ORIGINAL ARTICLE

Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups

David J. Hoeinghaus*, Kirk O. Winemiller and Jenny S. Birnbaum†

Section of Ecology, Evolutionary Biology & Systematics, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA

ABSTRACT

Aim To examine the roles of local and regional environmental variables and biotic interactions in determining the structure of local stream fish assemblages, and to compare results derived from analyses based on taxonomic and functional groups.

Location Texas, USA.

Methods Species abundance data were compiled for 157 stream fish assemblages in several river basins across Texas. Species were condensed into functional groups based on trophic and life-history characteristics. Local and regional environmental variables were either measured at each location or determined from scale maps and public-access data bases. The original taxonomic and functional group data sets were analysed using similarity indices, null models of co-occurrence, and direct and indirect ordination techniques. Results derived from taxonomic and functional group data sets are compared.

Results Inferences regarding the relative roles of local and larger-scale factors in determining stream fish assemblage structure differ dramatically between analyses of taxonomic and functional groups. Taxonomic analyses suggest a prominent role of regional-scale environmental factors, and local assemblages sorted according to a biogeographic pattern. Functional group analyses suggest almost equal roles of factors representative of local and larger scales, and assemblages were distinguished by a habitat template irrespective of geographic region.

Main conclusions The structure of local stream fish assemblages is determined ultimately by factors representing multiple scales, with the relative importance of each depending on the biological unit employed (species or functional groups). We suggest that analyses using functional groups can more directly infer ecological responses to environmental variation, and therefore may provide a more fruitful avenue for developing and testing ecological theory of community organization across biogeographic scales.

Keywords
Co-occurrence, diversity, historical factors, life-history strategies, scale, species interactions, stream fishes, Texas, trophic groups.

*Correspondence and present address: David J. Hoeinghaus, Division of Biology, Kansas State University, 104 Ackert Hall, Manhattan, KS 66506, USA.
E-mail: djhoeing@ksu.edu

†Present address: Mystic River Watershed Association, 20 Academy Street, Suite 203, Arlington, MA 02476, USA.*

INTRODUCTION

Several factors potentially contribute to the organization of local communities. Biotic interactions such as competition and predation, which are inherently local in scale, may affect local species abundances and distributions. Local habitat character-istics and regional environmental factors mediate biotic interactions and may limit the ability of species to persist in a local community. Historical factors such as speciation, extinction and dispersal may ultimately dictate the pool of species that potentially occur in a local community. Ecologists are increasingly aware that to interpret patterns in species

diversity and community assembly requires approaches integrating these factors representing multiple spatial and temporal scales (Ricklefs, 1987, 2004; Levin, 1992; Ricklefs & Schluter, 1993; Huston, 1999; Whittaker *et al.*, 2001; Leibold *et al.*, 2004).

Most large-scale studies have focused on determinants of species richness. For fish communities, diversity has been attributed to area (basin area, lake surface area), regional net primary production, habitat heterogeneity and historical factors (Barbour & Brown, 1974; Oberdorff *et al.*, 1995, 1997, 1999; Guégan *et al.*, 1998; Tedesco *et al.*, 2005). Relationships between local and regional diversity generally suggest that local fish diversity is determined by regional processes: local assemblages are unsaturated (Hugueny & Paugy, 1995; Griffiths, 1997; Oberdorff *et al.*, 1998; Irz *et al.*, 2004), although this interpretation may depend on the way the community (only native species, introduced species, both combined) and local and regional scales are defined (Angermeier & Winston, 1998; Loreau, 2000; Irz *et al.*, 2004).

Other important community attributes, such as assemblage structure or function, may respond to biotic, environmental and historical influences in a manner quite different from species richness (Tonn *et al.*, 1990; Marsh-Matthews & Matthews, 2000; Johnson *et al.*, 2004). Although generalizations derived for species richness cannot be applied directly to assemblage structure or function, few studies have examined relationships between combinations of some or all of these factors and fish assemblage structure (Tonn *et al.*, 1990; Oberdorff *et al.*, 1998; Marsh-Matthews & Matthews, 2000). We are unaware of any studies evaluating the roles of biotic interactions and local and regional environmental factors in determining the functional structure of fish assemblages.

The present study adopts a multi-scale approach to examine the influences of biotic interactions and environmental factors in determining the taxonomic and functional structure of stream fish assemblages across Texas. Analyses using species and functional groups examine: (1) regional patterns of composition, (2) local assemblage structure, (3) the relative strengths of association between assemblage structure and local- and regional-scale environmental factors, and (4) trends in co-occurrence among and within regions. Results from analyses based on species and functional groups are contrasted, and findings are compared with current models of stream fish assemblage organization.

METHODS

Regional description

Texas comprises a large geographic area (691,500 km^2) with strong climatic, geologic and vegetation gradients occurring across the state (Mallard *et al.*, 2005). For example, in the pinewoods of eastern Texas, rainfall averages almost 150 cm year^{-1}, whereas the trans-Pecos region in far-western Texas receives < 10 cm annually. Geology and topology range from Cenozoic sands and clays in north-eastern and east-
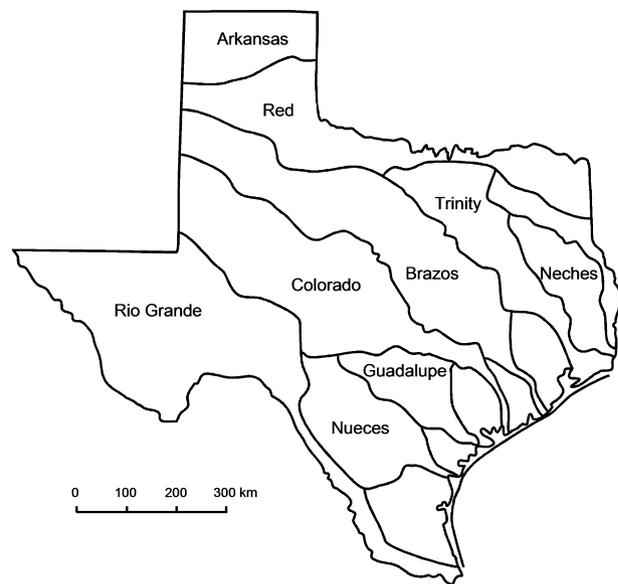

