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Multiscale Environmental Influences on Fish Assemblage Structure in Central Texas Streams

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ARTICLE

Multiscale Environmental Influences on Fish Assemblage Structure in Central Texas Streams

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Abstract

We investigated the influences of local and landscape-scale environmental variables on fish assemblage structure among 64 stream reaches in two large river basins in central Texas. The broad spatial extent of this study region provided an opportunity to examine fish assemblage–environment relationships at multiple scales across a range of stream types in landscapes exposed to varying degrees of anthropogenic alteration. We used nonmetric multidimensional scaling (NMS) combined with permutational analysis of variance, *k*-means cluster analysis, and indicator species analysis to evaluate broad-scale influences of ecoregional and large river basin boundaries on fish assemblage structure. We also estimated relationships between fish assemblage structure and environmental factors with NMS and rotational vector fitting across all ecoregions and within ecoregions. Ordinations of sites based on species composition grouped stream reaches together according to ecoregion, and *k*-means clustering identified three groups that corresponded with ecoregional membership. Several species had high affinities with specific ecoregions, a pattern that tracked broad-scale physiographic differences in climate, topography, terrestrial vegetation, and instream habitat. Within ecoregions, we observed that local-scale stream habitat variables as well as larger-scale landscape features were significantly related to fish assemblage composition. Substrate composition was a key local-scale habitat factor, and a gradient of rocky substrate to predominance of mud and silt correlated strongly with assemblage structure within all three ecoregions. The abundance of instream woody debris was also an important local-scale correlate for fish assemblage structure. At the landscape scale, patterns of agricultural and urban land development in the surrounding watersheds were consistently associated with fish assemblage structure in each ecoregion. This study adds important information toward a better understanding of how environmental factors structure fish assemblages across scales, which should facilitate refinement of existing habitat and biological indices for conservation of stream habitats and their biota.

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An understanding of how stream habitats and their surrounding landscapes shape assemblages of stream fishes is valuable for habitat assessment, stream restoration, and managing and conserving populations of focal fish species. Stream ecologists have long sought to understand how environmental variables at multiple spatial scales relate to fish distributions and the composition of local fish assemblages (Nikolski 1933; Gerking 1945). Previous work has shown that these relationships are complex. Local stream segments are nested within a larger fluvial hierarchy, and environmental variables at multiple spatial scales may ultimately shape local fish assemblages (Schlosser 1987; Poff 1997; Marsh-Matthews and Matthews 2000). Local, instream habitat variables, such as substrate composition, pool dimensions, and the amount of available cover, can correlate strongly with fish assemblage structure (e.g., Diana et al. 2006; Fischer and Paukert 2008; Rowe et al. 2009a), but these variables are shaped by larger-scale features such as underlying geology, riparian vegetation, and fluvial geomorphology (Frissell et al. 1986; Richards et al. 1996). In addition, anthropogenic alteration of landscapes in the surrounding watershed affects these relationships and may have a strong influence on stream habitat and fish assemblage composition (e.g., Snyder et al. 2003; Rowe et al. 2009b). For example, in Wisconsin and northern Michigan, Wang et al. (2006) found that fish assemblage characteristics were more influenced by local habitat variables in relatively undisturbed catchments, while landscape-scale and riparian conditions had a greater influence on fish assemblages in watersheds with greater agricultural and urban development.

Increasingly, the role of landscape-level factors in shaping stream communities is being recognized (Allan 2004). Altered stream-fish assemblage structure has been associated with the extent of agriculture (e.g., Roth et al. 1996; Rowe et al. 2009b) and urban development (e.g., Wang et al. 2001; Snyder et al. 2003) in surrounding catchments. Increased fish diversity and improved measures of biotic integrity have been associated with greater levels of forested land cover and intact wetlands in the landscape surrounding streams (e.g., Roth et al. 1996; Diana et al. 2006; Rowe et al. 2009b). These studies reveal that landscape-scale factors should be considered in addition to local-scale environmental variables typically measured for stream health assessment. Identification of significant relationships between environmental variables and stream-fish assemblage structure at appropriate scales can help to guide conservation efforts toward key factors that can be effectively managed.

Fish assemblage–environment relationships have been examined in many different regions, but conclusions regarding the relative importance of various local and landscape-scale environmental influences have been equivocal. Information from additional areas can potentially improve our general understanding of these relationships. Streams are susceptible to landscape alteration through increasing urbanization and conversion of land for pastures and other kinds of agricultural uses. Declining abundance of some families of native fishes (cyprinids, catostomids, ictalurids, and percids) in drainage basins throughout Texas (Anderson et al. 1995) and the surrounding region (Gido et al. 2010) has been documented following decades of environmental change. A better understanding of how fish assemblages respond to environmental variables at local and landscape levels may help to improve management and conservation strategies for Texas streams. Indices developed to assess the ecological status of Texas streams based on habitat characteristics can correlate poorly with regionalized indices of biotic integrity (IBI) (Kleinsasser et al. 2004), which indicates a need for a better understanding of fish–habitat relationships.

Discharge influences nearly all aspects of lotic ecosystems including habitat, nutrient cycling, sediment transport, water temperature, riverbank stability, groundwater recharge, and many other ecological factors (Allan 1995; Richter et al. 2003). Variability in discharge can lead to rapid changes in environmental conditions, such as temperature, turbidity, and conductivity, and limits the local abundance and distribution of aquatic organisms (Ostrand and Wilde 2002). As a result, variation in discharge between sample years may influence observed fish assemblage–environmental relationships. This influence requires further investigation to improve monitoring and conservation strategies for Texas streams.

Our objective was to examine the environmental factors shaping fish assemblages in streams within two river basins and three ecoregions of east-central Texas by (1) characterizing the patterns of stream fish assemblage structure across the region and (2) identifying environmental variables at the landscape and local-reach scales that were significantly associated with fish assemblage composition. Additionally, we evaluated fish assemblage and environmental data over 2 years to investigate how relationships varied between a period of extreme drought (2006) and normal low-water conditions (2008). The broad spatial extent of this study region provided an opportunity to examine environmental influences at multiple scales across a range of stream types within landscapes exposed to varying degrees of anthropogenic alteration.

METHODS

Study area.—Data were collected from 64 perennial, wadeable stream reaches within the Brazos and Trinity river basins in Texas. These streams lie within the Cross Timbers, Texas Blackland Prairies, and East-Central Texas Plains ecoregions (Figure 1). The Cross Timbers ecoregion, a mosaic of forests, woodlands, and prairies, currently is dominated by rangelands but also includes several major urban centers. The Texas Blackland Prairies ecoregion is distinguished from neighboring regions by having fine-textured, clay soils and less forest cover. This region was historically tallgrass prairie and now contains a higher percentage of cropland than do adjacent ecoregions. Large areas within the Blackland Prairies ecoregion are being converted to urban and industrial uses. The East-Central Texas Plains ecoregion was historically covered by post-oak savanna and currently is dominated by rangelands, but also contains row

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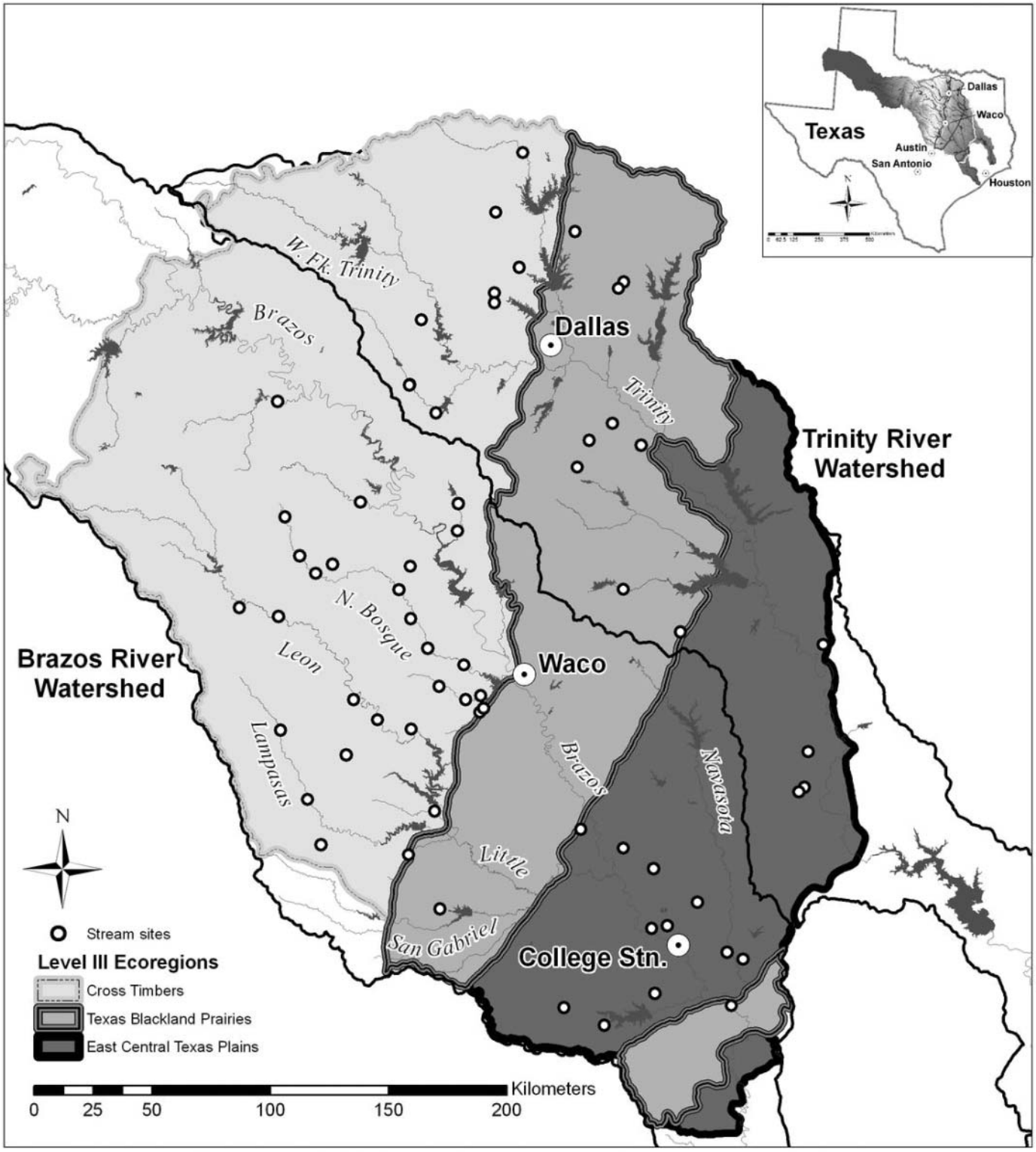

FIGURE 1. Locations of the 64 study sites in three ecoregions and two river basins (Trinity and Brazos).

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crops and urban development (Griffith et al. 2004). Owing to extreme drought conditions in 2006, study reach selection was dependent on habitat availability, resulting in unequal distribution of sampling sites among ecoregions. Despite this we selected sites that provided broad geographic coverage and a range of landscape features (including land use) and represented a range of stream habitat conditions.

Data collection.—We sampled 64 stream reaches during the summers (June–August) of 2006 and 2008. We were unable to survey several sites in 2007 owing to heavy rain and high discharge. Survey data for that year were not included in the analysis. At each study site, a 160–500-m reach was designated for fish collection and local habitat measurements. Reach length was determined based upon the wetted width of the stream (approximately 40 times the average width).

