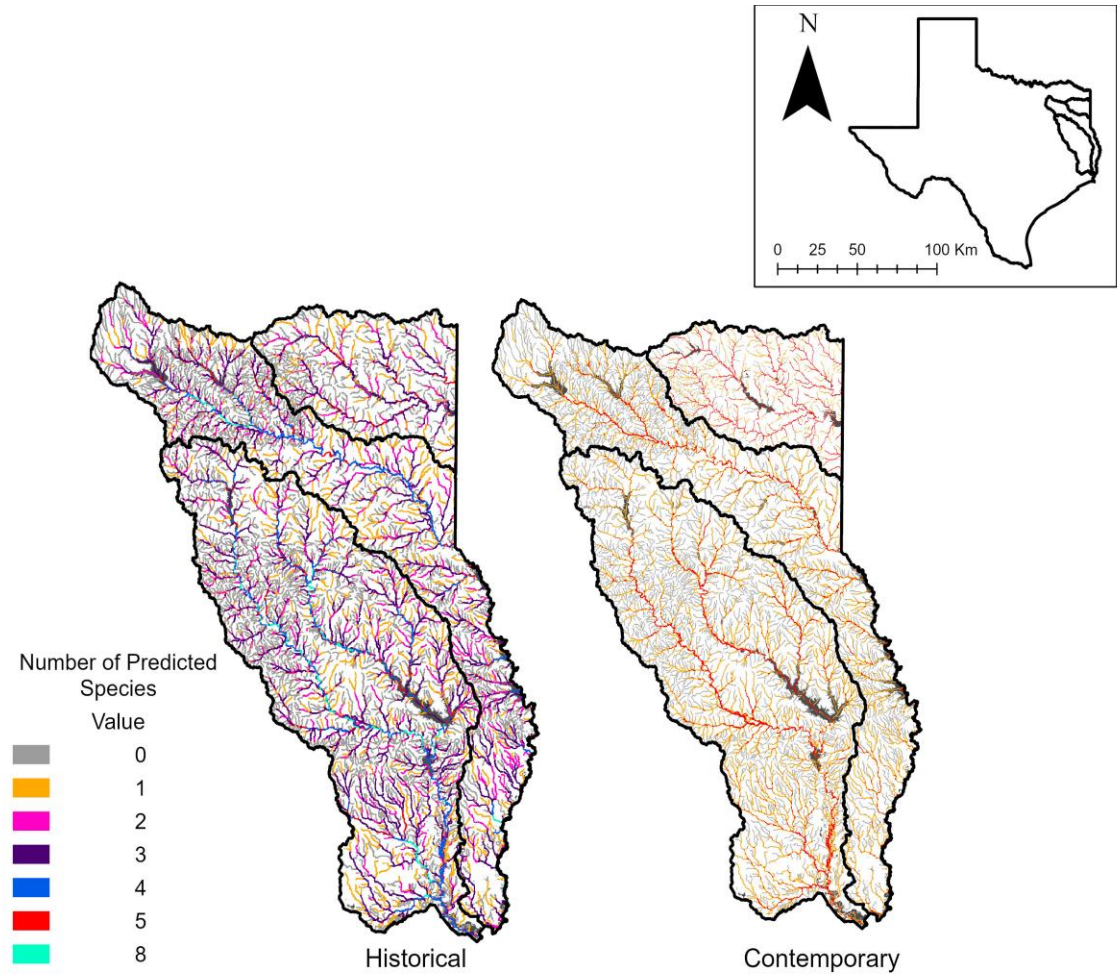

Figure 13. Map of Ecological niche model-based distributional predictions for all focal species across the Neches, Sabine, and Cypress River basins, east Texas. Color values represent the total number of SGCN predicted to occur within each stream reach during the (a) historical (1940–1999), and (b) contemporary (2000-2025) time periods.

Using the regional predictions from by the maxent models for all species, we created habitat suitability maps for all species between the two time periods and across all three river basins. These maps suggested that areas of the mainstem are more suitable for the occurrence of more focal species. This pattern was consistent across the two time periods (Figure 13).

Evaluation of Individual Species' Models. – Model response curves identified distinct environmental predictors contributing to habitat suitability for each focal species across the Neches, Sabine, and Cypress River basins during both historical (1940–1999) and contemporary (2000–2025) periods (Table 5). Among species in the family Leucisidae, streamflow consistently emerged as a key predictor across both time periods, with increased probability of occurrence of species at higher streamflows. For the Blackspot Shiner predictors such as slope, streamflow, percentage of pasture/crops, and stream order were the most important in both time periods (Figure 14). The predictive maps suggested high probability of occurrence for the species across a range of stream orders from the mainstems to lower-order streams throughout the basins (Figure 15). Between the two time periods, the habitat suitability predictions for the Blackspot Shiner changed ~39.78% overall from the historical to contemporary time period (Table 5; Figure 15).

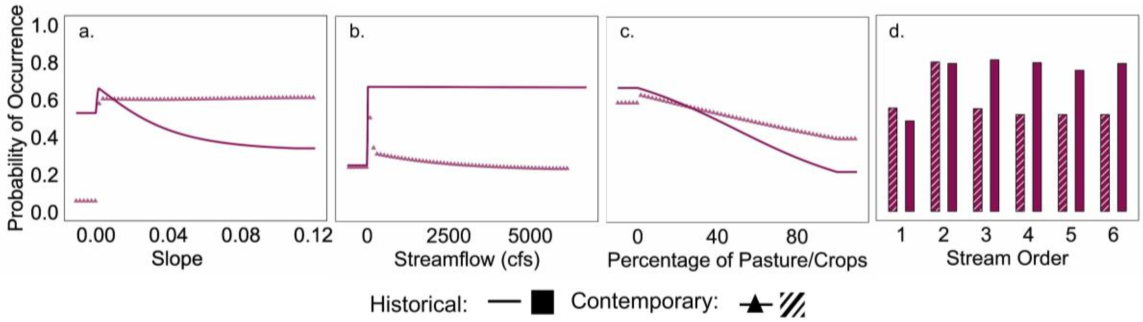

Figure 14. Model response curves depicting the environmental variables with high percent contribution to the probability of occurrence for the Blackspot Shiner in streams of the Neches, Sabine, and Cypress River basins, east Texas. Plots: (a) slope (%), (b) streamflow (cfs), (c) percent pasture/crops, (d) stream order.

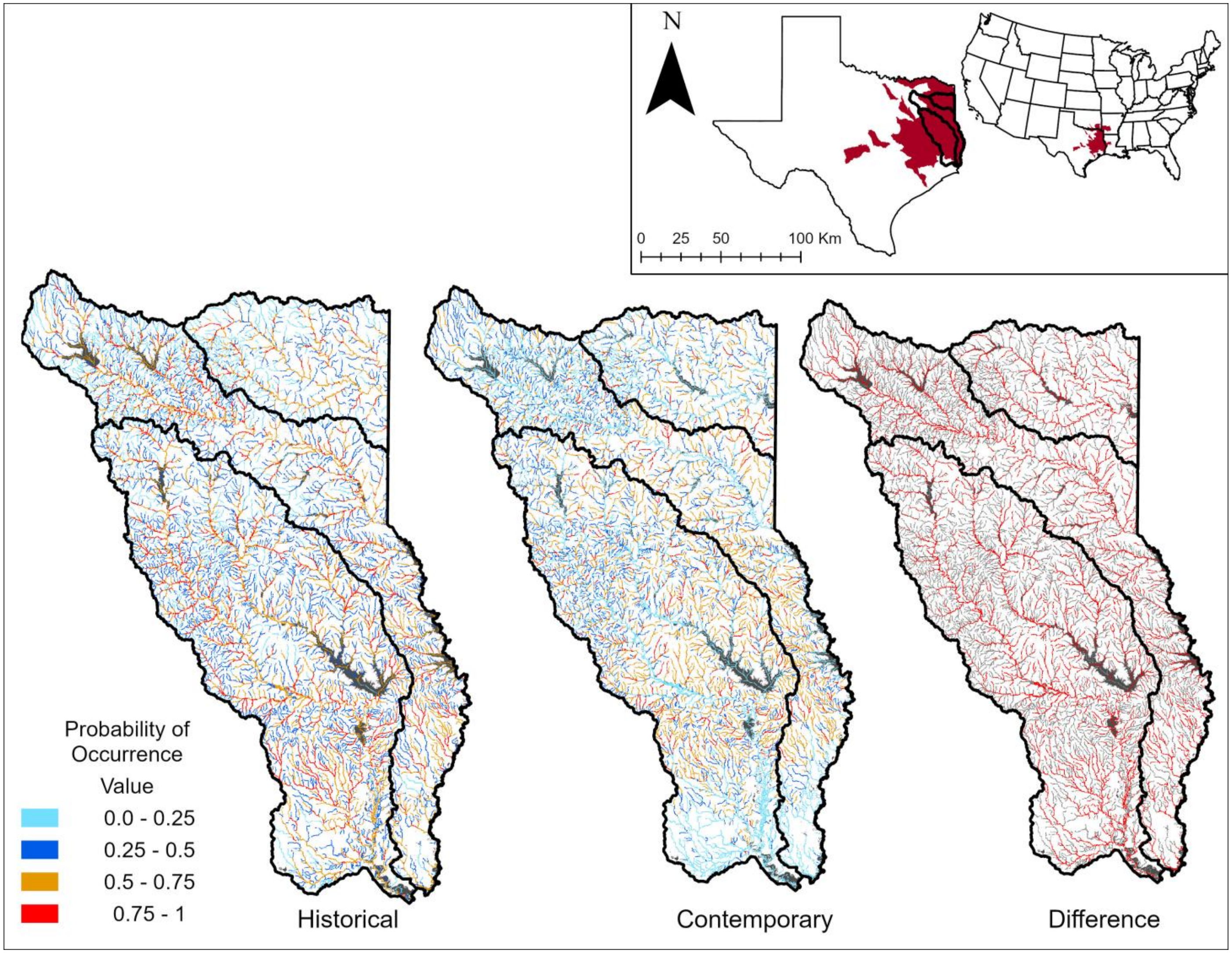

Figure 15. Predicted habitat suitability for the Blackspot Shiner in streams of the Neches, Sabine, and Cypress River basins, east Texas, based on Maxent model results for historical and contemporary time periods. Red and orange colors represent areas with higher predicted probability of suitable habitat, while light to dark blue indicate lower suitability. Reservoirs are shown in gray. The Difference maps depict spatial differences in predicted habitat suitability for each species, with red stream segments indicate significant changes in predicted suitability, while gray segments indicate no significant change. Maps in the top right corner depict the species' range in the United States and Texas.

The Ironcolor Shiner and Sabine Shiner had four important predictors including streamflow, percentage of forest cover, and stream order (Figure 16). In addition, stream slope was important for the Ironcolor Shiner. The predictive maps for each shiner species showed high probability of occurrence within the mainstem channels (Figures 17 and 18). Additionally, when compared between the historical and contemporary time periods, the predictive map showed 19.72% of predicted suitable habitats had changed for the Ironcolor Shiner. While for the Sabine Shiner, there was a 2.81% change of the predicted habitat suitability. For both species, especially the Ironcolor Shiner, the models indicate shift toward more areas within the basin suggesting higher probabilities of occurrence throughout the study area (Figures 17 and 18).

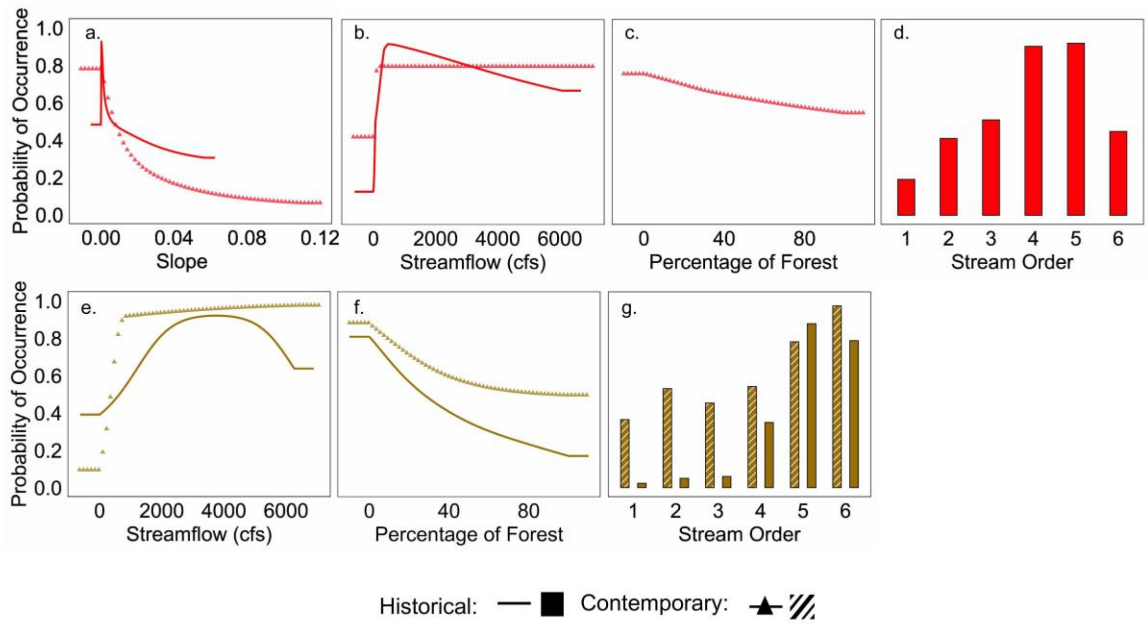

Figure 16. Model response curves depicting the environmental variables with high percent contribution to the probability of occurrence for each individual focal species in streams of the Neches, Sabine, and Cypress River basins, east Texas. Plots (a–d) represent variables for Ironcolor Shiner: (a) slope (%), (b) streamflow, (c) percent forest, (d) stream order. Plots (e–g) represent variables for Sabine Shiner: (e) streamflow, (f) percent forest, (g) stream order.

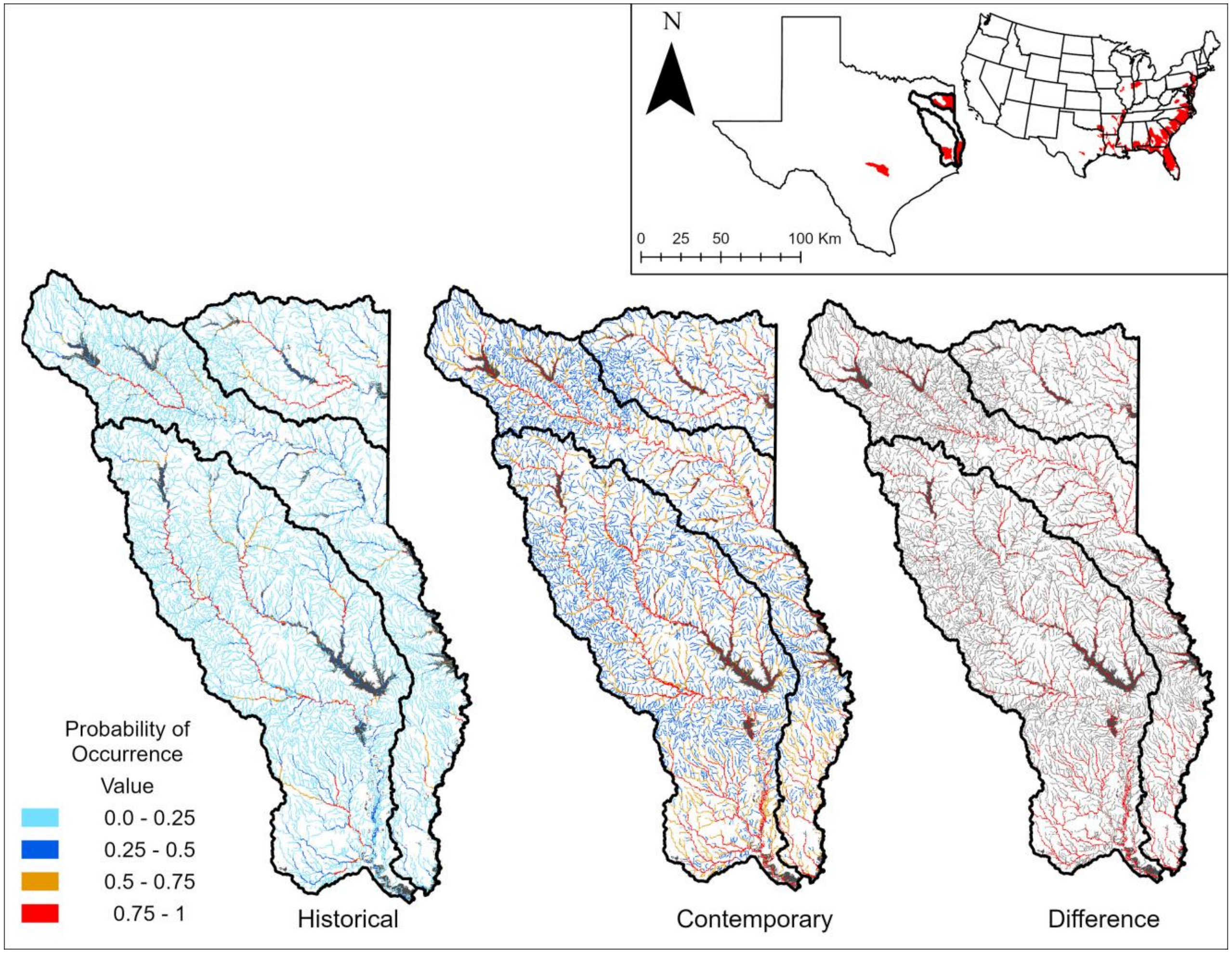

Figure 17. Predicted habitat suitability for the Ironcolor Shiner in streams of the Neches, Sabine, and Cypress River basins, east Texas, based on Maxent model results for historical and contemporary time periods. Red and orange colors represent areas with higher predicted probability of suitable habitat, while light to dark blue indicate lower suitability. Reservoirs are shown in gray. The Difference maps depict spatial differences in predicted habitat suitability for each species, with red stream segments indicate significant changes in predicted suitability, while gray segments indicate no significant change. Maps in the top right corner depict the species' range in the United States and Texas.

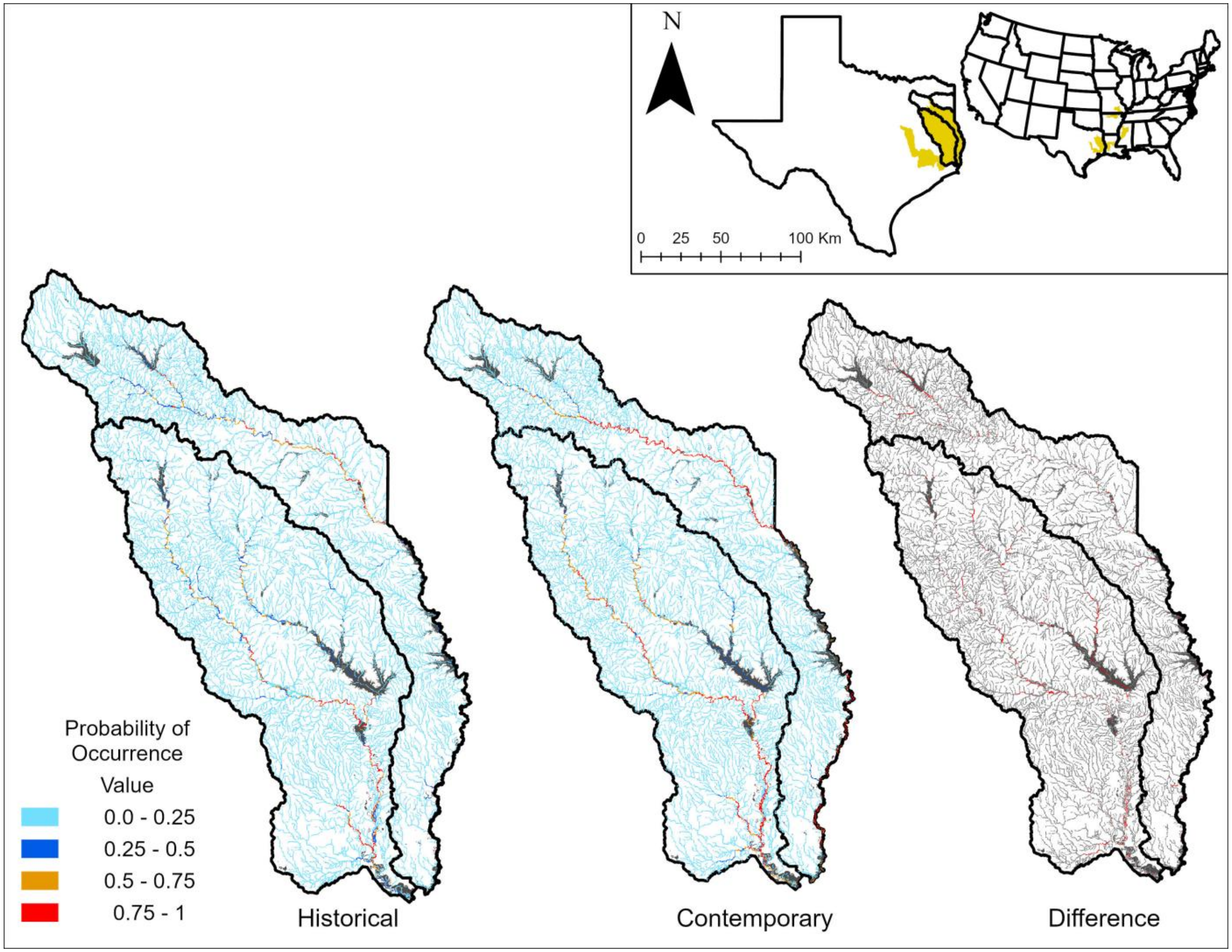

Figure 18. Predicted habitat suitability for the Sabine Shiner in streams of the Neches, Sabine, and Cypress River basins, east Texas, based on Maxent model results for historical and contemporary time periods. Red and orange colors represent areas with higher predicted probability of suitable habitat, while light to dark blue indicate lower suitability. Reservoirs are shown in gray. The Difference maps depict spatial differences in predicted habitat suitability for each species, with red stream segments indicate significant changes in predicted suitability, while gray segments indicate no significant change. Maps in the top right corner depict the species' range in the United States and Texas.

The Silverband Shiner was best predicted by streamflow, catchment area (km²), slope, and percentage of forest, while for the Suckermouth Minnow the best predictors were streamflow, percentage of forest cover, stream order, and percentage of pasture/crops (Figure 19). Streamflow remained an important predictor for both species in both time periods.

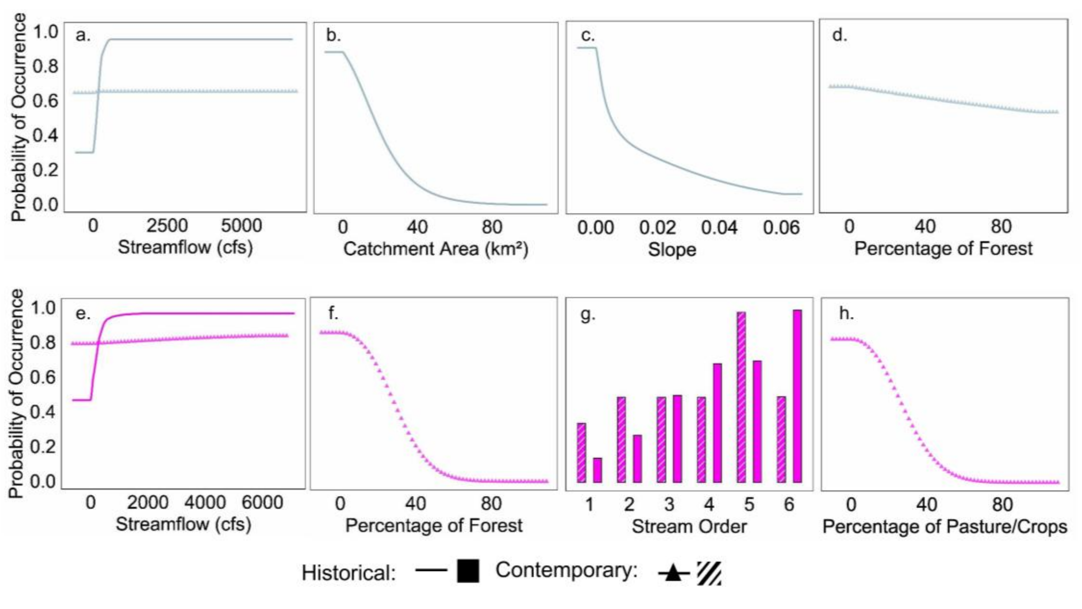

Figure 19. Model response curves depicting the environmental variables with high percent contribution to the probability of occurrence for each individual focal species in streams of the Neches, Sabine, and Cypress River basins. Plots (a–d) represent variables for Silverband Shiner: (a) streamflow, (b) catchment area (c) slope (%), (d) percent forest. Plots (e–h) represent variables for Suckermouth Minnow: (e) streamflow, (f) percent forest, (g) stream order, and (h) percent pasture/crops.