Figure 1 Major river basins of Texas.

central portions of the state to Pre-Cambrian granite and Cretaceous limestone in the Llano uplift and Edwards Plateau regions of central Texas, to mountains in the western trans-Pecos region, and recent alluvial deposits in river floodplains. Several vegetation zones follow this climatic and geologic gradient. The long-leaf pine forests of eastern Texas gradually give way to oak, hickory, juniper and mesquite forests and savannahs progressing westward, and prairies and plains in central and north-central regions. The major river drainages of Texas flow independently to the Gulf of Mexico across the vegetation and geologic regions following a general north-west to south-east trend (Fig. 1).

Data collection

A data base of fish species abundances and associated physicochemical habitat characteristics was compiled from collections made by K.O.W. and colleagues during summer months between 1993 and 2001. This data base includes 157 stream fish assemblages representing 40,677 individuals of 85 species. Collections were made in 10 sub-basins of six major river basins spanning the east–west gradient of the state: Neches River Basin (Village Creek, $n = 5$), Brazos River Basin (Middle Brazos River and tributaries, $n = 26$), Colorado River Basin (Spring Creek, $n = 16$; South Concho River, $n = 7$; Middle Concho River, $n = 15$), Guadalupe/San Antonio River Basin (Medina River, $n = 12$), Nueces River Basin (Frio River and tributaries, $n = 36$; Sabinal River and tributaries, $n = 21$; Hondo River, $n = 6$), and the Rio Grande River Basin (Devils River, $n = 13$).

Standardized methodology was employed in all surveys. For each survey, three stream transects spaced approximately 10 m apart were established for measuring or estimating in-stream variables. Each survey site was *c.* 30 m, from 5 m upstream to 5 m downstream of the first and third transects. Stream width

(m) was measured at each transect, and water temperature (°C), dissolved oxygen concentration (mg L^{-1}), conductivity (µm), water velocity (m s^{-1}), pH and depth were measured at three points evenly spaced along each transect (25%, 50% and 75% of the transect width) and the means were calculated for each site. Measurements were made using a YSI 85 water quality meter (temperature, dissolved oxygen, conductivity), pH meter and hand-held velocity meter. Substrate composition was estimated along each transect as percentage cover of several broad categories easily identified visually, or by grab samples (bedrock; cobble 6–25 cm; pebble/gravel 2–60 mm; sand 0.06–2 mm; mud/silt < 0.06 mm; clay and coarse detritus). The percentage of the site characterized by riffle, run and pool habitats was estimated from stream-side. Percentage cover of aquatic and riparian vegetation (within 3 m of the stream) was estimated for the length of the site. Following physicochemical measurements, all available habitats were seined until no new species were collected in three consecutive seine hauls. Species identification was according to Hubbs *et al.* (1991); taxonomic authorities for all species can be found therein. Sites were not surveyed more than once. Because standardized field-sampling methods were employed for all surveys, this data set allows for examination of patterns of assemblage structure (relative abundances of constituent species) in addition to species richness and composition. For the same reason, we did not add data available in the primary literature to our data set.

Field observation, scale maps and public-access data bases were used to compile a suite of 14 regional-scale environmental factors. In this study, environmental factors associated with processes occurring over an area larger than the in-stream scale are considered regional factors, such as stream order, predominant land use, geographic location, and annual precipitation and temperature extremes. Geographic location (decimal degrees) was determined using a hand-held GPS unit at the time of field sampling. Annual precipitation and temperature extremes (mean January and July temperatures) were obtained from the National Oceanic and Atmospheric Administration public-access data base (http://www.noaa.gov) and are based on 30-year averages or the longest available recent period. At sites for which climate data were not available, values were estimated based on two or more of the closest available survey points. Stream order was determined using 1 : 400,000 scale maps and cross-referenced with flow data publicly available from the US Geological Survey (http://www.usgs.gov). Predominant land use (percentage of watershed upstream from the site) was estimated from a 1 : 500,000 scale map compiled by the Texas Parks and Wildlife Department from Landsat overflights (Frye *et al.*, 1984). Land-use classifications were compared with field notes to identify potential changes in land use. Local and regional environmental factors included in analyses are presented in Table 1; summary data are provided in Appendices S1 & S2 in Supplementary Material.