Within each study reach, all available habitats were sampled by means of a backpack electrofisher (Smith-Root Model LR-24) and seine net (4.6 × 1.8 m or 1.8 × 1.8 m). Crews of 3–4 people electrofished each study reach in a single upstream pass with a minimum effort of 900 s. The reach was then sampled with a seine net with a minimum of six 10-m hauls. If the sixth haul yielded additional species in the sample of all available mesohabitats, additional seine hauls were made until no new species were captured. Sampled fishes were identified, counted, and either released into the habitat or preserved in 10% buffered formalin for later identification. Numerical abundance of each fish species was recorded for each study reach and sampling date for analyses of patterns in fish assemblage structure.

At each study reach, we measured 41 local habitat variables (Table A.1 in the appendix) including substrate composition, instream cover, wetted width, depth, canopy cover, bank slope, riparian buffer width, instantaneous dissolved oxygen, conductivity, and pH on the same dates as fish sampling. We made these measurements at five or six evenly spaced transects (depending on reach length). Some measurements, such as number of riffles, maximum pool depth, stream sinuosity, and composition of riparian vegetation, were summarized for the entire study reach. Total discharge (m^3/s) also was measured along a representative transect in each reach with a portable electromagnetic flowmeter (Marsh-McBirney Flo-Mate Model 2000). Dissolved oxygen, salinity, specific conductivity, water temperature, and pH were measured with a YSI 556 Multi-Probe meter with barometer (Yellow Springs Instruments).

Twenty-three landscape-scale variables describing the spatial relationships (coordinates), physical characteristics and topography, land use, and distribution of disturbance points (outfalls and dams) were calculated for each study reach (Table A.2). Watershed boundaries for each sample site were automatically digitized in ArcGIS version 9.2 with the ArcHYDRO 9 extension by using a 1:24,000-scale digital elevation model (DEM) expressed as a 30-m raster, available from the U.S. Geological Survey (http://ned.usgs.gov). Mean slope and elevation were calculated for each watershed with the DEM. Mean annual precipitation was calculated for each watershed from a polygon coverage of average monthly and annual precipitation for the climatological period 1961–1990. This data set was obtained from U.S. Department of Agriculture, Natural Resources Conservation Service (www.wcc.nrcs.usda.gov/climate). Number of wastewater outfalls and cumulative outfall (10^6 gal/d) were calculated for each watershed based on the Texas Commission on Environmental Quality (TCEQ) municipal and industrial wastewater outfall shapefile (available from www.tceq.state.tx.us/gis/sites.html). The cumulative outfall metric was based on cumulative amount of permitted discharge upstream of a study reach. Land cover class percentages were calculated for each watershed by using National Land Cover Database (NLCD 2001) (available from www.mrlc.gov/nlcd_multizone_map.php). All geographical information systems (GIS) analysis was performed with ArcGIS 9.2 (ESRI, Redlands, California.).

Data analysis: fish assemblage composition and species distributions among ecoregions.—We used a combination of nonmetric multidimensional scaling (NMS), permutational analysis of variance (ANOVA), permutational analysis of dispersion, *k*-means cluster analysis, and indicator species analysis (ISA) to compare fish assemblage composition and species distributions across ecoregions and basins. We used Bray–Curtis dissimilarity as the distance measure for all analyses, a coefficient that has been repeatedly demonstrated to be robust for ecological community data (Faith and Norris 1989). Before analyses, fish species occurring at only one study reach within each data set were excluded, which represented 1–9% occurrence depending on the data set (all sites combined or grouped by ecoregion). McCune and Grace (2002) suggested removing species with less than 5% occurrence across sampling units to remove noise. However, we found little difference in ordination results after removing rare species; thus, we retained all species except those that only occurred at a single survey site. All fish abundance data as well as environmental variables with high skewness (>1) were $\log_{10}$ transformed.

We assessed ecoregional and interbasin differences in fish assemblage structure within each year by conducting NMS ordinations on the combined sites × species matrix for all three ecoregions. Nonmetric multidimensional scaling is a distance-based procedure that ordinates study units based on rank dissimilarities (Minchin 1987; Clarke 1993). Stream reaches that have close proximity in ordination plots are assumed to have similar species composition and relative proportions of each species, whereas sites that are spaced farther apart have dissimilar species composition and relative proportions of each species. Because it avoids assumptions of linearity and accurately maps sample units in ordination space in proportion to ecological distance, NMS is considered well suited for analyzing patterns in assemblage structure without some of the problems associated with other commonly used methods such as correspondence analysis (McCune and Grace 2002). Site symbols were coded based on respective ecoregions and basins, and separation of sites grouped by ecoregion was assessed visually in ordination space.

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We tested for differences in fish assemblage structure among the three ecoregions and two basins and the dispersion of each group within ordination space by using permutational multivariate ANOVA (PERMANOVA) and permutational analysis of multivariate dispersion (PERMDISP). Permutational multivariate ANOVA is a nonparametric method that directly partitions the variation in a distance matrix according to any linear model, calculates a distance-based multivariate analog to the Fisher's F-ratio for each term in the model, and uses a permutation procedure to calculate P-values (Anderson 2001). We used PERMANOVA to describe differences in assemblage structure using Euclidean distances among sites in NMS ordination space. Distance comparisons in PERMANOVA can be sensitive to between-group differences in dispersions, so we used PERMDISP (Anderson 2006) to determine whether the dispersions (degree of variability among sites) of each group around their group centroid were significantly different from one another. Permutational analysis of multivariate dispersion is useful in determining whether the separations between groups indicated by PERMANOVA are affected by differences in the dispersions of groups, and this technique is a multivariate analog to Levene's test on the Euclidean distances of individual observations to their group centroid (Anderson 2006). It is also informative about differences in beta-diversity among groups, which may be driven by environmental variables. The NMS, PERMANOVA, and PERMDISP analyses were performed with the VEGAN package in R version 2.10.1 (R Foundation for Statistical Computing).

As a second test of affinities between fish assemblage structure and ecoregions, we used k-means cluster analysis to classify sites into three major groups based on fish assemblage structure. The k-means cluster analysis is a widely used nonhierarchical clustering technique that places sites into user-defined numbers of groups such that the sum of squares from points to the assigned cluster centers is minimized (Hartigan and Wong 1979). We hypothesized that a three-group cluster model would correspond with a priori ecoregional groups. To test this we calculated misclassification rates using a confusion matrix approach (Fielding and Bell 1997). A k-means cluster analysis was performed in R version 2.10.1 (©2010, The R Foundation for Statistical Computing).

We used ISA (Dufrêne and Legendre 1997) to test for the affinities of different species to ecoregions. Indicator species analysis assigns an indicator value (IV) to each taxon by calculating the product of the relative frequency (percent occurrence of a taxon among sample units in each group) and relative average abundance (percent of the total abundance of a taxon in each group) of each species to a group. The probability of achieving an equal or larger IV value among groups (p) was estimated by using 999 random permutations of the original data (Dufrêne and Legendre 1997). Species with significantly ($p \leq 0.1$) high IVs for a given group are probably found in other stream reaches of the same ecoregion and suggest an affinity by that species for environmental characteristics common to that ecoregion. We chose probabilities of $p \leq 0.1$ owing to our disproportionately low sample sizes in the Texas Blackland Prairie and East-Central Texas Plains when compared with the Cross Timbers ecoregion. Indicator species analysis was performed with the LABDSV package in R version 2.10.1 (©2010, The R Foundation for Statistical Computing).

Fish assemblage–environmental linkages.—In addition to NMS analysis of all sample sites within each year ($n = 64$ per year) to compare ecoregional and basin differences in fish assemblage structure, study reaches were divided into three groups according to ecoregion ($n = 38$ for Cross Timbers, $n = 11$ for Texas Blackland Prairies, and $n = 15$ for East-Central Texas Plains) for analysis of the 2006 and 2008 data sets. These groups of sites were used to examine potential relationships between assemblage structure and environmental variables that may have been obscured by ecoregional differences in fish assemblages and environmental variables. We used rotational vector fitting to relate local and landscape-scale environmental variables to gradients in fish assemblage structure quantified by the NMS ordinations at both the whole-study and within-ecoregion scales (Faith and Norris 1989). Vector fitting was used to find the direction of the maximum correlation for each environmental variable. Vectors represent the direction and magnitude of the correlation between environmental variables and fish assemblage structure. For example, the direction of a vector in a plot implies that sites in that direction have a higher value for the environmental variable and that changes in fish assemblage structure (quantified by the NMS ordination axes) are correlated with increasing values for the environmental value. Vector fitting was performed on all within-ecoregion ordinations. Significance ($P \leq 0.05$) of each environmental vector was estimated by using 1,000 random permutations of the data. Vector fitting was performed with the ECODIST package in R version 2.10.1 (©2010, The R Foundation for Statistical Computing).

RESULTS

Landscape and Local Habitat Structure

The general patterns of landscape factors varied across the 64 sites, with some factors differentiating along major longitudinal fluvial gradients within basins, which also corresponded to the west–east longitudinal gradient in accordance with the southeasterly flow of major Texas rivers (Figure 2). Watershed annual precipitation increased and elevation decreased along the west–east longitudinal gradient with the three ecoregions forming fairly distinct groups. The amount of forest and shrubland decreased and grassland increased within the Cross Timbers from west to east. The amount of forested land was relatively low within the Texas Blackland Prairies, but increased toward the west within the East-Central Texas Plains. Grasslands decreased toward the west within the Texas Blackland Prairies and had relatively low coverage throughout the East-Central Texas Plains. The amount of pasture increased across the three ecoregions in relation to longitude. Row-crop agriculture showed the

