CrossMark

PRIMARY RESEARCH PAPER

Ecoregional, catchment, and reach-scale environmental factors shape functional-trait structure of stream fish assemblages

Allison A. Pease · Jason M. Taylor · Kirk O. Winemiller · Ryan S. King

Abstract Patterns of association between functional traits and environmental gradients can improve understanding of species assemblage structure from local to regional scales, and therefore may be useful for natural resource management. We measured functional traits related to trophic ecology, habitat use, and life-history strategies of fishes and examined their associations with environmental factors in the Brazos and Trinity River basins in Central Texas. We also examined the relationship between functional diversity of fish assemblages and indices of biotic integrity and habitat quality. Environmental characteristics at the local reach and catchment scales, including the extent of forested area in the watershed, amount of land developed for urban and agricultural uses, stream size, substrate characteristics, and availability of riffle and pool habitats, were significantly associated with functional trait composition of fish assemblages. Broad physiographic differences between ecoregions also had a large influence on taxonomic and functional assemblage structure. In general, the volume of functional trait space occupied by fish assemblages was greatest in streams with high habitat quality scores located within landscapes having less alteration from agriculture and urban

A. A. Pease · K. O. Winemiller
Department of Wildlife and Fisheries Sciences, Texas
A&M University, 2258 TAMU, College Station,
TX 77843-2258, USA
e-mail: k-winemiller@tamu.edu

Present Address:
A. A. Pease (✉)
Department of Natural Resources Management, Texas
Tech University, Box 42125, Lubbock, TX 79409-2125,
USA
e-mail: allison.pease@ttu.edu

J. M. Taylor · R. S. King
Department of Biology, Center for Reservoir and Aquatic
Systems Research, Baylor University, One Bear Place
97388, Waco, TX 76798-7388, USA
e-mail: ryan_s_king@baylor.edu

Present Address:
J. M. Taylor
Water Quality and Ecology Research Unit, National
Sedimentation Laboratory, United States Department of
Agriculture, Agricultural Research Service, 598 McElroy
Drive, Oxford, MS 38655, USA
e-mail: jason.taylor@ars.usda.gov

development. Distributions of functional traits in fish assemblages might provide an additional basis for assessment of stream condition in relation to environmental impacts.

Introduction

The incorporation of species' functional traits into analyses of diversity has recently been promoted as a way to build a more general understanding of patterns and processes in community ecology (McGill et al., 2006; Webb et al., 2010). Compared to traditional approaches based on taxonomic composition of assemblages, analyses using species traits can reveal relationships that apply across zoogeographic regions (Poff et al., 2006; Olden & Kennard, 2010). Examining functional structure may also reveal more about the mechanisms by which ecological communities respond to environmental change (Poff et al., 2006; Kearney & Porter, 2009). Traits-based methods thus have potential for enhancing conservation applications, such as bioassessment metrics used by natural resource managers to evaluate ecological integrity (e.g., Garnier et al., 2004; Culp et al., 2011).

Documentation of relationships between environmental variables and species functional traits could improve stream bioassessment approaches that currently are based on taxonomic structure and coarse functional groups (Doledec & Statzner, 2010; Culp et al., 2011). Analyses that focus on species traits rather than taxonomic structure might reveal patterns more generally applicable across regions (Lamouroux et al., 2002; McGill et al., 2006; Poff et al., 2006). Whereas the occurrence of certain taxa in a local assemblage may reflect historical influences in addition to environmental factors, the functional composition of an assemblage more closely reflects constraints imposed by environmental gradients (Schlosser, 1982; Poff & Allan, 1995; Angermeier & Winston, 1999; Hoeinghaus et al., 2007). Functional-trait approaches may also improve upon methods, such as the index of biotic integrity (IBI; Karr et al., 1986), that categorize species into a handful of broad functional groups. Research on ecomorphology (e.g., Gatz, 1979; Webb, 1984;

Montaña & Winemiller, 2013) and life histories (e.g., Balon, 1975; Winemiller & Rose, 1992) of freshwater fishes have yielded a great deal of information on individual traits that can be used to make inferences about the ecology of poorly studied species based on established relationships between traits and ecology. Examining these traits may reveal finer-scale functional differences between species that might not be apparent when species are assigned to broad functional categories (Fonseca & Ganade, 2001; Villeger et al., 2008). The use of a larger suite of traits makes it possible to characterize multiple niche dimensions, whereas broadly defined functional groups usually focus on just a few aspects, such as feeding and habitat use (Wilson, 1999). Another advantage of using quantitative traits is that they can readily be used for newly developed multidimensional methods of estimating functional diversity (e.g., Villeger et al., 2008; Laliberte & Legendre, 2010). A lack of available data for large sets of quantitative traits for species poses a significant challenge for this approach, but museum collections may be used to supplement existing data in some cases (e.g., Ingram & Shurin, 2009).

Though many studies have suggested that functional-trait approaches using stream invertebrate assemblages are useful for assessing biotic responses to environmental change (e.g., Charvet et al., 2000; Doledec et al., 2006; Poff et al., 2006), our understanding of trait–environment relationships for stream fishes requires further development (Lamouroux et al., 2002; Olden et al., 2010). Building upon previous studies of stream invertebrate functional traits across gradients of watershed land use, Doledec et al. (2011) recently highlighted the value of using functional traits, such as generation time and tolerance of oxygen depletion, for assessing stream condition across large regions. For stream fish assemblages, some key trait–environment relationships have been described that are similarly useful for the assessment of ecological integrity. For example, Walser & Bart (1999) observed a reduction in fish species associated with coarse substrate in stream reaches where agriculture in the landscape led to increased silt and decreased complexity in substrate composition. Similarly, Berkman & Rabini (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. Perkin and colleagues (Perkin &

Bonner, 2011; Perkin & Gido, 2011) have demonstrated strong relationships between the presence of fish species within certain reproductive guilds and variables associated with anthropogenic flow alteration in streams. Other studies have shown that, at the landscape scale, agriculture and other land uses in a watershed are correlated with a decrease in species considered intolerant to anthropogenic disturbance (e.g., Roth et al., 1996; Brown, 2000; Wang et al., 2001). Further examination of trait–environment relationships across regions could contribute to a better understanding of how stream fish assemblages respond to environmental change (Pont et al., 2006; Heino et al., 2013).

The structure of stream fish assemblages is considered well suited for bioassessment due to the relative ease of conducting surveys and identification of species, availability of life-history information, and documented species responses to habitat alteration (Karr, 1981; Fausch et al., 1990). Following the IBI approach, stream reaches are scored based on relative abundances of indicator taxa assigned to categories based on feeding ecology, habitat use, and sensitivity to anthropogenic disturbance. In order to account for zoogeographic differences in species pools, such indices must be adjusted for different regions. Natural resource management agencies often calibrate fish-based indicators for different ecoregions that have been delineated based on climate, soil types, and vegetation (e.g., Simon, 1991; Linam et al., 2002). Identifying relationships between environmental conditions and stream fish assemblages that translate across regions remains a fundamental challenge.

In this study, we examined the influence of environmental variables at local and landscape scales on the functional trait structure of stream fish assemblages in a large region of central Texas, USA. Our related research in this region has shown that the taxonomic structure of these assemblages is shaped largely by broad physiographic differences across ecoregions, while influences of local, in-stream habitat features and watershed land use are more apparent when examined within ecoregions (Pease et al., 2011). This prior research suggested that taxonomic indicators of habitat quality are ecoregion specific. The present study aims to identify associations between environmental variables and the functional composition of local fish assemblages that may be more consistent across ecoregions. Specifically, our

objectives were (1) to characterize associations between species functional traits and environmental variables at catchment and local-reach scales within and across ecoregions, (2) to quantify relationships between measures of functional diversity of fish assemblages and environmental gradients, and (3) to examine relationships between functional diversity and established measures of habitat quality and biotic integrity. We predicted that feeding, habitat use, and life-history traits of fishes would be related to environmental variables associated with habitat diversity, flow regime, and watershed land use across ecoregions. Further, we predicted that functional trait diversity of local fish assemblages would be positively related to metrics of habitat quality and biotic integrity. These relationships may provide valuable information for determining the potential of functional traits of fish assemblages as a basis for assessing the condition of streams.