The series of analyses described below was performed using two data sets: the original species (hereafter 'taxonomic') data

Table 1 Local- and regional-scale environmental factors measured or obtained for each sampling site (summary statistics in Appendices S1 & S2)

Local (*n* = 19)	Regional (*n* = 14)
Site width (m)	Coordinate north (decimal degrees)
Site depth (m)	Coordinate west (decimal degrees)
Water velocity (m s^{-1})	1st order (categorical variable)
Sand (%)	2nd order (categorical variable)
Mud (%)	3rd order (categorical variable)
Clay (%)	4th order (categorical variable)
Pebble (%)	5th order (categorical variable)
Cobble (%)	Minimum January temperature (°C)
Bedrock (%)	Maximum July temperature (°C)
Detritus (%)	Annual precipitation (cm)
Water temperature (°C)	Shrub (%)
Dissolved oxygen (mg L^{-1})	Forest (%)
pH	Agriculture (%)
Conductivity (µm)	Grassland (%)
Riffle (%)	
Run (%)	
Pool (%)	
Riparian vegetation (%)	
Aquatic vegetation (%)	

set; and a functional group data set in which the 85 species collected were condensed into 14 functional groups based on trophic and life-history characteristics (Appendix S3). We chose to group species according to trophic and life-history characteristics because constituent species fill analogous ecological roles, that is they consume the same type of prey resources and have similar population dynamics. Trophic characterization was for adult stages following Linam *et al.* (2002) with modifications based on unpublished data (K.O. Winemiller); the life-history classification follows Winemiller (1992, 1996) and Winemiller & Rose (1992). Summary statistics of the biological data used in subsequent analyses are presented in Table 2.

While acknowledging that functional groupings have potential limitations (e.g. ontogenetic and temporal shifts in trophic ecology and habitat use), various types of functional groupings (e.g. life history, trophic category, morphology, body size) have been used successfully to develop community assembly rules (Fox & Brown, 1993, 1995; Brown *et al.*, 2000) and can provide a more comprehensive understanding of the communities of interest (Ricklefs *et al.*, 1981; Schlosser, 1982; Winemiller & Pianka, 1990; Simberloff & Dayan, 1991; Winemiller, 1991; Poff & Allan, 1995; Winston, 1995; Peres-Neto, 2004; Hoeinghaus *et al.*, in press; Olden *et al.*, 2006). Furthermore, a functional approach should facilitate the development of broadly applicable generalizations regarding patterns in community structure (Poff, 1997; Harris, 1999).

Analytical procedures

The following procedures were applied to both taxonomic and functional data sets.

Table 2 Number of surveys (*n*) and total, mean (± 1 SD) and range of taxonomic and functional diversity observed for each sub-basin

Sub-basin	*n*	Taxonomic diversity			Functional diversity		
		Total	Mean (± 1 SD)	Range	Total	Mean (± 1 SD)	Range
Village	5	35	13.40 (4.28)	8–20	10	6.20 (0.45)	6–7
Brazos	26	48	11.23 (4.31)	4–23	13	6.35 (1.65)	3–9
Spring	16	16	4.56 (1.41)	3–7	8	3.81 (0.91)	3–6
South Concho	7	17	7.29 (1.70)	4–9	9	5.29 (0.95)	4–7
Middle Concho	15	15	7.27 (2.22)	4–10	11	5.73 (1.10)	4–7
Medina	12	22	6.67 (1.78)	3–9	11	4.50 (1.31)	3–7
Frio	36	22	6.47 (2.08)	3–11	11	4.92 (1.48)	3–8
Sabinal	21	21	5.00 (1.58)	3–8	10	3.67 (1.11)	2–5
Hondo	6	14	8.33 (2.07)	6–11	8	5.83 (0.98)	5–7
Devils	13	14	6.08 (2.56)	3–10	8	3.92 (2.06)	1–8

Compositional similarity

Patterns of compositional similarity at the sub-basin-level (γ diversity, sub-basin species pools) were compared using Sørensen's qualitative index $C_s = 2j/(a + b)$, in which *j* is the number of species shared between sub-basins, and *a* and *b* are the species richness for the two sub-basins being compared (Magurran, 1988). To test if observed differences in sub-basin species richness were due to sampling effort, the number of assemblages sampled in each sub-basin was regressed independently against sub-basin richness using null regression. In this analysis, the slope of the observed regression was compared with a null distribution of slopes generated by randomizing the independent and dependent variables independently 5000 times. The null analysis tests whether the observed relationships are significantly different from those expected by chance (Gotelli & Graves, 1996). Analyses were performed using EcoSim ver. 7.69 (Gotelli & Entsminger, 2001). We used the *G*-test to determine if the life-history and trophic classifications, which were combined into functional groupings, were significantly associated.

Co-occurrence

Possible effects of biotic interactions can be examined using null models of species co-occurrence (Jackson *et al.*, 1992; Peres-Neto, 2004). Strong negative associations among species of the same functional group (species with the same trophic and life-history category) may be indicative of competitive exclusion. Species co-occurrence patterns were examined at multiple scales by comparing *C*-scores calculated based on the species presence–absence matrix with a null distribution based on 5000 Monte Carlo permutations calculated using EcoSim (Gotelli & Entsminger, 2001). The *C*-score is the average number of checkerboard units (CU) observed between all possible species pairs: an index of the tendency of species to not co-occur (Stone & Roberts, 1990). In the null model analysis, original row and column totals were maintained constant, whereas the composition within rows and columns was randomized. This algorithm has good type-1 properties, a low chance of falsely rejecting a true null hypothesis while maintaining sufficient

power for detecting non-random patterns in noisy data sets (Gotelli, 2000; Gotelli & Entsminger, 2001).

An observed mean *C*-score significantly greater than the simulated mean for the entire data set indicates non-random regional-scale structuring, whereas a significant difference in the variance among regional (sub-basin) *C*-scores indicates differences in the degree to which regions are structured. A similar co-occurrence analysis was performed for each sub-basin independently to test for local-scale patterns, using only those species collected in the respective sub-basin. Linear regressions of observed mean sub-basin *C*-scores with sub-basin species richness were compared with a null distribution of slopes based on 1000 randomizations.