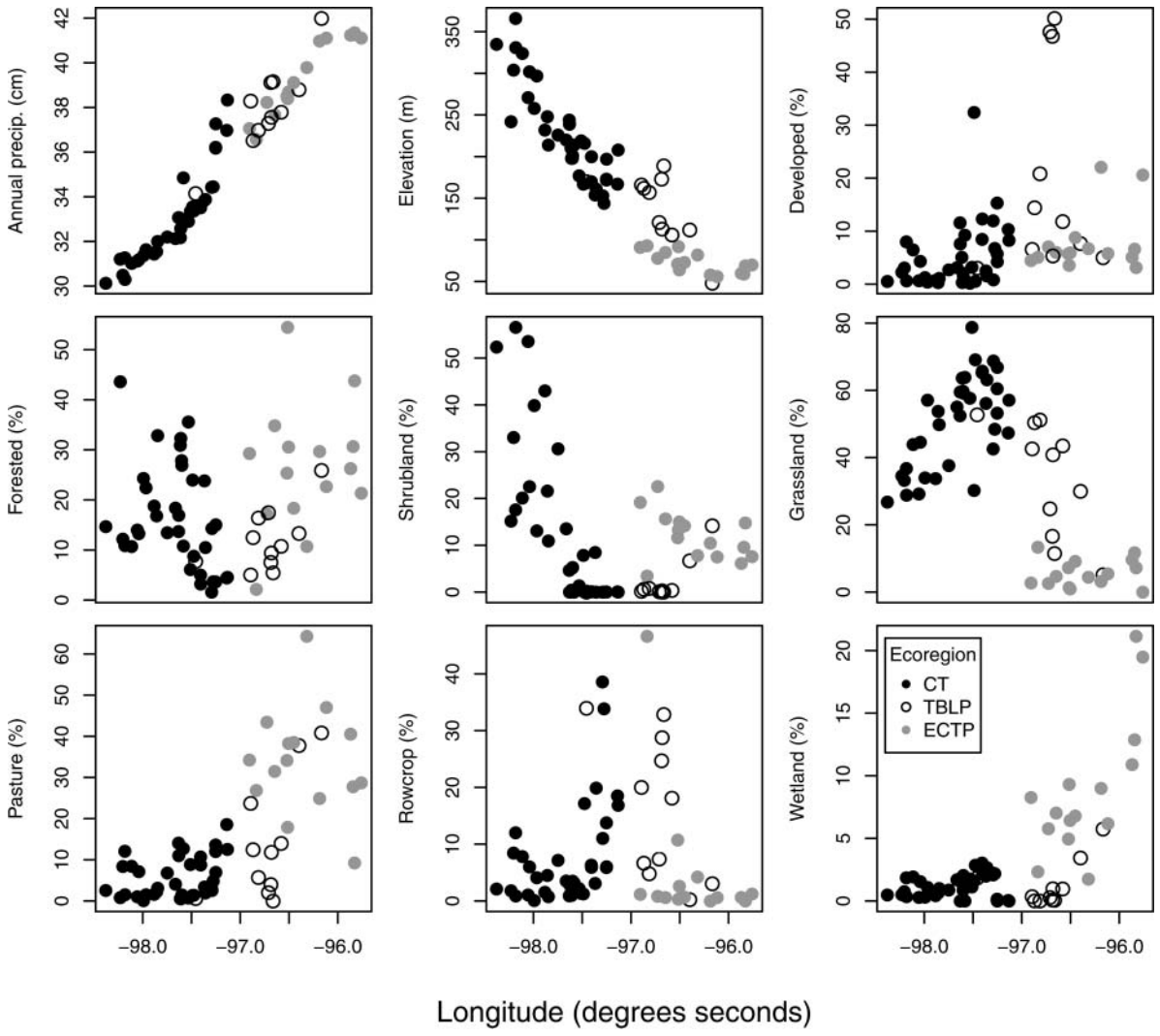

FIGURE 2. Relationships between ecoregion, longitude, and nine landscape-scale factors.

most variability in eastern regions of the Cross Timbers and the Texas Blackland Prairies, but was relatively low across the East-Central Texas Plains. Wetland cover was relatively low in the Cross Timbers and Texas Blackland Prairies ecoregions but was comparatively high throughout the East-Central Texas Plains. Impervious cover was relatively low across the 64 sites with most sites below 5% except for one site within the Cross Timbers (12%) and three sites within the Texas Blackland Prairies (17–21%). Watershed size varied among sites from 21.0 to 6,179.8 km^2 but showed no pattern across ecoregions.

Several stream habitat variables varied with ecoregion, including wetted width, discharge, substrate composition, woody debris, bank conditions, and canopy cover (Table A.1). Sites in the Cross Timbers ecoregion had greater stream widths, more riffle habitat, and rockier substrates. East-Central Plains streams generally had muddy or sandy substrates, more instream woody debris, and higher canopy cover. Most streams in the Blackland Prairies were in human-modified landscapes and had more homogeneous instream habitats. Blackland Prairies streams generally had substrate and woody debris characteristics that were intermediate between its two adjacent ecoregions. Both Blackland Prairies and East-Central Texas Plains streams had steeper banks with more exposed soil and erosion evident. In 2006 median discharge was lowest in the Cross Timbers and highest in the East-Central Texas Plains streams. In 2008 median discharge increased markedly in the Cross Timbers and Blackland Prairies and was greater than in the East-Central Texas Plains.

Fish Assemblage Structure across Ecoregions

A total of 108,895 fish specimens representing 58 species distributed across 16 families were sampled during the course of the study (Table 1). Richness per site varied from 6 to 26 species. Blacktail shiners, red shiners, western mosquitofish, central stonerollers, and longear sunfish constituted over 60% of the total abundance across study sites and years. Most species were captured throughout the entire study region, but some

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TABLE 1. Indicator values (IVs) from indicator species analysis for species collected during the study, with the corresponding ecoregions (CT = Cross Timbers, TBLP = Texas Blackland Prairies, and ECTP = East-Central Texas Plains) and probabilities for each sample year. Bold italics denote species that are significant indicators for an ecoregion. Species collected at too few sites for inclusion in the analysis or not collected during the year are denoted by "na."

		2006			2008		
Species	Species code	Ecoregion	IV	*P*	Ecoregion	IV	*P*
Lepisosteidae							
Spotted gar *Lepisosteus oculatus*	LEPIOCUL	ECTP	7.5	0.522	ECTP	10.3	0.326
Longnose gar *Lepisosteus osseus*	LEPIOSSE	***CT***	***24.7***	***0.054***	CT	18.8	0.153
Clupeidae							
Gizzard shad *Dorosoma cepedianum*	DOROCEPI	CT	11.7	0.664	CT	13	0.408
Threadfin shad *Dorosoma petenense*	DOROPETE	ECTP	4.7	0.843	na	na	na
Cyprinidae							
Central stoneroller *Campostoma anomalum*	CAMPANOM	***CT***	***53.2***	***0.001***	***CT***	***54.3***	***0.001***
Red shiner *Cyprinella lutrensis*	CYPRLUTR	***TBLP***	***38.2***	***0.063***	CT	36.5	0.17
Blacktail shiner *Cyprinella venusta*	CYPRVENU	***CT***	***47.9***	***0.001***	***CT***	***55.5***	***0.001***
Common carp *Cyprinus carpio*	CYPRCARP	***CT***	***29.5***	***0.046***	TBLP	15.9	0.335
Mississippi silvery minnow *Hybognathus nuchalis*	HYBONUCH	ECTP	na	na	TBLP	4.3	0.842
Ribbon shiner *Lythrurus fumeus*	LYTHFUME	***ECTP***	***63.6***	***0.001***	***ECTP***	***69.8***	***0.001***
Redfin shiner *Lythrurus umbratilis*	LYTHUMBR	CT	13.2	0.225	CT	10.5	0.326
Golden shiner *Notemigonus crysoleucas*	NOTECRYS	***ECTP***	***26.7***	***0.003***	***ECTP***	***13.3***	***0.085***
Blackspot shiner *Notropis atrocaudalis*	NOTRATRO	na	na	na	TBLP	4	0.848
Ghost shiner *Notropis buchanani*	NOTRBUCH	ECTP	8.5	0.376	ECTP	5	0.823
Weed shiner *Notropis texanus*	NOTRTEXA	TBLP	na	na	TBLP	8.3	0.37
Mimic shiner *Notropis volucellus*	NOTRVOLU	***CT***	***23.7***	***0.044***	***CT***	***36.8***	***0.004***
Pugnose minnow *Opsopoeodus emiliae*	OPSOEMIL	***ECTP***	***13.3***	***0.073***	ECTP	3	0.968
Bullhead minnow *Pimephales vigilax*	PIMEVIGI	CT	31	0.448	CT	37.4	0.147
Catostomidae							
River carpsucker *Carpiodes carpio*	CARPCARP	CT	11.4	0.424	CT	12.7	0.225
Lake chubsucker *Erimyzon sucetta*	ERIMSUCE	ECTP	na	na	ECTP	na	na
Smallmouth buffalo *Ictiobus bubalus*	ICTIBUBA	CT	7.9	0.423	TBLP	5.4	0.609
Spotted sucker *Minytrema melanops*	MINYMELA	***ECTP***	***18.4***	***0.096***	***TBLP***	***17.3***	***0.067***
Gray redhorse *Moxostoma congestum*	MOXOCONG	***CT***	***36.8***	***0.008***	***CT***	***34.2***	***0.009***
Blacktail redhorse *Moxostoma poecilurum*	MOXOPOEC	ECTP	na	na	***ECTP***	***13.3***	***0.079***
Characidae							
Mexican tetra *Astyanax mexicanus*	ASTYMEXI	CT	na	na	CT	na	na
Ictaluridae							
Black bullhead *Ameiurus melas*	AMEIMELA	TBLP	4.9	0.893	na	na	na
Yellow bullhead *Ameiurus natalis*	AMEINATA	TBLP	23.1	0.639	CT	27.1	0.663
Channel catfish *Ictalurus punctatus*	ICTAPUNC	***CT***	***52.5***	***0.003***	***CT***	***66.9***	***0.001***
Tadpole madtom *Noturus gyrinus*	NOTUGYRI	TBLP	9.3	0.772	CT	7.9	0.41
Freckled madtom *Noturus nocturnus*	NOTUNOCT	TBLP	3.8	0.761	TBLP	17.5	**0.067**
Flathead catfish *Pylodictis olivaris*	PYLOOLIV	CT	18.2	0.226	***CT***	***47.8***	***0.002***
Esocidae							
Grass pickerel *Esox americanus*	ESOXAMER	***ECTP***	***13.3***	***0.072***	na	na	na
Aphredoderidae							
Pirate perch *Aphredoderus sayanus*	APHRSAYA	***ECTP***	***26.7***	***0.003***	***ECTP***	***53.3***	***0.001***
Mugilidae							
Striped mullet *Mugil cephalus*	MUGICEPH	TBLP	7.4	0.241	na	na	na

(*Continued on next page*)

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TABLE 1. Continued.

Species	Species code	2006			2008		
		Ecoregion	IV	*P*	Ecoregion	IV	*P*
Atherinidae							
Brook silverside *Labidesthes sicculus*	LABISICC	ECTP	9.7	0.351	TBLP	10.9	0.29
Inland silverside *Menidia beryllina*	MENIBERY	CT	5.3	0.697	ECTP	na	na
Poeciliidae							
Western mosquitofish *Gambusia affinis*	GAMBAFFI	***CT***	***42.0***	***0.011***	***CT***	***42.7***	***0.029***
Fundulidae							
Blackstripe topminnow *Fundulus notatus*	FUNDNOTA	TBLP	33.2	0.238	ECTP	31.3	0.224
Plains killifish *Fundulus zebrinus*	FUNDZEBR	TBLP	na	na	TBLP	na	na
Moronidae							
White bass *Morone chrysops*	MOROCHRY	CT	5.3	0.713	CT	na	na
Centrarchidae							
Redbreast sunfish *Lepomis auritus*	LEPOAURI	CT	7.9	0.349	na	na	na
Green sunfish *Lepomis cyanellus*	LEPOCYAN	***CT***	***51.4***	***0.001***	***CT***	***59.3***	***0.001***
Warmouth *Lepomis gulosus*	LEPOGULO	TBLP	26	0.145	ECTP	23.5	0.328
Orangespotted sunfish *Lepomis humilis*	LEPOHUMI	ECTP	3.5	0.984	TBLP	11.6	0.249
Bluegill *Lepomis macrochirus*	LEPOMACR	***CT***	***38.8***	***0.084***	***CT***	***52.6***	***0.001***
Longear sunfish *Lepomis megalotis*	LEPOMEGA	***CT***	***45.8***	***0.001***	***CT***	***49.5***	***0.001***
Redear sunfish *Lepomis microlophus*	LEPOMICR	ECTP	14.7	0.102	***CT***	***23.7***	***0.046***
Redspotted sunfish *Lepomis miniatus*	LEPOMINI	ECTP	na	na	***ECTP***	***13.3***	***0.077***
Spotted bass *Micropterus punctulatus*	MICRPUNC	CT	***24.5***	0.233	***CT***	***35.6***	***0.038***
Largemouth bass *Micropterus salmoides*	MICRSALM	***CT***	***42.6***	***0.031***	***CT***	***52.8***	***0.001***
White crappie *Pomoxis annularis*	POMOANNU	ECTP	14.4	0.343	TBLP	8.8	0.567
Percidae							
Bluntnose darter *Etheostoma chlorosoma*	ETHECHLO	ECTP	5.2	0.777	TBLP	4.2	0.857
Slough darter *Etheostoma gracile*	ETHEGRAC	ECTP	9.6	0.34	***ECTP***	***33.3***	***0.004***
Orangethroat darter *Etheostoma spectabile*	ETHESPEC	***CT***	***76.3***	***0.001***	***CT***	***63.2***	***0.001***
Texas logperch *Percina carbonaria*	PERCCARB	CT	na	na	na	na	na
Bigscale logperch *Percina macrolepida*	PERCMACR	CT	10.5	0.276	CT	10.5	0.334
Dusky darter *Percina sciera*	PERCSCIE	ECTP	7.4	0.864	ECTP	12.8	0.355
Sciaenidae							
Freshwater drum *Aplodinotus grunniens*	APLOGRUN	CT	6.5	0.669	CT	10.5	0.298