Materials and methods

Study area

Data were collected from 64 perennial, wadeable streams within the Brazos and Trinity River basins in Texas (Fig. 1). These streams lie within the Cross Timbers, Texas Blackland Prairies, and East Central Texas Plains ecoregions. Each ecoregion contained sites within a range of stream sizes (watershed areas of 30–6200 km^2). The Cross Timbers ecoregion, a mosaic of forests, woodlands and prairies, 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 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 crops and urban development (Griffith et al., 2004). Study sites were selected to provide broad geographic coverage, a range of landscape features (including land use), and representation of a range of stream habitat conditions.
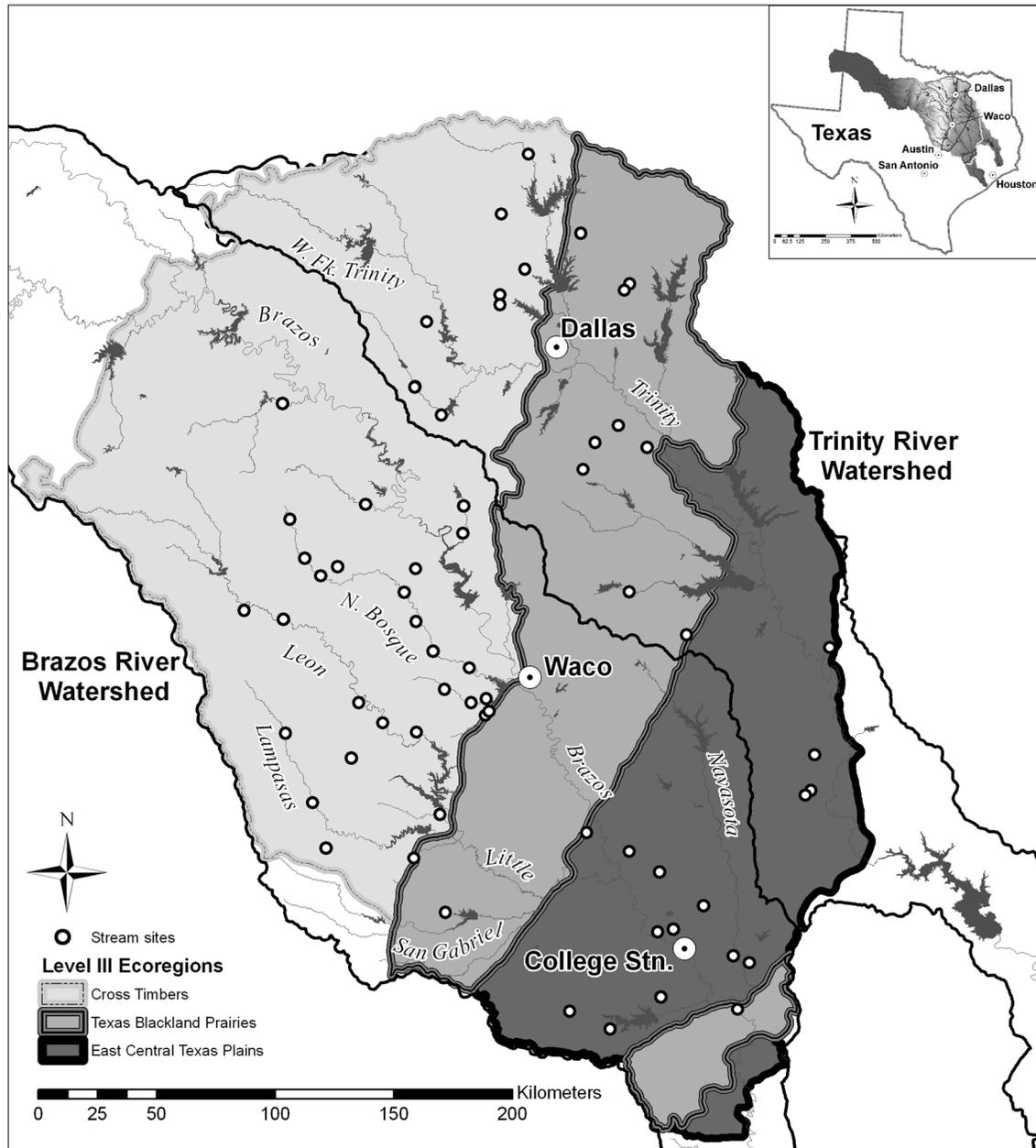
Fig. 1 Map of study region in the Brazos and Trinity Basins of Texas. *Solid dots* indicate locations of surveyed stream reaches

Data collection

We sampled stream reaches during the summer (June–August) of 2008 following methods used by the Texas Commission on Environmental Quality (2007). At each survey site, fish assemblage and local habitat data were collected within a 160–500 m stream reach. 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 using a backpack electrofisher (Smith-Root Model LR-24) and seine net (4.6 m × 1.8 m or 1.8 m x 1.8 m, 5-mm mesh). 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 within the study reach, additional seine hauls were made until no additional species were captured. Collected fishes were identified, separated into juvenile and adult age classes, 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 event for analyses of patterns in fish assemblage structure. Methods for handling and preserving fishes were approved by the Texas A&M University Institutional Animal Care and Use Committee.

At each study site, we measured 32 local habitat variables (Table 1) including substrate composition, in-stream cover, wetted width, depth, canopy cover, bank slope, riparian buffer width, instantaneous

Table 1 Local-scale environmental variables measured at Central Texas stream reaches

Category	Abbreviation	Variable
Substrate	BEDROCK	Percent of substrate bedrock
	LG_BLDR	Percent of substrate large boulders (>45 cm)
	SM_BLDR	Percent of substrate small boulders (25–45 cm)
	COBBLE	Percent of substrate cobble (6–25 cm)
	GRAVEL	Percent of substrate gravel (2–60 mm)
	SAND	Percent of substrate sand (0.06–2 mm)
	MUDSILT	Percent of substrate mud or silt (<0.06 mm)
	GRV_LRG	Percent of substrate gravel or larger
	EMBEDDED	Substrate embeddedness (percent of boulders and cobble covered in fine sediment)
Algae/macrophytes	ALGAE_AB	Abundance of algae in study reach (scored as abundant, common, rare, or absent)
	MCRPH_AB	Abundance of aquatic macrophytes in study reach (scored as abundant, common, rare, or absent)
Instream cover	STRM_COV	Visually estimated percent cover
	LWD	Percent of in-stream cover large woody debris
	SWD	Percent of in-stream cover small woody debris
	ROOTS	Percent of in-stream cover submerged roots
Stream morphology	STRMBEND	Number of stream bends in study reach
	WETWIDTH	Wetted width of stream (averaged across transects)
	AVG_DEP	Average stream depth
	THAL_DEP	Thalweg depth (averaged across transects)
	POOL_WID	Maximum pool width
	POOL_DEP	Maximum pool depth
	VELDEPTH	Velocity/depth regime score (optimal, suboptimal, marginal, or poor)
	NO_RIFF	Number of riffles in study reach
Flow	DISCHARG	Discharge (instantaneous stream flow in ft3/s)
Riparian	BUFFER	Width of riparian buffer (averaged across transects)
Characteristics	CANOPY	Percent of stream shaded by tree canopy (measured with densitometer)
Bank	BNK_SLOP	Bank slope (averaged across transects)
Characteristics	SOIL_EXP	Percentage of exposed soil on banks
Water	DO	Instantaneous dissolved oxygen (mg/L)
Parameters	PH	pH
	SPCOND	Specific conductivity (µs)
	TEMP	Water temperature (°C)

Table 2 Landscape-scale environmental variables estimated for Central Texas streams

Abbreviation	Variable
LAT_DS	Latitude, decimal degrees
LONG_DS	Longitude, decimal degrees
PRECIP	Mean annual precipitation, calculated for watershed
ELEV_M	Mean elevation (m)
WSLOPE	Mean watershed slope
WSHEDKM2	Watershed area (km^2)
DAMS_CT	Number of dams in watershed
OUT_MGD	Cumulative permitted outfall discharge rate within watershed (million gallons per day)
OUT_CT	Number of outfalls within watershed
RESV_PCT	% Land covered in reservoirs
WATER	% Land covered by water
DEV_TOT	% Developed land
FOR_TOT	% Forest land, including forested wetlands
SHRUB	% Shrubland
GRASS	% Grassland
PASTURE	% Land converted for pasture
ROWCROP	% Land converted for row crops
WET_TOT	% Wetland
IMP_PCT	% Impervious cover
CNPY_PCT	% Canopy cover

Land-cover percentages are for the watershed of a study stream

dissolved oxygen, conductivity, and pH on the same dates as fish sampling. These measurements were made at 5–6 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. Discharge (in m^3/s) was also measured along a representative transect within each reach using a portable electromagnetic flow meter (Marsh-McBirney Flo-Mate Model 2000). Dissolved oxygen, salinity, specific conductivity, water temperature, and pH were measured using a YSI 556 Multi-Probe Meter with Barometer (Yellow Springs Instruments).