Pairwise comparisons were made to identify species and functional groups with strong negative co-occurrence patterns within each sub-basin based on the number of CU observed for each pairing, calculated as $CU = (r_i − s)(r_j − s)$, where r_i and r_j are the number of sites occupied by species *i* and *j* respectively, and *s* is the number of shared sites. Because the number of localities occupied by each species influences CU values, adjusted values were calculated for each pairwise comparison by dividing the observed CU by the maximum possible for the pair, which occurs at the lowest possible value of *s*: $s_{min} = \max(0, r_i − r_j − n)$, where *n* is the number of sites in the sub-basin. Adjusting CU values in this manner results in a scale from 0–100% of the maximum possible CU for the pair. Original and adjusted values were examined together, so that pairings with the highest negative co-occurrence patterns could be identified without overweighting the influence of either very common or rare species. Pairwise comparisons that are indicative of strong negative co-occurrences have both high CU and adjusted CU values.

Assemblage structure

Canonical correspondence analysis (CCA) was used to compare patterns of environmental correlations of fish assemblage structure among sites for local and regional environmental variables separately, as well as the full suite of environmental factors together. For each analysis, only significant and non-redundant environmental variables were retained. Significance

of each environmental variable was tested by manual selection using 1000 Monte Carlo permutations and α = 0.05. A variable was considered redundant if its variance inflation factor was > 20 (ter Braak & Šmilauer, 1998). Retained variables were ranked according to their contribution to the total explained variation. Because CCA constrains species data to be correlated with the associated environmental data, correspondence analysis (CA) was also performed to examine patterns of community structure based solely on species abundances.

Only the first two canonical axes from these multivariate analyses were retained for interpretation. Species abundances were log $(x + 1)$ transformed and rare species were down-weighted because they have a relatively large contribution in resulting ordination patterns (Gauch, 1982; ter Braak, 1986; ter Braak & Šmilauer, 1998) and also are more likely than common species to be inadequately sampled. Down-weighting rare species thus provides a more conservative evaluation of patterns of community structure among sites. Correspondence analysis and CCA are not affected adversely by data sets containing large numbers of zeros, and the resulting axis scores maintain relative distances among samples (Gauch, 1982; ter Braak, 1986; Palmer, 1993). These qualities make ordination techniques amenable to analyses of community structure within and across geographic scales (Jackson & Harvey, 1989).

To determine if assemblage structure differed significantly among sub-basins, multivariate analysis of variance (MANOVA) was performed using sample scores from the first two CA axes as dependent variables and sub-basin as a categorical variable. Site species richness (α diversity) and the number of individuals collected were regressed independently against CA axis scores using null regression (Gotelli & Entsminger, 2001).

RESULTS

Compositional similarity

Functional richness was observed to increase logarithmically with species richness ($r^2 = 0.71$). The geographic gradient in species richness in Texas (higher diversity in the east) also appears to represent a trend in functional richness. Sub-basin-scale compositional diversity (γ diversity) was not significantly correlated with the number of assemblages sampled within a sub-basin for either the taxonomic ($r^2 = 0.08$, $P = 0.20$) or functional data set ($r^2 = 0.30$, $P = 0.06$). Species life history and trophic categories were significantly associated (G-adjusted = 34.59, d.f. = 15, $P < 0.005$).

For the taxonomic data set, patterns of compositional similarity followed a geographic trend. Village, Brazos and Devils sub-basins (eastern and western geographic extremes) were compositionally unique, whereas the other sub-basins formed a group with higher inter-basin similarity in species composition (Table 3). Most similarity values were < 0.40 for Village and Brazos sub-basins, with values *c.* 0.50 for comparisons between the Devils sub-basin and the nearest geographical sub-basins (Frio, Hondo, Medina, Sabinal). Some species, such as *Cyprinella venusta*, *Gambusia affinis* and *Lepomis megalotis*, were collected in every sub-basin, creating a similarity baseline of about 0.12 (the minimum similarity observed; comparisons between western and eastern geographical extremes).

As expected, several functional groups were present in all sub-basins, resulting in a minimum functional similarity of 0.48, with most values > 0.70 (Table 3). Although a longitudinal gradient in functional diversity may exist, sub-basin functional group composition did not follow the geographical trend in regional similarity observed for the taxonomic data set. For example, functional group composition of the Village sub-basin was most similar to the two other taxonomically unique sub-basins (Brazos and Devils; Table 3).

Co-occurrence

The observed mean taxonomic C-score of 8.29 was significantly greater than the simulated mean of 3.92 ($P < 0.001$), indicating non-randomness in our full taxonomic data set.

Table 3 Sørensen's index values for between-sub-basin compositional similarity of taxonomic (above diagonal) and functional diversity (below diagonal)

| Functional similarity | Taxonomic similarity | | | | | | | | | |
	Devils	Frio	Hondo	Sabinal	Medina	Spring	South Concho	Middle Concho	Brazos	Village
Devils		0.500	0.500	0.457	**0.556**	0.333	0.387	0.343	0.129	0.122
Frio	**0.842**		**0.778**	**0.744**	**0.773**	**0.684**	**0.667**	**0.651**	0.314	0.211
Hondo	0.750	**0.842**		**0.686**	0.667	**0.600**	**0.581**	0.457	0.226	0.163
Sabinal	**0.889**	**0.952**	**0.778**		**0.791**	**0.811**	**0.789**	**0.667**	0.290	0.179
Medina	**0.842**	**1.000**	**0.842**	0.476		**0.789**	**0.769**	**0.651**	0.257	0.175
Spring	0.750	**0.842**	0.750	**0.889**	**0.842**		**0.909**	**0.649**	0.313	0.196
South Concho	0.706	**0.900**	0.706	**0.947**	**0.900**	**0.941**		**0.632**	0.308	0.231
Middle Concho	0.737	**0.909**	0.737	**0.857**	**0.909**	**0.842**	**0.900**		0.406	0.250
Brazos	**0.762**	**0.833**	0.667	**0.783**	**0.833**	0.667	0.727	**0.833**		0.434
Village	**0.778**	0.667	0.556	0.700	0.667	0.556	0.632	0.667	**0.870**	

Values in bold type are > 50% and 75% similarity for taxonomic and functional data sets, respectively (higher similarity values are emphasized for functional diversity given the higher baseline similarity across all sub-basins; see Results).