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were restricted to certain ecoregions or river basins. Mississippi silvery minnow were captured only in Brazos River tributaries in the Blackland Prairies and East-Central Plains ecoregions. Mimic shiners were only captured at sites in the Brazos drainage basin in the Cross Timbers. Blackspot shiners were restricted to Trinity River tributaries in the Blackland Prairies and East-Central Texas Plains whereas redfin shiners were only captured in the Cross Timbers ecoregion. Lake chubsuckers and plains killifish were only collected from the Trinity River drainages in the East-Central Texas Plains and Texas Blackland Prairies ecoregions, respectively. We collected freckled madtoms in all three ecoregions, but only in Trinity River drainages. Nonnative fish species sampled in our study included common carp that were sampled throughout the study area and redbreast sunfish collected in the Cross Timbers ecoregion in 2006. Mexican tetras, which are native to Texas but historically limited to the Rio Grande drainage, were sampled in Salado Creek (Brazos drainage, Cross Timbers ecoregion).

Nonmetric dimensional scaling analysis identified three axes for 2006 and two axes for 2008 that explained 85.9% (stress = 14.75, instability = 0.028, 500 iterations) and 93.4% (stress = 16.68, instability = 0.034, 500 iterations) of the variation in the original distances among sites based on fish assemblage composition (Figure 3). Species composition differed among ecoregions for both 2006 (PERMANOVA: $F = 7.87$, $P < 0.001$; Figure 3a) and 2008 (PERMANOVA: $F = 13.31$, $P < 0.001$; Figure 3b). Dispersion among sites within each ecoregion also differed with Texas Blackland Prairies and East-Central Texas Plains sites having more dispersion in assemblage space than Cross Timbers sites during both 2006 (PERMDISP: $F = 5.21$,

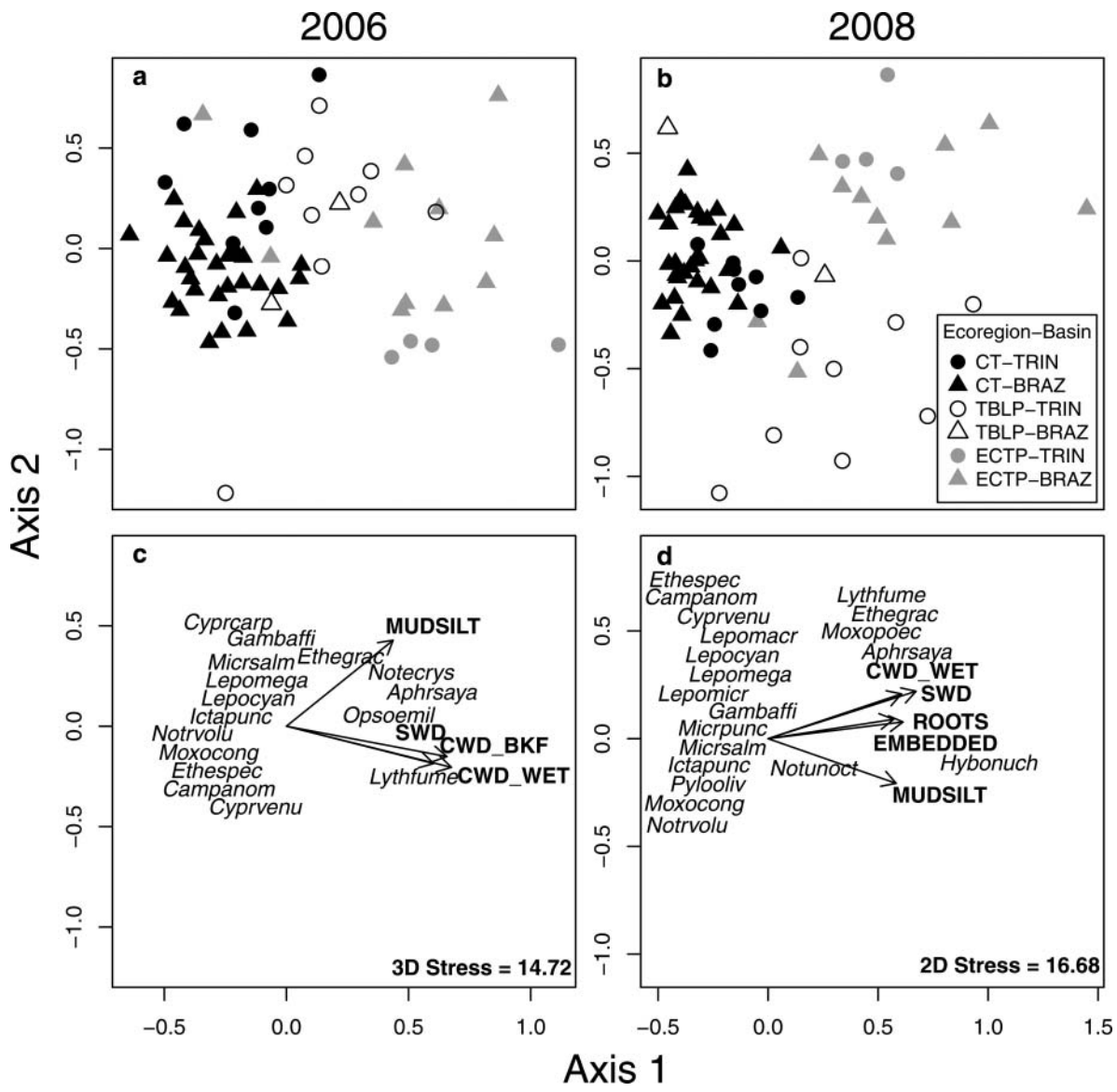

FIGURE 3. Nonmetric multidimensional scaling ordination of **(a)**–**(b)** individual sites and **(c)**–**(d)** species centroids using fish species composition for 2006 and 2008. Symbols indicate membership among the three ecoregions (CT = Cross Timbers, TBLP = Texas Blackland Prairies, and ECTP = East-Central Texas Plains) and two river basins (TRIN = Trinity and BRAZ = Brazos). Environmental vectors show the directions and magnitudes of significant correlations within the ordination space; abbreviations are as follows: MUDSILT = percentage of mud and silt, CWD_BKF = number of coarse woody debris units within the high-water zone, CWD_WET = number of coarse woody debris units within the wetted channel, SWD = percentage of instream cover small woody debris, ROOTS = percentage of instream cover roots, EMBEDDED = degree of riffle embeddedness (%), and RIP_SHRB = percentage of riparian zone in shrub cover. See Table 1 for species codes.

$P = 0.007$; Figure 3a) and 2008 (PERMDISP: $F = 12.44$, $P < 0.001$; Figure 3b). Species composition also differed between basins in 2006 (PERMANOVA: $F = 3.18$, $P = 0.007$) and 2008 (PERMANOVA: $F = 4.68$, $P < 0.001$) but without accompanying differences in dispersion within assemblage space (PERMDISP: $F = 2.06$, $P = 0.15$ and $F = 1.64$, $P = 0.23$, respectively). The NMS did not separate sites according to basin. Most sites in the Cross Timbers ecoregion and the East-Central Texas Plains separated along the primary NMS axis (Figure 3a, b). Sites in the Texas Blackland Prairies were intermediate along axis 1 in 2006, and these sites generally separated from the other two ecoregions along axis 2 in 2008.

The *k*-means clustering corroborated groupings of sites based on fish assemblage structure that corresponded with ecoregions, especially for the Cross Timbers sites. Correspondence between *k*-means clusters and ecoregion was relatively high with misclassification rates of 18.8% and 7.8% for 2006 and 2008, respectively (Table 2). In 2006, misclassifications only occurred between adjacent ecoregions with lower relative number of misclassifications for the Cross Timbers and

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TABLE 2. Confusion matrix between *k*-means cluster results and ecoregions for 2006 and 2008. Bold italics denote instances in which the *k*-means clusters corresponded to the appropriate ecoregions (see Table 1 for ecoregion abbreviations).

k-means cluster	CT	TBLP	ECTP
	2006		
1	***33***	2	0
2	5	***7***	3
3	0	2	***12***
	(Misclassification rate = 18.75%)		
	2008		
1	***38***	2	1
2	0	***8***	1
3	0	1	***13***
	(Misclassification rate = 7.8%)		

East-Central Texas Plains relative to the Texas Blackland Prairies sites. In 2008, none of the Cross Timbers sites were misclassified and compared with 2006, there were fewer misclassifications for the other two ecoregions.

The strong clustering of sites by ecoregion reflected differences in the geographic distributional patterns of species in this region. Indicator species analysis revealed affinities of several species for certain ecoregions that were higher than expected by chance (Table 1). For example, central stonerollers, blacktail shiners, mimic shiners, gray redhorses, channel catfish, western mosquitofish, green sunfish, bluegills, longear sunfish, largemouth bass, and orangethroat darters had high IVs for the Cross Timbers ecoregion in both 2006 and 2008 (Table 1; Figure 3c, d). Ribbon shiners, golden shiners, grass pickerel, pirate perch, redspotted sunfish, and slough darters had high affinities with the East-Central Texas Plains (Table 1; Figure 3c, d). No species showed consistently strong IVs for the Texas Blackland Prairies.

The instream habitat features that corresponded with differentiation of sites based on fish assemblage structure tended to be associated with ecoregional differences (Table A.1). For ease of interpretation, only those relationships having correlation coefficients greater than 0.60 are plotted in NMS ordinations, but several other habitat variables had significant correlations with fish assemblage structure (Figure 3c, d; Table A.1). Variables related to substrate size and instream coarse woody debris had strong correlations with fish assemblage structure during both 2006 and 2008 (Figure 3c, d; Table A.1). Sites that supported fish assemblages associated with the East-Central Texas Plains had embedded substrates with more mud–silt and less gravel substrates. These reaches also had more coarse woody debris within the wetted and bankfull channel, more small woody debris, and more rootwads. Banks were more erosional with steeper slopes and more exposed soil in streams of the East-Central Texas Plains. Stream reaches that supported fish assemblages with high affinities for the Cross Timbers had wider stream widths, higher amounts of gravel or larger substrates, and more filamentous algae cover (Figure 3c, d; Table A.1).