Historically, the predictive maps for both species showed a high probability of occurrence mainly within the mainstem channels and some higher order streams (e.g., order 4 and 5; Figures 20 and 21). However, in the contemporary time period, there was a 35.12% overall change in predicted habitat suitability, for the Silverband Shiner with equal probability of occurrence for the species throughout the study area (Table 5; Figure 20). For the Suckermouth Minnow, on the other hand, there was a smaller overall change of 7.11% of habitat suitability, indicating more areas of higher probability of occurrence (Table 5; Figure 21).

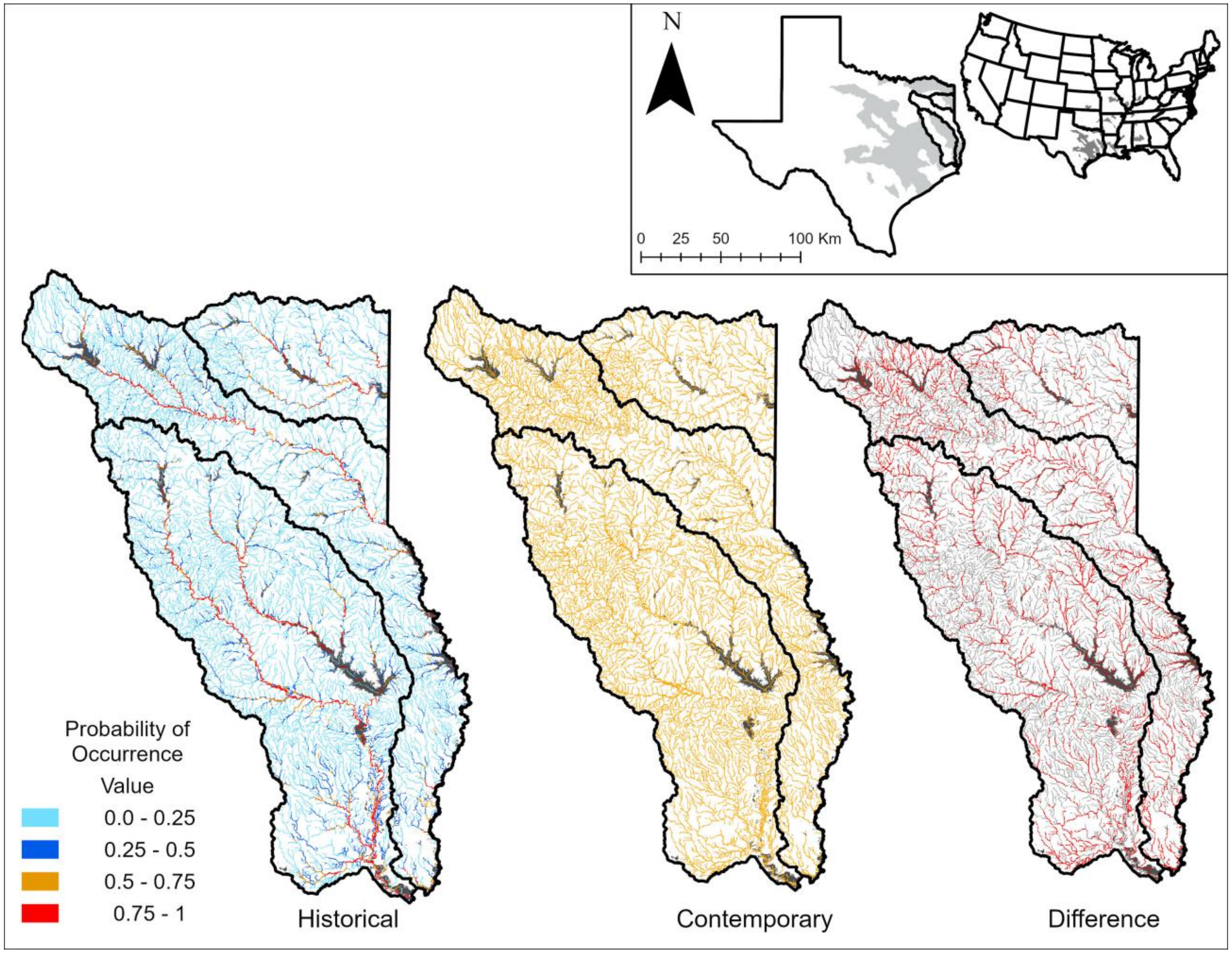

Figure 20. Predicted habitat suitability for the Silverband Shiner in streams of the Neches, Sabine, and Cypress River basins, east Texas, based on Maxent model results for historical and contemporary time periods. Red and orange colors represent areas with higher predicted probability of suitable habitat, while light to dark blue indicate lower suitability. Reservoirs are shown in gray. The Difference maps depict spatial differences in predicted habitat suitability for each species, with red stream segments indicate significant changes in predicted suitability, while gray segments indicate no significant change. Maps in the top right corner depict the species' range in the United States and Texas.

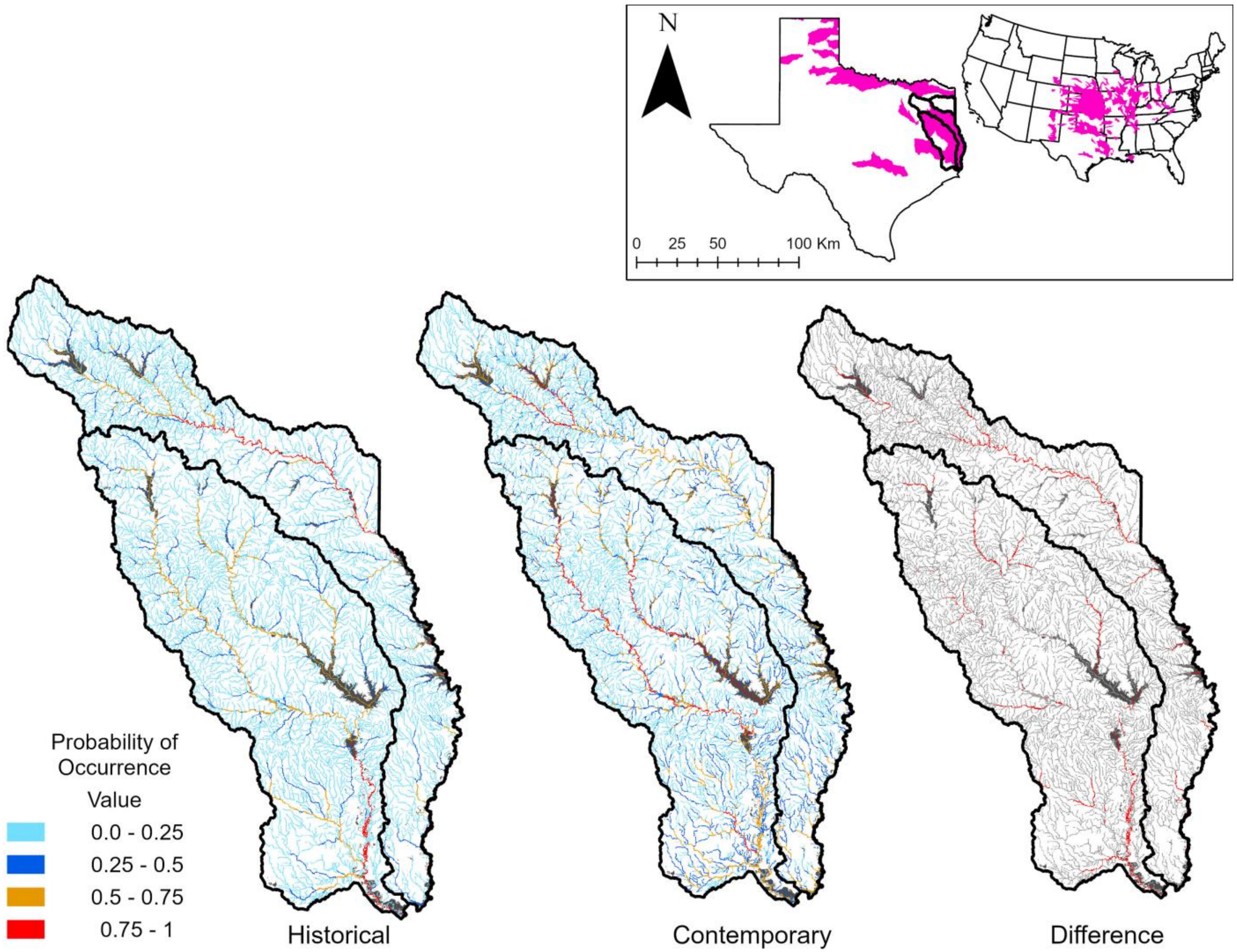

Figure 21. Predicted habitat suitability for the Suckermouth Minnow in streams of the Neches, Sabine, and Cypress River basins, east Texas, based on Maxent model results for historical and contemporary time periods. Red and orange colors represent areas with higher predicted probability of suitable habitat, while light to dark blue indicate lower suitability. Reservoirs are shown in gray. The Difference maps depict spatial differences in predicted habitat suitability for each species, with red stream segments indicate significant changes in predicted suitability, while gray segments indicate no significant change. Maps in the top right corner depict the species' range in the United States and Texas.

Among Percidae species, streamflow and stream order were consistent for the occurrence of the species across the two time periods (Figure 22). Although, for the Orangebelly Darter, only historical data was available and the results suggested that the species is most likely to occur in lower-order streams (i.e., stream order 2). While an increase in percent developed land cover decreases their probability of occurrence in these basins (Figure 25).

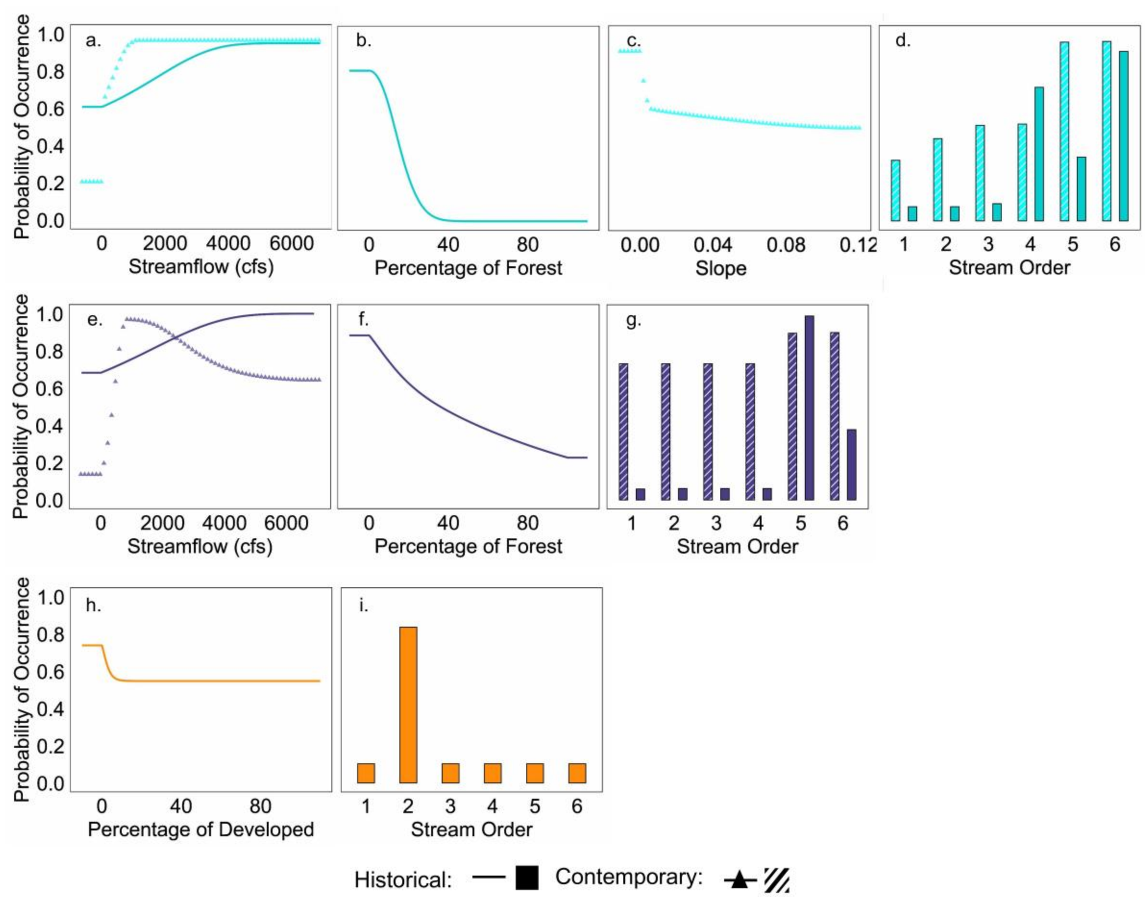

Figure 22. Model response curves depicting the environmental variables with high percent contribution to the probability of occurrence for each individual focal species in streams of the Neches, Sabine, and Cypress River basins, east Texas. Plots (a–d) represent variables for Gumbo Darter: (a) streamflow, (b) percent forest, (c) slope (%), (d) stream order. Plots (e–g) represent variables for Western Sand Darter: (e) streamflow, (f) percent forest, (g) stream order. Plots (h–i) represent variables for Orangebelly Darter: (h) percent developed, (i) stream order.

For both the Gumbo Darter and Western Sand Darter, probability of occurrence increased with high order streams that also have high flow. Such results are reflected in the predictive maps, in which both darters have high probability of occurrence within the mainstem channels of the study area (Figures 23 and 24). Although predictive maps showed low changes overall for both darters between the two time periods (8.67% Gumbo Darter and 3.02% Western Sand Darter), it was observed that model predictions for the Gumbo Darter show more area with higher probability of occurrence within the mainstem channels and tributaries in the contemporary period (Figures 23).

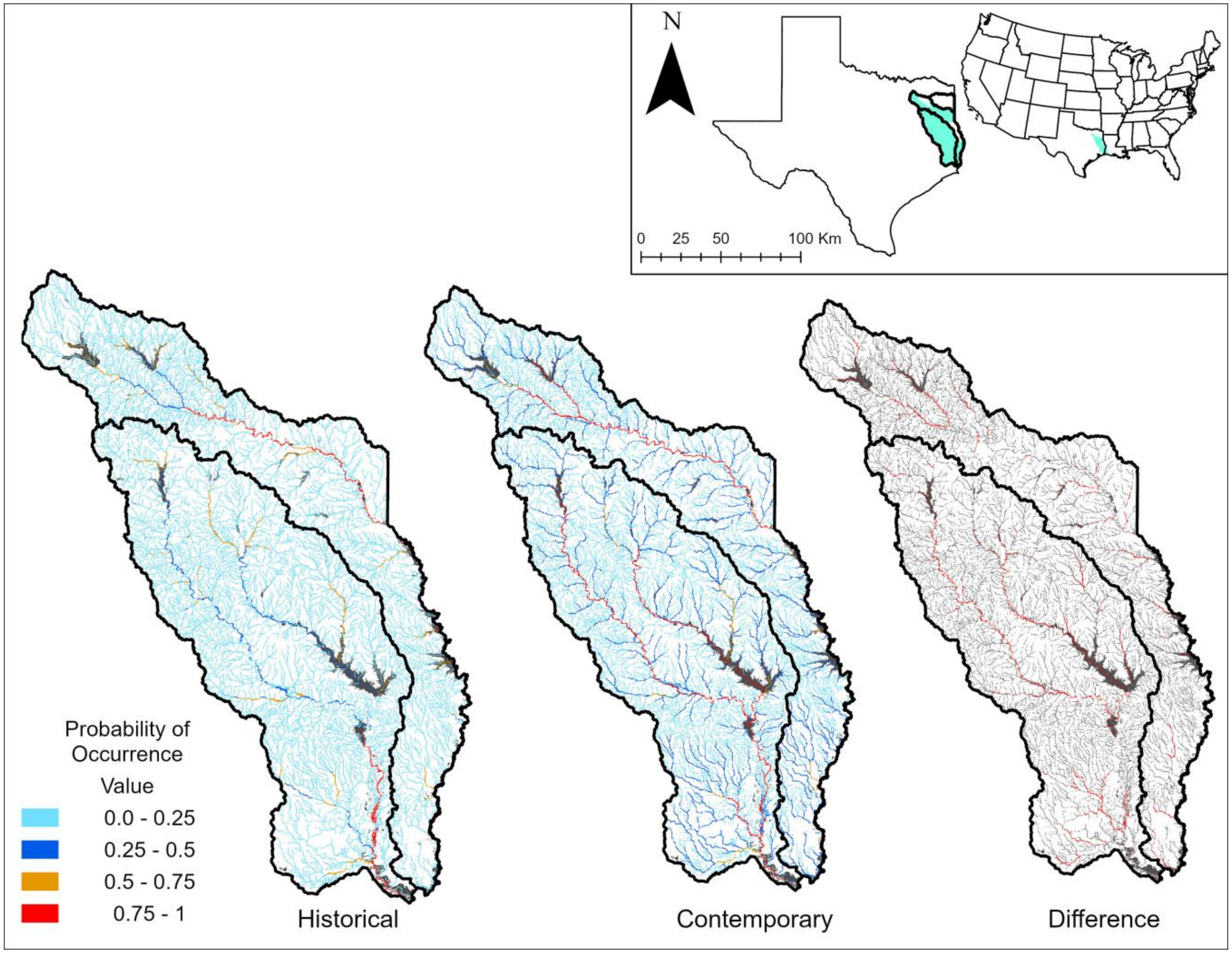

Figure 23. Predicted habitat suitability for the Gumbo Darter in streams of the Neches, Sabine, and Cypress River basins, east Texas, based on Maxent model results for historical and contemporary time periods. Red and orange colors represent areas with higher predicted probability of suitable habitat, while light to dark blue indicate lower suitability. Reservoirs are shown in gray. The Difference maps depict spatial differences in predicted habitat suitability for each species, with red stream segments indicate significant changes in predicted suitability, while gray segments indicate no significant change. Maps in the top right corner depict the species' range in the United States and Texas.

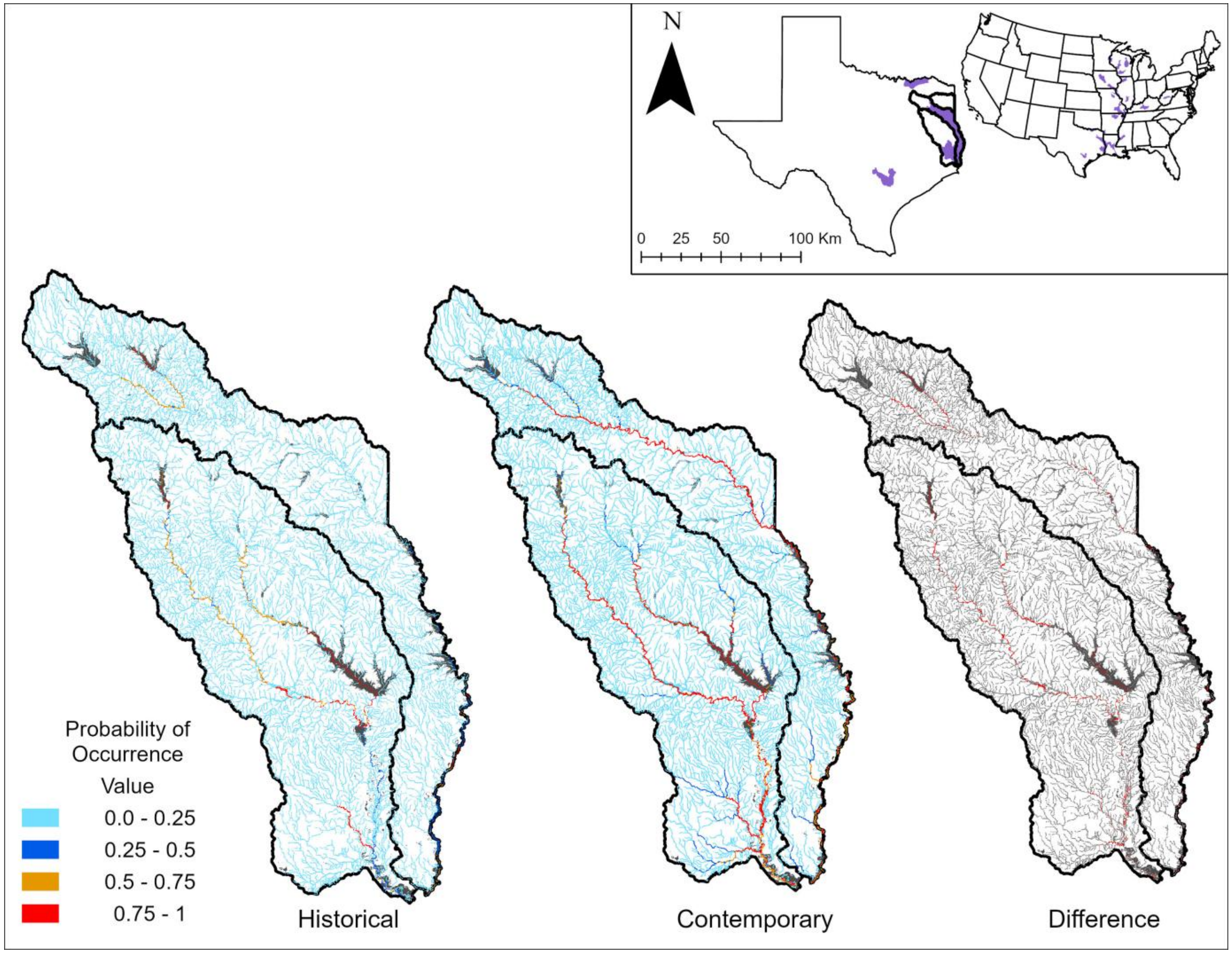

Figure 24. Predicted habitat suitability for the Western Sand Darter in streams of the Neches, Sabine, and Cypress River basins, east Texas, based on Maxent model results for historical and contemporary time periods. Red and orange colors represent areas with higher predicted probability of suitable habitat, while light to dark blue indicate lower suitability. Reservoirs are shown in gray. The Difference maps depict spatial differences in predicted habitat suitability for each species, with red stream segments indicate significant changes in predicted suitability, while gray segments indicate no significant change. Maps in the top right corner depict the species' range in the United States and Texas.