Species negative co-occurrence patterns at the regional scale are due to differences in regional species pools. In contrast, the observed mean *C*-score calculated from the entire functional data set did not differ from random ($P = 0.22$); negative co-occurrence of functional groups at the regional scale was not observed. Variance of mean *C*-scores indicated that co-occurrence patterns differed significantly among sub-basins for both taxonomic and functional data sets ($P < 0.001$ and $P = 0.03$, respectively). Relationships between sub-basin *C*-score and sub-basin taxonomic or functional diversity were not significantly different from random ($P = 0.26$ and $P = 0.15$, respectively).

Non-random sub-basin-level species co-occurrence patterns were observed for only four of the 10 sub-basins using the taxonomic data set, and for three sub-basins using the functional data set. Regardless, strong negative species associations were observed in all sub-basins for both data sets (Appendices S4–S7). For the taxonomic data set, most of the strongly negative associations were observed between species of different life-history groups, either in the same trophic group or for predator and prey pairs. Few negative associations were observed between species that shared both the same trophic and life-history groups (Appendices S4 & S5). A somewhat different trend was observed for pairwise species comparisons within sub-basins for the functional data set; functional groups with the strongest negative associations were predator–prey combinations and different life-history groups (Appendices S6 & S7).

Assemblage structure

Correspondence analysis of the taxonomic data set separated assemblages into significantly different sub-basin groupings (Fig. 2; Wilks's λ, $F_{18,292} = 47.19$, $P < 0.001$). Axis 1 describes a general east–west gradient, with eastern sub-basins at lower values and western sub-basins at higher values. The eastern and western extremes (Neches and Brazos, and Rio Grande drainages, respectively) were relatively more distinct compared with the other drainages. Axis 2 separated the Rio Grande basin, and to a lesser degree the Neches and Brazos basins, from the others. This apparent similarity on axis 2 probably results from involution: the closeness in ordination space of opposite extremes of a gradient due to a shared lack of species rather than actual similarity in species composition (Wartenberg *et al.*, 1987). This interpretation is corroborated by results of sub-basin-level taxonomic similarity analyses presented above.

A different pattern resulted from CA ordination of the functional data set. Although sub-basins were found to be significantly different (Wilks' λ, $F_{18,292} = 9.48$, $P < 0.001$), the observed pattern does not correspond with geographic position (Fig. 3), and all basins had high overlap in ordination space. Instead of a geographic relationship, CA axis 1 described assemblage trophic composition. Local assemblages with high piscivore densities had the most negative values, whereas sites dominated by omnivory and invertivory progressed from slightly negative values to positive values (Fig. 3).
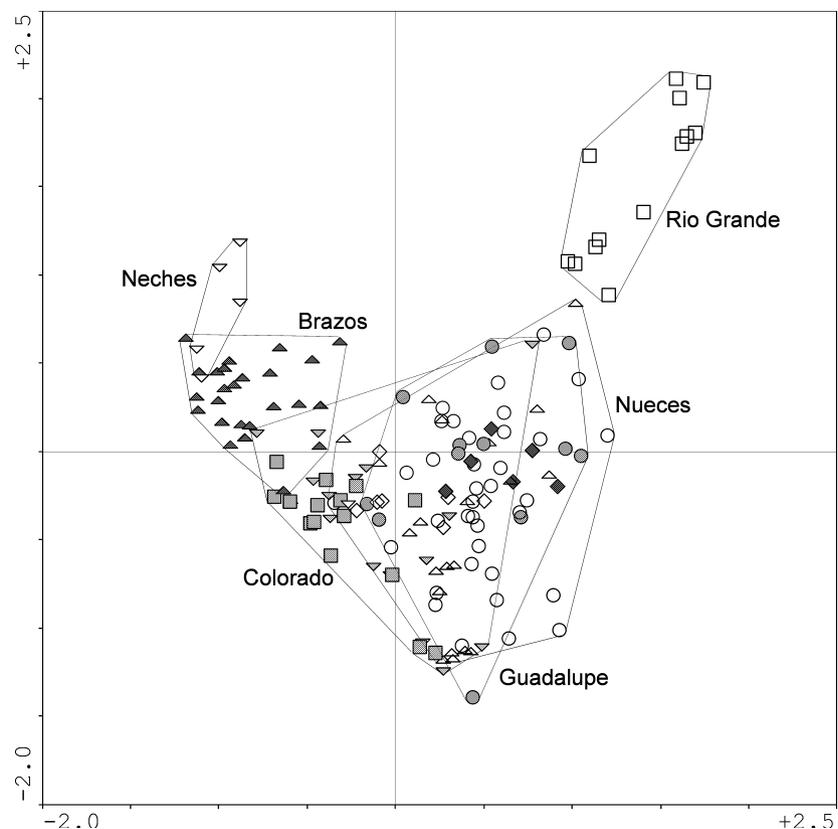