Twenty-one landscape-scale variables describing spatial relationships (coordinates), physical characteristics and topography, land use, and distribution of disturbance points (outfalls and dams) were calculated for each site (Table 2). Watershed boundaries for each sample site were automatically digitized in ArcGIS 9.2 with the ArcHYDRO 9 extension 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 using the digital elevation model. Mean annual precipitation was calculated for each watershed from polygon coverage of average monthly and annual precipitation for the climatological period 1961–1990. This dataset was obtained from USDA-NRCS (http://www.wcc.nrcs.usda.gov). Number of wastewater outfalls and cumulative outfall (million gallons/day) were calculated for each watershed based on the Texas Commission on Environmental Quality (TCEQ) municipal and industrial wastewater outfall shapefile available from http://www.tceq.state.tx.us/gis/sites.html. The cumulative outfall metric was based on cumulative amount of permitted discharge upstream of a site. Land-cover class percentages were calculated for each watershed using National Land Cover Database (NLCD 2001) available from http://www.mrlc.gov/nlcd_multizone_map.php. All GIS analysis was performed with ArcGIS 9.2 (ESRI, Redlands, CA).

We measured 29 functional traits (Table 3) of five adult individuals of each fish species collected in the study region. Traits were selected that have known associations with feeding, habitat preference, locomotion, or reproductive strategies of fish species. For

Table 3 List of the 29 morphological and life-history traits, measurement methods, and their functional significance

Trait	Trait code	Trait definition	Category
Maximum standard length	MAX_SL	Maximum standard length from published records	Habitat use, feeding, life history
Head length	HEAD_L	Distance from the tip of the jaw to the posterior edge of the operculum	Feeding
Head depth	HEAD_D	Vertical distance from dorsum to ventrum passing through the pupil	Feeding
Oral gape	GAPE	Vertical distance measured inside of fully open mouth at tallest point	Feeding
Mouth position	MOUTH_P	The angle between an imaginary line connecting the tips of the open jaws and an imaginary line running between the center of the pupil and the posterior-most vertebra (e.g., 90° representing a terminal mouth)	Feeding, habitat use
Eye position	EYE_POS	Vertical distance from the center of the pupil to the ventrum	Habitat use
Eye diameter	EYE_D	Horizontal distance from eye margin to eye margin	Feeding
Snout length	SNT_L	Distance from the pupil to the tip of the upper jaw with mouth shut	Feeding
Jaw protrusion	JAW_PR	Additional distance from the pupil to the tip of the upper jaw with mouth fully open and extended	Feeding
Body depth	BOD_D	Maximum vertical distance from dorsum to ventrum	Locomotion, habitat use
Body width	BOD_W	Maximum horizontal distance	Locomotion
Caudal peduncle length	PED_L	Distance from the posterior proximal margin of the anal fin to the caudal margin of the ultimate vertebra	Locomotion
Caudal peduncle depth	PED_D	Minimum vertical distance from dorsum to ventrum of caudal peduncle	Locomotion
Caudal peduncle width	PED_W	Horizontal width of the caudal peduncle at midlength	Locomotion
Body depth below midline	DEP_MID	Vertical distance from midline to ventrum	Locomotion, habitat use
Dorsal fin length	DORS_L	Distance from the anterior proximal margin to the posterior proximal margin of the dorsal fin	Locomotion
Dorsal fin height	DORS_HT	Maximum distance from the proximal to distal margin of the dorsal fin	Locomotion
Anal fin length	ANAL_L	Distance from anterior proximal margin to posterior proximal margin of the anal fin	Locomotion
Anal fin height	ANAL_HT	Maximum distance from proximal to distal margin of the anal fin	Locomotion
Caudal fin depth	CAUD_D	Maximum vertical distance across the fully spread caudal fin	Locomotion
Caudal fin length	CAUD_L	Maximum distance from proximal to distal margin of the caudal fin	Locomotion
Pectoral fin length	PEC_L	Maximum distance from proximal to distal margin of pectoral fin	Locomotion, habitat use
Pelvic fin length	PELV_L	Maximum distance from proximal to distal margin of pelvic fin	Locomotion, habitat use

Table 3 continued

Trait	Trait code	Trait definition	Category
Gut length	GUT_L	Length of gut from beginning of esophagus to the anus	Feeding
Gill raker length	RAKER_L	Length of the longest gill raker	Feeding
Egg diameter	EGG_D	Mean diameter of mature (fully yolked) oocytes	Life history
Clutch size	CLUTCH	Average clutch size	Life history
Longevity	LONGEV	Average life span in years	Life history
Age at maturation	AGE_MAT	Average age for reproductive maturity (in years)	Life history

Trait definitions and functional categories follow Gatz (1979), Webb (1984), Winemiller (1991), Winemiller & Rose (1992), and Sibbing & Nagelkerke (2001)

example, gape dimensions, mouth orientation, head size, and gut length are associated with dietary resources used by fishes (Gatz, 1979). Morphological traits related to habitat use and swimming behavior include maximum body depth, fin lengths, and caudal peduncle dimensions (Gatz, 1979; Webb, 1984). Morphological traits were measured to the nearest 0.1 mm using vernier calipers following the methods of Winemiller (1991). For species with sexually dimorphic features (e.g., the anal fin of Western Mosquitofish *Gambusia affinis*), we measured females only. Mean egg diameter, mean clutch size, age at maturation, and longevity were obtained from published studies and the FishTraits database (Frimpong & Angermeier, 2009). These characteristics are associated with life-history variation among species (Winemiller & Rose, 1992). Whereas most studies of functional structure of stream fish assemblages use categorical traits or functional groups (e.g., Goldstein & Meador, 2004; Ibañez et al., 2007), we based our analyses on an array of quantitative traits associated with multiple niche dimensions which allowed for calculation of multidimensional functional diversity indices (Villeger et al., 2008; Laliberte & Legendre, 2010).

Statistical analyses

A prior study (Pease et al., 2011) performed non-metric multidimensional scaling (NMS) on species abundances across the study region and within each ecoregion to estimate differences in taxonomic assemblage structure among these sites. To identify the main gradients of environmental variation among stream reaches across the study region, we performed principal component analysis (PCA) on the correlation matrix of log-transformed environmental variables (local and landscape-scale). Interspecific differences in functional traits were also analyzed with PCA. Because traits were expected to be influenced by body size, we regressed traits against standard length and used the residuals as size-standardized values for the traits PCA (following Pease et al., 2012). Log-transformed values for mouth position and clutch size were used instead of residuals because those traits had no correlation with body size. Mean values for each species for each transformed functional trait were used for the traits PCA. We used PC-ORD software version 5.2 (MjM Software, Gleneden Beach, OR, USA) to perform PCA analyses. To estimate the extent of taxonomic constraints on functional trait differences among species, a Mantel test was performed to evaluate the correlation between taxonomic and trait distance matrices. The taxonomic distance matrix was constructed following Tedesco et al. (2008) and Olden & Kennard (2010).

We used RLQ analysis to examine relationships between environmental variables and functional traits of fish assemblages following Pease et al. (2012). RLQ is a multivariate ordination analysis developed by Doledec et al. (1996) that simultaneously performs ordinations on three matrices (species abundance, environmental variables, species traits). Prior studies show that RLQ is a useful tool for revealing trait–environment relationships among species assemblages (e.g., Mellado Díaz et al., 2008; Brind'Amour et al., 2011). We tested the significance of the relationship between environmental factors and functional trait

composition of fish assemblages with a Monte Carlo permutation test (1000 random permutations of rows of the matrices of traits and environmental variables). RLQ analyses were performed for each ecoregion separately and for the full study region (all ecoregions combined). We used the ADE-4 package (Dray & Dufour, 2007) for R version 2.10.1 (The R Foundation for Statistical Computing) for the RLQ and associated analyses.

Functional trait diversity was calculated for each fish assemblage using the convex hull volume method of Cornwell et al. (2006). The convex hull volume represents the multidimensional functional space filled by an assemblage, and it is calculated by measuring the volume within the minimum convex hull, which includes the trait values for all of the species present. A higher convex hull volume indicates higher total functional richness in an assemblage. Because trait dimensions cannot be greater than the number of species when calculating the convex hull volume for local assemblages, we used the scores for the first six PC axes from the functional traits PCA for species' traits. Volumes were calculated using the Quickhull algorithm (Barber et al., 1996) in MATLAB (Mathworks Inc., 2009). Functional evenness, which measures the distribution of species in trait space, was calculated using the evenness index of Villeger et al. (2008). Values for this index range from zero to one, with lower scores for assemblages dominated by functionally similar species. Functional divergence, calculated with the FDiv equation developed by Villeger et al. (2008), estimates how abundance is distributed relative to the centroid of the trait space occupied by an assemblage. FDiv ranges from zero to one, with low scores for assemblages with highly abundant species distributed near the centroid of trait volume, and high scores for assemblages with abundances distributed far away from the centroid. Functional evenness and divergence were calculated using the FD package (Laliberte & Legendre, 2010) for R version 2.10.1 (The R Foundation for Statistical Computing). Linear regressions were used to examine relationships between functional-trait diversity of assemblages, species richness, and local and landscape-scale environmental variables as well as the primary axis from the environmental PCA. The three functional diversity metrics of assemblages were also regressed against IBI and habitat quality index (HQI) scores calculated for the stream reaches. The IBI for this region is calculated based on metrics including fish species richness, number of cyprinid and centrarchid species, number of non-native species, and relative abundance of feeding guilds (Linam et al., 2002). The HQI is a multi-metric index developed to assess streams in this region based on physical characteristics of in-stream and riparian habitat. Sites with high HQI scores have abundant in-stream cover, greater availability of pools and riffles, stable banks, and broad riparian buffers (Texas Commission on Environmental Quality, 2007).