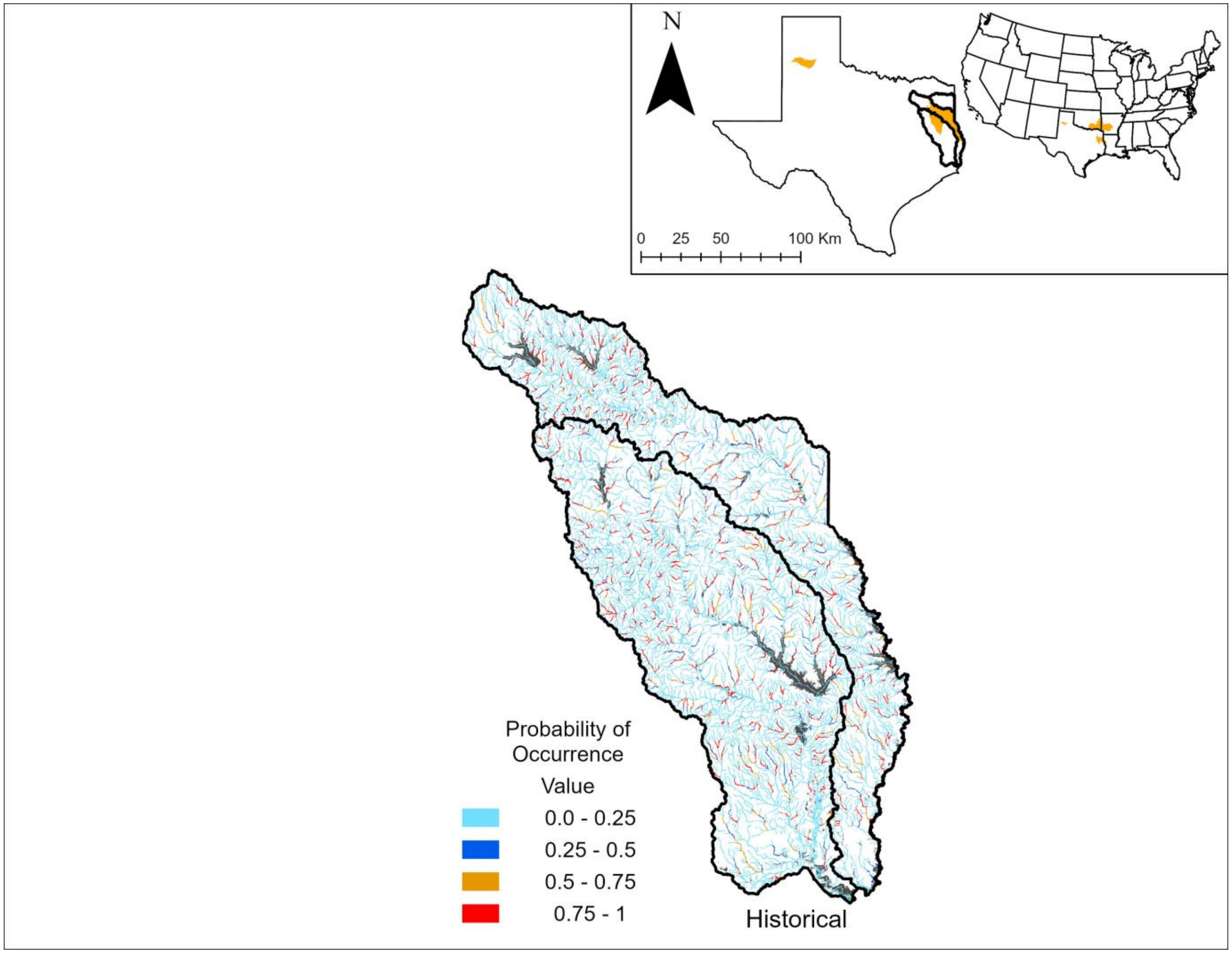

Figure 25. Predicted habitat suitability for the Orangebelly Darter in streams of the Neches, Sabine, and Cypress River basins, east Texas, based on Maxent model results for historical and contemporary time periods. Red and orange colors represent areas with higher predicted probability of suitable habitat, while light to dark blue indicate lower suitability. Reservoirs are shown in gray. The Difference maps depict spatial differences in predicted habitat suitability for each species, with red stream segments indicate significant changes in predicted suitability, while gray segments indicate no significant change. Maps in the top right corner depict the species' range in the United States and Texas.

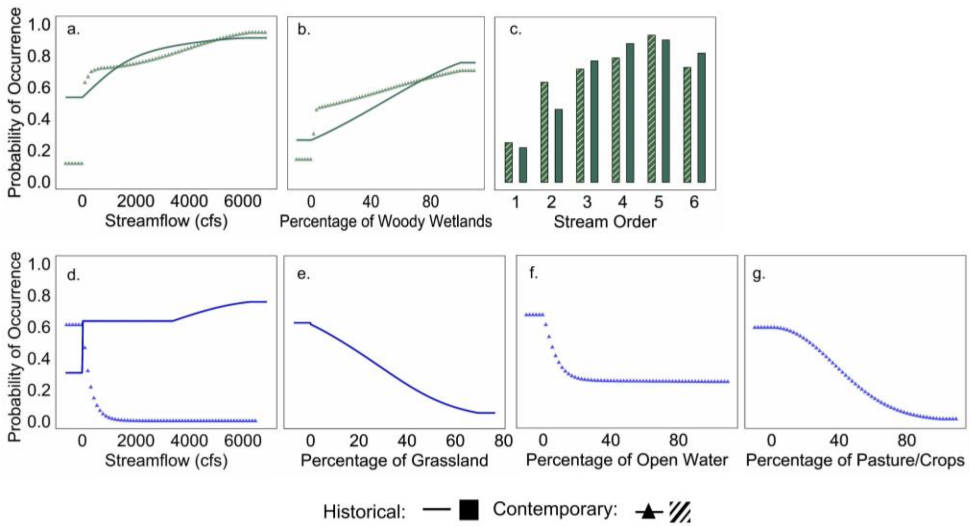

Figure 26. Model response curves depicting the environmental variables with high percent contribution to the probability of occurrence for each individual focal species in streams of the Neches, Sabine, and Cypress River basins, east Texas. Plots (a–c) represent variables for Spotted Sucker: (a) streamflow (cfs), (b) percent woody wetlands (c) stream order. Plots (d–g) represent variables for Western Creek Chubsucker: (d) streamflow (cfs), (e) percent pasture/crops, (f) percent grassland, and (g) percent open water.

Predictor variables for Catostomidae species slightly differed by species, although streamflow continued to be an important variable. For the Spotted Sucker, higher streamflow, higher percentage of woody wetlands, and higher stream order were the best predictors of occurrence for the species in both time periods (Figure 26a−c). The Western Creek Chubsucker was also influenced by streamflow in the historical model, with high streamflow values associated with greater probabilities of occurrence. In contrast, in the contemporary model, lower streamflow values resulted in high probability of occurrence (Figure 26d). The model also predicted higher probability of occurrence of the Chubsucker at lower percentages of pasture/crops, grassland, and open water (Figure 26, d−g).

The predictive maps for the Spotted Sucker show a 11.44% change in predicted habitat suitability from the historical and contemporary time period, while the Western Creek Chubsucker has a 52.96% change in habitat suitability (Table 5).

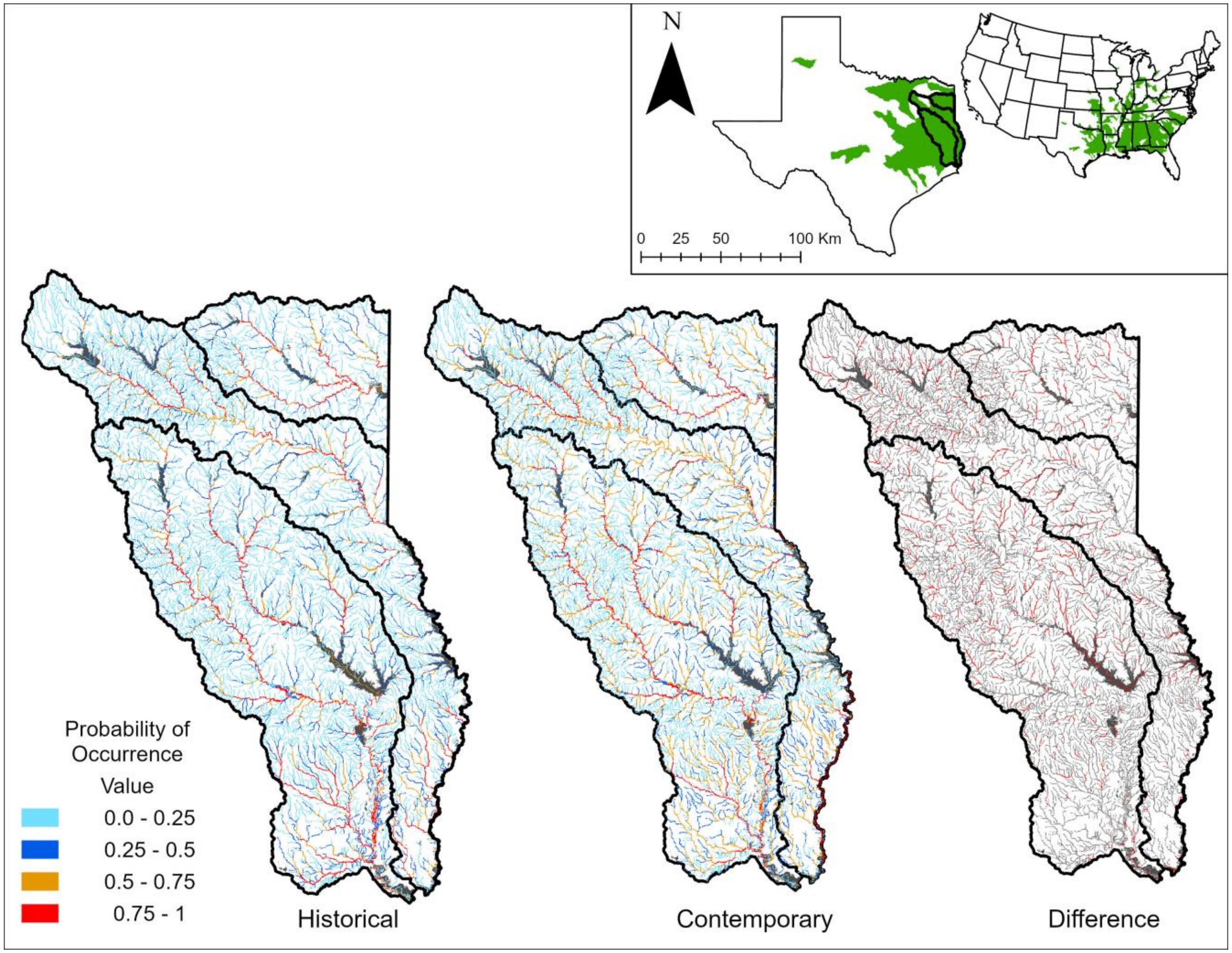

Figure 27. Predicted habitat suitability for the Spotted Sucker in streams of the Neches, Sabine, and Cypress River basins, east Texas, based on Maxent model results for historical and contemporary time periods. Red and orange colors represent areas with higher predicted probability of suitable habitat, while light to dark blue indicate lower suitability. Reservoirs are shown in gray. The Difference maps depict spatial differences in predicted habitat suitability for each species, with red stream segments indicate significant changes in predicted suitability, while gray segments indicate no significant change. Maps in the top right corner depict the species' range in the United States and Texas.

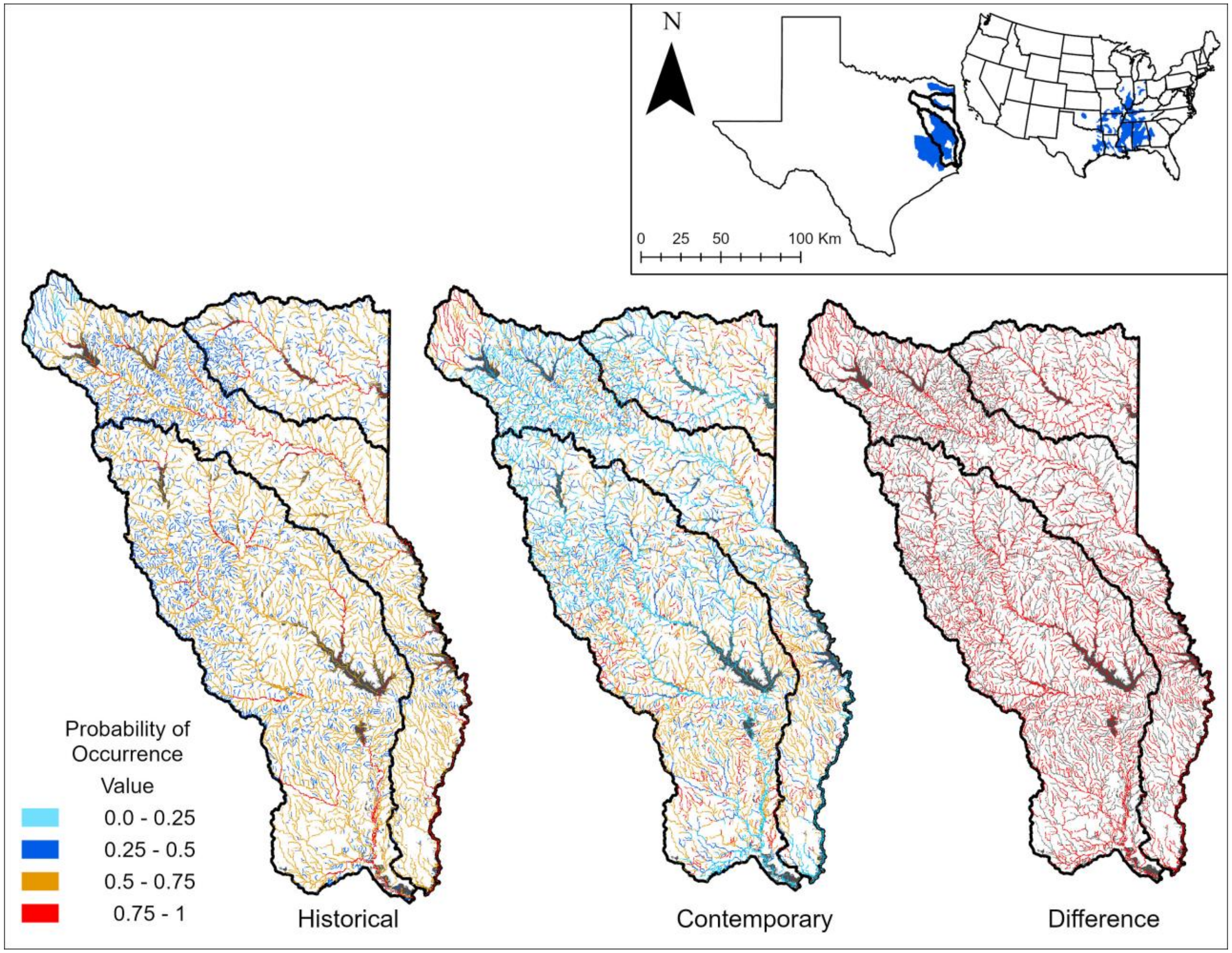

Figure 28. Predicted habitat suitability for the Western Creek Chubsucker in streams of the Neches, Sabine, and Cypress River basins, east Texas, based on Maxent model results for historical and contemporary time periods. Red and orange colors represent areas with higher predicted probability of suitable habitat, while light to dark blue indicate lower suitability. Reservoirs are shown in gray. The Difference maps depict spatial differences in predicted habitat suitability for each species, with red stream segments indicate significant changes in predicted suitability, while gray segments indicate no significant change. Maps in the top right corner depict the species' range in the United States and Texas.

B. Local Environmental Predictors and Fish Assemblage

Fish Assemblage and Environmental Variables by Season and Basin

The NMDS ordination analysis performed on fish assemblages in the mainstem of the Neches and Sabine suggested differences during the summer season (Pseudo-$F_{1,52}$ = 21.02, p = 0.001). Although these two rivers share similar species, SIMPER and IndVal analyses indicated that differences were primarily influenced by higher abundances of Weed Shiner, Ribbon Shiner, and Blacktail Shiner in the Neches, while the Red Shiner was more abundant in the Sabine. In addition, results indicated that several species were unique to individual basins. For example, the Mississippi Silvery Minnow, Suckermouth Minnow, and Cypress Darter were only collected in the Neches, while the Flathead Catfish, River Carpsucker, and Mud Darter were only collected in the Sabine.

Among streams, the NMDS showed some overlapping in the fish assemblage of the three river basins and across seasons. However, when a PERMANOVA was performed, fish assemblages of the Neches and Sabine revealed significant differences during the summer (Pseudo-$F_{1,64}$ = 5.00, $p < 0.001$). These differences were influenced by the Blackspotted Topminnow, Longear Sunfish, which were more abundant in the Sabine, and the Blackstripe Topminnow and Bluntnose Darter, which were more abundant in the Neches. Significant differences were also observed in assemblages of the Neches and Cypress (Pseudo-$F_{1,40}$ = 2.74, p = 0.003) and Sabine and Cypress (Pseudo-$F_{1,38}$ = 3.53, $p < 0.001$) during the summer (Figure 29). Differences between the Neches and the Cypress were influenced by the Ribbon Shiner and Bluegill Sunfish, which were more abundant in the Cypress, and by the Western Mosquitofish in the Neches. For the Sabine and the Cypress, the Ribbon Shiner again contributed to differences in the Cypress, while the Blackspotted Topminnow and Western Mosquitofish were more abundant in the Sabine. Furthermore, results indicated that several species were collected only at individual basins. For example, the Mississippi Silvery Minnow, Sabine Shiner, and Pallid Shiner were restricted to the Neches, whereas the Flathead Catfish, Suckermouth Minnow and Starhead Minnow were only found in the Sabine. Likewise, Striped Shiner, Ironcolor Shiner, and Orangespotted Sunfish were collected only in the Cypress basin.

In the Fall season, significant differences in stream assemblages was observed in the Neches and Sabine (Pseudo-$F_{1,53}$ = 3.64, p = 0.001), Neches and Cypress (Pseudo-$F_{1,37}$ = 4.17, $p < 0.001$), and Sabine and Cypress (Pseudo-$F_{1,34}$ = 3.78, $p < 0.001$; Figure 29). Differences between the Neches and Sabine sites could be explained by high abundance of the Blackstripe Topminnow and Blacktail Shiner in the Neches, while the Blackspotted Topminnow was more abundant in the Sabine. Differences between the Neches and Cypress were influenced by higher abundances of the Western Mosquitofish in the Neches and the Redfin Shiner in the Cypress. Similarly, comparisons between the Sabine and Cypress indicated greater abundance of the Western Mosquitofish in the Sabine, while the Redfin Shiner and Pirate Perch were more abundant in the Cypress. In addition, results from the fall indicated that the Mississippi Silvery Minnow, Black Crappie, and Suckermouth Minnow were collected only in the Neches, and the Chestnut Lamprey, and the Banded Pygmy Sunfish were only found in the Sabine, and the Striped Shiner, Flier, and Redear Sunfish were only collected in the Cypress.

Only assemblages from the Neches and Sabine were compared during the spring (Pseudo-$F_{1,54}$ = 5.12, p = 0.001) and were found to be statistically different. Such differences were influenced by the abundance of Blackstripe Topminnow in the Neches, and Blackspotted Topminnow and Redfin Shiner in the Sabine. In the spring, the Neches and Sabine basins differed in species composition, with the Goldstripe Darter, Pallid Shiner, and Channel Catfish collected only in the Neches, whereas the Scaly Sand Darter was only collected in the Sabine.

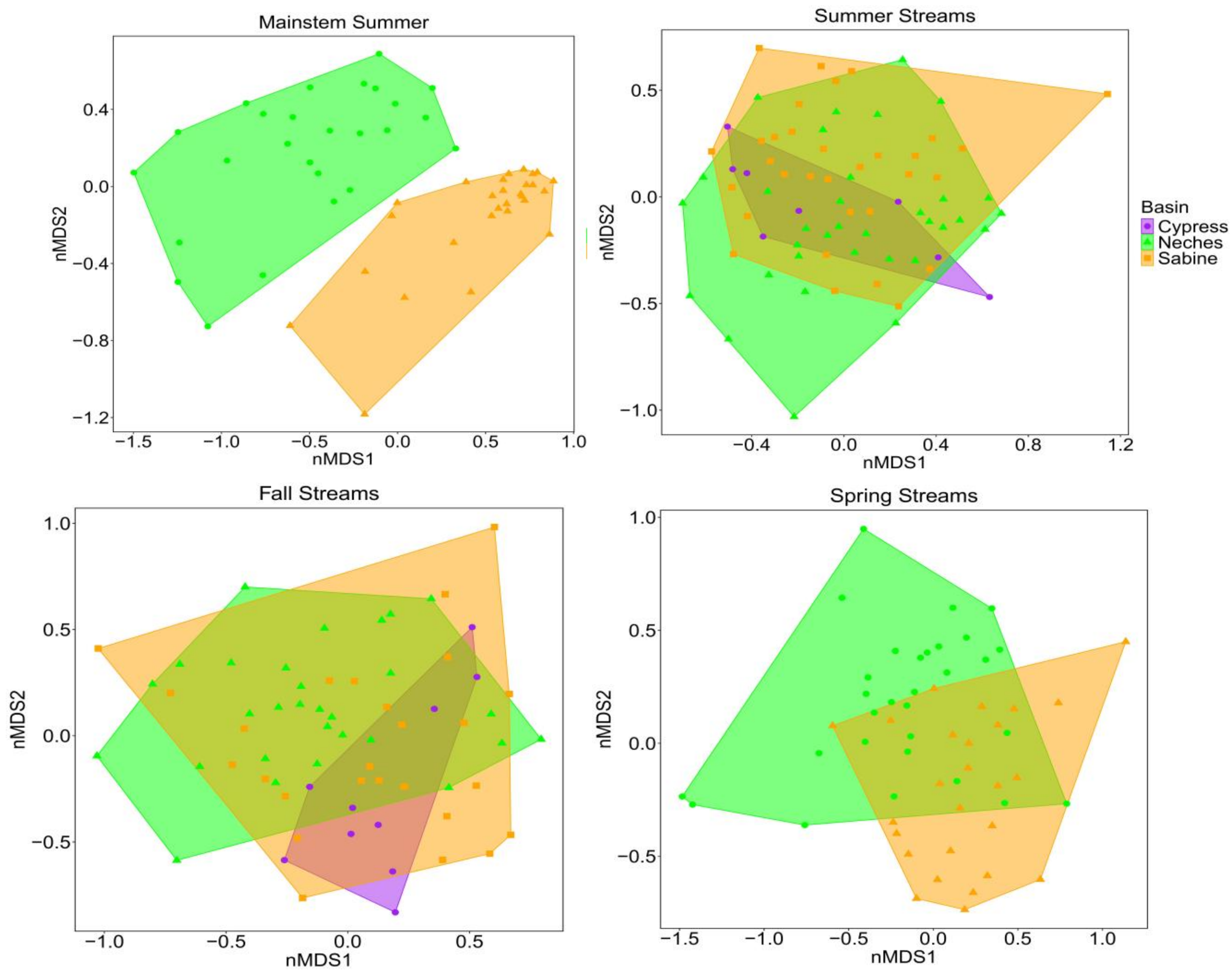

Figure 29. Non-metric multidimensional scaling (NMDS) analyses of fish assemblage based on the species abundance for the mainstem of the Neches and Sabine sampled in summer 2023, and streams of Neches, Sabine, and Cypress surveyed in summer 2023−24, Fall 2023−24, and spring 2024−25. The River basins are represented by different colors (i.e., Neches = green; Sabine = Orange; and Cypress = purple). Symbols (i.e., circle, triangle, square) within the polygons represent the sites sampled in each river basin.

The RDA model performed for the fish assemblages in sites of the mainstem rivers of the Neches and Sabine indicated a significant relationship between fish assemblage composition and the measured environmental variables ($F_{7,45} = 5.72$, $p = 0.001$, adjusted $R^2 = 0.47$; Figure 30), RDA1 and RDA2 axes yielded 37.9% of variation of the factors explaining fish assemblage due to local variables associated with hydrological and habitat characteristics. The RDA1 (29.4%) separated sites based on flow and canopy coverage, with positive values associated with sites of the Neches, containing greater canopy coverage, and negative values corresponded with sites in the Neches that had reduced flow. RDA2 (8.3%) reflected a gradient of macrophyte cover and water conductivity, with high values grouping sites in the Sabine.