Fish Assemblage Structure within Ecoregions

Cross Timbers ecoregion.—For stream reaches in the Cross Timbers ecoregion, ordination of fish species composition at the 38 sites in 2006 identified two major axes that explained 70.6% of the original distances in *n*-dimensional space (stress = 22.34, instability = 0.023, 500 iterations). The 2008 species composition data sorted sites along two major axes that explained 73.3% of the original distances in *n*-dimensional space (stress = 20.93, instability = 0.028, 500 iterations). Several landscape variables were significantly correlated with fish assemblage structure in both years including pasture, precipitation, watershed size, watershed slope, number of dams, wastewater treatment plant (WWTP) outfalls, total developed land, total agriculture, and canopy percent (Figure 4; Table A.2). Instream habitat variables that were correlated with fish assemblage structure for both years included discharge, the proportion of mud and silt in substrate, coarse woody debris within the wetted channel, and erosion potential. Several relationships between instream habitat and fish assemblage structure varied between years. Pool width, number of riffles, overhanging vegetation, leaf packs, artificial cover, and exposed soil were correlated with fish assemblage structure during 2006, which was a dry year. During 2008, these habitat variables were not significantly correlated with fish assemblage structure. Average depth, cobble substrates, microalgal cover, large woody debris, bank slope, tree and grass cover within the riparian buffer, and specific conductivity were significantly correlated with fish assemblage structure in 2008.

Within the Cross Timbers ecoregion, several species were strongly associated with the environmental gradients associated with the ordination axes derived for each year (Figure 4). Yellow bullhead abundance in 2006 and 2008 was positively associated with axis 2, which represented a gradient of decreasing watershed size. During both years, central stonerollers, blacktail shiners, and orangethroat darters had consistent negative correlations with axis 1, which represented an environmental gradient of increasing pasture and mud–silt substrates. Abundance of red shiners and bluntnose minnow tended to be lower at sites associated with higher scores on axis 2 in 2006, and tended to be higher at sites associated with higher scores on axis 1 in 2008. Abundance of these species was positively correlated with WWTP outfalls and dams in both years.

Texas Blackland Prairies ecoregion.—The NMS ordination of abundance data for the 11 sites in the Texas Blackland Prairies ecoregion for 2006 resulted in two axes that explained 89.5% of the variation in assemblage structure (stress = 11.39). For 2008, the sites sorted in multidimensional species-space along two axes that explained 85.6% of the variation (stress = 10.64, instability = 0.032, 500 iterations). The percentage of watershed area with impervious cover was significantly correlated with fish assemblage structure during both years, and pasture and total area developed were significant landscape variables associated

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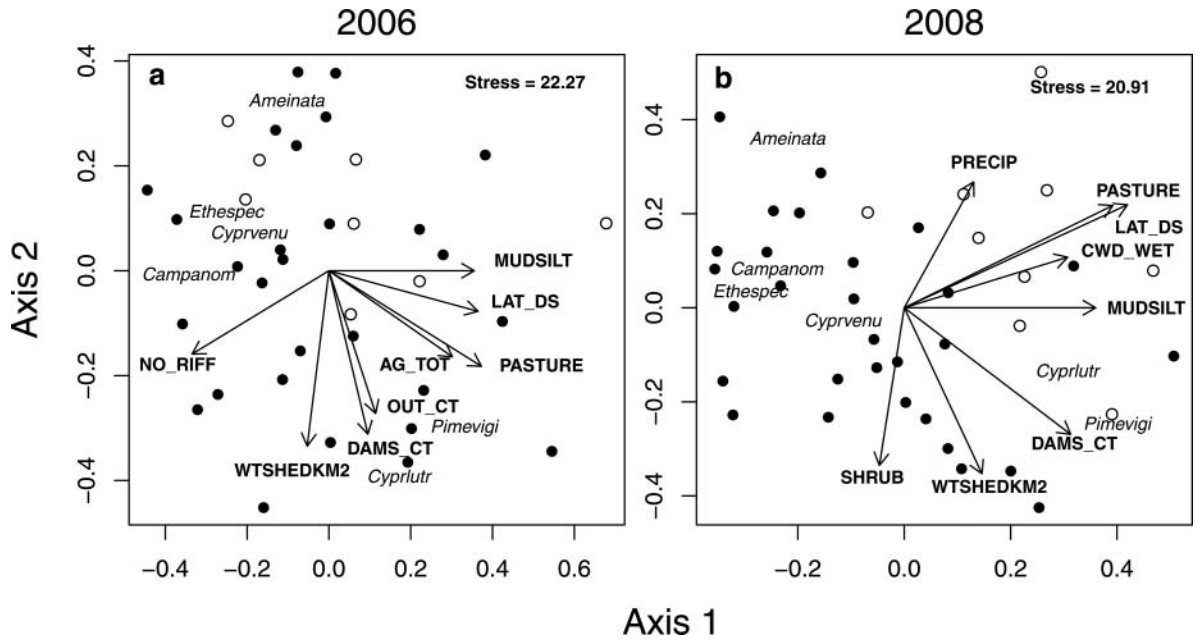

FIGURE 4. Nonmetric multidimensional scaling ordination of individual sites and species centroids in the Cross Timbers region using fish species composition for **(a)** 2006 and **(b)** 2008. Filled symbols represent Brazos River basin sites and open symbols represent Trinity River basin sites. Environmental vectors show the directions and magnitudes of significant correlations within the ordination space; abbreviations are as follows: MUDSILT = percentage of mud and silt, CWD_WET = number of coarse woody debris units within the wetted width, NO_RIFF = number of riffles, SHRUB = percentage of shrub land cover, IMP_PCT = percentage of impervious land cover, PASTURE = percentage of pasture, AG_TOT = percentage of agricultural land cover, PRECIP = average annual precipitation, CONN = degree of connectivity to a reservoir, LAT_DS = latitude, OUT_CT = number of wastewater outfalls upstream, DAM_CT = number of dams, and WTSHEDKM2 = watershed area. See Table 1 for species codes.

with assemblage structure in 2006 (Figure 5; Table A.2). The number of riffles and percent cobble in substrate were local-scale variables and had a consistently significant relationship with assemblage structure in both years (Table A.2). Discharge, amount of large woody debris, percent embeddedness, percent mud and silt in substrate, riparian vegetation composition, and thalweg depth were also significantly correlated with species composition in 2008. The number of rootwads along the bank was an additional significant variable in 2006.

Several fish species strongly influenced the NMS ordinations and likewise had abundance patterns that were correlated with environmental gradients. In 2006, yellow bullheads were negatively correlated with NMS axis 2, which was associated with increasing impervious cover in the watershed. In 2008, abundance of this species had a negative correlation with axis 1, which was associated with a gradient of increasing mud and silt substrates. Central stonerollers and blacktail shiners showed negative correlations with axis 1 in 2006, and abundance of these species was correlated positively with the number of riffles and negatively with land converted to pasture. In 2008, abundance of both species showed a negative correlation with increasing mud and silt. Red shiners were positively associated with impervious land cover and stream discharge. In 2006, bullhead minnow and blackstripe topminnow were more abundant in sites with more development and impervious land cover, but this relationship did not hold in 2008.

East-Central Texas Plains ecoregion.—The NMS ordination of the fish abundance data for the 15 sites in the East-Central Texas Plains for 2006 resulted in two axes that explained 74.1% of the variation (stress = 15.87, instability = 0.035, 500 iterations). For 2008, sites sorted along two axes that explained 89.3% of the variation (stress = 10.20, instability = 0.032, 500 iterations). Seven landscape-scale variables showed consistently significant relationships with fish assemblage structure during both years: precipitation, watershed slope, percent of land in reservoirs and surface water, percent of land in row crops, percent of land classified as wetlands, total area used for agriculture, and percent canopy cover (Figure 6; Table A.2). Total forest cover and pasture cover were significant in 2006. The amount of small woody debris, percent canopy cover, and dissolved oxygen within study reaches were the three local-scale variables significantly related to fish species composition in both years (Table A.2). In 2006, the proportion of small boulders, large woody debris, composition of riparian vegetation, and temperature were also significantly correlated with fish assemblage structure. In 2008, percent of cobble in substrate, proportion of mud and silt substrate, leaf packs, coarse woody debris on the bank, composition of riparian vegetation, canopy cover, and pH were significantly correlated with fish assemblage structure as revealed by NMS gradients.

Red shiners and western mosquitofish had positive correlations with axis 1 in 2006 and 2008, and these species were

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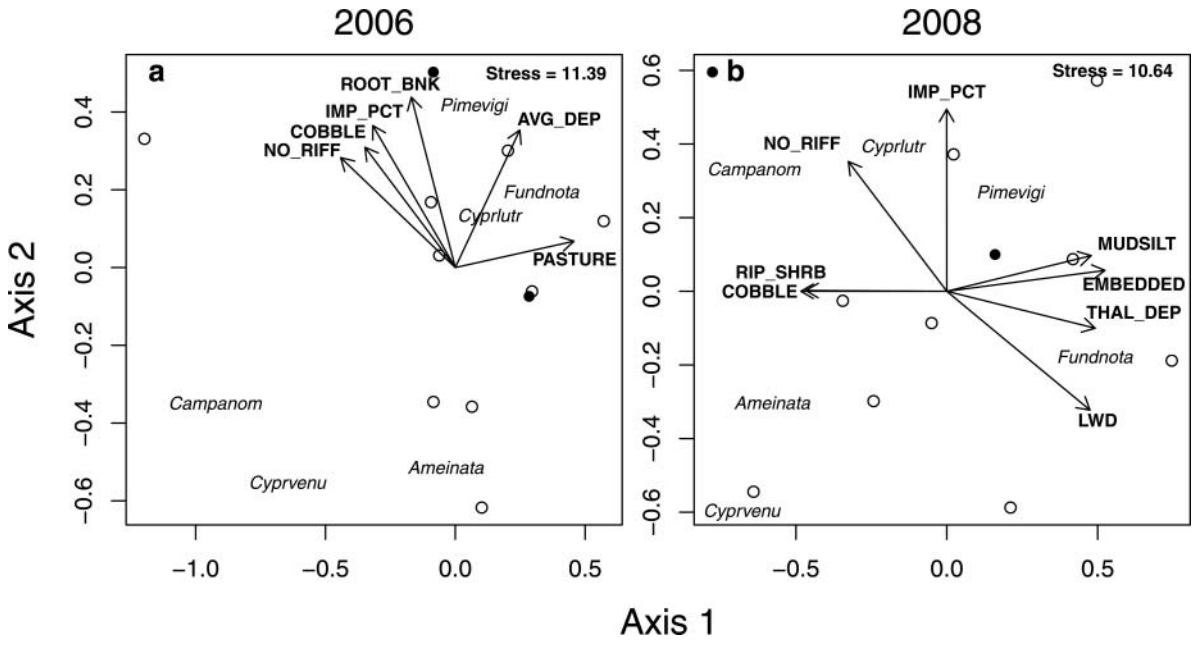

FIGURE 5. Nonmetric multidimensional scaling ordination of individual sites and species centroids in the Texas Blackland Prairies region using fish species composition for **(a)** 2006 and **(b)** 2008. Filled symbols represent Brazos River basin sites and open symbols represent Trinity River basin sites. Environmental vectors show the directions and magnitudes of significant correlations within the ordination space; abbreviations are as follows: MUDSILT = percentage of mud and silt, ROOT_BKF = number of coarse woody debris units within the high-water zone, LWD = percentage of instream cover large woody debris, COBBLE = percentage of cobble, EMBEDDED = degree of riffle embeddedness (%), RIP_SHRB = percentage of of riparian zone in shrub cover, NO_RIFF = number of riffles, IMP_PCT = percentage of impervious land cover, PASTURE = percentage of pasture, THAL_DEP = average thalweg depth, and AVG_DEP = average depth. See Table 1 for species codes.