Figure 2 Sample score ordination on correspondence analysis (CA) axes 1 and 2 (axes *x* and *y*, respectively) of the taxonomic data set. Envelopes designate basins (Fig. 1); symbols designate sub-basins: Brazos (▲), Devils (□), Frio (◯), Hondo (◆), Medina (◕), Middle Concho (▦), Sabinal (△), South Concho (◇), Spring (▼), Village (▽).
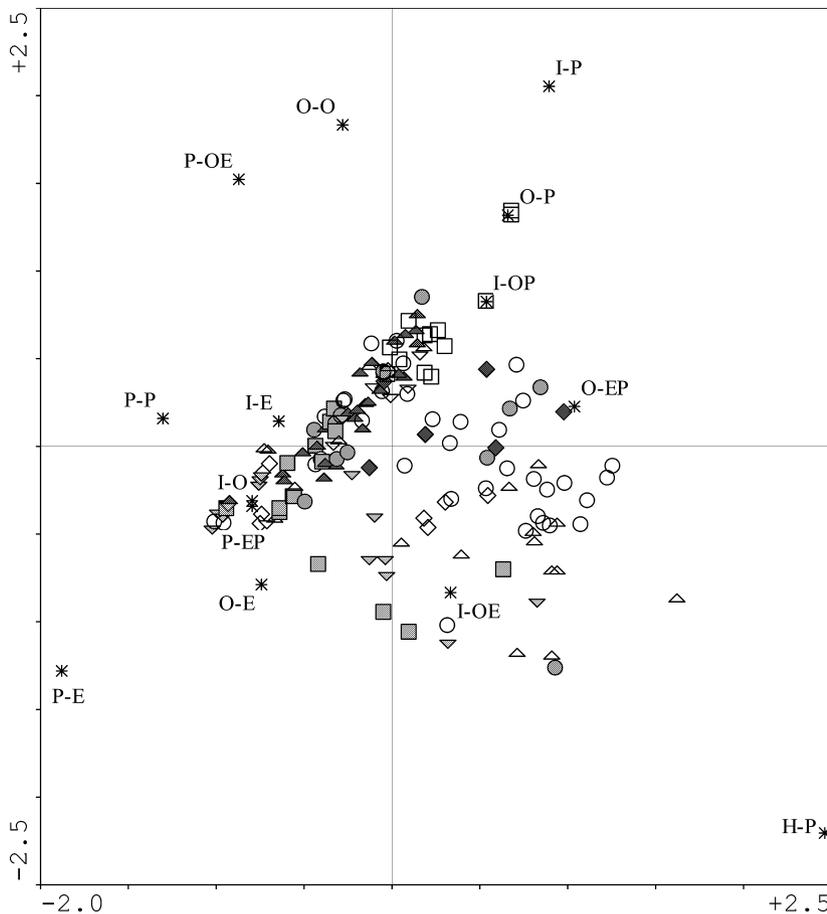
Figure 3 Ordination of sample and functional group scores on correspondence analysis (CA) axes 1 and 2 (axes *x* and *y*, respectively) resulting from correspondence analysis of the functional group data set. Ordination scores for functional groups are designated by stars. Functional group labels are in trophic–life-history format, where trophic = invertivore (I), herbivore (H), omnivore (O) or piscivore (P); life-history = opportunistic (O), periodic (P) or equilibrium (E). Functional groups with two life-history designations (e.g. P–EP) are species with intermediate life histories in Winemiller's (1992) life-history continuum. Symbols designate sub-basins: (▲), Devils (□), Frio (○), Hondo (◆), Medina (◑), Middle Concho (▨), Sabinal (△), South Concho (◇), Spring (▼), Village (▽).

Axis 2 appears to correlate, to some degree, with the distribution of life-history strategies in assemblages. Higher values on axis 2 were associated with abundant opportunistic and periodic species, whereas equilibrium species dominated assemblages with lower axis 2 values (Fig. 3). In general, sites appear to be positioned along a gradient of habitat stability or depth: shallow, temporally variable sites had positive values on both axes; deep, stable sites had negative values on both axes.

Both species richness and abundance were significantly, but weakly, correlated with taxonomic CA axis 1 (richness, $r^2 = 0.24$, $P < 0.001$; abundance, $r^2 = 0.22$, $P < 0.001$), with more diverse assemblages having negative axis values. This pattern corresponds to the longitudinal gradient in Texas, with higher diversity found in the eastern part of the state. The second taxonomic CA axis was significantly, although extremely weakly, correlated with species richness ($r^2 = 0.08$, $P < 0.001$) but not abundance ($r^2 = 0.01$, $P = 0.09$). Neither site functional diversity nor abundance was correlated with sample scores on functional CA axis 1 ($r^2 = 0.01$, $P = 0.10$; $r^2 = 0.01$, $P = 0.14$, respectively), whereas very weak significant correlations were observed for axis 2 ($r^2 = 0.03$, $P = 0.018$; $r^2 = 0.07$, $P < 0.001$, respectively).