Results

Fifty-eight fish species distributed within 16 families were sampled during the course of the study. Richness per site ranged from 6 to 26 species with a mean of 14. Blacktail Shiners *Cyprinella venusta*, Red Shiners *Cyprinella lutrensis*, Western Mosquitofish, Central Stonerollers *Campostoma anomalum*, and Longear Sunfish *Lepomis megalotis* constituted over 60% of the total sample. Most species were captured throughout the entire study region, but some were restricted to certain ecoregions and/or river basins. Nine species were collected at more than 40 sites, while 27 species were found at fewer than 10 sites. Common Carp *Cyprinus carpio*, Redbreast Sunfish *Lepomis auritus*, and Mexican Tetras *Astyanax mexicanus* were the only non-native fish species collected in these streams.

The 64 sites encompassed a variety of stream habitat conditions. Sites within the Cross Timbers ecoregion had greater stream widths, rockier substrates and more riffle habitats within study reaches. East Central Plains streams generally had muddy or sandy substrates, more in-stream woody debris, and fewer riffles. Most stream reaches in the Blackland Prairies were in human-modified landscapes, had more homogeneous in-stream habitats, low canopy cover, and were intermediate between streams in the other two ecoregions in terms of substrate. The first two axes of the PCA on local and landscape-scale environmental variables explained 33.8% of total variation among stream sites (Fig. 2). The dominant gradient (PC1, 23.5% of variance) was most strongly associated with substrate type, number of riffles, in-stream woody debris and roots, stream width, elevation, longitude, precipitation, percentage of grassland in the watershed, and percentage of land converted to
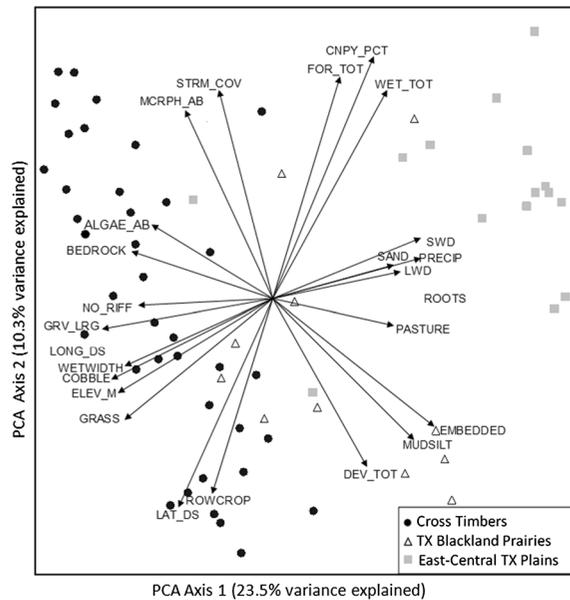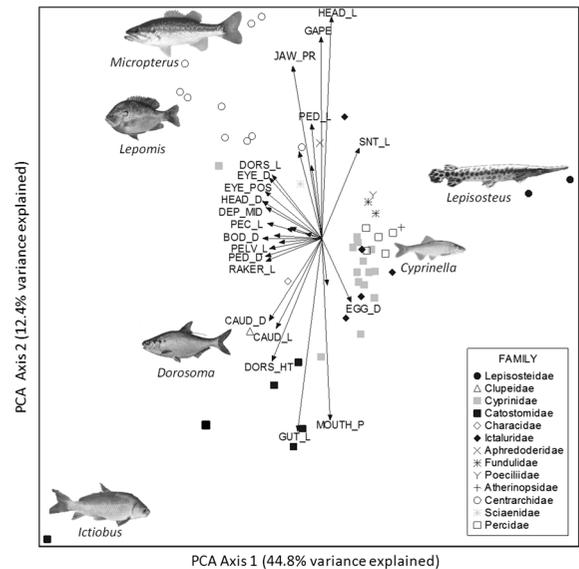
Fig. 2 PCA ordination of Central Texas stream reaches based on local and landscape-scale environmental variables. *Symbols* represent the three ecoregions as in Fig. 2. See Tables 1 and 2 for variable abbreviations

Fig. 3 PCA ordination of Central Texas fish species in two dimensions of functional trait space. Trait loadings on the two axes are depicted as vectors. *Symbols* represent the families of species. See Table 3 for trait abbreviations. Fish images from Brian Gratwicke and public domain

pasture. Sites with high scores on PC1 were generally within the East Central Plains and had fine substrate, more roots and woody debris for in-stream cover, few riffles, and a greater percentage of pastureland in the surrounding landscape. Most stream reaches with low scores on PC1 were in the Cross Timbers ecoregion and had rocky substrates, more riffles, wider channels, and more grassland in the watershed. The second gradient (PC2, 10.3% of variance) revealed a gradient that contrasted sites having more forest cover, more wetlands in the watershed and more in-stream cover with sites having less forest cover, more row-crop agriculture, extensive urban development, and more wastewater outfalls in the watershed. Sites with low scores on PC2 were generally located in the northern portions of the Cross Timbers and the Blackland Prairies (near the Dallas and Fort Worth urban areas).

Functional trait structure

The first two axes of the PCA performed on functional traits explained 57.2% of variance among species (Fig. 3). The primary axis (PC1, 44.8% of variance) largely reflected differences in head depth, body depth, fin lengths, gill raker length, eye diameter,

and eye position. Gar species (family Lepisosteidae), with very low body and head depths and relatively short fins, had high scores on PC1. Species with low scores on PC1 included centrarchids with relatively deep bodies, long fins and large eyes. Catostomids (Smallmouth Buffalo *Ictiobus bubalus*, River Carpsucker *Carpiodes carpio*), and Common Carp also had low scores on PC1. Axis 2 (PC2, 12.4% of variance) contrasted species with differences in trophic traits including head length, gape size, jaw protrusion, gut length, and mouth position. Highly predatory species, such as black basses (*Micropterus* species) and Warmouth *Lepomis gulosus* with highly protrusible jaws, large mouth gapes and relatively short guts, had high PC2 scores. Flathead Catfish *Pylodictis olivaris* also had a high score on PC2. Catostomid species (omnivorous benthic feeders) had subterminal mouths, long guts and small gapes, and these species had very low scores on PC2. Gizzard Shad *Dorosoma cepedianum* and two herbivorous cyprinids (Mississippi Silvery Minnow *Hybognathus nuchalis* and Central Stoneroller) also had low scores on PC2. The Mantel test showed a significant correlation ($R = 0.455$, $P = 0.001$) between trait and taxonomic distance matrices.

**Table 4** Results of the RLQ analyses for Central Texas stream fish assemblages

	RLQ axis 1	RLQ axis 2
Eigenvalue	0.015	0.006
Covariance	0.122	0.077
Correlation	0.128	0.128
R/RLQ	75.6	78.2
L/RLQ	23.6	27.5
Q/RLQ	66.0	89.1

The ratios R/RLQ, L/RLQ, and Q/RLQ represent the percentage of variance in the separate analyses of the environmental variables (R), species composition (L), and functional traits (Q) accounted for by the first two RLQ axes

RLQ analysis of the dataset that encompassed the entire study region revealed a statistically significant ($P < 0.005$, 1000 permutations) association between local and landscape-scale environmental variables and species traits. The first two axes of the RLQ accounted for 25.6% of total variance in the matrix that related the environmental characteristics of sites to species functional traits (Table 4). On RLQ axis 1, wider streams with grasslands in the surrounding landscape, wide riparian buffers, rocky substrate, and large pool habitats plotted on the left side of axis 1 and contained species with larger body sizes, deeper bodies, longer fins, and larger clutch sizes (Fig. 4). Plotted on the right side of axis 1 were reaches with narrower channels, finer substrates, more in-stream woody debris, and more wetlands in the watershed and that generally contained greater proportions of small fishes with more streamlined body shapes, shorter gill rakers, and smaller clutches. Stream reaches within larger, more forested watersheds with higher discharge, more riffle habitats, and more heterogeneous flow regimes were positively associated with RLQ axis 2. Functional traits that correlated with RLQ axis 2 include inferior mouth position, body width, gut length, and age at maturation. Environmental variables associated negatively with RLQ axis 2 include precipitation, amount of large woody debris, proportion of mud and silt in substrate, and the percentage of land in the watershed converted for pasture, row crops, and urban development. Stream reaches plotted at the bottom of axis two contained species with superior mouths (e.g., Western Mosquitofish), relatively long heads and snouts, and long lifespan (e.g., sunfishes, gars).