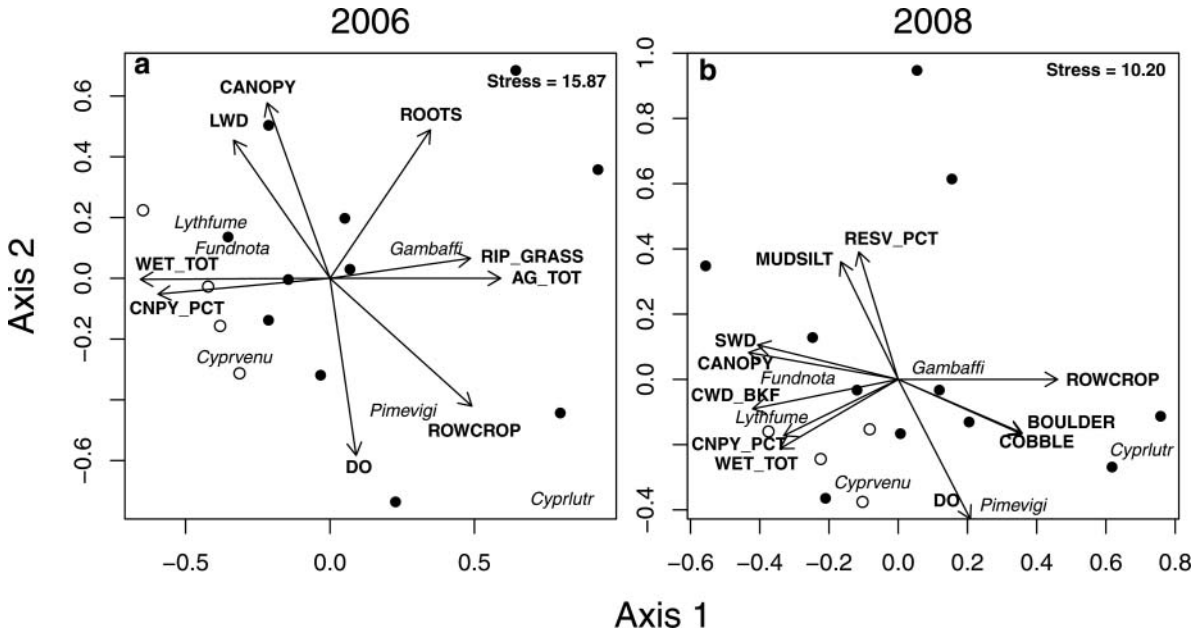

FIGURE 6. Nonmetric multidimensional scaling ordination of individual sites and species centroids in the East-Central Texas Plains region using fish species composition for **(a)** 2006 and **(b)** 2008. Filled symbols represent Brazos River basin sites and open symbols represent Trinity River basin sites. Environmental vectors show the directions and magnitudes of significant correlations within the ordination space; abbreviations are as follows: CANOPY = percentage of canopy cover over stream, LWD = percentage of instream cover large woody debris, SWD = percentage of instream cover small woody debris, ROOTS = percentage of instream cover roots, RIP-GRASS = percentage of riparian zone in grass and forb cover, DO = instantaneous dissolved oxygen concentration, BOULDER = percentage of boulder substrate, COBBLE = percentage of cobble substrate, MUDSILT = percentage of mud and silt substrate, CWD_BKF = number of coarse woody debris units within the high-water zone, AG_TOT = percentage of agricultural land cover, ROWCROP = percentage of row-crop land cover, CNPY_PCT = percentage of landscape canopy cover, WET_TOT = percentage of wetland land cover, and RESV_PCT = percentage of reservoir land cover. See Table 1 for species codes.

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more abundant at sites within more agricultural landscapes with fewer forests and wetlands. Blacktail shiners and ribbon shiners showed the opposite relationship with this agricultural gradient. These species were associated negatively with mud and silt and positively with dissolved oxygen, two environmental variables that correlated with NMS axis 2 in 2008. In 2006, ribbon shiners strongly influenced NMS axis 2, and the abundance of this species was positively correlated with woody debris and channel sinuosity. Like blacktail shiners and ribbon shiners, bullhead minnow were negatively associated with the gradient of increasing mud and silt and reservoir influence and decreasing dissolved oxygen in 2008. Blackstripe topminnow were negatively associated with the agricultural gradient during both years.

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DISCUSSION

Freshwater biodiversity is quickly becoming the most threatened component of biodiversity globally (Sala et al. 2000; Jenkins 2003; Dudgeon et al. 2006). Fish are an important component of freshwater biodiversity and a better understanding of how assemblages respond to environmental factors at multiple scales of space and time is important for developing effective conservation strategies. We found that fish assemblage structure was distinct among ecoregions, a pattern that reflects broad-scale influences of climate and physiography, which in turn, influence patterns of land cover and instream habitat for fish. The strength of the spatial pattern varied with hydrologic conditions with weaker differences between ecoregions in assemblage structure during the year that experienced prolonged drought. Within ecoregions, fish assemblage–environment relationships were observed at both the landscape and local habitat scales. Our results support calibrating stream biotic indices based on ecoregion-specific characteristics of environmental features and fish assemblage structure, sampling across multiple years of differing hydrological conditions to determine species–environment relationships, and developing conservation strategies that include management and restoration practices for both instream habitat and the surrounding landscape.

Factors Driving Ecoregional Differences in Fish Assemblages

Fish assemblage structure revealed weak grouping of samples according to river basin (i.e., Brazos versus Trinity rivers) in a manner reflecting the general east–west faunal turnover documented for Texas freshwater fishes (Hubbs 1991; Hoeinghaus et al. 2007). Sites within ecoregions consistently grouped together in ordination space. Additionally, *k*-means cluster analysis identified groups that corresponded well with ecoregional groupings. The ecoregional framework tracks broad-scale physiographic differences in geology and terrestrial vegetation across central and eastern Texas (Griffith et al. 2004). These regional-scale patterns in turn influence watershed landscape features, fluvial geomorphology, and reach-scale stream characteristics (Frissell et al. 1986). Along the physiographic gradient from the Cross Timbers to the Blackland Prairies and the East-Central Plains, habitats generally changed from rockier streams with more riffles to streams with finer substrate and more woody debris. Several species were strongly associated with ecoregional differences in habitat and were found in either the Cross Timbers or East-Central Texas Plains.

Fish assemblage structure was more divergent between ecoregions in 2008 than in 2006. Our study area experienced a severe drought during 2006, with many stream reaches restricted to perennial pools with little or no connectivity. Strong associations between functional and taxonomic composition of stream fish assemblages and hydrologic regimes have been demonstrated at regional scales (Poff and Allan 1995). The strong east–west gradient of average precipitation across the three ecoregions greatly contributes to differences in habitat features. During years with normal precipitation (e.g., 2008) differences in hydrology and habitat across this gradient strongly influence species spatial distributions and abundance. In 2006, lack of flow, loss of riffle habitats, and loss of longitudinal connectivity probably resulted in greater crowding, more intense biotic interactions, and environmental stress. Love et al. (2008) inferred that short-term changes in fish assemblages in Arkansas streams during summer drought were associated with local extinction and immigration dynamics of isolated pools. Assemblage variability was greater for stream reaches with greater hydrological variability, and abundant species had higher immigration rates and lower extinction rates (Taylor and Warren 2001). This has also been observed in Texas where streams that were disconnected during a summer drought showed more interannual variation in habitat and fish assemblage structure than streams that maintained flow (C. E. Stanley, J. M. Taylor, and R. S. King, unpublished results). Those authors inferred that streams with disconnected pools had species compositions resulting from local species extinctions due to changes in habitat and predation pressure and increases in species that were tolerant of abiotic stressors (e.g., high temperature, low dissolved oxygen) associated with nonflowing conditions. These factors may have reduced differences in fish assemblage structure between adjacent ecoregions in 2006, resulting in less separation of ecoregional groups in ordination space and greater misclassification rates between *k*-means clusters and ecoregional groups. Our results suggest that decreases in precipitation and stream flows predicted by climate change models for Texas (Ward 2011) have the potential to homogenize fish assemblages at regional scales (Perkin and Bonner 2011). Although we surveyed over 3 years, our data nonetheless provide evidence that, during periods of extreme drought, taxonomic structure of fish assemblages becomes less distinctive according to ecoregion.

Fish Assemblage–Habitat Associations within Ecoregions

Despite differences between years with contrasting hydrologic regimes, there were consistent ecoregional assemblage groupings, indicator species, and associated habitat variables

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across both years. The strength of ecoregional differences was greater in this study than other, similar studies on ecoregional classifications of North American stream communities (Hawkins et al. 2000; Van Sickle and Hughes 2000). Our results support recent efforts by state natural resource agencies to develop regionalized fish assemblage IBI metrics (e.g., Linam et al. 2002). We examined ecoregions separately to identify relationships between fish assemblages and environmental variables at landscape and local scales. Within the Cross Timbers ecoregion, fish assemblage structure was correlated with both natural (e.g., precipitation, watershed size) and anthropogenic (e.g., pasture, number of dams, WWTP outfalls, development, total agriculture, canopy percent) landscape factors during both years. Instream habitat variables that were correlated with fish assemblage structure within the Cross Timbers ecoregion for both years included discharge, mud–silt, coarse woody debris within the wetted channel, and erosion potential. There also appeared to be a latitudinal gradient underlying some of the variation in fish assemblage structure. This suggests that dominant landscape and habitat gradients within the Cross Timbers ecoregion are highly influential, and correlations with latitude may be an artifact of Trinity River sites having relatively more pasture than do Brazos River sites. Gradients in fish species composition were correlated with amount of impervious surface, number of riffles, and cobble substrates within the Blackland Prairies ecoregion for both years. In the East-Central Plains ecoregion, differences in fish assemblage structure were strongly associated with a gradient of agricultural development, ranging from landscapes dominated by forest and wetlands to those heavily planted in crops. The amount of small woody debris and canopy cover decreased along this land-use gradient. These landscape- and local-scale environmental variables appear to be important influences on stream fish assemblage structure within ecoregions. However, interpretations for the Blackland Prairie and East-Central Plains ecoregions should be viewed with caution. Even though some consistent relationships were observed for both of these ecoregions, dry conditions during 2006 reduced the number of study sites and could have influenced fish distributions and abundance patterns within stream reaches. Future studies would benefit from additional sampling within these ecoregions.

Stream fish assemblages are structured by environmental factors that interact at multiple scales (Poff 1997; Marsh-Matthews and Matthews 2000; Hugueny et al. 2010). We found that local-scale stream habitat variables as well as larger-scale natural and anthropogenic landscape features were significantly correlated with fish assemblage composition in central Texas. At the local scale, substrate composition was a key factor in all three ecoregions, with a gradient of rocky substrate to predominance of mud and silt correlating strongly with assemblage structure. This is consistent with findings from studies of wadeable streams in other regions of North America (Diana et al. 2006; D'Ambrosio et al. 2008; Rowe et al. 2009a). Berkman and Rabeni (1987) showed that as the percentage of fine substrates increased, the abundance of benthic invertebrate feeders, herbivores, and lithophilous spawners in stream fish assemblages declined in Missouri streams. The abundance of instream woody debris was also an important local-scale correlate for fish assemblage structure in our study area. The amount of woody debris was measured as a local habitat variable, but it is related to riparian conditions and the presence of intact forests and wetlands in the surrounding catchment (Richards et al. 1996).