For fish assemblage in the streams of the Neches, Sabine, and Cypress basins, the RDA models revealed significant relationships ($F_{7,65} = 2.33$, $p = 0.001$, adjusted $R^2 = 0.11$; Figure 30) for the summer season. Overall, RDA1 and RDA2 explained 10.0% of the total variation. RDA1 (6.6%) represented a gradient of turbidity and mud/silt substrate, with positive values grouping sites in the Sabine and Cypress with higher turbidity and mud/silt substrates. RDA2 (5.7%) represented a gradient of DO and gravel substrate, with positive values grouping sites in the Sabine having higher DO values, and negative values corresponded to sites in the Neches with lower gravel percentages.

In the fall season, the RDA model revealed significant relationships between fish assemblage composition and the measured environmental variables ($F_{8,55} = 3.11$, $p = 0.001$, adjusted $R^2 = 0.21$; Figure 30), with axes RDA1 and RDA2 together explaining 18.9% of the total variation. The RDA1 (12.2%) showed a gradient separating sites based on water chemistry and stream morphology, with positive values along RDA1 associated with sites with greater depth and higher DO values and negative values associated with sites having lower water conductivity. RDA2 (6.7%) separated sites based on temperature and flow, with negative scores corresponding to sites with lower temperature and flows, such as seen in the Sabine.

Finally, in the spring season, an RDA model was performed on the fish assemblages within the Neches and Sabine streams only. Cypress sites were not sampled in the spring due to high flow conditions. The relationships between fish assemblage composition and the measured environmental variables was also significant ($F_{8,47} = 2.48$, $p = 0.001$, adjusted $R^2 = 0.18$; Figure 30), with axes RDA1 and RDA2 together explaining 19.0% of the total variation. RDA1 (5.9%) represented a gradient of wetted width, with positive scores corresponding to greater wetted widths as seen in most Neches sites. RDA2 (4.9%) represented a gradient of macrophyte density, with negative scores corresponding to lower percentages of macrophytes also corresponding to sites within the Neches.

All RDA models suggested that several environmental variables are important for structuring community composition across sites and seasons. However, the RDAs did not reveal any specific associations among focal individual species and environmental variables measured in this study.

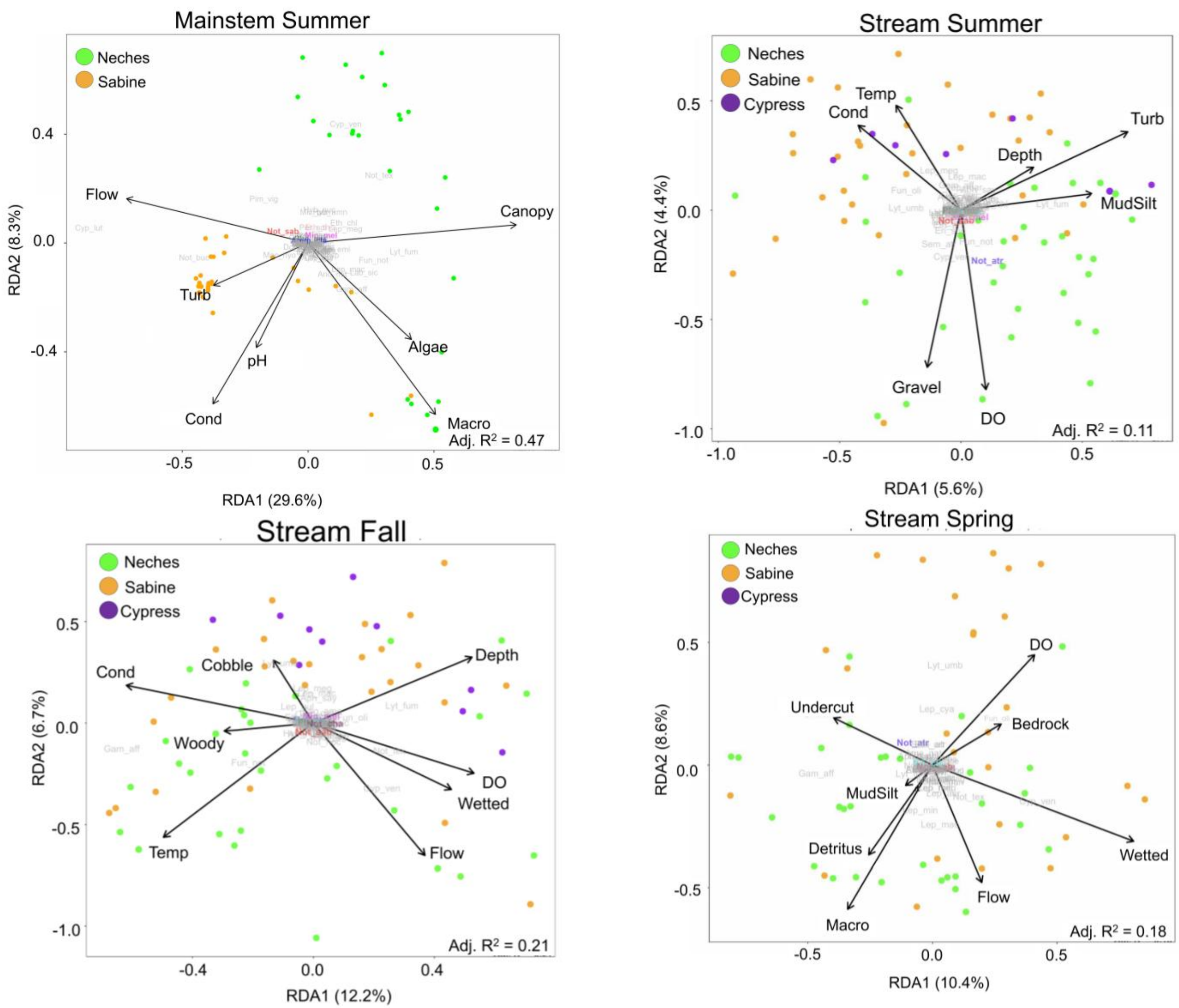

Figure 30. Redundancy analysis (RDA) biplots showing the relationship between environmental variables and fish assemblage containing the focal species in the mainstem (Summer 2023) and streams (Summer 2023–24, Fall 2023–24, and Spring 2024–25).

Local Stream Predictors of Imperiled Species Distribution in East Texas

The Random Forest Models' performance varied by species, with out-of-bag (OOB) classification error rates ranging from 6.94% for the Sabine Shiner to 23.08% for the Western Creek Chubsucker (Table 6). Variable importance plots (Figure 31) and partial dependence plots (Figures 32 and 33) revealed the top five local habitat predictor variables for the occurrence of the focal species in this study.

The three leucisids: Blackspot Shiner, Sabine Shiner, and Suckermouth Minnow, all shared several key local predictors including woody debris, stream order, temperature, and depth. In addition, other predictors were unique for each species (Figure 32). For instance, stream slope was unique to the Blackspot Shiner (Figure 32e), whereas canopy cover was for Sabine Shiner and Suckermouth Minnow (Figure 32f,o). The Blackspot Shiner had high probability of occurrence in shallow, first and second order streams with available woody debris and greater slope (Figure 32 a–e). For the Sabine Shiner the best predictors were canopy cover (higher probability of occurrence in streams with less canopy cover < 30), less woody debris, higher temperature, depth (variable), and stream orders 4−6 (Figure 32 f–j). The occurrence of the Suckermouth Minnow was primarily associated with the presence of woody debris, larger streams of 3–5 order, depth (i.e., highest probability at 0.6 m), higher temperature, and canopy cover between 25−60% (Figure 32 k–o).

The occurrence of the Gumbo Darter was predicted by water conductivity (~ 300 um/cm), larger stream orders 3 and 5, lower dissolved oxygen (DO), lower stream flow, and deeper area of the stream (Figure 33 a–e). For the sucker species, the models suggest that the Spotted Sucker was likely to occur in streams with more percent macrophyte cover (>20%), slope, mud/silt substrate (~30% <), woody debris (~20% >), and pH (Figure 33 f–j). While the Western Creek Chubsucker was more likely to occur in sites with lower temperature (i.e., ~25^{o} C or less), clay substrate (~25% or more), woody debris (> ~25%), depth (< ~ 0.5m), and conductivity (< ~ 100 µS/cm; Figure 33 k–o).

Table 6. Out-of-Bag (OOB) estimated error rate percentages for Random Forest models of focal imperiled species.

Species	***OOB Estimated Error Rate***
Blackspot Shiner	11.69%
Sabine Shiner	6.94%
Suckermouth Minnow	8.33%
Gumbo Dater	10.94%
Spotted Sucker	21.05%
Wester Creek Chubsucker	23.08%

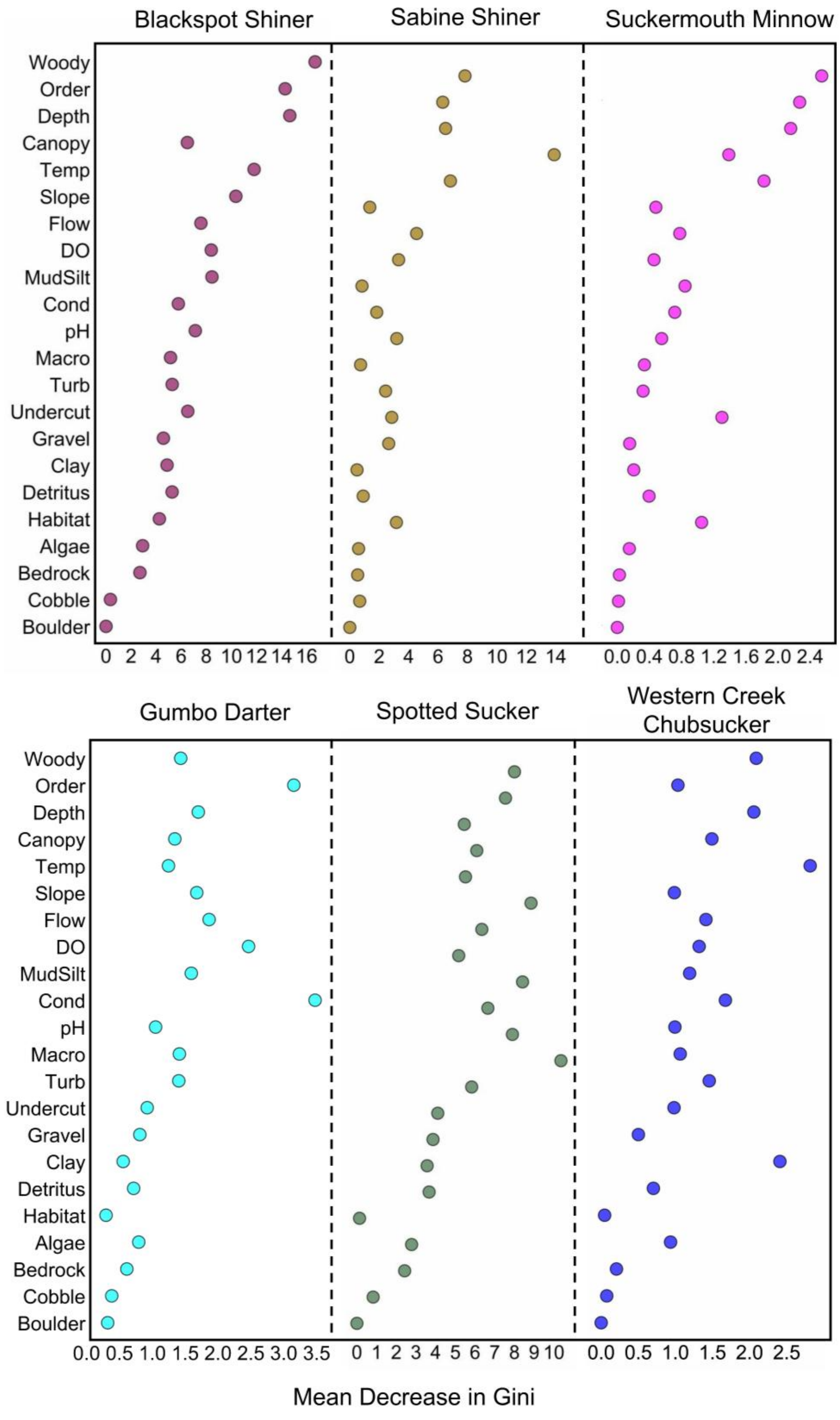

Figure 31. Variable importance plots for each species-specific random forest model ranked by overall contribution to the model, with greater mean decrease in Gini indicating higher predictor importance.

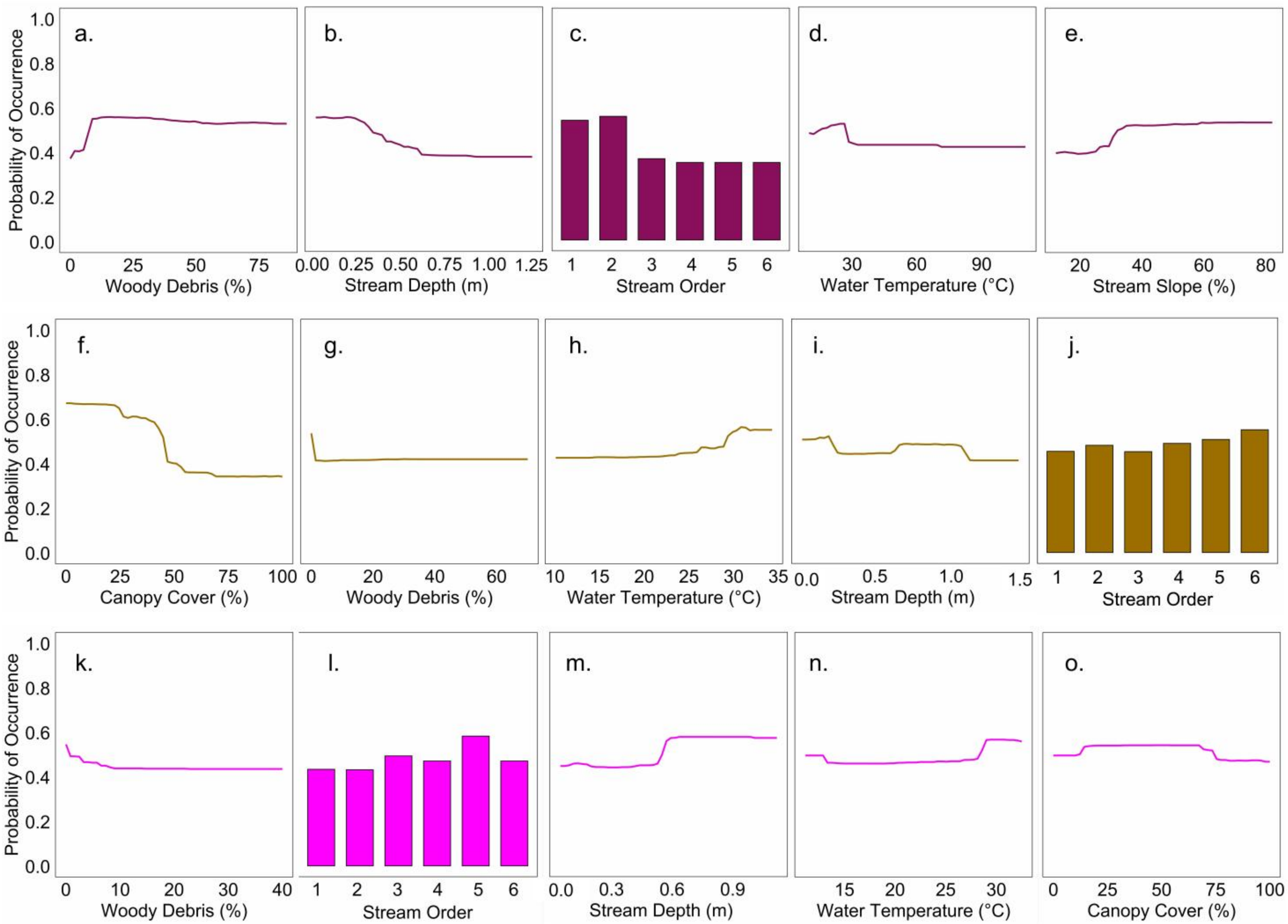

Figure 32. Partial dependence plots of the five most important local variables contributing to random forest models predicting the probability of occurrence of focal species in the Neches, Sabine, and Cypress River basins. Panels a–e corresponds to Blackspot Shiner, panels f–j corresponds to Sabine Shiner, and panels k–o corresponds to Suckermouth Minnow.

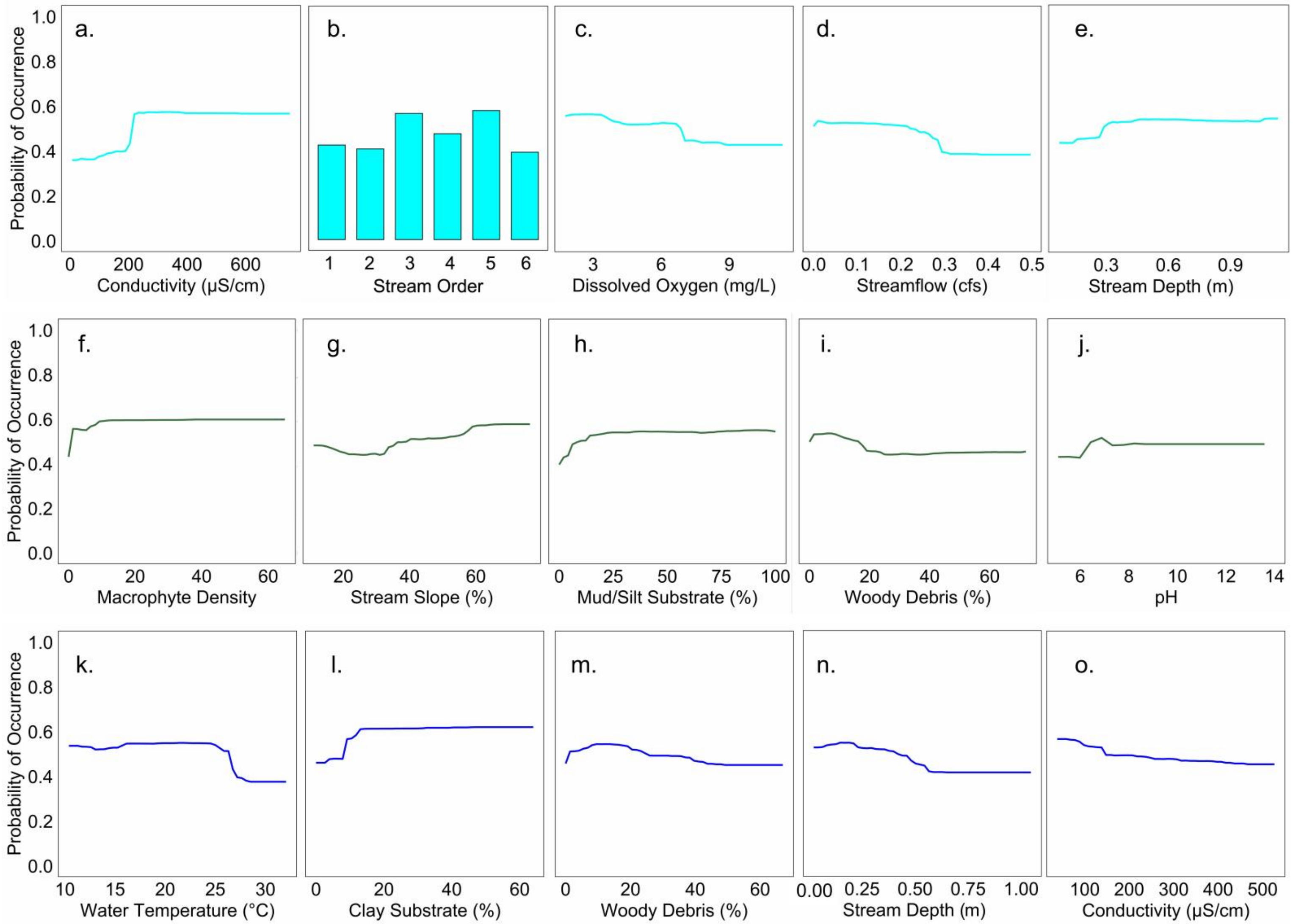

Figure 33. Partial dependence plots of the five most important local variables contributing to random forest models predicting the probability of occurrence of focal species in the Neches, Sabine, and Cypress River basins. Panels a–e corresponds to Gumbo Darter, panels f–j corresponds to Spotted Sucker, and panels k–o corresponds to Western Creek Chubsucker.

Co−Occurrence Models Predicting Associations among Imperiled Fish Species and Associated Assemblages

When assemblages were combined and examined at the annual scale, most species pair relationships were positive (aggregated) within the community (Figure 34). However, individual species relationships, suggested that Blackspot Shiner and Sabine Shiner exhibited the high (~60%) negative associations (i.e., segregation from other fish species) within the assemblage (Figure 34). All other focal species revealed high positive association (~80%; Figure 34). Co-occurrence analysis by season also suggested positive associations for most species across the total assemblage (Figures 35–37). Consistently, the Sabine and Blackspot shiners had high percentages of negative associations compared to the other focal species across seasons (Figures 35–37).

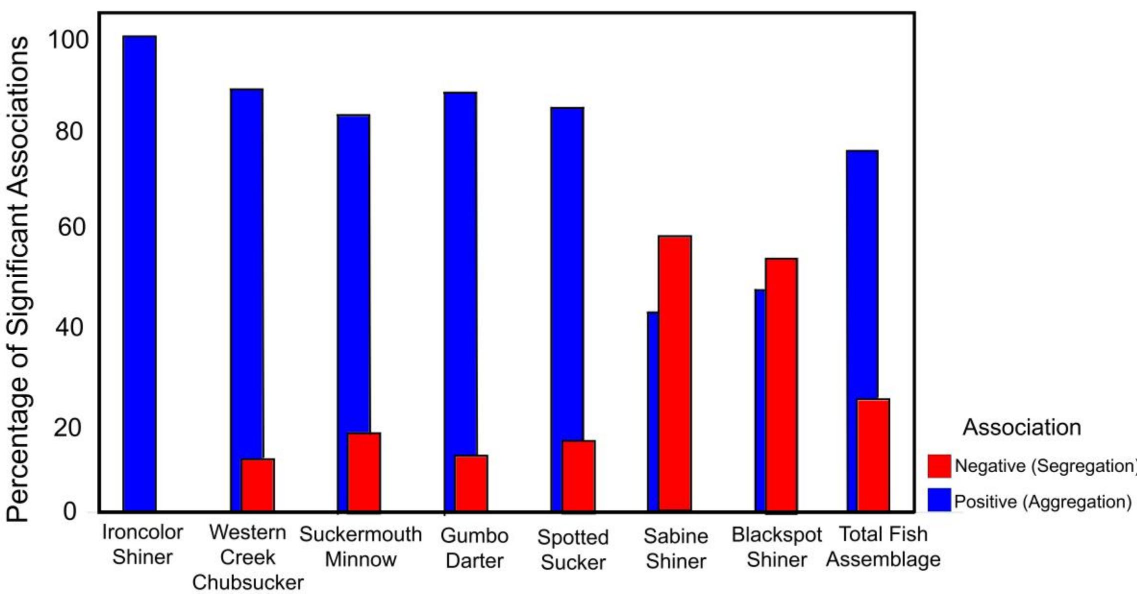

Figure 34. Bar plot showing the percent of total significant pairings for each focal species at the annual scale. The right-most bar represents the assemblage-wide percentages. Positive associations are in red and negative associations are in red.