Within the Cross Timbers ecoregion, RLQ analysis revealed a statistically significant association between multi-scale environmental variables and fish functional traits ($P = 0.014$, 1000 permutations). The first two axes of the RLQ accounted for 28.5% of the total variance in the matrix that related the environmental characteristics of sites to the functional traits of species. Stream reaches with lower discharge and greater abundance of algae, shoreline vegetation cover, and woody debris that contained fishes with longer fins, deeper bodies, and more subterminal mouths were associated with low scores on RLQ axis 1 (Appendix—Supplementary Material). High scores on axis 1 were associated with stream segments within larger watersheds that had greater discharge and greater availability of run and riffle habitats. These reaches generally contained fishes with more streamlined body shapes, shorter gill rakers, and more terminal mouth positions. Stream reaches within watersheds containing more pasturelands and receiving more municipal wastewater discharges had high scores on RLQ axis 2. Functional traits including gut length, egg diameter, and age at maturation were negatively correlated with RLQ axis 2. Environmental variables negatively correlated with RLQ axis 2 include the percentage of forested land cover in the watershed and abundance of benthic algae.

In the Texas Blackland Prairies, RLQ revealed similar relationships between environmental variables and functional trait composition of fish assemblages, but these associations had lower statistical significance ($P = 0.075$, 1000 permutations). The first two RLQ axes accounted for 46.4% of total variance in the matrix that related environmental characteristics to species functional traits. Axis 1 of the RLQ separated sites with deeper habitats and finer substrates from sites with more riffle habitats and coarser substrates within more urbanized landscapes (Appendix—Supplementary Material). Fishes with longer fins were associated with deeper habitats with finer substrates, whereas species with longer relative gut lengths and larger eggs were more common in sites with riffles containing coarse substrates. Axis 2 separated reaches with more cover (structural complexity) within less impacted landscapes with a greater percentage of wetlands and shrublands that contained species with longer snouts and heads and more terminal mouth orientations from other reaches.
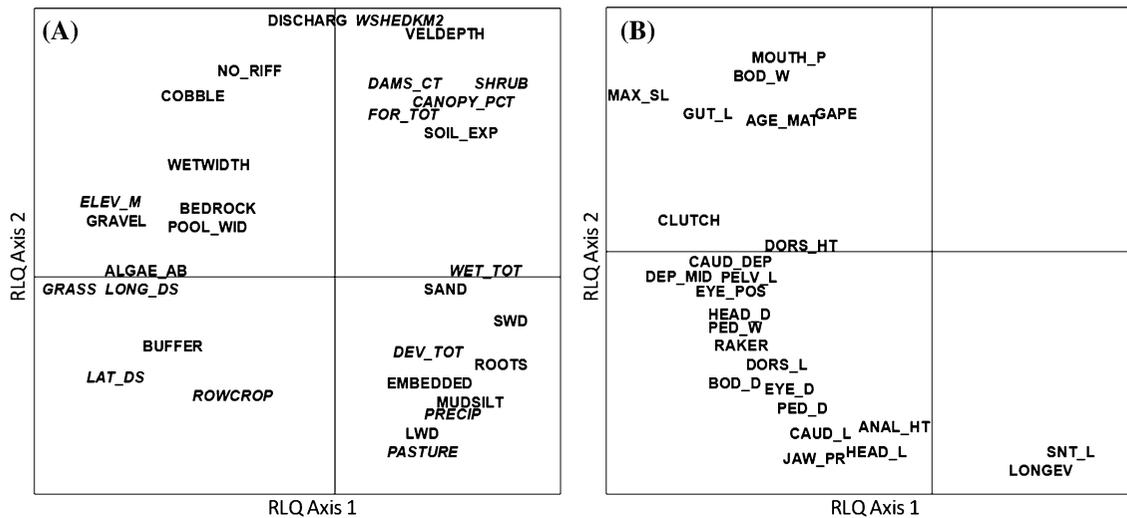
Fig. 4 Ordination of RLQ scores of **A** environmental variables and **B** functional traits of fish species for Central Texas stream reaches. Ecoregional and catchment-scale variables are *italicized*. See Tables 1, 2, and 3 for environmental variables and functional traits that correspond to abbreviations

RLQ performed for the East Central Texas Plains ecoregion showed a relatively poor correlation between local and landscape-scale habitat variables and fish functional traits ($P = 0.344$, 1000 permutations). Strongest correlations between traits and environmental variables revealed by RLQ included a greater abundance of larger fishes and species with longer fins, longer guts, and larger eyes in reaches with deeper pools, rocky substrates, and more woody debris (Appendix—Supplementary Material). These reaches also tended to have broader riparian buffer zones.

The volume of functional trait space occupied by fish assemblages across the study region was significantly correlated with species richness of stream sites ($R^2 = 0.697$, $P < 0.0001$) (Fig. 5). Sites with the largest functional convex hull volumes contained species from a broad spectrum of families and a variety of trophic guilds. Sites with higher IBI scores tended to occupy greater volumes of functional trait space ($R^2 = 0.347$, $P < 0.0001$). Some assemblages with intermediate species richness and IBI scores had the greatest functional trait volumes. These sites were characterized by species with distinctive morphology or life histories, such as gars (*Lepisosteus* species), large suckers (*Ictiobus*, *Carpiodes*, *Moxostoma* species), herbivorous minnows (e.g., Central Stoneroller, Mississippi Silvery Minnow), Gizzard Shad, madtoms (*Noturus* species), Flathead Catfish, black bass (*Micropterus* species), and darters (*Etheostoma* species).

Functional trait-space occupation also showed a weak but significant relationship with HQI score ($R^2 = 0.193$, $P = 0.0003$) and the first axis of the environmental PCA ($R^2 = 0.183$, $P = 0.0004$). Individual environmental variables significantly related to trait-space occupation were percent of the watershed altered for agriculture (negatively correlated, $R^2 = 0.147$, $P = 0.002$), elevation (positively correlated, $R^2 = 0.135$, $P = 0.003$), watershed area (positively correlated, $R^2 = 0.298$, $P < 0.0001$), and average channel width (positively correlated, $R^2 = 0.185$, $P = 0.0005$). Stream reaches with higher HQI scores tended to occupy greater volumes of trait space, but there were many exceptions to this general pattern. Some sites that were rated highly in terms of habitat quality had relatively low species richness and functional trait diversity, whereas some of the most taxonomically and functionally diverse fish assemblages were at sites rated "intermediate" for habitat quality. Streams in the Blackland Prairies and East Central Texas Plains ecoregions had high scores on axis 1 of the environmental PCA (Fig. 2) and tended to have assemblages occupying a smaller volume of trait space (Fig. 5). In contrast, sites in the Cross Timbers ecoregion with rocky substrate, more riffle habitats, wider channels, and less human impacts within the watershed (negative loadings on PC1) supported more functionally diverse assemblages (Figs. 2, 5). However, certain streams with high PC1 scores also
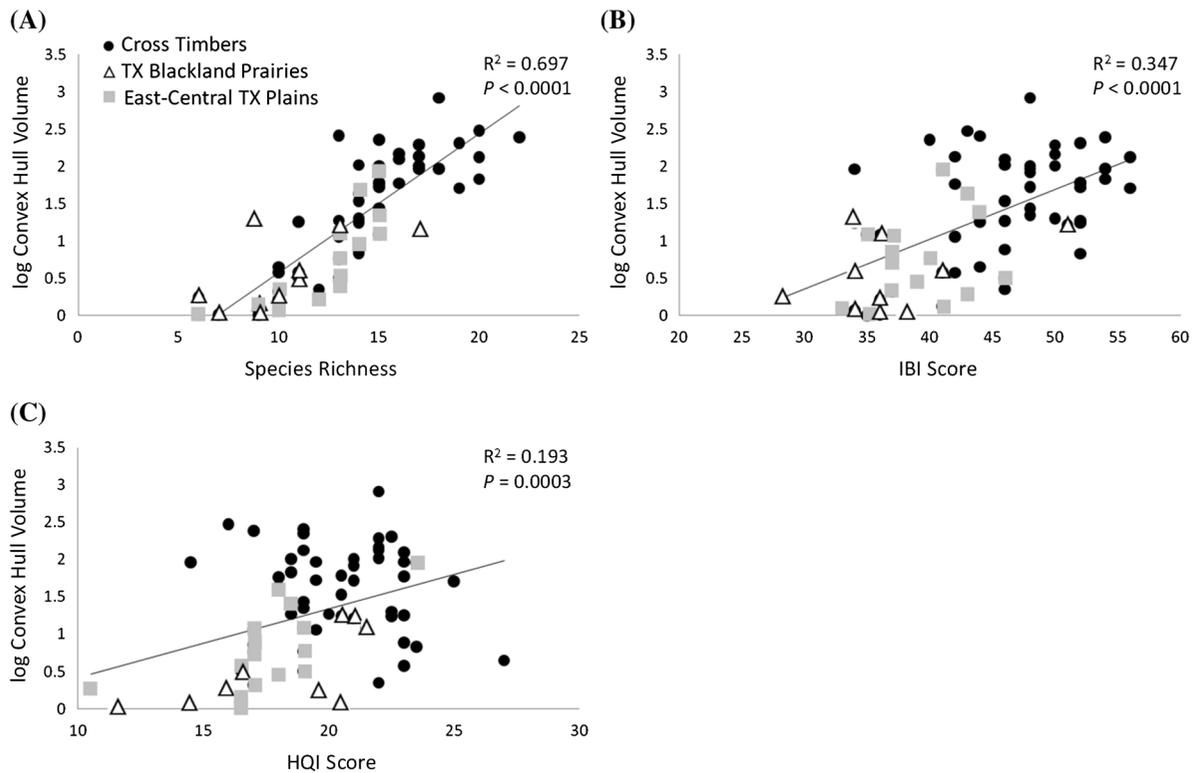
Fig. 5 Regressions of convex hull volumes of functional trait occupation of Central Texas fish assemblages against **A** species richness, **B** IBI, and **C** HQI scores