At broader spatial scales, patterns of agricultural and urban land development were consistently associated with fish assemblage structure within all three ecoregions. The influence of land use in the surrounding watershed on stream fish assemblages has been demonstrated in studies conducted throughout the United States (e.g., Roth et al. 1996; Wang et al. 2001; Snyder et al. 2003; Rowe et al. 2009b). Conversion of natural landscapes for agricultural and urban development is considered an important cause of global decline in the integrity of lotic ecosystems (Allan 2004) and loss of aquatic biodiversity (Allan and Flecker 1993). In our study, landscape-scale factors were just as influential as the local habitat characteristics that typically are included in biological assessment protocols. Urban and agricultural development created landscape patterns that were correlated with fish assemblage structure, but may have been confounded by other spatial factors such as underlying geology or spatial contagion of land use (King et al. 2005). These land-use patterns, in turn, were correlated with a suite of instream environmental variables, and these local abiotic factors directly influence the distribution and abundance of fishes. In a study of headwater streams in the Pedernales River basin of central Texas, Birnbaum et al. (2007) found that local-scale environmental factors had strong correlations with fish and crayfish assemblage structure, and landscape-scale variables were weakly correlated. Those authors noted, however, that the amount of forest cover was positively associated with local-scale factors that define high quality habitat for species intolerant of high temperatures, turbidity, and low dissolved oxygen.

Conservation of stream habitats and their biota requires an understanding of how environmental factors, both natural and human-influenced, structure aquatic assemblages across different scales of space and time (Fausch 2010; Grossman and Sabo 2010). Many previous studies have focused on the importance of variables at the local habitat scale or across relatively small study regions. By including a comprehensive suite of variables at multiple spatial scales in a large region, our study contributes to understanding how these environmental factors may interact to structure stream fish assemblages. By examining years with contrasting hydrologic conditions, our study also provides clues to how decreased rainfall and its effect on stream habitat may contribute to homogenization of fish assemblages under the growing threat of climate change. In addition to contributing to a more general understanding of fish–habitat relationships, these kinds of studies will greatly assist natural resource managers tasked with assessing the ecological status of surface waters and watersheds.

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Appendix: Supplemental Data on Environmental Variables and Community Structure

TABLE A.1. Local-scale environmental variables used in this study, with median values (interquartile ranges in parentheses) for each ecoregion in each year.

	Cross Timbers		Texas Blackland Prairies		East-Central Texas Plains	
Variable	2006	2008	2006	2008	2006	2008
Wetted width (m)	8.16 (5.8–9.98)	9.23 (7.05–12.02)	4.95 (3.78–6)	6.78 (5.62–7.53)	4.58 (3.86–5.58)	5.32 (4.13–5.84)
Average depth (m)	0.22 (0.17–0.28)	0.28 (0.19–0.39)	0.25 (0.2–0.3)	0.34 (0.29–0.46)	0.27 (0.19–0.39)	0.31 (0.2–0.51)
Thalweg depth (m)	0.39 (0.3–0.52)	0.48 (0.37–0.64)	0.36 (0.31–0.44)	0.55 (0.49–0.66)	0.39 (0.31–0.67)	0.45 (0.34–0.79)
Discharge (m^3/s)	0 (0–1.04)	1.24 (0.3–4)	0.26 (0–0.68)	1.45 (0.01–6.36)	0.44 (0.1–1.35)	0.7 (0.01–2.09)
Pool width (m)	12 (8.5–15)	10.2 (8.2–14.9)	1.81 (0–7.1)	8 (6–10)	0 (0–6.3)	4 (2–6)
Pool depth (m)	0.85 (0.72–1.25)	1.2 (0.9–1.6)	0.85 (0–1.23)	1.1 (0.7–1.5)	0.8 (0–1.3)	1.1 (0.75–1.5)
Number of riffles	2 (0–2)	3 (3–3)	1 (0–3)	0 (0–2)	0 (0–1)	0 (0–1)
% Embeddedness	35 (17.5–50)	35 (15–53.33)	35 (30–100)	35 (30–100)	100 (33.33–100)	100 (40–100)
% Bedrock	22 (8.33–42)	16.5 (0–36.25)	0 (0–55)	5 (0–36)	0	0
% Large boulder	0 (0–1.67)	0 (0–1.4)	0	0	0	0
% Small boulder	3.17 (0.60–5.17)	2 (0–4.67)	0 (0–1)	0 (0–3)	0 (0–1)	0
% Cobble	9 (3.67–21)	13 (7.83–18)	3 (0.4–20.4)	6 (0–15)	0 (0–4)	0 (0–2)
% Gravel	26.2 (13.33–39)	29 (7.83–45.83)	20.83 (4–39)	7 (3–25)	1.17 (0–16)	5.33 (0–19)
% Sand	8.33 (3.33–23)	13.33 (3.83–28.33)	7 (2–25)	21 (9–32)	43 (11–72.6)	53 (25–79)
% Mud–silt	3.8 (0–19.67)	2 (0–15)	16 (8.2–48)	19.8 (13–66)	31 (7.4–49)	21 (14–52)
% Stream cover	25 (20.17–34.17)	29.17 (18.33–45)	26 (14–71.67)	24 (22–30)	51 (35.83–63)	32 (25–34.17)
% Filamentous algae	9 (2.6–23.17)	6 (3–22)	2.5 (0.2–17.2)	2.8 (0.2–9.4)	2.2 (0–9.4)	0 (0–1.25)
% Microalgae	1 (0–4.67)	0 (0–10)	2.6 (0–18.2)	0	2 (0–19.2)	0
% Macrophytes	2.83 (0.67–9.2)	0 (0–1.2)	0 (0–13.2)	0	0.4 (0–1.5)	0 (0–0.4)
% Large woody debris	0 (0–1)	0.33 (0–2)	2.6 (0.4–6)	1 (0–7)	10 (4.8–20)	8 (3.75–17)
% Small woody debris	1 (0.17–2.5)	1.8 (0.4–4.17)	2.6 (1.6–5)	37 (13–43)	24 (1.2–38)	47 (39.8–61)
% Roots	0.2 (0–1.33)	0.83 (0–2)	0 (0–0.6)	17 (11.6–31)	0.2 (0–1)	18 (9–32)
% Overhanging vegetation	1.2 (0–3.6)	1 (0.33–2.2)	1 (0–1.2)	1 (0–2)	0.6 (0.4–1.2)	1.4 (0–2.2)

TABLE A.1. Continued.

Variable	Cross Timbers		Texas Blackland Prairies		East-Central Texas Plains	
	2006	2008	2006	2008	2006	2008
% Undercut bank	1 (0–2.4)	1.17 (0.4–2.4)	0	7 (2–16)	0 (0–0.2)	1.4 (0–4)
% Leafpack	0 (0–1)	0	1.8 (1–4.2)	0 (0–3)	19 (6–29)	2.2 (0.5–4.6)
% Artificial substrate	0 (0–0.2)	0	0.6 (0–4.2)	0.4 (0–3)	0	0 (0–1)
Number coarse woody debris (wet)	0.6 (0.25–1.40)	0.8 (0.5–1.6)	3 (1.5–4.5)	4 (1.75–8.5)	11.75 (5.75–20.5)	11.4 (8–19.25)
Number coarse woody debris (bankfull)	0.5 (0.2–1)	1 (0.5–1.8)	3.25 (1.75–4.5)	3.75 (1–6)	6 (4–11.75)	1.75 (1–3.75)
Number rootwads (wet)	0.2 (0–0.8)	0.5 (0–1)	0.25 (0–0.4)	0.75 (0.5–1)	0.5 (0.5–2)	1.75 (0.67–4)
Number rootwads (bankfull)	1 (0.4–1.8)	1.4 (0.5–3)	0.67 (0–1)	2 (0.5–2.5)	1.33 (1–21)	1.25 (0.4–2.25)
Erosion potential	25.5 (15.5–32.5)	32.08 (20.5–40.42)	36 (23–52.5)	46.5 (33.5–54)	36.67–26.5–46)	48.5 (40–57.5)
% Exposed soil	29.5 (17.4–43)	38.33 (28.7–50)	35.5 (24.7–57.5)	51 (36–62.5)	38.75 (19.5–49.5)	49 (36.5–63)
Bank slope	30.83 (24.9–43.7)	33.92 (25.7–40)	30.42 (19.5–38.15)	45.5 (38.2–59.25)	37.5 (25.5–44)	49.7 (35–56.56)
Buffer width	17.75 (14.7–19)	17.92 (15–19.5)	8.4 (2.9–10.4)	18 (16–18.3)	12.1 (5.3–20)	17 (15.5–19.5)
% Riparian trees	50 (40–70)	45 (40–57.5)	47.5 (37.5–55)	40 (32.5–42.5)	47.5 (30–62.5)	35 (25–42.5)
% Riparian shrubs	12.5 (7.5–20)	25 (20–30)	10 (5–32.5)	2.5 (0–15)	7.5 (5–12.5)	10 (2.5–12.5)
% Riparian grass	22.5 (17.5–32.5)	25 (15–35)	42.5 (15–50)	47.5 (32.5–65)	32.5 (22.5–50)	47.5 (40–57.5)
% Canopy cover	59 (45–80.33)	62 (47.4–84.2)	82.66 (45.3–92.64)	87.06 (65.3–92.64)	80 (70.88–95)	90.88 (82–98.54)
Dissolved oxygen (mg/L)	5.95 (4.31–8.43)	6 (4.77–8.56)	9.08 (6.87–10.23)	6.37 (5.77–7.96)	5.23 (4.35–7.36)	4.12 (3.8–5.54)
pH	7.85 (7.66–8.22)	7.82 (7.58–7.96)	7.9 (7.8–8.2)	7.96 (7.76–8.11)	7.7 (7.3–7.9)	7.47 (7.29–7.6)
Specific conductance (μS/cm)	551 (405–754)	604 (476–752)	619 (411–849)	616 (497–663)	334 (236–1037)	564 (413–815)
Temperature (°C)	27.12 (26.1–29.51)	27.36 (26.62–28.62)	28.2 (26.52–32.06)	27.3 (26–28.8)	26.84 (25.52–28.5)	26.4 (25.2–26.8)

TABLE A.2. Correlation coefficients (r) and P-values for the environmental vectors that best describe the relationships between environmental variables and community structure across and within ecoregions. Values are based on rotational vector fitting between variables and nonmetric multidimensional scaling scores for each site. Values in bold italics represent significant relationships.

	All ecoregions				Cross Timbers				Texas Blackland Prairies				East-Central Texas Plains			
	2006		2008		2006		2008		2006		2008		2006		2008	
Environmental variable	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Landscape																
Latitude					*0.665*	*0.001*	*0.813*	*0.001*	0.463	0.375	0.649	0.125	0.369	0.412	0.237	0.686
Longitude					0.185	0.542	***0.478***	***0.013***	0.388	0.473	0.539	0.251	***0.629***	***0.050***	0.540	0.137
Ecoregion					0.720	0.260	0.720	0.289	0.000	1.000	0.000	1.000	0.751	0.585	0.756	0.440
Precipitation (annual average)					0.404	0.053	***0.511***	***0.006***	0.335	0.595	0.554	0.220	***0.678***	***0.022***	***0.656***	***0.035***
Elevation (m)					0.142	0.696	0.412	0.051	0.485	0.329	0.329	0.640	***0.649***	***0.038***	0.483	0.238
Watershed slope					0.162	0.628	0.326	0.144	0.392	0.538	0.350	0.590	***0.730***	***0.012***	***0.692***	***0.014***
Watershed area					***0.604***	***0.002***	***0.656***	***0.001***	0.615	0.147	0.581	0.188	0.459	0.245	0.622	0.056
Number of dams					***0.581***	***0.003***	***0.709***	***0.001***	0.428	0.450	0.426	0.446	0.139	0.897	0.234	0.718
Outfalls (million gal/d)					***0.461***	***0.015***	***0.482***	***0.012***	0.351	0.540	0.489	0.356	0.355	0.433	0.317	0.531
Number of outfalls					***0.527***	***0.006***	***0.477***	***0.010***	0.405	0.497	0.473	0.358	0.234	0.709	0.219	0.739
Number of reservoirs					***0.508***	***0.005***	0.294	0.207	0.219	0.718	0.580	0.279	0.306	0.560	0.371	0.384
% Reservoir					***0.425***	***0.031***	0.218	0.425	0.219	0.684	0.580	0.263	***0.688***	***0.038***	***0.764***	***0.015***
% Surface water					***0.418***	***0.050***	***0.502***	***0.006***	0.622	0.146	0.597	0.170	***0.642***	***0.044***	***0.698***	***0.011***
% Developed					***0.420***	***0.042***	***0.483***	***0.010***	***0.875***	***0.002***	0.673	0.097	0.368	0.407	0.242	0.719
% Forestland					0.392	0.060	0.401	0.053	0.292	0.699	0.039	0.995	***0.654***	***0.022***	0.585	0.069
% Shrubland					0.331	0.137	***0.581***	***0.003***	0.383	0.475	0.276	0.712	0.097	0.955	0.219	0.748

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TABLE A.2. Continued.