For both the taxonomic and functional data sets, combined CCAs (both local and regional variables included) explained a greater percentage of variance than either local or regional analysis separately. Therefore, only results from the combined analyses are presented here. Ordination of the taxonomic data set by CCA resulted in a pattern similar to that obtained by CA ordination and similarity analyses. In the combined taxonomic CCA, the Rio Grande, Brazos and Neches drainages are distinguished from the rest of the basin (Fig. 4). Geographical coordinates were significant but highly redundant with climatic and landscape factors, and were therefore excluded from the analysis. Evaluation of the relative contribution of local and regional factors to the explained variation suggests that regional factors are the dominant influence on the observed pattern of assemblage structure (Table 4). Temperature extremes (January and July temperatures) and two land-use classifications (shrub and forest) accounted for 50% of the explained taxonomic variation, with all significant non-redundant regional variables together accounting for 67% of the explained variation (Table 4). The local factors with the greatest contribution to the model were percentage riffle and pH (7.3% and 5.8%, respectively, of the explained variation). For the taxonomic analysis, regional environmental factors separated sub-basins into biotic provinces, and local factors explained within-sub-basin variation in assemblage structure.

Although CCA ordination of the functional data set separated sub-basins to some degree, there was a large amount of overlap among sub-basins (Fig. 5). As in the functional CA ordination, sub-basins are not positioned in ordination space according to geographic proximity. Instead of a geographical

Figure 4 Sample score ordination on canonical correspondence analysis (CCA) axes 1 and 2 (axes *x* and *y*, respectively) from CCA of the taxonomic data set, with significant local- and regional-scale environmental variables (Table 3). Brazos (▲), Devils (□), Frio (○), Hondo (◆), Medina (◑), Middle Concho (▣)Concho (▨), Sabinal (△), South Concho (◇), Spring (▼), Village (▽).
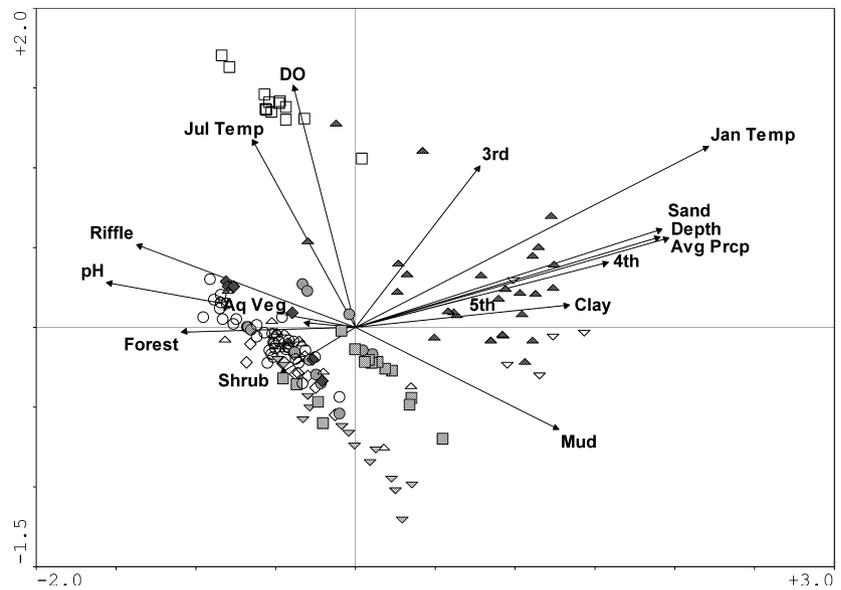
Table 4 Individual ranks and sum of significant regional (R) and local (L) environmental variables based on percentage contribution to variance explained by the composite canonical correspondence analysis (CCA) using the taxonomic and functional data sets (22% and 23.7%, respectively; see Results)

Taxonomic			Functional		
Variable (scale)	Percentage contribution	*P*	Variable (scale)	Percentage contribution	*P*
January temperature (R)	19.0	0.001	Riffle (L)	21.2	0.001
Forest (R)	12.4	0.001	January temperature (R)	18.2	0.001
July temperature (R)	10.9	0.001	Dissolved oxygen (L)	12.1	0.001
Shrub (R)	8.0	0.001	Shrub (R)	12.1	0.001
Riffle (L)	7.3	0.001	Width (L)	6.1	0.002
pH (L)	5.8	0.001	Precipitation (R)	6.1	0.002
Sand (L)	4.4	0.001	Conductivity (L)	6.1	0.003
4th order (R)	4.4	0.001	3rd order (R)	6.1	0.006
3rd order (R)	4.4	0.001	Bedrock (L)	3.0	0.008
Dissolved oxygen (L)	4.4	0.001	Cobble (L)	3.0	0.022
5th order (R)	4.4	0.001	July temperature (R)	3.0	0.029
Depth (L)	3.6	0.001	1st order (R)	3.0	0.036
Precipitation (R)	3.6	0.002			
Clay (L)	2.9	0.018			
Aquatic vegetation (L)	2.2	0.020			
Mud (L)	2.2	0.030			
Regional	67.1		Regional	48.5	
Local	32.8		Local	51.5	

pattern, samples appear to be positioned with respect to habitat type and stability. The dominant axis (axis 1) separates riffle assemblages (negative values) from those in other habitat types (e.g. pools and runs, having positive values); whereas axis 2 appears to correlate with position along longitudinal stream gradients (headwaters with negative values and lower stream reaches with positive values) and environmental stability (temperature extremes and precipitation). Sites with positive values on both axes (pool and run habitats at lower positions in the longitudinal gradient) had greater relative densities of piscivores. The dominant environmental variables in the analysis were percentage riffle (21.2% of the explained

variation); January temperature (18.1%); and dissolved oxygen and shrub landscape (Table 4). Overall, regional- and local-scale variables contributed approximately equally to the explained variation in the functional analysis (48.5% and 51.5%, respectively).