contained assemblages that had high trait-space volumes. Functional evenness and functional divergence showed no clear relationship with environmental variables or with IBI, HQI, or environmental PCA scores.

Discussion

Functional trait structure of stream fish assemblages in central Texas can be explained by statistical models that incorporate ecoregion-scale physiographic differences, landscape-scale gradients of urban and agricultural development, and local habitat variables. In a related study, Pease et al. (2011) showed that taxonomic structure of stream fish assemblages was distinct among ecoregions and that clustering of sites by ecoregion reflected differences in the geographic distributional patterns of species, with several species having affinities for certain ecoregions. Prior studies in this region have found that fish distribution patterns based on taxonomic classification also tracked broad,

physiographic gradients (Hubbs, 1957, Hoeinghaus et al. 2007). Despite the influence of ecoregional differences in species distribution on taxonomic assemblage composition and structure, several general trait–environment relationships were noted. This suggests that incorporating functional traits in studies examining assemblage structure may improve our ability to identify consistent environmental associations across large regions.

The dominant environmental gradient among stream sites in the study region (environmental PC1) separated sites according to elevation, precipitation, substrate type, and the presence of riffles, in-stream woody debris, and other features correlated with broad-scale physiographic differences in climate, geology, and terrestrial vegetation among the three ecoregions (Griffith et al., 2004). Along this 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 substrates composed of finer sediments and containing more woody debris. The secondary environmental

gradient among sites (environmental PC2) reflected differences in the amount of landscape developed for agriculture and urban uses. This gradient contrasted stream segments with watersheds having high percentages of forest and canopy cover and more wetlands with segments draining watersheds with more land impacted by human uses and municipal wastewater inputs. In terms of species traits, the set of principal environmental variables related to functional structure of fish assemblages (highest correlations with RLQ axis 1 and 2 for all ecoregions combined) also included characteristics associated with physiography, such as elevation, substrate type, and amount of woody debris. Environmental variables reflecting the extent of human land use in watersheds (e.g., amount of forest, total developed land, and percentage of land converted for row crops and pasture) were also associated with functional trait composition of fish assemblages. However, it is important to acknowledge that patterns of land use were strongly correlated to ecoregion, and some of the relationship between functional trait composition and land use was likely driven by historical differences in fish distributions that are independent of modern land use in the region (Allan, 2004; King et al., 2005). Nevertheless, many of these patterns remained evident when analyzing data within each of the three ecoregions separately, particularly the Cross Timbers, where nutrient enrichment associated with pasture land and wastewater treatment inputs has been shown to influence taxonomic fish assemblage structure (Taylor et al., 2014). This suggests that human land use in watersheds was at least partially responsible for differences in functional trait composition.

Functional trait–environment relationships

The PCA based on species traits revealed that principal functional differences among species were associated with locomotion and habitat use (e.g., body depth, caudal peduncle dimensions, fin length), trophic ecology (gut length, gape size, head length, snout length, jaw protrusion, eye diameter, mouth position), and life-history strategy (egg diameter). The use of measurements from a limited number of specimens for each species prevented examination of intraspecific variation in traits across sites, which may affect evaluation of functional diversity (Schleuter et al., 2010) and influence the strength of trait–environment

relationships (Brind'Amour et al., 2011). It also should be noted that a significant taxonomic component influenced differences in traits among species in the region (e.g., body depth and fin lengths associated with sunfish species). Results from RLQ analyses revealed the manner in which differences in the trait composition of local assemblages were related to environmental differences among stream sites. Across the full study region and within the Blackland Prairies and East Central Plains ecoregions, large streams with more pool habitats contained larger species with deeper bodies, longer fins, and longer gill rakers. This finding is consistent with other studies that found fish body size correlated with stream size (e.g., Schlosser, 1982; Hoagstrom & Berry, 2008) and body shape associated with presence of pools in stream reaches (e.g., Lamouroux et al., 2002). Deep, laterally compressed bodies and long fins are traits known to improve maneuverability in low-velocity habitats containing aquatic vegetation and other structures (Gatz, 1979; Webb, 1984). Similarly, species with longer fins and deeper bodies were associated with abundance of in-stream woody debris in the Cross Timbers ecoregion. Gill raker length is associated with filter feeding in fishes (Gatz, 1979), which is expected to be more common in larger, low-gradient streams with large pools (Vannote et al., 1980; Poff & Allan, 1995). In agreement with studies in other regions, smaller streams with narrow channels and few pools contained smaller species and species with more streamlined body shapes (Scarnecchia, 1988; Lamouroux et al., 2002). Such traits should enhance the ability of fishes to occupy refuges from both predation and high water velocities among microhabitats available in smaller headwater streams (Schlosser, 1982; Townsend & Hildrew, 1994).

Fishes with long intestines and subterminal mouths, such as omnivorous catostomids and cyprinids, were more abundant in wider stream reaches with rocky substrate and riffles within forested landscapes. This pattern was observed across the entire study region as well as within the Blackland Prairie and East Central Plains ecoregions. Long intestines and subterminal mouths in fishes are strongly associated with benthic omnivory (Gatz, 1979; Hugueny & Pouilly, 1999), and this trophic group has been found to be more abundant in larger streams with more vegetative detritus (e.g., Schlosser, 1982; Goldstein & Meador, 2004; Hoagstrom & Berry, 2008). The amount of forested land

cover in a watershed influences the quantity and type of detritus and in-stream cover in streams (Richards et al., 1996), and these factors likely enhance habitat quality for benthic omnivores. Throughout the study region, streams with mud and silt substrates within more developed landscapes had more small species with short reproductive cycles. Similarly, within the Cross Timbers ecoregion, age at maturity was negatively correlated with the percentage of land converted to pasture and total percentage of watershed development. Rapid maturation is associated with an opportunistic life history strategy that confers high population resilience (Townsend & Hildrew, 1994), which is advantageous in habitats subjected to frequent and/or unpredictable disturbances (Winemiller & Rose, 1992). Stanley et al. (2012) found that species with small body size and rapid life cycles were abundant in streams of the Cross Timbers ecoregion that experience periodic drying of segments and loss of hydrologic connectivity. Contrary to theoretical expectations for life-history strategies in relation to environmental disturbance regimes (Winemiller & Rose, 1992; Townsend & Hildrew, 1994), we found that species with long lifespans were relatively abundant in reaches within landscapes strongly impacted by human activities. This result seems to be driven largely by the relative abundance of gars, long-lived species that are highly tolerant of high temperatures, aquatic hypoxia, and other aspects indicative of degraded aquatic habitats (Linam et al., 2002). Streams in developed landscapes also contained greater proportions of species with superior mouth positions, such as Western Mosquitofish. These fishes forage near the water surface and can effectively use aquatic surface respiration to tolerate aquatic hypoxia, a condition more common in streams receiving nutrient enrichment and draining landscapes with other impacts (Allan, 2004).