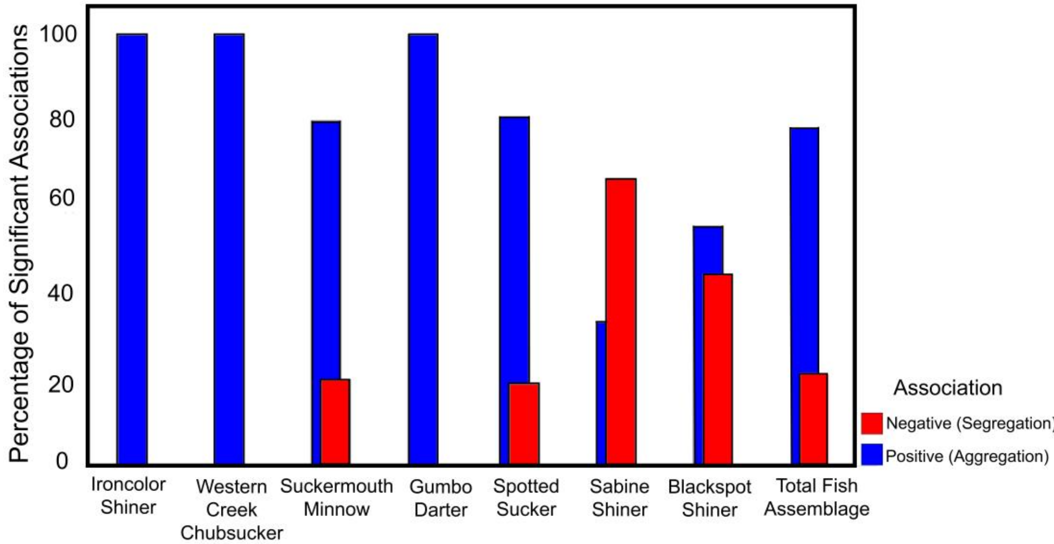

Figure 35. Bar plot showing the percent of total significant pairings for each focal species for summer. The right-most bar represents the assemblage-wide percentages. Positive associations are in red and negative associations are in red.

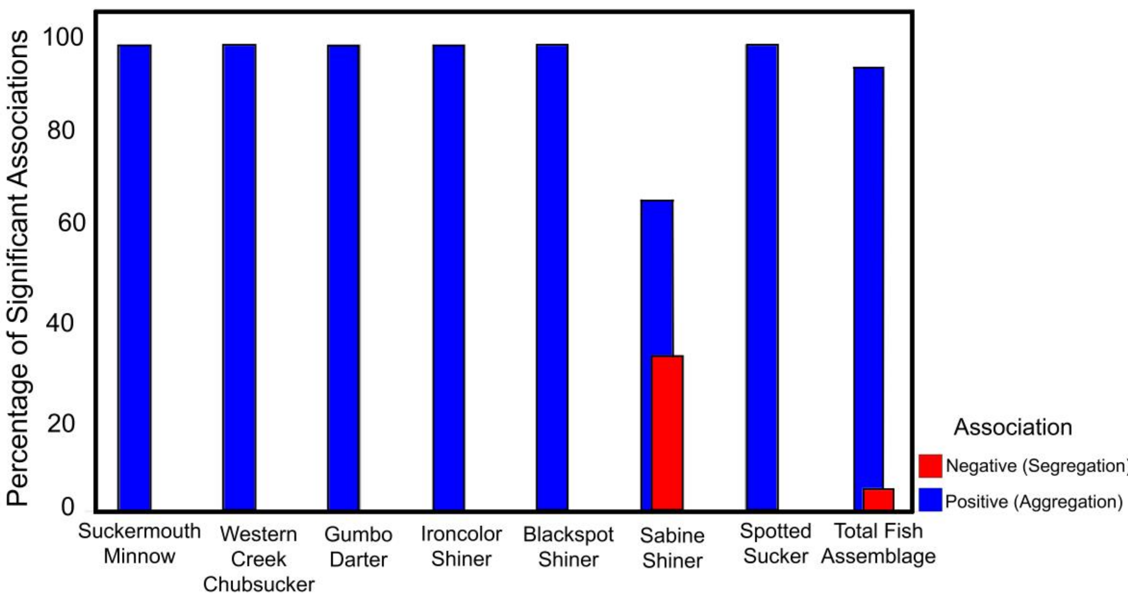

Figure 36. Bar plot showing the percent of total significant pairings for each focal species for fall. The right-most bar represents the assemblage-wide percentages. Positive associations are in red and negative associations are in red.

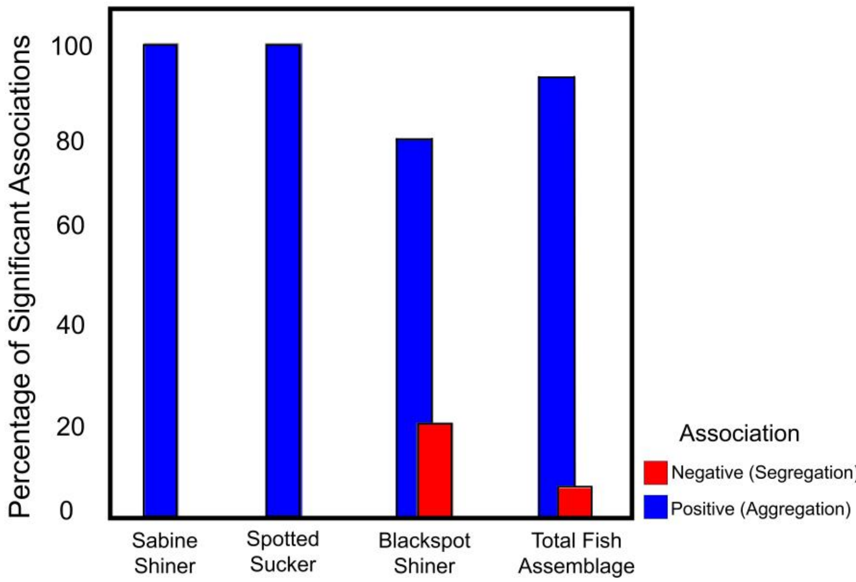

Figure 37. Bar plot showing the percent of total significant pairings for each focal species for spring. The right-most bar represents the assemblage-wide percentages. Positive associations are in red and negative associations are in red.

When co-occurrence patterns were examined by each focal species, both positive and negative associations were observed at the seasonal and annual scale for each species (Figures 38−44; Table 7). First, the Blackspot Shiner displayed negative associations, with other focal species. In the summer, it was negatively associated with both the Suckermouth Minnow and the Sabine Shiner (Figures 38), also it showed negative association with the Sabine Shiner at the annual scale (Figure 38 and 40). In contrast, the Blackspot Shiner was positively associated with the Spotted Sucker on the annual scale (Figures 38 and 43). The Ironcolor Shiner, was only found at one creek in the Cypress during the fall and summer and had positive associations with three species in the community including the Banded Pygmy Sunfish, Cypress Minnow, and Cypress Darter (Figure 39).

The Sabine Shiner, Suckermouth Minnow, and Gumbo Darter were all positively associated to one another, and also with the Mississippi Silvery Minnow, a species of conservation concern not addressed in this study. All three species were segregated from sunfishes (Figures 40–42), particularly the Bluegill, Green, and Warmouth sunfishes. The Spotted Sucker and Western Creek Chubsucker exhibited mostly positive associations with a variety of species, including the Bluegill and Redspotted sunfishes, and two catfishes, the Yellow Bullhead and Black Bullhead (Figures 42 and 43).

Table 7. List of species and corresponding abbreviations used for the species co–occurrence figures (Figures 38–43).

Common Name	Scientific Name	Name Abbreviation
Banded Pygmy Sunfish	*Elassoma zonatum*	BPS
Bigscale Logperch	*Percina macrolepida*	BLP
Black Bullhead	*Ameiurus melas*	BBH
Black Crappie	*Pomoxis nigromaculatus*	BC
Blackspot Shiner	*Notropis atrocaudalis*	BSS
Blackspotted Topminnow	*Fundulus olivaceus*	BSTM
Blackstripe Topminnow	*Fundulus notatus*	BTM
Blacktail Redhorse	*Moxostoma poecilurum*	BTR
Blacktail Shiner	*Cyprinella venusta*	BTS
Blue Catfish	*Ictalurus furcatus*	BCF
Bluegill Sunfish	*Lepomis macrochirus*	BGS
Bluntnose Darter	*Etheostoma chlorosoma*	BND
Bowfin	*Amia calva*	BF
Brook Silverside	*Labidesthes sicculus*	BS
Bullhead Minnow	*Pimephales vigilax*	BHM
Channel Catfish	*Ictalurus punctatus*	CCF
Chestnut Lamprey	*Ichthyomyzon castaneus*	CL
Creek Chub	*Semotilus atromaculatus*	CC
Cypress Darter	*Etheostoma proeliare*	CD
Cypress Minnow	*Hybognathus hayi*	CM
Bowfin	*Amia calva*	BF
Brook Silverside	*Labidesthes sicculus*	BS
Leuciscidae Species	NA	LUSP
Dollar Sunfish	*Lepomis marginatus*	DSF

Table 7. Continued.

Common Name	Scientific Name	Name Abbreviation
Dusky Darter	*Percina sciera*	DD
Flier	*Centrarchus macropterus*	FLR
Ghost Shiner	*Notropis buchanani*	GHS
Gizzard Shad	*Dorosoma cepedianum*	GS
Golden Shiner	*Notemigonus crysoleucas*	GOS
Goldstripe Darter	*Etheostoma parvipinne*	GSD
Green Sunfish	*Lepomis cyanellus*	GSF
Gumbo Darter	*Etheostoma thompsoni*	GD
Harlequin Darter	*Etheostoma histrio*	HD
Inland Silverside	*Menidia beryllina*	ISS
Lake Chubsucker	*Erimyzon sucetta*	LCS
Largemouth Bass	*Micropterus salmoides*	LMB
Lepomis Species	*Lepomis spp.*	LSP
Longear Sunfish	*Lepomis megalotis*	LES
Mississippi Silvery Minnow	*Hybognathus nuchalis*	MSM
Orangespotted Sunfish	*Lepomis humilis*	OSS
Pallid Shiner	*Hybopsis amnis*	PS
Pirate Perch	*Aphredoderus sayanus*	PP
Pugnose Minnow	*Opsopoeodus emiliae*	PNM
Red Shiner	*Cyprinella lutrensis*	RS
Redbreast Sunfish	*Lepomis auritus*	RBSF
Redear Sunfish	*Lepomis microlophus*	RES
Redfin Pickerel	*Esox americanus*	RFP
Redfin Shiner	*Lythrurus umbratilis*	RFS

Table 7. Continued.

Common Name	Scientific Name	Name Abbreviation
Redspot Darter	*Etheostoma artesiae*	RSD
Redspotted Sunfish	*Lepomis miniatus*	RSS
Ribbon Shiner	*Lythrurus fumeus*	RBS
River Darter	*Percina shumardi*	RD
Sabine Shiner	*Notropis sabinae*	SS
Scaly Sand Darter	*Ammocrypta vivax*	SSD
Shoal Chub	*Macrhybopsis hyostoma*	SC
Slough Darter	*Etheostoma gracile*	SLD
Spotted Bass	*Micropterus punctulatus*	SPB
Spotted Gar	*Lepisosteus oculatus*	SG
Spotted Sucker	*Minytrema melanops*	SSK
Striped Shiner	*Luxilus chrysocephalus*	STS
Suckermouth Minnow	*Phenacobius mirabilis*	SMM
Tadpole Madtom	*Noturus gyrinus*	TM
Threadfin Shad	*Dorosoma petenense*	TFS
Warmouth	*Lepomis gulosus*	WM
Weed Shiner	*Notropis texanus*	WS
Western Mosquitofish	*Gambusia affinis*	WMF
White Crappie	*Pomoxis annularis*	WC
Yellow Bullhead	*Ameiurus natalis*	YBH

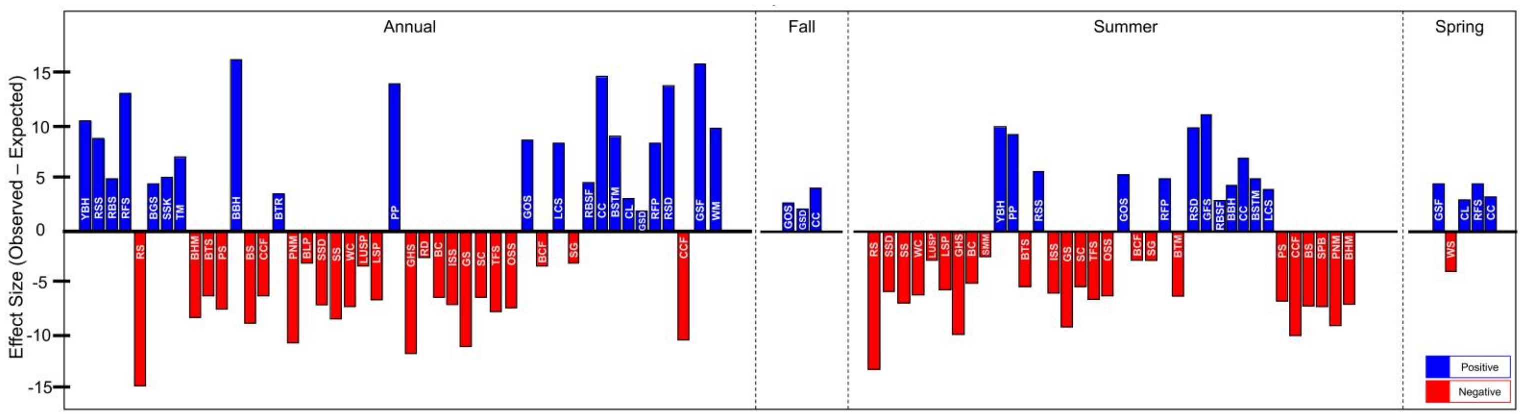

Figure 38. Bar plot showing species significantly associated with the Blackspot Shiner at the annual and seasonal (i.e., Fall, Summer, Spring) scale, based on a probabilistic co-occurrence model. Blue bars indicate positive (aggregated) associations, and red bars indicate negative (segregated) associations. Bar height reflects effect size, calculated as the difference between observed and expected co-occurrence.

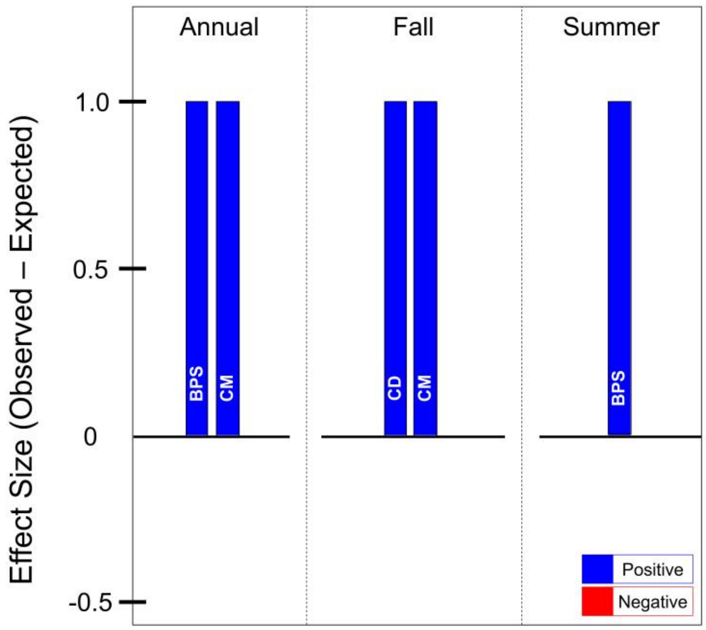

Figure 39. Bar plot showing species significantly associated with the Ironcolor Shiner at the annual, and seasonal (i.e., Fall and Summer) scale, based on a probabilistic co-occurrence model. Blue bars indicate positive (aggregated) associations, and red bars indicate negative (segregated) associations. Bar height reflects effect size, calculated as the difference between observed and expected co-occurrence. Species names are labeled within or below each bar.

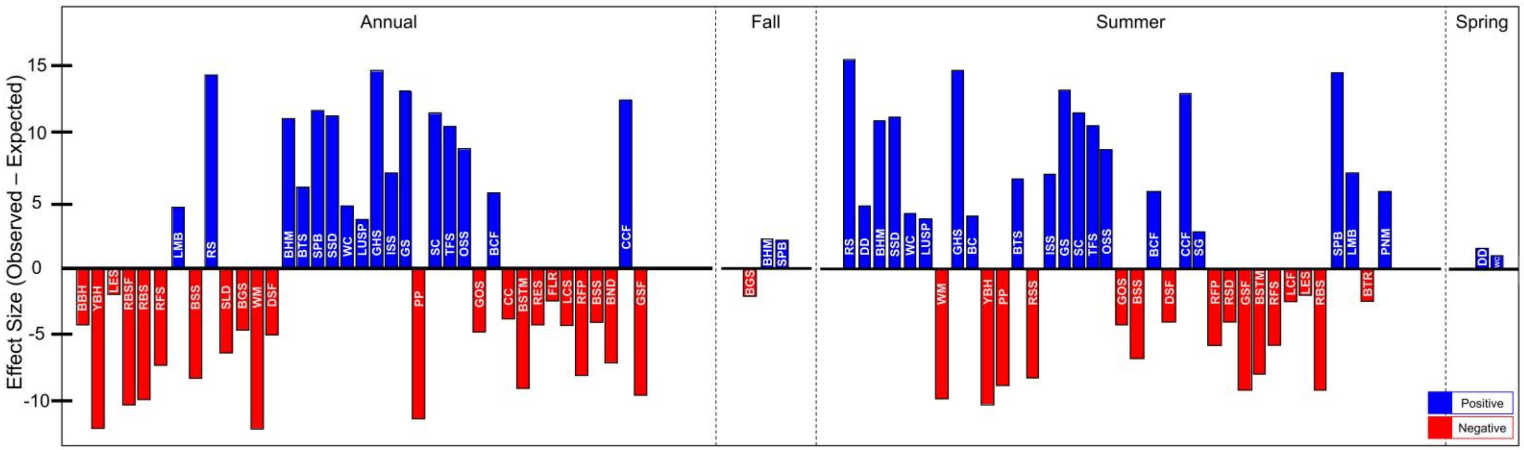

Figure 40. Bar plot showing species significantly associated with the Sabine Shiner at the at the annual and seasonal (i.e., Fall, Summer, Spring) scale, based on a probabilistic co-occurrence model. Blue bars indicate positive (aggregated) associations, and red bars indicate negative (segregated) associations. Bar height reflects effect size, calculated as the difference between observed and expected co-occurrence. Species names are labeled within or below each bar.

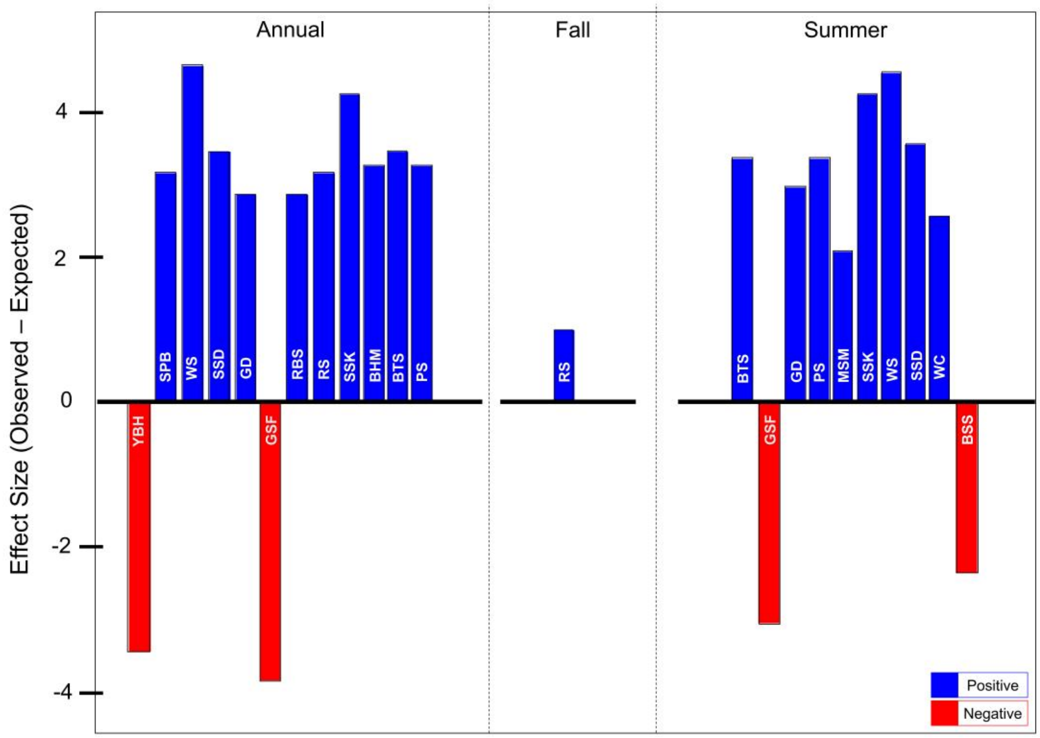

Figure 41. Bar plot showing species significantly associated with the Suckermouth Minnow at the annual and seasonal (i.e., Fall, Summer) scale, based on a probabilistic co-occurrence model. Blue bars indicate positive (aggregated) associations, and red bars indicate negative (segregated) associations. Bar height reflects effect size, calculated as the difference between observed and expected co-occurrence. Species names are labeled within or below each bar.

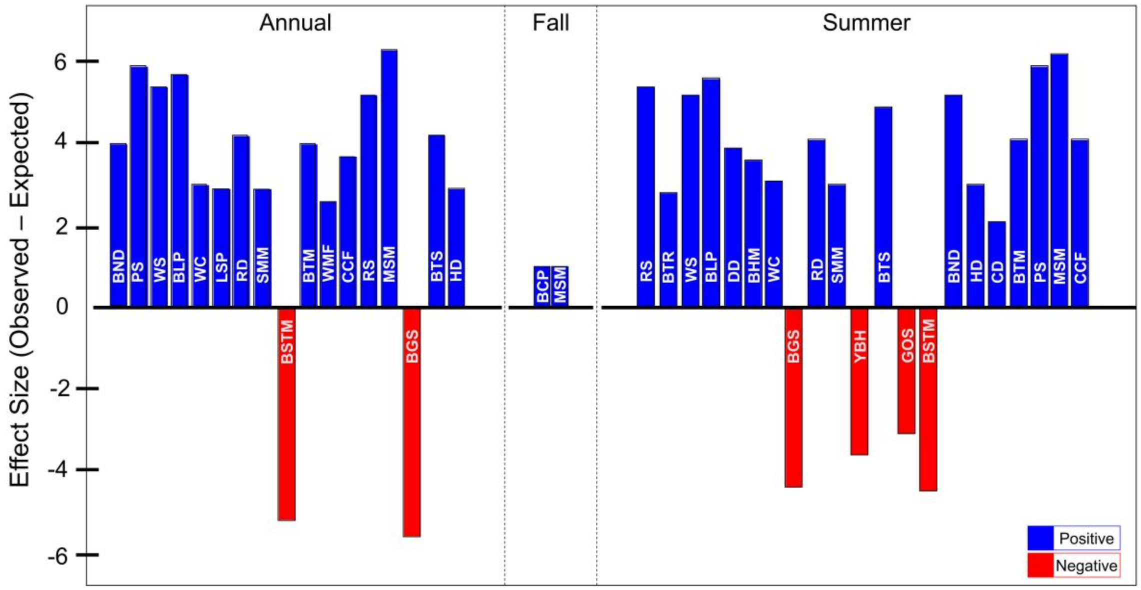

Figure 42. Bar plot showing species significantly associated with the Gumbo Darter at the annual, and seasonal (i.e., Fall, Summer) scale, based on a probabilistic co-occurrence model. Blue bars indicate positive (aggregated) associations, and red bars indicate negative (segregated) associations. Bar height reflects effect size, calculated as the difference between observed and expected co-occurrence. Species names are labeled within or below each bar.