	All ecoregions				Cross Timbers				Texas Blackland Prairies				East-Central Texas Plains			
	2006		2008		2006		2008		2006		2008		2006		2008	
Environmental variable	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
% Grassland					0.203	0.473	***0.481***	***0.010***	0.477	0.347	0.370	0.574	0.247	0.703	0.311	0.531
% Pasture					***0.740***	***0.001***	***0.770***	***0.001***	***0.765***	***0.024***	0.633	0.127	***0.656***	***0.045***	0.468	0.223
% Row crop					***0.502***	***0.012***	0.314	0.177	0.344	0.622	0.123	0.925	***0.843***	***0.002***	***0.865***	***0.004***
% Wetland					0.316	0.175	0.369	0.075	0.462	0.378	0.454	0.414	***0.856***	***0.002***	***0.756***	***0.009***
% Total agriculture					***0.613***	***0.001***	***0.496***	***0.014***	0.462	0.370	0.493	0.348	***0.771***	***0.007***	***0.679***	***0.028***
% Impervious cover					0.381	0.070	***0.398***	***0.044***	***0.800***	***0.012***	***0.774***	***0.030***	0.582	0.081	0.376	0.401
% Canopy cover					***0.419***	***0.041***	***0.447***	***0.024***	0.213	0.821	0.128	0.941	***0.780***	***0.005***	***0.701***	***0.011***
Geomorphology and hydrology																
Wetted width (m)	***0.499***	***0.001***	***0.442***	***0.003***	***0.432***	***0.032***	0.201	0.457	0.134	0.935	0.389	0.502	0.328	0.498	0.375	0.372
Average depth (m)	***0.383***	***0.009***	***0.488***	***0.001***	0.304	0.199	***0.444***	***0.015***	0.715	0.061	0.612	0.160	0.584	0.085	0.564	0.100
Thalweg depth (m)	0.271	0.088	0.051	0.914	0.232	0.388	0.279	0.258	0.651	0.118	***0.786***	***0.019***	0.543	0.111	0.518	0.141
Discharge	0.234	0.169	0.27	0.104	***0.477***	***0.011***	***0.388***	***0.043***	0.533	0.258	0.724	0.054	0.277	0.617	0.423	0.301
Pool width (m)	***0.618***	***0.001***	***0.429***	***0.002***	***0.499***	***0.006***	0.238	0.334	0.422	0.464	0.240	0.793	0.066	0.973	0.376	0.409
Pool depth (m)	0.239	0.155	0.046	0.938	0.240	0.394	0.248	0.324	0.311	0.683	0.481	0.355	0.074	0.968	0.069	0.972
Number of riffles	***0.487***	***0.003***	***0.586***	***0.001***	***0.661***	***0.001***	0.164	0.626	***0.867***	***0.001***	***0.752***	***0.049***	0.371	0.414	0.490	0.194
Substrate																
% Embeddedness	***0.518***	***0.001***	***0.689***	***0.001***	0.229	0.424	0.390	0.056	0.470	0.385	***0.826***	***0.011***	0.437	0.286	0.472	0.241
% Bedrock	***0.469***	***0.001***	***0.445***	***0.001***	0.120	0.797	0.207	0.466	0.688	0.082	0.540	0.235	0.515	0.132	0.476	0.169
% Large boulder	0.159	0.456	0.241	0.151	0.098	0.872	0.074	0.928	0.383	0.450	0.308	0.492	0.574	0.275	0.522	0.169
% Small boulder	***0.421***	***0.005***	***0.335***	***0.022***	0.152	0.698	0.030	0.982	0.531	0.280	0.370	0.526	***0.620***	***0.050***	0.473	0.169
% Cobble	***0.366***	***0.011***	***0.579***	***0.001***	0.117	0.789	0.088	0.861	***0.769***	***0.025***	***0.757***	***0.041***	0.517	0.141	***0.742***	***0.008***
% Gravel	***0.383***	***0.006***	***0.586***	***0.001***	0.229	0.411	***0.438***	***0.035***	0.165	0.888	0.731	0.054	0.240	0.707	0.291	0.578
% Sand	***0.487***	***0.002***	***0.536***	***0.001***	0.255	0.321	0.250	0.331	0.569	0.211	0.328	0.628	0.480	0.206	0.338	0.497
% Mud–silt	***0.645***	***0.001***	***0.737***	***0.001***	***0.634***	***0.002***	***0.618***	***0.001***	0.353	0.573	***0.765***	***0.025***	0.610	0.078	***0.745***	***0.014***
Fish cover																
% Stream cover	***0.381***	***0.015***	0.252	0.126	0.362	0.095	0.222	0.428	0.383	0.568	0.616	0.153	0.418	0.316	0.390	0.375
% Filamentous algae	0.155	0.496	***0.425***	***0.008***	0.180	0.574	0.391	0.051	0.487	0.350	0.594	0.175	0.337	0.478	0.639	0.049
% Microalgae	0.252	0.146	***0.360***	***0.012***	0.276	0.277	***0.449***	***0.026***	0.503	0.309	0.137	0.838	0.294	0.580	0.132	0.898
% Macrophyte	0.261	0.111	0.186	0.344	0.234	0.401	0.258	0.309	0.387	0.549	0.241	0.724	0.565	0.113	0.287	0.586
% Large woody debris	***0.707***	***0.001***	***0.655***	***0.001***	0.201	0.545	***0.471***	***0.012***	0.521	0.273	***0.899***	***0.002***	***0.735***	***0.009***	0.267	0.643
% Small woody debris	***0.665***	***0.001***	***0.844***	***0.001***	0.273	0.283	0.073	0.923	0.179	0.865	0.463	0.361	***0.605***	***0.066***	***0.789***	***0.002***
% Roots	0.106	0.693	***0.738***	***0.001***	0.161	0.652	0.291	0.207	0.345	0.569	0.420	0.482	***0.782***	***0.010***	0.241	0.705
% Overhanging vegetation	0.272	0.095	0.035	0.954	***0.414***	***0.042***	0.176	0.597	0.548	0.237	0.181	0.871	0.321	0.508	0.587	0.079
% Undercut bank	***0.333***	***0.021***	***0.398***	***0.009***	0.120	0.802	0.166	0.625	0.294	0.618	0.066	0.978	0.426	0.311	0.205	0.776
% Leafpack	***0.578***	***0.001***	***0.360***	***0.024***	***0.426***	***0.034***	0.209	0.478	0.274	0.719	0.597	0.176	0.330	0.492	***0.681***	***0.024***
% Artificial substrate	0.259	0.105	***0.477***	***0.002***	***0.426***	***0.035***	0.295	0.205	0.611	0.168	0.605	0.161	0.595	0.156	0.398	0.332
Number coarse woody debris (wet)	***0.745***	***0.001***	***0.765***	***0.001***	***0.471***	***0.029***	***0.559***	***0.002***	0.252	0.772	0.434	0.420	0.545	0.113	0.374	0.391
Number coarse woody debris (bankfull)	***0.711***	***0.001***	0.252	0.150	0.137	0.756	0.105	0.837	0.226	0.812	0.276	0.747	0.545	0.122	***0.808***	***0.006***
Number rootwads (wet)	0.290	0.067	***0.504***	***0.001***	0.215	0.450	0.270	0.258	0.621	0.116	0.451	0.402	0.274	0.575	0.234	0.702
Number rootwads (bankfull)	***0.375***	***0.013***	0.038	0.950	0.231	0.388	0.257	0.297	***0.776***	***0.025***	0.212	0.853	0.300	0.578	0.612	0.059
Bank and riparian characteristics																
Erosion potential	***0.470***	***0.001***	***0.484***	***0.001***	***0.442***	***0.024***	***0.433***	***0.025***	0.209	0.861	0.345	0.592	0.407	0.319	0.062	0.981
% Exposed soil	***0.373***	***0.009***	***0.320***	***0.034***	***0.467***	***0.020***	0.385	0.059	0.217	0.855	0.388	0.511	0.520	0.146	0.028	0.995
Bank slope	0.175	0.368	***0.590***	***0.001***	0.110	0.837	***0.539***	***0.005***	0.612	0.155	0.622	0.148	0.614	0.066	0.280	0.629
Buffer width	0.073	0.850	0.125	0.617	0.044	0.975	0.139	0.699	0.106	0.964	0.330	0.633	0.165	0.854	0.406	0.319

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TABLE A.2. Continued.

	All ecoregions				Cross Timbers				Texas Blackland Prairies				East-Central Texas Plains			
	2006		2008		2006		2008		2006		2008		2006		2008	
Environmental variable	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
% Riparian trees	***0.318***	***0.032***	***0.456***	***0.002***	0.316	0.195	***0.419***	***0.035***	0.158	0.889	0.180	0.892	0.493	0.177	0.299	0.581
% Riparian shrubs	0.142	0.541	***0.614***	***0.001***	0.051	0.954	0.246	0.318	0.183	0.877	***0.732***	***0.041***	***0.711***	***0.018***	0.184	0.807
% Riparian grass	***0.353***	***0.012***	***0.590***	***0.001***	0.277	0.272	***0.428***	***0.032***	0.165	0.919	0.526	0.279	***0.640***	***0.050***	0.490	0.212
% Canopy cover	***0.485***	***0.001***	***0.548***	***0.001***	0.205	0.532	0.324	0.144	0.450	0.402	0.422	0.438	***0.804***	***0.006***	***0.827***	***0.009***
Water chemistry																
Dissolved oxygen (mg/L)	0.114	0.659	***0.514***	***0.001***	0.115	0.802	0.260	0.280	0.454	0.353	0.502	0.316	***0.769***	***0.008***	***0.894***	***0.002***
pH	***0.328***	***0.027***	***0.428***	***0.002***	0.244	0.364	0.125	0.751	0.212	0.829	0.390	0.521	0.525	0.149	***0.681***	***0.027***
Specific conductivity (μS/cm)	0.250	0.142	0.185	0.336	0.364	0.132	***0.410***	***0.047***	0.210	0.868	0.440	0.451	0.420	0.278	0.340	0.480
Temperature (°C)	***0.341***	***0.020***	***0.367***	***0.015***	0.203	0.499	0.340	0.104	0.389	0.520	0.073	0.980	***0.674***	***0.026***	0.550	0.103

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