As has been shown in studies comparing stream fish assemblages within regions (e.g., Hoagstrom & Berry, 2008) and across continents (e.g., Winemiller, 1991), functional trait-space occupation tended to be greater in more species-rich assemblages. Exceptions to this pattern occurred, however, with assemblages having intermediate levels of species richness occupying the largest trait space. Exceptions to the trend of higher functional diversity with increasing species richness are consistent with the idea that habitat filters at the local-scale limit the potential trait space that can be occupied (Keddy, 1992; Cornwell et al., 2006). Assemblage functional trait volume also was correlated with watershed size, confirming patterns found in other studies (e.g., Hoagstrom & Berry, 2008; Pease et al., 2012), suggesting that larger streams support a greater diversity of ecological niches. In the present study, trait-space volume was also correlated with IBI and HQI scores, two indices used by managers to assess stream health. Indices of biotic integrity scores are based on both taxonomic and functional attributes of fish assemblages (Linam et al., 2002). Despite correlations with HQI, many sites with high HQI scores in the Cross Timbers ecoregion had fish assemblages with relatively small trait volumes. This may be due to the strong association between fish diversity in Cross Timbers streams and environmental variables not included in the HQI metrics, such as agricultural land use, wastewater treatment discharges, and nutrient concentrations (Taylor et al., 2014). In general, the functional trait space occupied by fish assemblages increased in streams located within landscapes having less agricultural and urban development. Conversion of natural landscapes for agriculture 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 & Flecker, 1993). Watershed alteration usually impacts native fish communities indirectly through its effects on water quality, productivity, and other aspects of in-stream habitat (Wang et al., 2006; Rowe et al., 2009). The influence of land use on the taxonomic structure of stream fish assemblages has been demonstrated frequently (e.g., Roth et al., 1996; Walser & Bart, 1999; Wang et al., 2001; Snyder et al., 2003), but the relationship between functional trait diversity and landscape alteration is poorly understood. Recent work evaluating conservation priorities for freshwater fishes in the southwestern United States in relation to different measures of diversity suggests that functional diversity may be at greater risk from landscape-scale threats than taxonomic diversity (Strecker et al., 2011).

Implications for Environmental Assessment

Current indices of biotic integrity incorporate several functional aspects of fish assemblage structure (e.g., basic trophic guilds, pollution tolerance), but the identification of specific functional traits or suites of

traits related to stream habitat quality could enhance these approaches and provide more sensitive and generally applicable metrics. Functional trait composition of fish assemblages in central Texas streams was related to local and landscape-scale variables that are influenced by anthropogenic impacts to watersheds. For example, traits related to locomotion and feeding ecology were related to the presence of pools and riffles in stream reaches, a geomorphological characteristic that is sensitive to flow regime alteration. Further study of these relationships could be particularly useful for water resource management in Texas and many other regions of the world that are struggling to determine environmental flow requirements in order to balance competing needs for limited supplies of freshwater. Also, the prevalence of trophic and life-history traits shifted along a land use gradient, with larger species and herbivore/detritivores more common in streams within forested watersheds having less agricultural and urban development. In streams within more impacted landscapes, small species with shorter life cycles were more abundant. These results suggest that watershed impacts have significant functional consequences for fish assemblages and stream ecosystems in this region. The trait–environment relationships identified here also support the idea that multiple trait types (trophic, habitat use, life history) respond to local and regional environmental gradients (Hoeinghaus et al., 2007). Analysis of functional traits representing multiple niche dimensions instead of categorization of species into general functional groups could enhance the precision, reliability, and transferability of stream bioassessment protocols.

Functional trait–environment relationships should be relatively consistent across regions, and future research should aim to determine the predictability of assemblage-level functional responses to habitat degradation at larger geographic scales (Heino et al., 2013). Extensive research on functional traits along gradients of anthropogenic disturbance in stream invertebrate assemblages has yielded predictable relationships between land use and trait responses (e.g., Gayraud et al., 2003; Doledec et al., 2006; Tomanova et al., 2008). Our results provide insight into responses of fishes to anthropogenic disturbance by revealing the most responsive functional traits, but more research on how these and other traits relate to landscape alteration, flow regime modification, nutrient loading, pollution, and climate change is needed.

In summary, we found that local and landscape-scale environmental factors associated with regional physiography and human impacts to watersheds were significantly correlated with functional traits in stream fish assemblages. Functional descriptors of fish assemblage responses to environmental gradients complement traditional taxonomic approaches (Angermeier & Winston, 1999), but functional descriptors should transfer more reliably across drainage basins, ecoregions, and perhaps even continents (Winemiller, 1991; Lamouroux et al., 2002). Further investigation of patterns of functional diversity, including trait–environment relationships, will provide a more mechanistic understanding of how environmental factors affect species assemblages, which ultimately will improve our ability to predict ecological responses to environmental change (Poff, 1997; Poff et al., 2006; Olden et al., 2010).

References

Allan, J. D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology, Evolution & Systematics 35: 257–284.

Allan, J. D. & A. S. Flecker, 1993. Biodiversity conservation in running waters. BioScience 43: 32–43.

Angermeier, P. L. & M. R. Winston, 1999. Characterizing fish community diversity across Virginia landscapes: prerequisite for conservation. Ecological Applications 9: 335–349.

Balon, E. K., 1975. Reproductive guilds of fishes: a proposal and definition. Journal of the Fisheries Resource Board of Canada 32: 821–864.

Barber, C. B., D. P. Dobkin & H. Huhdanpaa, 1996. The Quickhull algorithm for convex hulls. Association for Computing Machinery Transactions on Mathematical Software 22: 469–483.

Berkman, H. E. & C. F. Rabini, 1987. Effect of siltation on stream fish communities. Environmental Biology of Fishes 18: 285–294.

Brind'Amour, A., D. Boisclair, S. Dray & P. Legendre, 2011. Relationships between species feeding traits and environmental conditions in fish communities: a three-matrix approach. Ecological Applications 21: 363–377.

Brown, L. R., 2000. Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. Environmental Biology of Fishes 57: 251–269.

Charvet, S., B. Statzner, P. Usseglio-Polatera & B. Dumont, 2000. Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. Freshwater Biology 43: 277–296.

Cornwell, W. K., D. W. Schwilk & D. D. Ackerly, 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87: 1465–1471.

Culp, J. M., D. G. Armanini, M. J. Dunbar, J. M. Orlofske, N. L. Poff, A. I. Pollard, A. G. Yates & G. C. Hose, 2011. Incorporating traits in aquatic biomonitoring to enhance causal diagnosis and prediction. Integrated Environmental Assessment and Management 7: 187–197.

Doledec, S. & B. Statzner, 2010. Responses of freshwater biota to human disturbances: contribution of J-NABS to developments in ecological integrity assessments. Journal of the North American Benthological Society 29: 286–311.

Doledec, S., D. Chessel, C. F. J. TerBraak & S. Champley, 1996. Matching species traits to environmental variables: a new three-table ordination method. Environmental and Ecological Statistics 3: 143–166.

Doledec, S., N. Phillips, M. R. Scarsbrook, R. H. Riley & C. R. Townsend, 2006. Comparison of structural and functional approaches to determining landuse effects on grassland stream invertebrate communities. Journal of the North American Benthological Society 25: 44–60.

Doledec, S., N. Phillips & C. R. Townsend, 2011. Invertebrate community responses to land use at a broad spatial scale: trait and taxonomic measures compared in New Zealand rivers. Freshwater Biology 56: 1670–1688.

Dray, S. & A. B. Dufour, 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22: 1–20.

Fausch, K. D., J. Lyons, J. R. Karr & P. L. Angermeier, 1990. Fish communities as indicators of environmental degradation. American Fisheries Society Symposium 8: 123–144.

Fonseca, C. R. & G. Ganade, 2001. Species functional redundancy, random extinctions and the stability of ecosystems. Journal of Ecology 89: 118–125.

Frimpong, E. A. & P. L. Angermeier, 2009. Fish traits: a database of ecological and life-history traits of freshwater fishes of the United States. Fisheries 34: 487–495.

Garnier, E., J. Cortez, G. Billes, M. Navas, C. Roumet, M. Debussche, G. Laurent, A. Blanchard, D. Aubry, A. Bellmann, C. Neill & J. Toussaint, 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85: 2630–2637.

Gatz, A. J., 1979. Ecological morphology of freshwater stream fishes. Tulane Studies in Zoology and Botany 21: 91–124.

Gayraud, S., B. Statzner, P. Bady, A. Haybach, F. Scholl, P. Usseglio-Polatera & M. Bacchi, 2003. Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. Freshwater Biology 48: 2045–2064.

Goldstein, R. M. & M. R. Meador, 2004. Comparison of fish species traits from small streams to large rivers. Transactions of the American Fisheries Society 133: 971–983.