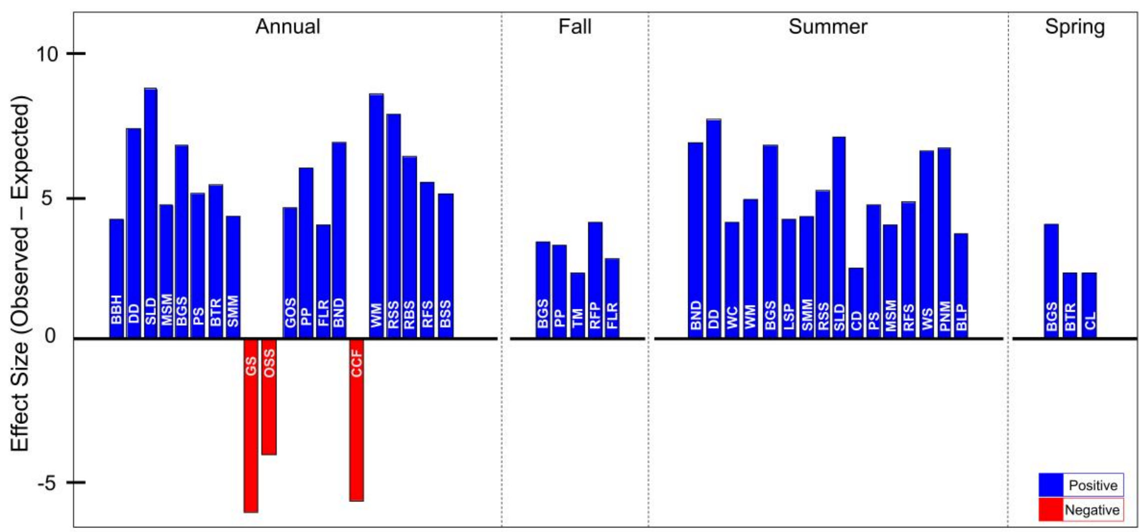

Figure 43. Bar plot showing species significantly associated with the Spotted Sucker at the annual and seasonal (i.e., Fall, Summer, Spring) scale, based on a probabilistic co-occurrence model. Blue bars indicate positive (aggregated) associations, and red bars indicate negative (segregated) associations. Bar height reflects effect size, calculated as the difference between observed and expected co-occurrence. Species names are labeled within or below each bar.

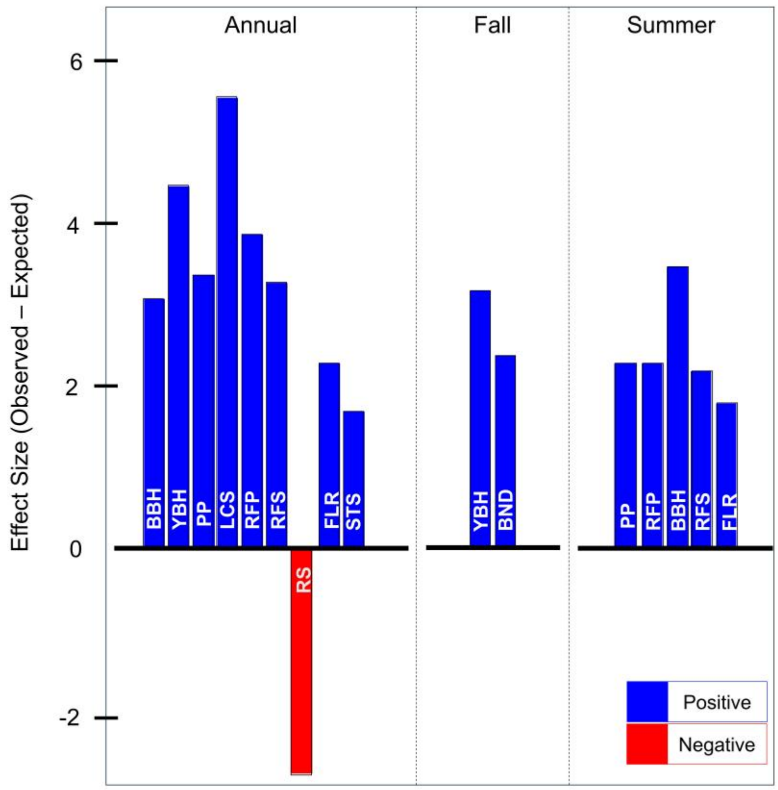

Figure 44. Bar plot showing species significantly associated with the Western Creek Chubsucker at the annual and seasonal (i.e., Fall and Summer) scale, based on a probabilistic co-occurrence model. Blue bars indicate positive (aggregated) associations, and red bars indicate negative (segregated) associations. Bar height reflects effect size, calculated as the difference between observed and expected co-occurrence. Species names are labeled within or below each bar.

Discussion

Species distributions are influenced by multiple interacting factors which operate at various (i.e., spatial and/or temporal) scales. East Texas, which contains a very high freshwater diversity, is considered a hotspot for emerging human development (TPWD 2012). Therefore, distributional data of freshwater fishes across spatial and temporal scales can provide valuable information, especially for native freshwater fish species that are facing high rates of imperilment. In this study, we provided information on the distribution and occurrence for ten imperiled fish species inhabiting streams within the Neches, Sabine, and Cypress River basins in east Texas. First, we used ecological niche modeling (MaxEnt) to identify environmental variables at the regional scale that could help predict the probability of occurrence and distribution of targeted species in these river basins across two time periods (i.e., historical and contemporary). Findings from the models reveal that two hydrological variables, stream flow and stream order, were important top predictors of focal fish species in both time periods. Land use variables associated with percentage of forest cover and pasture-crop also helped to predict the distribution of some shiners, darters, and suckers across time periods. My results showed that flow dependent species (e.g., shiners and darters) were highly influenced by flow and have high probabilities of occurrence at higher stream flow. Sucker species also showed responses to flow and stream order inferring the importance of these variables for species movements which could be related to spawning and recruitment within the studied basins. These results supported my hypothesis in that some land cover variables and hydrological factors were important predictors for focal species distributions (H1). However, while niche modeling appeared informative for most fish species across both time periods, it was less informative for species that had limited or missing occurrence data (e.g., Orangebelly Darter).

I also examined local environmental variables (e.g., abiotic and biotic) to help predict the occurrence of focal fish species in streams within these three river basins and across three seasons (i.e., summer, fall, spring). we found water chemistry, water depth, stream order, and substrate diversity were primary predictors of local species occurrence in east Texas streams. This result supports the regional hydrological predictors discussed above and strengthens the importance of these variables for persistence and conservation of imperiled species within these river basins. Additionally, given that most of the focal fish species in this study are small-medium sized body and habitat and/or fluvial specialists, we predicted high patterns of aggregation (i.e., co-occurrence) as result of similar habitat requirements. This prediction was partially supported with my data and co-occurrence patterns appeared to be influenced by seasonal environmental conditions and also species life histories. For example, when species co-occurrence patterns were examined at the annual scale (i.e., all seasons together), the Black Shiner and Sabine Shiner segregate from each other (i.e., less likely to co-occur) and these patterns persisted when compared by season (e.g., summer). These two shiners are known as habitat specialists, typically found in riffle-run habitat with sand-cobble substrate (William & Bonner, 2006; Bean et al., 2010; Swanson, 2022), therefore negative associations predicted by the model might suggest coexistence of these shiners in the same streams can be mediated by finer microhabitat variables (not measured in this study) that allow segregation (e.g., food, habitat use) within these streams.

Regional environmental predictors and species distribution

Among regional environmental predictors, my results suggest that stream flow and stream order were key predictors for most focal species across both time periods. In freshwater ecosystems, these variables have been recognized as important factors for community organization. Travnichek and Maceina (1994) examined flow regulation effects on fish assemblages in the Tallapoosa River, Alabama. Their results suggested that more fluvial specialist species, including Cyprinids and Catostomids, were found in un-regulated rivers, while more generalist species were in regulated rivers. Natural flow regimes influence ecological processes of species such as spawning, growth, and their dispersal (Poff et al., 1997; Freeman et al., 2022). For broadcaster spawning fish species, flow is an importantfactor because these species rely heavily on consistent flows for successful development of their eggs and aides in dispersal of the species (Williams & Bonner, 2006; Bean et al., 2010; Steffensmeier et al., 2024). Stream order compliments stream flow as it is a reflection of the stream size and the physical and biological transitions that accompany it (Platts, 1979; Argent et al., 2002).

Stream flow and stream order have been identified as important predictors of the occurrence of imperiled fish species in other studies conducted in Texas streams (Acre et al., 2021, Parker et al., 2021; Evans et al., 2023). Recruitment, survival, and reproduction of the two endangered Texas shiners, the Smalleye Shiner *Notropis buccula* and Sharpnose Shiner *N. oxyrhynchus* have been linked to natural flow regime of the Brazos River in Texas (Moss & Mayes, 1993; Wilde & Urbanczyk, 2013). The Blue Sucker *Cycleptus elongatus,* a Texas state threatened species, is also associated with higher flows, and recent studies suggest that the species occurred in areas where flow was less regulated and the natural flow regime was maintained (Evans et al., 2023). Findings from this study somewhat agree that water flow influences of stream fishes, for instance, most of the shiners (Leuciscidae), darters (Percidae), and suckers (Catostomidae) in this study increased probability of occurrence when flows increased.

The Western Creek Chubsucker and Orangebelly Darter were two species in this study whose probability of occurrence decreased as flow increased. Few information is available in Texas for these two species. However, studies in Oklahoma suggest that the Orangebelly Darter is typically found in riffle and run habitats in lower order streams (Scalet, 1971; 1973). These lower order streams typically have lower overall flow compared to higher order streams but still contain locally fast-flowing habitats suitable for this species, in agreement with my findings. The Western Creek Chubsucker showed high probability of occurrence across a range of stream orders and high flows in the historical model, but in the contemporary model, the species was predicted to have high probability of occurrence at lower flows. The chubsucker typically occupies smaller streams with moderate flow but has been observed to move into even smaller streams for spawning (Wall & Gilbert, 1980; Carman, 2001). The shift in flow influence between the historical and contemporary models may reflect the species movement associated with this reproductive behavior. Further studies focusing on the spawning and reproductive behavior of sucker species in east Texas streams can fill these gaps.

Across both time periods, most focal species also showed higher probabilities of occurrence in medium to high order streams (i.e., orders 3–6). The Sabine Shiner and Suckermouth Minnow were predicted to be in high order streams, while the Blackspot Shiner and Spotted Sucker appeared to occur in a greater range of stream orders with swiftly flowing water. In Arkansas, the Spotted Sucker has been reported from small to moderate streams, backwaters of large rivers, and even in reservoirs (Robison & Buchanan, 2020). A recent study in

East Texas, reported that stream order was an important predictor for the Spotted Sucker, with the species preferring sites in the mainstem river channels (Umstott, 2025).

Variations in the probability of species occurrence across stream orders may reflect differences in species life history and habitat needs. For example, larger order streams generally provide greater habitat availability and more stable environmental conditions, but sand and gravel substrates tend to be less abundant as stream order increases (Platts, 1979). Given its spawning behavior as a substrate spawner, the Orangebelly Darter might prefer low order streams because there may be more available habitat that allows the species to bury their eggs in loose gravel substrate. The Spotted Sucker is generally associated with larger order streams, it has migratory behaviors and has been known to migrate into lower order streams to spawn over sand and gravel substrates (Jackson, 1958; Mettee et al., 1996). Juvenile suckers remain in these smaller streams as they grow and develop, which aligns with model predictions showing high probabilities of occurrence across a range of stream orders. The Suckermouth Minnow is also a substrate spawner, and while it was consistently predicted by high order streams, there were moderate probabilities of occurrence in stream orders 2–4. This is consistent with Robison & Buchanan, 2020, who reported that over most of the species' range, the Suckermouth Minnow occurs in streams of all sizes.

Land cover variables including pasture/crop, developed, and forest cover were also important for the occurrence of the focal species in this study. Changes in land use have been linked to approximately 39% of the impacts on imperiled freshwater fishes in North America (Jelks et al., 2008; Utz et al., 2010). All focal species in this study exhibited higher probabilities of occurrence at lower percentages of this pasture/crop land cover, both historically and contemporarily. Agricultural and urban land use are typically associated with siltation, nutrient and chemical inputs, and channel modification, all of which degrade stream habitats (Wang et al., 1997; Allan, 2004; Brown et al., 2005). While urbanization and agriculture degrade streams, forest land cover is generally associated with higher habitat quality, and the loss of forests (i.e., deforestation) has been shown to negatively influence streams (Wang et al., 1997; Jacobson et al., 2001). Here, we found that higher forest coverage showed lower probability of occurrence for the focal species, except for the Western Creek Chubsucker in the contemporary period. This pattern could result from land use practices in east Texas, particularly within the Neches, Sabine, and Cypress River basins. These river basins are a part of the "piney woods" ecoregion and have a history of silviculture (i.e., management of trees for timber production) practices, including timber harvesting and commercial pine plantations (Griffith et al., 2007; Joshi et al., 2012). As a result, these forested land cover areas may not represent only natural, undisturbed forests, but can also include pine plantations and harvest stands. When the trees are harvested (i.e., through clearcutting or selective removal), the process can affect streams in ways similar to development and agriculture, such as through increased sedimentation and reduced water quality (Campbell & Doeg, 1989; Lunn et al., 2017).

Besides silviculture practices, some forested streams in east Texas are generally deeper and contain fine sediments and greater amounts of woody debris (Swanson, 2022). These conditions may not be suitable for many stream fishes, including the focal species in this study, which have showed high associations with flowing water in run and riffle habitats dominated by sand and gravel substrates. In Illinois, Smith (1979) found that the Suckermouth Minnow occurred primarily in open, prairie streams rather than heavily forested ones, suggesting that dense canopy cover may reduce habitat suitability for this species. While land use was not revealed as strong predictor compared to hydrological variables, the effects of different land cover types on stream conditions highlight the importance of considering large-scale land use alongside hydrology when assessing fish species distributions, both historically and contemporarily.

Local environmental variables predicting the local fish species in streams of east Texas

Studies at local scales are essential for revealing local environmental variables and species interactions affecting the occurrence of species, such patterns that may not be evident at the regional scale. While the ordination analyses in this study did not identify specific environmental variables for individual focal species, they indicated that the overall fish assemblages were primarily influenced by water quality, substrate diversity, and hydrology. Stream habitats in the Neches, Sabine are characterized by sandy, silty, and clay substrates with both large and small woody debris (Robertson et al., 2018; SRA, 2018), streams within the Cypress River basin also contain abundant woody debris and sand–silt substrates but tends to support deeper pools (Robertson et al., 2016).

At the species level, the three leucisids (i.e., Blackspot Shiner, Sabine Shiner, and Suckermouth Minnow) shared woody debris, stream depth, water temperature, and stream order as top predictor variables. However, the order of importance varied by species, for example woody debris was the top predictor for the Blackspot Shiner and Suckermouth Minnow, but the second-best predictor for the Sabine Shiner. Additionally, increased slope resulted as key predictor of Blackspot Shiner while decreased percent canopy cover was important for the Sabine Shiner and Suckermouth Minnow. The latter agrees with other studies reporting how dense canopy cover and heavily forested area can reduce habitat suitability for the Suckermouth Minnow (Smith,1979). Additionally, the Suckermouth Minnow inhabiting streams in Colorado was found consistently associated with flow and gravel substrate (Bestgen et al., 1999). As predicted, the Sabine and Blackspot shiners were associated with sand and gravel substrate in riffle and run habitats within these streams and rivers. Williams and Bonner (2006) found that the Sabine Shiner was abundant in streams of the Angelina River, in particular, LaNana Bayou, with relatively shallow water (<0.25 m depth) and slow velocities (0–0.2 m/s). Swanson (2022) also reported high probability for the Blackspot Shiner in shallow water dominated by sand or gravel substrate in streams of east Texas,. The Gumbo Darter, the only darter species able to be modeled at the local scale, is known to have similar habitat requirements (substrates dominated by sand and gravel) as the three Leucisidae species (Suttkus et al., 2012). Random forest models revealed that stream order and depth were important local predictors for the occurrence of the Gumbo Darter. However, woody debris and macrophyte coverage were not identified as important predictors, despite Suttkus et al. (2012) reporting that the species was associated with stream banks with grasses, weeds, and exposed roots.

The catostomidae species (i.e., Spotted Sucker and Western Creek Chubsucker) were influenced more by substrate diversity (i.e., mud/silt, clay, and woody debris) and water quality variables. These findings agree with Edwards (1997), who reported that the Spotted Sucker is more likely to occur in slow, turbid, low-gradient streams with submerged vegetation and soft substrates of silt, organic debris, and sand. Like other Catostomidae species, the Western Creek Chubsucker also shares many of the habitat requirements as the Spotted Sucker. However, my results indicate some differences between the two species, primarily associated with the stream order were they were predicted to occur. The Western Creek Chubsucker is typically found in smaller order streams (Wall & Gilbert, 1980), whereas the Spotted Sucker occurs in larger streams, except during spawning periods (White, 1974; Hooley-Underwood et al., 2019). Such preferences were evident in my results, as the Western Creek Chubsucker showed a higher probability of occurrence in shallower areas of the streams.

Local co-occurrence patterns of fish species in streams of East Texas

Interspecific interactions can influence species' occurrences even when environmental conditions appear suitable. For instance, the presence of predators may alter the abundance, habitat use, or behavior of prey species (Jackson et al., 2001; Pfaff et al., 2024). These local-scale variables can ultimately shape the broader distribution patterns observed at the regional scale. For species having similar habitat preferences, such as the focal species in this study, local environmental variables may act as filters so that species with similar life-history traits and habitat requirements would be more likely to co-occur together (i.e., aggregated). In dynamic ecosystems, such as streams, this may be more likely to explain co-occurrence patterns than direct interspecific interactions (Blanchet et al., 2020). Probabilistic null models of pairwise species co-occurrence are good tools to identify species pairs that are found more than just by chance (Veech, 2013). Here, we found that most of the focal fish species exhibited co-occurrence patterns that were consistent with similar patterns of life histories and habitat preferences. For example, the Western Creek Chubsucker is known to spawn on the nests of other species such as the Creek Chub, or alongside species with similar reproductive behaviors, such as the Striped Shiner (Johnston et al., 1996). These patterns may reflect the positive annual-scale associations observed between the Western Creek Chubsucker and the Striped Shiner in this study.

When evaluating species co-occurrence patterns, it is essential to interpret the results with caution. As noted by Blanchet et al. (2020), observed associations may not always reflect true ecological interactions but can instead result from factors such as sampling methods, spatial scale, and model assumptions. However, some of the observed co-occurrence patterns from my results indicate that species interactions still may play an important role. Both the Sabine and Blackspot shiners are habitat specialists that prefer shallow riffle and run habitats containing sand and gravel substrates (William & Bonner, 2006; Swanson, 2022). Additionally, as congeneric species, they share similar life-history traits, including being classified as broadcast spawners (Williams & Bonner, 2006; Bean et al., 2010). However, in my study, the Blackspot Shiner exhibited a negative association with both the Sabine Shiner and the Suckermouth Minnow, another fluvial specialist associated with sand and gravel substrates. Species in the genus *Notropis* often occur in multispecies aggregations, using habitats and food resources that superficially appear similar. Studies have shown that coexistence of *Notropis* species appear mediated by vertical segregation in microhabitat types (Baker & Ross, 1981; Gorman, 1988; Dibble & Harrel, 2000) and feeding ecology (Mendelson, 1975). This indicates that while environmental conditions and habitat availability primarily shape the species composition, interspecific interactions could also be influencing species occurrence throughout the streams of east Texas.

Implications for Conservation

Understanding species distributions, and the environmental variables influencing their occurrence, is essential for conservation and management decisions, especially for prioritizing species and habitats for protection. As biodiversity loss continues, especially in freshwater ecosystems, and factors such as land use change, stream alteration, pollution, and invasive species further threaten native aquatic fauna (Dudgeon et al., 2006; Strayer & Dudgeon, 2010), continued research is crucial to understand and conserve native freshwater fish species. The rate of these influences on aquatic systems through increased urbanization and expansion make it challenging to monitor species status effectively, which can lead to unnoticed declines in the species populations. Furthermore, gaps in information for many imperiled species make it difficult to assess population trends, ultimately hindering conservation and management efforts. Studies at both the regional and local scale have provided insights into environmental variables influencing other imperiled freshwater fish species worldwide, which have been used to help guide management decisions. Results from this study highlight both regional (historical and contemporary) distribution patterns and local (contemporary abiotic and biotic) environmental factors influencing the occurrence of ten SGCN freshwater fish species within the Neches, Sabine, and Cypress River basins in east Texas.

At the regional scale, my results offer insights into the potential distribution of the ten focal species and how their ranges have shifted over time due to habitat changes within each basin. The ecological niche model predictions highlight key areas within the Neches, Sabine, and Cypress River basins that can be targeted for conservation, both for individual species and through a comprehensive map identifying regions of overlap among multiple focal species. Additionally, these highlighted conservation areas could guide the next step of ground-truthing the model predictions for the imperiled species, a common practice in ecological niche modeling. This process could both confirm areas of persistence or uncover new locations where these species may occur (Laszlo et al., 2022). Practices could involve targeted sampling efforts in areas that contemporarily showed high probabilities of occurrence, as well as areas that historically had high probabilities of occurrence, that appear to have declined. Additionally, expanding the study beyond the Sabine, Neches, and Cypress basins to include the Trinity, Sulfur, or Red River basins, where several focal species have also been reported could deepen our understanding of these imperiled species. This would make it possible to test whether similar environmental factors shape their distributions across Texas waters. This could be done through additional ENMs or through applying what we learned in this study.

At the local scale, my results provide insights into the local abiotic and biotic factors that are influencing the occurrence of these focal species. While most species co-occurrence patterns appear to be influenced by local habitat conditions (i.e., local filters), there still may be some biotic interactions, specifically for the Blackspot and Sabine shiners that may be influencing their distribution and occurrences. Further investigating these relationships through detailed microhabitat studies or lab experiments could help improve our understanding of how both abiotic and biotic factors shape distributions for imperiled species in East Texas streams.

Across both spatial scales, hydrological and water quality variables were the most influential variables predicting the occurrence and distribution of the focal species. This emphasizes the importance of maintaining the natural flow regime in order to aide these imperiled species within east Texas. Therefore, protecting mainstem habitats where most focal species exhibited the highest probabilities of occurrence should be prioritized for all three river basins. For example, a section of the Neches River, from below Lake Palestine to the upper region of B.A. Steinhagen Lake, was nominated to be a part of National Wild and Scenic Rivers program in 2012. Though it did not initially pass, the results from my study may reinforce available information for continue promoting this area for conservation of habitats for imperiled species. Finally, my findings emphasize that management and conservation actions in these river basins not only benefit the ten focal imperiled species, but also native species and other SGCN in east Texas that were not included in this study.

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Appendix

S 1. List of site locations sampled within the Neches River, Sabine River, and Cypress River Basins in East Texas from Summer 2023 – Spring 2025.

#	Site	River Basin	County	Latitude	Longitude
1	Turkey Creek	Neches	San Augustine	31.3945	-94.1948
2	Lick Creek	Neches	San Augustine	31.4232	-94.2080
3	Running Branch	Neches	San Augustine	31.3887	-94.2470
4	Boykin Creek	Neches	Jasper	31.0661	-94.2816
5	Graham Creek	Neches	Angelina	31.0481	-94.3880
6	Hickory Creek	Neches	Houston	31.4658	-95.1294
7	Walnut Creek	Neches	Houston	31.4678	-95.1308
8	Lee Creek	Neches	Houston	31.3831	-95.1529
9	Hackberry Creek	Neches	Trinity	31.2263	-94.9143
10	Sandy Creek DCNF	Neches	Trinity	31.2025	-94.8939
11	Piney Creek	Neches	Trinity	31.0659	-95.0559
12	Naconiche Creek	Neches	Nacogdoches	31.7121	-94.4497
13	Banita Creek	Neches	Nacogdoches	31.5933	-94.6536
14	La Nana Creek	Neches	Nacogdoches	31.6233	-94.6420
15	Beech Creek	Neches	Nacogdoches	31.8412	-94.6815
16	Tuscosso Creek	Neches	Nacogdoches	31.6026	-94.5155
17	Carrizo Bayou	Neches	Nacogdoches	31.6031	-94.5729
18	Ham Creek	Neches	Rusk	31.9662	-94.7037
19	Sandy Creek ANF	Neches	San Augustine	31.2931	-94.1387
20	Harvey Creek	Neches	San Augustine	31.3207	-94.2378
21	Scott Creek	Neches	San Augustine	31.3393	-94.2463
22	Hurricane Creek	Neches	Angelina	31.2990	-94.7355
23	Jack Creek	Neches	Angelina	31.3528	-94.7974
24	Hager Creek	Neches	Houston	31.3475	-95.0816
25	Cochino Bayou	Neches	Houston	31.3294	-95.0767

S1. Continued

#	Site	River Basin	County	Latitude	Longitude
26	Lynch Creek	Neches	Houston	31.2823	-95.2047
27	Bonaldo Creek	Neches	Nacogdoches	31.5161	-94.7876
28	Alazan Bayou	Neches	Nacogdoches	31.5848	-94.7681
29	Mill Creek	Neches	Nacogdoches	31.6267	-94.7340
30	Legg Creek	Neches	Nacogdoches	31.5962	-94.8790
31	Murvaul Creek	Sabine	Panola	32.0759	-94.2506
32	Socagee Creek	Sabine	Panola	32.2316	-94.0925
33	Morris Creek	Sabine	Shelby	31.9774	-94.0667
34	McFaddin Creek	Sabine	Panola	31.9768	-94.2345
35	Styles Creek	Sabine	Shelby	31.9258	-93.9997
36	Carroll Creek	Sabine	Shelby	31.8216	-93.9671
37	Brawley Creek	Sabine	Shelby	31.7650	-93.9282
38	Siepe Bayou	Sabine	Shelby	31.7186	-93.9103
39	Blue Bayou South	Sabine	Shelby	31.6820	-93.9059
40	Mill Creek	Sabine	Panola	32.2318	-94.1944
41	Respass Creek	Sabine	Panola	32.1840	-94.2706
42	Grace Creek	Sabine	Gregg	32.5225	-94.7600
43	Peavine Creek	Sabine	Gregg	32.4195	-94.8688
44	Rabbit Creek	Sabine	Gregg	32.3884	-94.9029
45	Potters Creek	Sabine	Harrison	32.4343	-94.4244
46	Eightmile Creek	Sabine	Harrison	32.3764	-94.3258
47	Irons Bayou	Sabine	Harrison	32.1491	-94.4859
48	Brittain Creek	Sabine	Shelby	31.6356	-93.8920
49	Martinez Bayou	Sabine	Shelby	31.6119	-93.8969
50	Indian Creek off 2261	Sabine	Shelby	31.6142	-93.9510
51	Bourghs Creek	Sabine	Sabine	31.5414	-93.8618

S1. Continued

#	Site	River Basin	County	Latitude	Longitude
52	Reeves Creek	Sabine	Sabine	31.5288	-93.8565
53	Colorow Creek	Sabine	Sabine	31.5582	-93.8976
54	Buckley Creek	Sabine	Shelby	31.5901	-93.9549
55	Indian Creek off 944	Sabine	Sabine	31.3109	-93.7775
56	Housen Bayou	Sabine	Sabine	31.3032	-93.8443
57	Tebo Creek	Sabine	Sabine	31.3809	-93.8915
58	Big Sandy Creek	Sabine	Sabine	31.2077	-93.7518
59	Walnut Creek	Sabine	Sabine	31.2614	-93.8367
60	South Prong Creek	Sabine	Sabine	31.1993	-93.7350
61	Mill Creek	Neches	Angelina	31.090438	-94.396301
62	Moral Bayou	Neches	Nacogdoches	31.624	-94.725
63	Jones Creek	Neches	Nacogdoches	31.824	-94.780
64	Owens Creek	Neches	Rusk	32.030	-94.715
65	Terrapin Creek	Neches	Nacogdoches	31.639	-94.396
66	Atascoso Creek	Neches	Nacogdoches	31.588	-94.415
67	Little Cow Creek	Sabine	Newton	30.996	-94.251
68	Yellow Bayou	Sabine	Newton	30.960	-93.682
69	Boregas Creek	Sabine	Sabine	31.431	-93.682
70	Cypress Creek	Sabine	San Augustine	31.522	-94.008
71	Irons Bayou	Sabine	Panola	32.098	-94.610
72	Black Cypress Creek	Cypress	Cass	33.001	-94.517
73	Lilly Creek	Cypress	Upshur	32.814	-94.953
74	Little Cypress Creek	Cypress	Upshur	32.776	-94.946
75	Eagle Creek	Cypress	Harrison	32.676	-94.636
76	Pope Creek	Cypress	Harrison	32.667	-94.601

S1. Continued

#	Site	River Basin	County	Latitude	Longitude
77	Scotts Creek	Cypress	Marion	32.810	-94.348
78	French Creek	Cypress	Marion	32.762	-94.437
79	Karnack Creek	Cypress	Harrison	32.621	-94.210
80	Haggerty Creek	Cypress	Harrison	32.592	-94.251
81	Little Creek	Cypress	Morris	32.902	-94.785
82	N-27	Neches	Hardin	30.18914	-94.3889
83	N-26	Neches	Jefferson	30.17561	-94.219
84	N-25	Neches	Jefferson	30.18743	-94.2008
85	N-24	Neches	Jefferson	30.18546	-94.1785
86	N-17 @ HWY 96	Neches	Jasper	30.35899	-94.0949
87	N-19 @ Lakeview	Neches	Hall	30.21595	-94.1168
88	N-23	Neches	Jefferson	30.17176	-94.1533
89	N-16	Neches	Tyler	30.67955	-94.0907
90	11-AR	Neches	Angelina	31.45762	-94.7288
91	N-30	Neches	Angeliina	31.39521	-94.9646
92	29-AR	Neches	Angelina	31.48785	-94.8254
93	25-AR	Neches	Rusk	31.87147	-94.94099
94	57-AR	Neches	Rusk	31.91816	-94.9032
95	N-2 @ HWY 31	Neches	Henderson	32.31516	-95.4523
96	N-1 @ HWY 64	Neches	Smith	32.37393	-95.4736
97	10-AR @HWY 21	Neches	Cherokee	31.67148	-94.9526
98	28- AR @ FM 1911	Neches	Cherokee	31.57726	-94.8916
99	27-AR @HWY 343	Neches	Cherokee	31.75308	-94.9605
101	N-8 @HWY 84	Neches	Cherokee	31.77626	-95.3969
102	N-9 @HWY 294	Neches	Anderson	31.62958	-95.2857
103	N-10 @HWY 21	Neches	Cherokee	31.58003	-95.1679

S1. Continued

#	Site	River Basin	County	Latitude	Longitude
104	N-12 @HWY 94	Neches	Angelina	31.29132	-94.8843
104	N-7 @HWY 79	Neches	Anderson	31.89405	-95.4335
105	N-6 @HWY 175	Neches	Cherokee	32.03953	-95.4363
106	N-14	Neches	Tyler	31.02527	-94.3993
107	N-13 @HWY 59	Neches	Angelina	31.13266	-94.8101
108	43-SR	Sabine	Shelby	31.99463	-94.0272
109	42-SR	Sabine	Shelby	31.99689	-94.0771
110	33-SR	Sabine	Panola	32.2287	-94.2391
111	32-SR	Sabine	Panola	32.22666	-94.2912
112	31-SR	Sabine	Panola	32.26803	-94.3123
113	30-SR	Sabine	Panola	32.31393	-94.3414
114	35-SR	Sabine	Panola	32.14555	-94.1928
115	34-SR	Sabine	Panola	32.18281	-94.2233
116	25-SR	Sabine	Gregg	32.39824	-94.5248
117	20-SR	Sabine	Gregg	32.39167	-94.5887
118	19-SR	Sabine	Gregg	32.40823	-94.6577
119	29-SR	Sabine	Harrison	32.34646	-94.3674
120	28-SR	Sabine	Harrison	32.3695	-94.4008
121	41-SR	Sabine	Shelby	32.00122	-94.1129
122	38-SR	Sabine	Shelby	32.02917	-94.1587
123	37-SR	Sabine	Panola	32.06269	-94.1875
124	36-SR	Sabine	Panola	32.10599	-94.1894
125	17-SR	Sabine	Panola	32.43528	-94.7594
126	12-SR	Sabine	Upshur	32.56416	-95.1444
127	10-SR	Sabine	Wood	32.55896	-95.2069

S1. Continued

#	Site	River Basin	County	Latitude	Longitude
128	9-SR	Sabine	Wood	32.61338	-95.4853
129	5-SR	Sabine	Wood	32.67374	-95.5685
130	4-SR	Sabine	Wood	32.72616	-95.6352
131	2-SR	Sabine	Rains	32.77366	-95.7989
132	1-SR	Sabine	Van Zandt	32.80639	-95.9189
133	18-SR	Sabine	Gregg	32.42044	-94.7073
134	26-SR	Sabine		32.9465	-94.4968
135	27-SR	Sabine	Panola	32.37154	-94.4608

S 2. List of fish species collected from the Neches, Sabine, and Cypress River basins in east Texas, across three seasons throughout 2023-2025. Species are listed based on taxonomic group.

				River Basin		
Order	**Family**	**Scientific Name**	**Common Name**	**Neches**	**Sabine**	**Cypress**
Petromyzontidae	Petromyzontidae	*Ichthyomyzon castaneus*	Chestnut Lamprey	3	25	0
Petromyzontidae	Petromyzontidae	*Ichthyomyzon gagei*	Southern Brook Lamprey	16	39	0
Lepisosteiformes	Lepisosteidae	*Lepisosteus oculatus*	Spotted Gar	3	7	3
Lepisosteiformes	Lepisosteidae	*Lepisosteus osseus*	Longnose Gar	1	5	0
Cypriniformes	Cyprinidae	*Notemigonus crysoleucas*	Golden Shiner	71	85	10
Cypriniformes	Leuciscidae	*Cyprinella lutrensis*	Red Shiner	1775	34058	0
Cypriniformes	Leuciscidae	*Cyprinella venusta*	Blacktail Shiner	3187	762	5
Cypriniformes	Leuciscidae	*Hybopsis amnis*	Pallid Shiner	788	70	0
Cypriniformes	Leuciscidae	*Hybognathus nuchalis*	Mississippi Silvery Minnow	795	0	0
Cypriniformes	Leuciscidae	*Lythrurus fumeus*	Ribbon Shiner	3040	801	658
Cypriniformes	Leuciscidae	*Lythrurus umbratilis*	Redfin Shiner	414	1793	179
Cypriniformes	Leuciscidae	*Notropis atrocaudalis*	Blackspot Shiner	412	237	13
Cypriniformes	Leuciscidae	*Notropis sabinae*	Sabine Shiner	208	443	0
Cypriniformes	Leuciscidae	*Notropis texanus*	Weed Shiner	3152	307	196
Cypriniformes	Leuciscidae	*Notropis volucellus*	Mimic Shiner	18	57	9
Cypriniformes	Leuciscidae	*Opsopoeodus emiliae*	Pugnose Minnow	287	215	4

S2. Continued.

Order	Family	Scientific Name	Common Name	River Basin Neches	Sabine	Cypress
Cypriniformes	Leuciscidae	*Phenacobius mirabilis*	Suckermouth Minnow	13	2	0
Cypriniformes	Leuciscidae	*Pimephales promelas*	Fathead Minnow	1	0	0
Cypriniformes	Leuciscidae	*Pimephales vigilax*	Bullhead Minnow	2791	7224	47
Cypriniformes	Leuciscidae	*Semotilus atromaculatus*	Creek Chub	118	124	11
Cypriniformes	Catostomidae	*Erimyzon claviformis*	Western Creek Chubsucker	17	7	3
Cypriniformes	Catostomidae	*Erimyzon sucetta*	Creek Chubsucker	142	42	1
Cypriniformes	Catostomidae	*Minytrema melanops*	Spotted Sucker	205	44	9
Cypriniformes	Catostomidae	*Moxostoma poecilurum*	Blacktail Redhorse	49	20	0
Siluriformes	Ictaluridae	*Amerius melas*	Black Bullhead	39	17	6
Siluriformes	Ictaluridae	*Amerius natalis*	Yellow Bullhead	123	177	21
Siluriformes	Ictaluridae	*Ictalurus punctatus*	Channel Catfish	69	194	4
Siluriformes	Ictaluridae	*Noturus gyrinus*	Tadpole Madtom	13	4	3
Siluriformes	Ictaluridae	*Noturus nocturnus*	Freckled Madtom	84	49	1
Esociformes	Esocidae	*Esox americanus*	Redfin Pickerel	45	30	40
Percopsiformes	Aphredoderidae	*Aphredoderus sayanus*	Pirate Perch	247	351	204
Atheriniformes	Atherinidae	*Labidesthes sicculus*	Brook Silverside	364	100	50

S2. Continued.

Order	Family	Scientific Name	Common Name	River Basin		
				Neches	Sabine	Cypress
Poeciliidae	Poeciliidae	*Gambusia affinis*	Western Mosquitofish	3996	4364	79
Cyprinodontiformes	Fundulidae	*Fundulus chrysotus*	Golden Topminnow	2	3	0
Cyprinodontiformes	Fundulidae	*Fundulus dispar*	Starhead Minnow	0	1	0
Cyprinodontiformes	Fundulidae	*Fundulus notatus*	Blackstriped Topminnow	1789	225	108
Cyprinodontiformes	Fundulidae	*Fundulus olivaceus*	Blackspotted Topminnow	144	866	0
Perciformes	Centrarchidae	*Centrarchus macropterus*	Flier	4	14	11
Perciformes	Centrarchidae	*Micropterus punctulatus*	Spotted Bass	222	160	5
Perciformes	Centrarchidae	*Micropterus nigricans*	Largemouth Bass	138	213	11
Perciformes	Centrarchidae	*Lepomis auritus*	Redbreast Sunfish	91	39	0
Perciformes	Centrarchidae	*Lepomis cyanellus*	Green Sunfish	130	234	42
Perciformes	Centrarchidae	*Lepomis gulosus*	Warmouth	177	162	29
Perciformes	Centrarchidae	*Lepomis macrochirus*	Bluegill	772	499	191
Perciformes	Centrarchidae	*Lepomis marginatus*	Dollar Sunfish	13	57	8
Perciformes	Centrarchidae	*Lepomis megalotis*	Longear Sunfish	2076	2372	296
Perciformes	Centrarchidae	*Lepomis microlophus*	Redear Sunfish	38	39	9
Perciformes	Centrarchidae	*Lepomis miniatus*	Redspotted Sunfish	188	151	13

S2. Continued.

Order	Family	Scientific Name	Common Name	River Basin		
				Neches	**Sabine**	**Cypress**
Perciformes	Centrarchidae	*Pomoxis annularis*	White Crappie	101	81	4
Perciformes	Centrarchidae	Pomoxis nigromaculatus	Black Crappie	19	25	1
Perciformes	Percidae	*Ammocrypta vivax*	Scaly Sand Darter	52	48	0
Perciformes	Percidae	Etheostoma artesiae	Redspot Darter	43	109	0
Perciformes	Percidae	Etheostoma chlorosoma	Bluntnose Darter	782	155	25
Perciformes	Percidae	Etheostoma gracile	Slough Darter	294	167	24
Perciformes	Percidae	*Etheostoma histrio*	Harlequin Darter	14	3	0
Perciformes	Percidae	*Etheostoma parvippine*	Goldstripe Darter	12	1	0
Perciformes	Percidae	*Etheostoma proeliare*	Cypress Darter	71	0	3
Perciformes	Percidae	*Etheostoma thompsoni*	Gumbo Darter	215	24	0
Perciformes	Percidae	*Percina macroplepida*	Bigscale Logperch	44	4	0
Perciformes	Percidae	*Percina sciera*	Dusky Darter	143	101	3
Perciformes	Sciaenidae	*Aplodinotus grunniens*	Freshwater Drum	2	0	0
Perciformes	Elassomatidae	*Elassoma zonatum*	Banded Pygmy Sunfish	3	4	1
Amiiformes	Amiidae	*Amia calva*	Bowfin	0	0	1
Perciformes	Percidae	*Ammocrypta clara*	Western Sand Darter	9	0	0

S2. Continued.

Order	Family	Scientific Name	Common Name	River Basin		
				Neches	**Sabine**	**Cypress**
Clupeiformes	Engraulidae	*Anchoa mitchilli*	Bay Anchovy	657	0	0
Cypriniformes	Catostomidae	*Carpiodes carpio*	River Carpsucker	0	4	0
Cypriniformes	Cyprinidae	*Cyprinus carpio*	Common Carp	0	0	1
Clupeiformes	Dorosomatidae	*Dorosoma cepedianum*	Gizzard Shad	11	203	0
Clupeiformes	Dorosomatidae	*Dorosoma petenense*	Threadfin Shad	460	1279	0
Esociformes	Esocidae	*Esox niger*	Chain Pickerel	1	0	0
Perciformes	Percidae	*etheostoma asprigene*	Mud Darter	0	2	0
Cyprinodontiformes	Fundulidae	*Fundulus blairae*	Western Starhead Topminnow	7	0	0
Cypriniformes	Leuciscidae	*Hybognathus hayi*	Cypress Minnow	0	0	1
Cypriniformes	Catostomidae	*Ictiobus bubalus*	Smallmouth Buffalo	0	0	1
Siluriformes	Ictaluridae	*Ictalurus furcatus*	Blue Catfish	4	26	0
Perciformes	Centrarchidae	*Lepomis humilis*	Orangespotted Sunfish	1	133	6
Perciformes	Centrarchidae	*Lepomis symmetricus*	Bantam Sunfish	0	1	2
Cypriniformes	Leuciscidae	*Luxilus chrysocephalus*	Striped Shiner	0	0	26
Cypriniformes	Leuciscidae	*Macrhybopsis hyostoma*	Shoal Chub	13	1018	0
Atheriniformes	Atherinidae	*Menidia beryllina*	Inland Silverside	43	763	0

S2. Continued.

Order	Family	Scientific Name	Common Name	River Basin		
				Neches	Sabine	Cypress
Acanthuriformes	Moronidae	*Morone chrysops*	White Bass	1	0	0
Cypriniformes	Leuciscidae	*Notropis buchanani*	Ghost Shiner	288	8085	0
Cypriniformes	Leuciscidae	*Notropis chalybaeus*	Ironcolor Shiner	0	0	106
Cichliformes	Cichlidae	*Oreochromis aureus*	Blue Tilapia	1	0	0
Perciformes	Percidae	*Percina shumardi*	River Darter	23	1	0
Siluriformes	Ictaluridae	*Pylodictis olivaris*	Flathead Catfish	0	3	0
Carangiformes	Achiridae	*Trinectes maculatus*	Hogchoker	2	0	0

S 3. List of the number of sites that contained focal species in this study by basin, and habitat type.

Basin	Habitat Type	Number of Sites	Number of Focal Species
Cypress	Stream	7	4
Neches	Mainstem	18	5
Neches	Stream	32	6
Sabine	Mainstem	23	3
Sabine	Stream	23	6

S 4. List of the number of sites that contained focal species in this study by season, basin, and habitat type.

Basin	Season	Habitat Type	Number of Sites	Number of Focal Species
Cypress	Fall	Stream	6	4
Cypress	Summer	Stream	2	2
Neches	Fall	Stream	18	6
Neches	Summer	Mainstem	18	5
Neches	Summer	Stream	29	5
Neches	Spring	Stream	20	4
Sabine	Fall	Stream	10	4
Sabine	Summer	Mainstem	23	3
Sabine	Summer	Stream	17	5
Sabine	Spring	Stream	10	3

CHAPTER VI: VALIDITY OF GUMBO DARTER

Background

The gumbo darter (*Etheostoma thompsoni*) was described as a distinct species most similar to the mud darter (*E. asprigene*) by Suttkus, Bart, and Etnier in 2012 based on subtle morphological differentiation. The gumbo darter possesses a narrow distribution and is found only within the Neches and Sabine River drainages of Texas, and the Calcasieu River of Louisiana, while the mud darter is broadly distributed throughout almost the entirety of the central Mississippi River basin, as well as within Texas (Red River drainage). The narrow distribution of the gumbo darter within the states of Texas and Louisiana, a pattern of endemism not shared by any other freshwater fish, prompted both states to list it as an imperiled Species of Greatest Conservation Need. This component of the project levied novel genetic and morphological data, as well as analytical methods not applied in the earlier taxonomic work of Suttkus et al. (2012), to assess the taxonomic validity of the gumbo darter.

Methods

Both mud and gumbo darters were collected from across their respective distributions to obtain suitable geographic coverage necessary to examine interrelatedness of geographically disparate populations. Additional whole specimens and tissue samples were obtained from several natural history museums to supplement project coverage. Molecular data was obtained from 76 mud darters, 19 gumbo darters, and 28 outgroup taxa via PCR and consisted of two mitochondrial loci (CO1, cyt b) and three nuclear loci (glyt, RAG1, zic1) known to be phylogenetically informative among closely related darters based on previous studies.

Phylogenetic relationships were inferenced utilizing two methods, maximum likelihood (ML) and Bayesian methods. Additional analyses were conducted utilizing the molecular data, including the creation of two haplotype networks to further visualize interrelatedness and divergence from a subset of the sampled mitochondrial and nuclear loci. Pairwise genetic distances, measured as p-distance, were also calculated from the molecular data to determine inter- and intra-lineage divergence among groupings of individuals. Morphological datasets were constructed consisting of 12 common meristic characters measured from 116 mud and 40 gumbo darters, and 1 area measurement (total area of nape unscaled) along with 15 common linear measurements were obtained from 114 mud and 40 gumbo darters. Geometric morphometric analyses were also performed on 125 mud and 56 gumbo darters to examine putative differences in body shape between the species. PERMANOVA analyses were performed on the morphological datasets to test for a significant difference between different groupings of mud and gumbo darters. Principle Component Analyses (PCA) were conducted on the same datasets as well as results from geometric morphometric analyses. Random forest analyses were also conducted utilizing the morphological datasets to determine influential characters in delineating the two species and groupings of the species.

Results

Topologies resulting from phylogenetic analysis of the nuclear loci indicate the mud and gumbo darter are not reciprocally monophyletic and were instead recovered as polyphyletic with respect to one another. This result is consistent with a population level divergence, rather than species level divergence, existing between the two species. Pairwise genetic distances between lineages of mud and gumbo darters, as well as closely related outgroup taxa, inferred from the nuclear phylograms substantiate that molecular divergence of the nuclear loci is low, and more closely reflects that of populations rather than two distinct species. Results from phylogenetic analysis of the mitochondrial loci indicate historic hybridization events having occurred between mud darters from the Red River basin in Texas and the creole darter (Etheostoma collettei), a species not known to occur in Texas. Evidence of past hybridization events, in which the mitochondrial genome of the offspring is maternally inherited, in this case from closely related congeners, was uncovered throughout numerous individuals included in this study and obscure taxonomically informative relationships.

Morphological results from both species indicate a high degree of variability across the meristic and linear measurements collected and analyzed. Although PERMANOVA results indicate a significant morphological difference exists between the mud and gumbo darters, these analyses fail to capture the variation observed in both species. Very few appreciable, diagnostic characters, able to reliably distinguish between the two species morphologically were uncovered. A diagnostic character outlined by Suttkus et al. (2012) was a partially scaled nape being present in gumbo darters, versus fully scaled in mud darters. We found variation in this character, however, in which individuals from several populations of mud darter possessed a portion of the nape unscaled, and several gumbo darters that possessed a fully scaled nape. Although differences in meristic and linear measurements were found to exist between the two species, these differences are typically minor, and the characters often broadly overlapped between the species. PCAs generated from meristic, linear measurement, and geometric morphometric datasets revealed virtually no separation between groupings of the two species in multivariate space and instead revealed a strong association between recorded characters of the mud and gumbo darter.

Summary

Results from molecular phylogenetic analyses of the nuclear loci do not support the current classification of the gumbo darter as a species distinct from the mud darter, and instead indicates their evolutionary histories remain intertwined. This is counter to what would be expected of a valid species that should exhibit a distinct evolutionary history independent of other taxa (i.e., Evolutionary Species Concept; Wiley, 1978). Results from phylogenetic analyses of the mitochondrial loci are largely uninformative in a taxonomic sense due to widespread mitochondrial introgression (hybridization) between numerous, closely related species of darter. Results from morphological analyses of the two species indicate that differences exist between the two groups (mud vs. gumbo darters), but we interpret these rather subtle differences to be population rather than species-level differences due to broad overlap in both linear measurements and meristic characters. Taken together, our results do not support the taxonomic validity of the gumbo darter as it is currently described. Updating classification to reflect evolutionary relationships could be most easily achieved by placing *Etheostoma thompsoni* in the synonymy of *E. asprigene*.