Griffith, G. E., S. A. Bryce, J. M. Omernik, J. A. Comstock, A. C. Rogers, B. Harrison, S. L. Hatch & D. Bezanson, 2004. Ecoregions of Texas (Color Poster with Map, Descriptive Text, and Photographs). U.S. Geological Survey, Reston, VA.

Heino, J., D. Schmera & T. Eros, 2013. A macroecological perspective of trait patterns in stream communities. Freshwater Biology 58: 1539–1555.

Hoagstrom, C. W. & C. R. Berry, 2008. Morphological diversity among fishes in a Great Plains river drainage. Hydrobiologia 596: 367–386.

Hoeinghaus, D. J., K. O. Winemiller & J. S. Birnbaum, 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. Journal of Biogeography 34: 324–338.

Hubbs, C., 1957. Distributional patterns of Texas freshwater fishes. Southwestern Naturalist 2: 89–104.

Hugueny, B. & M. Pouilly, 1999. Morphological correlates of diet in an assemblage of West African freshwater fishes. Journal of Fish Biology 54: 1310–1325.

Ibañez, C., T. Oberdorff, G. Teugels, V. Mamononekene, S. Lavoué, Y. Fermon, D. Paugy & A. K. Toham, 2007. Fish assemblage structure and function along environmental gradients in rivers of Gabon (Africa). Ecology of Freshwater Fish 16: 315–334.

Ingram, T. & J. B. Shurin, 2009. Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblages. Ecology 90: 2444–2453.

Karr, J. R., 1981. Assessment of biotic integrity using fish communities. Fisheries 6: 21–27.

Karr, J. R., K. D. Fausch, P. L. Angermeier, P. R. Yant & I. J. Schlosser, 1986. Assessing biological integrity in running waters: a method and its rationale. Illinois Natural History Survey Special Publication 5. Champaign, IL.

Kearney, M. & W. Porter, 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12: 334–350.

Keddy, P. A., 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3: 157–164.

King, R. S., M. E. Baker, D. F. Whigham, D. E. Weller, T. E. Jordan, P. F. Kazyak & M. K. Hurd, 2005. Spatial considerations for linking watershed land cover to ecological indicators in streams. Ecological Applications 15: 137–153.

Laliberte, E. & P. Legendre, 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91: 299–305.

Lamouroux, N., N. L. Poff & P. L. Angermeier, 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. Ecology 83: 1792–1807.

Linam, G. W., R. J. Kleinsasser & K. B. Mayes, 2002. Regionalization of the Index of Biotic Integrity for Texas streams. Texas Parks and Wildlife Department River Studies Report No. 17. TPWD, Austin, TX.

McGill, B. J., B. J. Enquist, E. Weiher & M. Westoby, 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21: 178–185.

Mellado Díaz, A., M. L. Suarez Alonso & M. R. Vidal-Abarca Gutiérrez, 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. Freshwater Biology 53: 1–21.

Montaña, C. G. & K. O. Winemiller, 2013. Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: evidence from morphology, diet and stable isotope analysis. Biological Journal of the Linnean Society 109: 146–164.

Olden, J. D. & M. J. Kennard, 2010. Intercontinental comparison of fish life history strategies along a gradient of hydrological variability. American Fisheries Society Symposium 73: 83–107.

Olden, J. D., M. J. Kennard, F. Leprieur, P. A. Tedesco, K. O. Winemiller & E. Garcia-Berthou, 2010. Conservation biogeography of freshwater fishes: recent progress and future challenges. Diversity and Distributions 16: 496–513.

Pease, A. A., J. M. Taylor, K. O. Winemiller & R. S. King, 2011. Multi-scale environmental influences on fish assemblage structure in central Texas streams. Transactions of the American Fisheries Society 140: 1409–1427.

Pease, A. A., A. A. Gonzalez-Diaz, R. Rodiles-Hernandez & K. O. Winemiller, 2012. Functional diversity and trait-environment relationships of stream fish assemblages in a large tropical catchment. Freshwater Biology 57: 1060–1075.

Perkin, J. S. & T. H. Bonner, 2011. Long-term changes in flow regime and fish assemblage composition in the Guadalupe and San Marcos Rivers of Texas. River Research and Applications 27: 566–579.

Perkin, J. S. & K. B. Gido, 2011. Stream fragmentation thresholds for a reproductive guild of Great Plains fishes. Fisheries 36: 371–383.

Poff, N. L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16: 391–409.

Poff, N. L. & J. D. Allan, 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76: 606–627.

Poff, N. L., J. D. Olden, N. K. M. Vieira, D. S. Finn, M. P. Simmons & B. C. Kondratieff, 2006. Functional trait niches of North American lotic insects:traits-based ecological applications in light of phylogenetic relationships. Journal of the North American Benthological Society 25: 730–755.

Pont, D., B. Hugueny, U. Beier, D. Goffaux, A. Melcher, R. Noble, C. Rogers, N. Roset & S. Schmutz, 2006. Assessing river biotic condition at a continental scale: a European approach using functional metrics and fish assemblages. Journal of Applied Ecology 43: 70–80.

Richards, C., L. B. Johnson & G. E. Host, 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences 53: 95–311.

Roth, N. E., J. D. Allan & D. L. Erickson, 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11: 141–156.

Rowe, D. C., C. L. Pierce & T. F. Wilton, 1988. Physical habitat and fish assemblage relationships with landscape variables at multiple spatial scales in wadeable Iowa streams. North American Journal of Fisheries Management 29: 1333–1351.

Scarnecchia, D. L., 1988. The importance of streamlining in influencing fish community structure in channelized and unchannelized reaches of a Prairie stream. Regulated Rivers: Research and Management 2: 155–166.

Schlosser, I. J., 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs 52: 395–414.

Schleuter, D., M. Daufresne, F. Massol & C. Argillier, 2010. A user's guide to functional diversity indices. Ecological Monographs 80: 469–484.

Sibbing, F. A. & L. A. J. Nagelkerke, 2001. Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. Reviews in Fish Biology and Fisheries 10: 393–437.

Simon, T. P., 1991. Development of index of biotic integrity expectations for the ecoregions of Indiana. I. Central Corn Belt Plain. EPA 905/9-91/025. U.S. Environmental Protection Agency, Chicago, IL.

Snyder, C. D., J. A. Young, R. Villella & D. P. Lemarie, 2003. Influences of upland and riparian land use patterns on stream biotic integrity. Landscape Ecology 18: 647–664.

Stanley, C. E., J. M. Taylor & R. S. King, 2012. Coupling fish community structure with instream flow and habitat connectivity between two hydrologically extreme years. Transactions of the American Fisheries Society 141: 1000–1015.

Strecker, A. L., J. D. Olden, J. B. Whittier & C. P. Paukert, 2011. Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity. Ecological Applications 21: 3002–3013.

Taylor, J. M., R. S. King, A. A. Pease & K. O. Winemiller, 2014. Nonlinear response of stream ecosystem structure to low-level phosphorus enrichment. Freshwater Biology 59: 969–984.

Tedesco, P., B. Hugueny, T. Oberdorff, H. H. Durr, S. Merigoux & B. de Merona, 2008. River hydrological seasonality influences life history strategies of tropical riverine fishes. Oecologia 156: 691–702.

Texas Commission on Environmental Quality, 2007. Surface Water Quality Monitoring Procedures, Vol. 2. Report No. RG-416. Texas Commission on Environmental Quality, Austin, TX.

Tomanova, S., N. Moya & T. Oberdorff, 2008. Using macroinvertebrate biological traits for assessing biotic integrity of neotropical streams. River Research and Applications 24: 1230–1239.

Townsend, C. R. & A. G. Hildrew, 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology 31: 265–275.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

Villeger, S., N. W. H. Mason & D. Mouillot, 2008. New multidimensional functional diversity indices for a multi-faceted framework in functional ecology. Ecology 89: 2290–2301.

Walser, C. A. & H. L. Bart, 1999. Influence of agriculture on instream habitat and fish community structure in piedmont watersheds of the Chattahoochie River system. Ecology of Freshwater Fish 8: 237–246.

Wang, L., J. Lyons, P. Kanehl & R. Bannerman, 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management 28: 255–266.

Wang, L., P. W. Seelbach & J. Lyons, 2006. Effects of levels of human disturbance on the influence of catchment, riparian, and reach-scale factors on fish assemblages. American Fisheries Society Symposium 48: 199–219.

Webb, P. W., 1984. Body form, locomotion and foraging in aquatic vertebrates. American Zoologist 24: 107–120.

Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne & N. L. Poff, 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecology Letters 13: 267–283.

Wilson, J. B., 1999. Guilds, functional types and ecological groups. Oikos 86: 507–522.

Winemiller, K. O., 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecological Monographs 61: 343–365.

Winemiller, K. O. & K. A. Rose, 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49: 2196–2218.