References

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CHAPTER VII: LOWER NECHES RIVER

Background

Royal Dallas Suttkus surveyed the fish assemblage in the lower Neches River downstream of Dam B in the late 1970s and early 1980s (Suttkus and Clemer 1979). These data represent the most comprehensive baseline data for the lower Neches River outside of the sparse surveys conducted by the Texas Game and Fish Commission in the 1950s (reviewed in Mangold et al. 2025). Repeating these surveys represents a useful approach for determining trajectories of fishes farther upstream from the long-term surveys conducted by the Academy of Natural Sciences (Academy of Natural Sciences n.d.) and surveys focused on a saltwater barrier near the downstream terminus of the river (Pizano-Torres et al. 2017).

Methods

Study area. – All 36 of Suttkus' historical sampling sites on the Neches River in the Big Thicket Preserve were selected for sampling (Figure 1). Due to accessibility issues and prohibitively deep water that was not able to be seined, the site just below Town Bluff Dam (NR01) and the Evadale site at Highway 96 (NR29) were dropped from sampling leaving a total of 34 sampling sites (Figure map) spanning a range of ~112 river kilometers. These sites range from ~1.5 km below Town Bluff Dam to Lakeview, below the entrance to the Lower Neches Valley Authority Canal. Most sites were sampled at the exact recorded locations of Suttkus's historical sampling. However, 6 sites were moved to opposite banks or adjacent sandbars due to habitat that was too deep to effectively seine. We consider the change in location to be negligible in these cases and a natural consequence of a changing riverscape.

Historical fish assemblage data. – Historical sampling data collected by Suttkus for the Neches River in the Big Thicket National Preserve was downloaded from iDigBio (www.idigbio.org, downloaded 5/24/2023). To attempt to mitigate potential effects of seasonal changes in assemblages, only samples from the month of December were used. NR01 and NR29 were removed from the data because we were unable to replicate the samples. One site, NR36, was sampled by Suttkus in both December of 1978 and 1984. To avoid doubling sampling effort for the site and to minimize annual changes in abundance, only the 1978 sample was retained as this sample is consistent with the timing of the majority of samples. The retained historical data spanned the years 1977-1981 and contained a single sampling event for each site. The historical data was then combined with the 2024 data and the resulting dataset contains a total of 68 sampling events across 34 geographical sites and 2 time periods (1977-1981 and 2024). Taxa were then updated to current taxonomic status (Fishbase, Suttkus et al. 2012).

Fish sampling. – Contemporary sampling was conducted on December 18-19, 2024. Fish were collected using a 10' x 5' seine with 1/8" mesh size to conform with Suttkus's traditional sampling methodology. All sample-able habitat and flow regimes were sampled at each site to encompass all microhabitat types. All sites where Suttkus had recorded sampling time (n=17) were sampled for the same duration as Suttkus's original sample and at the same time of day to standardize effort and minimize diel changes in assemblage structure. The remaining sites were each sampled for approximately 20-30 minutes. The low of the range was chosen to approximately match the average of the timed samples (22 minutes) and the high of the range was chosen to match what Suttkus considered a 'typical' sample in past studies (Gunning and

Suttkus 1991). All fish were vouchered and fixed in 10% formalin in the field. Specimens were later transferred to 70% ethanol, identified, and enumerated in the lab. Specimens were then deposited into the Biodiversity Research and Teaching Collection at Texas A&M University.

Statistical analysis. – Species richness was calculated for both time periods separately and combined. Abundance data was subsequently used for all assemblage analyses. We believe the use of abundance data is justifiable in this case due to both the known rigidity and consistency of Suttkus's sampling methodology and its prior use in evaluating long term changes of fish assemblages (Geheber and Piller 2012, Perkin et al. 2017). Our replication of methodology and sampling effort also justifies abundance derived analyses across time periods. To minimize the effect of 'rare' species on assemblage analyses, species with an abundance less than 3 individuals for both time periods combined were excluded from further analysis. Two sites, NR21 and NR24, were statistical outliers and were dropped from assemblage analyses. For each species, abundance data was fourth root transformed and a Bray-Curtis Similarity matrix was constructed. PERMANOVA (Anderson 2001) was conducted in Primer 7 (Clarke and Gorley 2015) using the Bray-Curtis Similarity matrix with unrestricted permutation of raw data and type III sums of squares (partial) in order to test for significance between the two time periods. PERMDISP analysis (Anderson 2006) was also conducted to test for significant effects of dispersion in the data. To visualize groupings in the case of significant differences in dispersion, a non-metric multi-dimensional scaling plot (NMDS) was generated. To test for differences between time periods while disregarding the effect of different dispersion among groups, Canonical analysis of principal coordinates (CAP)(Anderson and Willis 2003) was also conducted. Indicator species analysis (Dufrêne and Legendre 1997, De Caćeres and Legendre 2009, De Caćeres et al. 2012) in R was also used to assess individual species most characteristic of the assemblage in their respective time periods.

Results

Total species richness for the data analyzed across both time periods was 48 species (Table 1). Period-specific species richness was 42 species for historical (1977-1981) and 41 species for contemporary (2024). In total, 7 species were unique to 1977-1981 and 6 species were unique to 2024. PERMANOVA analysis shows significant differences between the two time periods ($p = <0.0001$, Pseudo-$F = 2.2891$) while PERMDISP analysis reveals a significant difference of dispersion between time periods ($p = 0.44$, $F = 0.7007$). NMDS revealed separate groupings of periods in multivariate space and CAP demonstrated significant differences between the two time periods (trace test, $p = <0.0001$; Figure 2). Cross-validation of the CAP model showed an allocation success rate of 98.438% ($m=7$). Indicator species analysis showed 8 species characteristic of the 1977-1981 samples (*Notropis sabinae*, *Ammocrypta vivax*, *Notropis atherinoides*, *Macrhybopsis aestivalis*, *Pomoxis annularis*, *Opsopoeodus emiliae*, *Percina sciera*, and *Carpiodes carpio*) and 3 species characteristic of the 2024 samples (*Lythrurus fumeus*, *Notropis texanus*, and *Ictalurus furcatus*; Table 2).

Discussion

The data collected a part of this study represent a second time step for the comprehensive surveys conducted by Suttkus and Clemmer (1979). Based on two sampling periods, evidence suggests that the fish assemblage in the lower Neches River changed between the historical and contemporary periods, and our work helps to identify the species that can contributed most to the observed change and might represent priority species for conservation and management actions.

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Table 1. Species present and their total abundance for the two periods of surveys of the Lower Neches River downstream of Dam B.

Species	Historical Abundance	Contemporary Abundance
Ammocrypta vivax	281	46
Aphredoderus sayanus	0	5
Aplodinotus grunniens	5	5
Carpiodes carpio	24	0
Cyprinella lutrensis	7307	5652
Cyprinella venusta	8915	5261
Dorosoma cepedianum	10	6
Dorosoma petenense	80	31
Etheostoma chlorosoma	16	3
Etheostoma histrio	41	0
Etheostoma proeliare	10	0
Etheostoma thompsoni	7	10
Fundulus notatus	198	196
Fundulus olivaceus	6	2
Gambusia affinis	146	220
Hybognathus nuchalis	10	4
Hybopsis amnis	233	265
Ictalurus furcatus	0	47
Ictalurus punctatus	176	229
Labidesthes sicculus	227	114
Lepisosteus osseus	0	6
Lepomis gulosus	32	13
Lepomis humilis	0	9
Lepomis macrochirus	202	424
Lepomis megalotis	522	957
Lepomis microlophus	71	44
Lythrurus fumeus	16	84
Macrhybopsis aestivalis	271	0
Menidia beryllina	0	19
Micropterus punctulatus	52	52
Micropterus salmoides	4	6
Minytrema melanops	5	0
Morone chrysops	3	1
Notropis atherinoides	90	0
Notropis buchanani	602	204
Notropis sabinae	3644	151
Notropis texanus	111	402
Notropis volucellus	802	414
Noturus nocturnus	4	1
Opsopoeodus emiliae	143	1

Percina macrolepida	6	1
Percina sciera	50	11
Percina shumardi	6	0
Phenacobius mirabilis	18	5
Pimephales vigilax	12510	4783
Pomoxis annularis	284	8
Pomoxis nigromaculatus	10	12
Trinectes maculatus	0	48
Richness	42	41

Table 2. Indicator species analysis results illustrating species indicative of each period (historical or contemporary) and their long-term trend.

Period	Species	Test Statistic	p value	Trend
Historical	*Notropis sabinae*	0.965	0.005	Decreasing
Historical	*Ammocrypta vivax*	0.841	0.005	Decreasing
Historical	*Notropis atherinoides*	0.804	0.005	Decreasing
Historical	*Macrhybopsis aestivalis*	0.748	0.005	Decreasing
Historical	*Pomoxis annularis*	0.697	0.005	Decreasing
Historical	*Opsopoeodus emiliae*	0.684	0.005	Decreasing
Historical	*Percina sciera*	0.64	0.01	Decreasing
Historical	*Carpiodes carpio*	0.42	0.025	Decreasing
Contemporary	*Lythrurus fumeus*	0.737	0.005	Increasing
Contemporary	*Notropis texanus*	0.696	0.04	Increasing
Contemporary	*Ictalurus furcatus*	0.514	0.005	Increasing

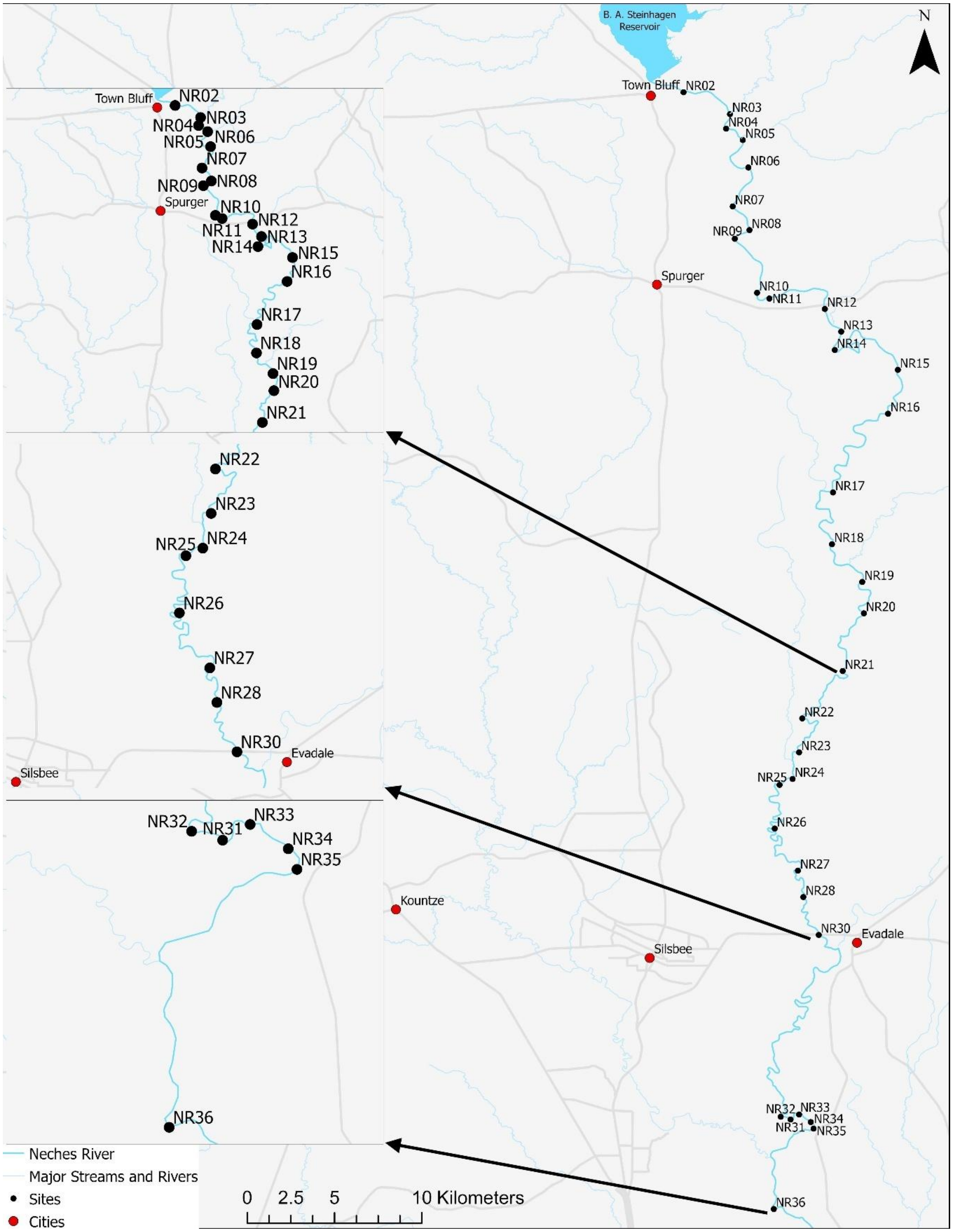

Figure 1. Map of the lower Neches River where fish assemblage collections were made in the historical and contemporary time periods.

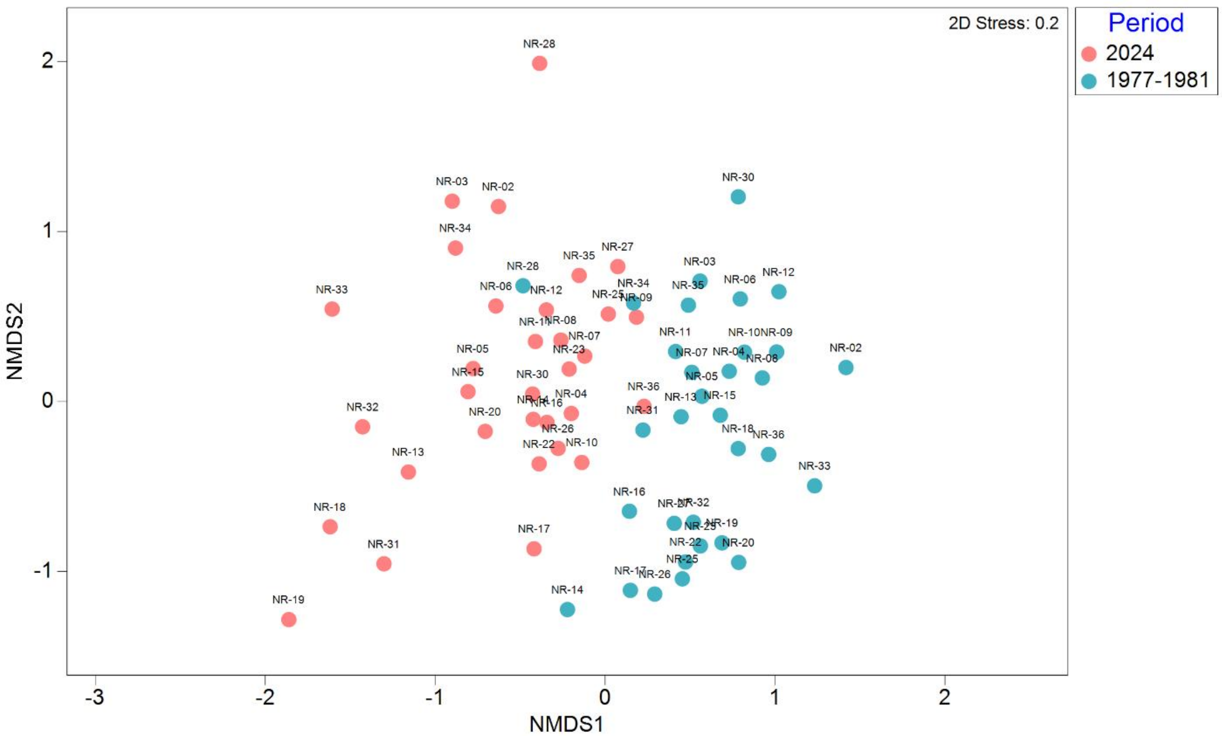

Figure 2. Non-metric multi-dimensional scaling (NMDS) plot illustrating differences in fish assemblage composition between historical (blue) and contemporary (red) time periods.

CHAPTER VIII: UPPER SABINE RIVER TRIBUTARY DATA

Introduction

Though repeating surveys at the locations of historical surveys is informative for understanding trajectories of change in fish assemblages as reported in Chapters I and II of this study, assessment of un-surveyed locations can be useful for filling gaps in the distribution of fishes. Changes to Sabine River fish assemblages are notable in the mainstem near reservoirs (Chapter II of this study), but evidence suggests small stream fish assemblages might have changed little between 1953 and 1986 (Anderson et al. 1995). However, inference from past work is limited to locations with existing data and there is a need for surveys distributed in other areas that have not been surveyed in the past. The goal of this Chapter is to fill gaps in coverage for fish assemblage structure in multiple tributary streams in the upper Sabine River basin.

Methods

Study area. – We targeted small order (2^{nd} and 3^{rd}) streams in the Upper Sabine River Basin of Texas in the summer of 2024 and surveyed fish assemblages using standard methods. A total of 48 sites were distributed to cover gradients of forest, agriculture, and developed landcover (Figure 1).

Field surveys. – Methods for fish collections in this chapter were identical to Chapter III of this report. Briefly, at each site, we established a 150-meter reach and conducted ten 15-meter seine hauls. We then conducted 900 seconds backpack electrofishing through the reach. All fishes were euthanized in clove oil, fixed in 10% formalin and brought back to the lab for identification. Five equidistant transects were established within the reach. At each transect, environmental variables (water depth/velocity/quality, bank angle, substrate, canopy cover, woody debris, wetted/channel width) were collected.

Results

Collections across the upper Sabine River tributaries yielded 6,174 specimens across 58 species (Table1). Thirty-four specimens from five genera were too small to identify to species level.

Discussion

The data collected from previously un-surveyed tributaries in the upper Sabine River basin and included in the database from this project can be used by researchers or stakeholders interested in species present in these locations. When combined with the trait data presented in Chapter I, the distribution of mussel host fishes in these tributaries can also be assessed.

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Table 1. Fishes collected from 48 tributaries to the upper Sabine River during summer of 2024.

Species	Total abundance
Ameiurus melas	37
Ameiurus natalis	63
Ameiurus umbratilis	6
Amia calva	13
Aphredoderus sayanus	143
Atherinopsidae sp	1
Catostomidae sp	1
Centrarchus macropterus	337
Cyprinella lutrensis	144
Cyprinella venusta	108
Cyprinus carpio	226
Dorosoma cepedianum	2
Elassoma zonatum	8
Erimyzon oblongus	1
Erimyzon sucetta	39
Esox americanus	34
Etheostoma artesiae	3
Etheostoma chlorosoma	56
Etheostoma gracile	163
Etheostoma histrio	6
Etheostoma parvipinne	12
Etheostoma thompsoni	39
Fundulus chrysotus	3
Fundulus dispar	3
Fundulus notatus	42
Fundulus olivaceus	227
Gambusia affinis	1099
Hybognathus hayi	1
Ictalurus punctatus	1
Ictiobus bubalus	7
Lepisosteus sp	2
Lepomis cyanellus	283
Lepomis gulosus	48
Lepomis humilis	3
Lepomis macrochirus	845
Lepomis marginatus	28
Lepomis megalotis	738
Lepomis microlophus	43

Lepomis miniatus	30
Lepomis sp	13
Lepomis symmetricus	2
Lythrurus fumeus	356
Lythrurus umbratilis	115
Micropterus punctulatus	115
Micropterus salmoides	175
Minytrema melanops	1
Moxostoma poecilurum	9
Notemigonus crysoleucas	252
Notropis atrocaudalis	124
Notropis buchanani	4
Notropis sabinae	7
Notropis sp	18
Notropis texanus	16
Notropis volucellus	5
Noturus gyrinus	2
Noturus nocturnus	3
Opsopoeodus emiliae	15
Percina sciera	35
Pimephales promelas	10
Pimephales vigilax	13
Pomoxis annularis	5
Pomoxis nigromaculatus	13
Semotilus atromaculatus	21

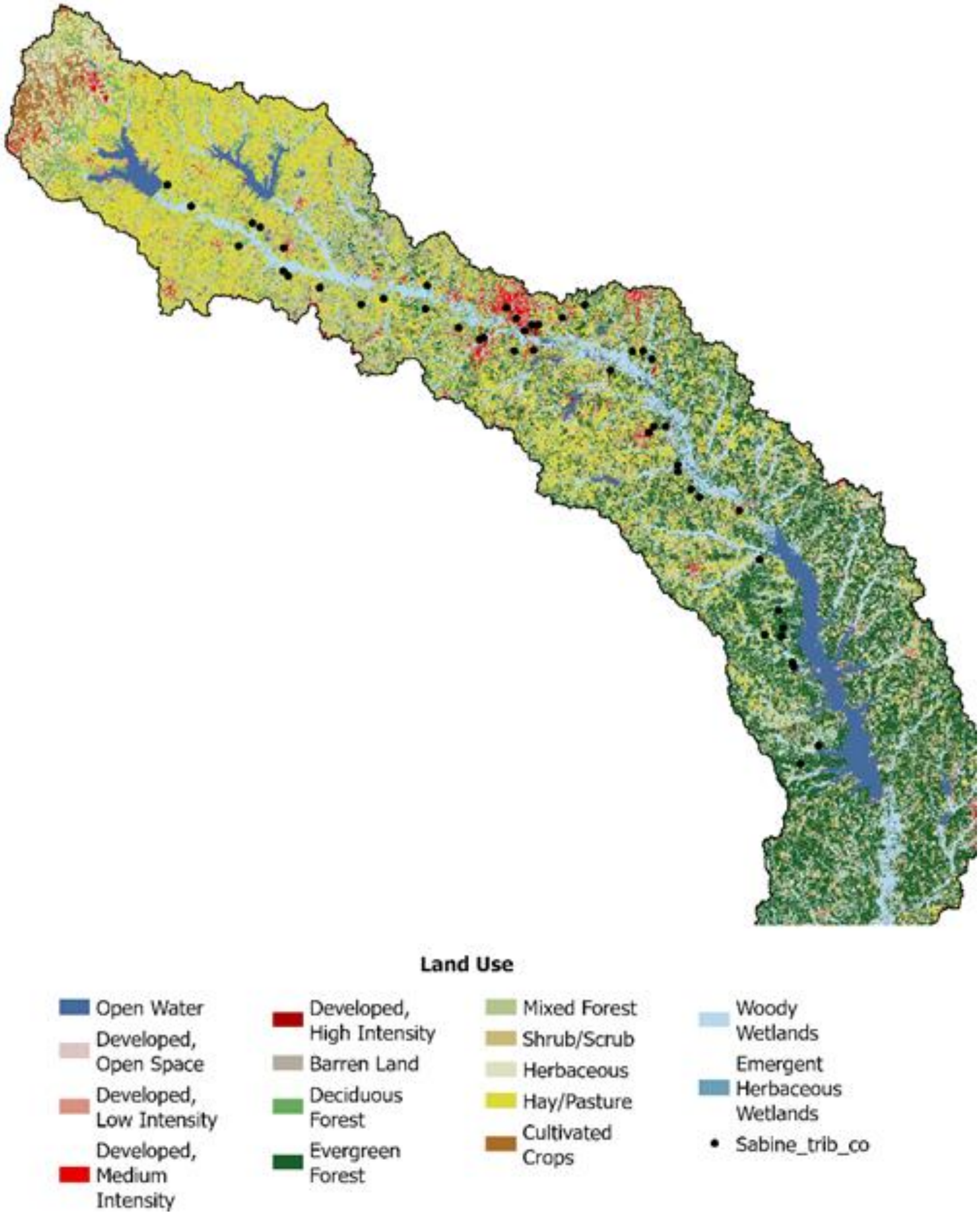

Figure 1. Locations of 48 tributary stream survey site locations distributed across a landcover gradient in the upper Sabine River basin.