Total variance explained by CA of our taxonomic and functional data sets was 32.5% and 57.2%, respectively. Because CCA constrains species data to be correlated with environmental variables, the percentage variance explained is generally lower than for CA (22.0% and 23.7% for taxonomic CCA and functional CCA, respectively). Because broad geographic and temporal scales tend to increase the amount of
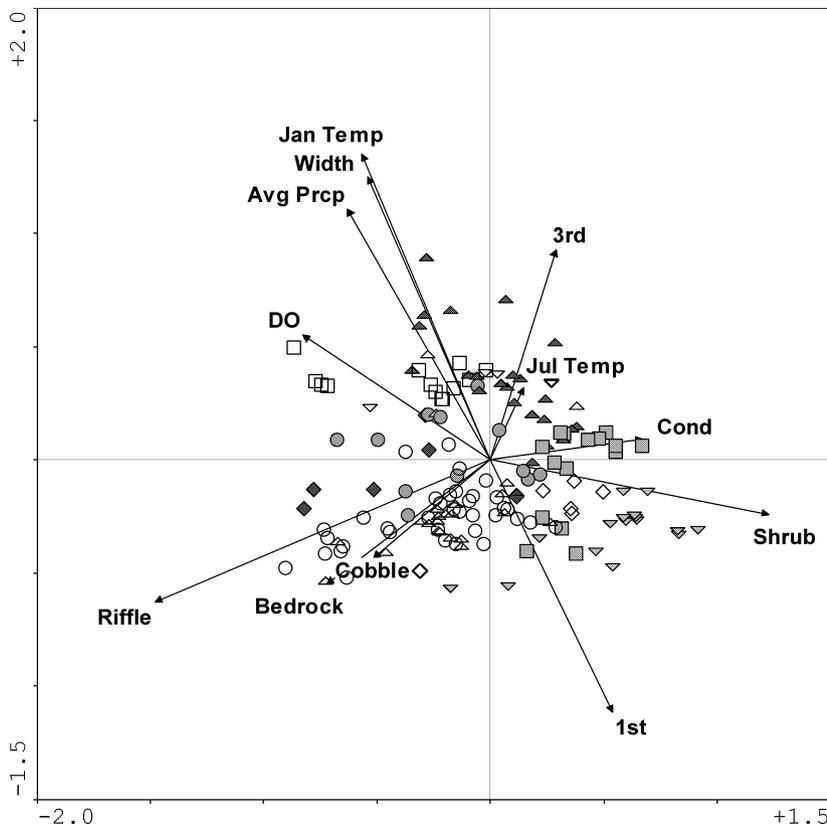
Figure 5 Sample score ordination from canonical correspondence analysis (CCA) of the functional group data set, with significant local- and regional-scale environmental variables (Table 3). Brazos (▲), Devils (▣), Frio (○), Hondo (◆), Medina (◐), Middle Concho (▨), Sabinal (△), South Concho (◇), Spring (▼), Village (▽).

unaccountable variation in species relative abundances, low percentage variances modelled by CA and CCA are expected, and resulting relationships in ordination space reveal meaningful ecological patterns (ter Braak & Šmilauer, 1998). Additionally, CCA only extracts variation in species distributions that can be attributed to specific environmental relationships. Due to the lack of, or extremely weak, relationships between CA axes and species richness and abundance, as well as the lack of a relationship between the number of sites sampled in a sub-basin and sub-basin diversity, we can infer that the observed patterns in assemblage structure are real and are not likely to result from differences in sample size or species richness among sub-basins for either data set.

DISCUSSION

Local and regional determinants of assemblage structure

Patterns in regional composition, fish assemblage structure and co-occurrences depended on the type of biological data used (taxonomic identity or functional group). Patterns derived from taxonomic analyses were driven by species' geographic distributions. Taxonomic analyses suggested that local assemblage structure was influenced predominantly by regional-scale environmental factors, especially seasonal temperature extremes and shrub and forest landscapes. The biogeographic trend observed, combined with the relatively isolated nature of river drainages, may also represent the role

of historical factors such as speciation and dispersal in regulating the composition of regional species pools. In contrast, analyses using functional groupings based on trophic and life-history characteristics distinguished assemblages along gradients of habitat type (riffle, pool) and stability (stream order, climate characteristics, presence of piscivores) irrespective of sub-basin, and revealed an approximately equal influence of local- and regional-scale factors.

For all sub-basins, we observed extremely few negative associations among species in both the same trophic and functional group. This result suggests that competitive interactions probably do not play a strong role in structuring Texas stream fish assemblages, and corresponds with null model analyses by Jackson et al. (1992) for north-temperate lakes, and Peres-Neto (2004) for a Brazilian stream system (but cf. Winston, 1995). Although Brown et al. (2000) demonstrated that interspecific competition may scale up to shape the boundaries of species distributions, competition is unlikely to result in complementary species distributions in streams because populations in these temporally variable environments may not reach levels at which resource limitation occurs (Grossman et al., 1998; Peres-Neto, 2004). Even in comparatively stable lake fish assemblages, competition has generally been reported to result in niche segregation and character displacement rather than exclusion (Robinson & Wilson, 1994).

Instead, strong negative associations were most commonly observed for species in different life-history groups. Assuming environmental factors constrain the life-history characteristics

of species (e.g. equilibrium species are restricted to more stable environments), this result suggests a dominant structuring effect of habitat on species assemblages. Within sub-basins, species tend not to co-occur because they occupy different habitat types, such as riffles vs. pools. Approximately half the above-mentioned negative associations were for species in the same trophic group, the other half were for predator–prey comparisons. Because species life-history and trophic categories were significantly associated, it is not initially apparent which characteristic is the dominant structuring mechanism.

Variation in distribution patterns within trophic groups or among non-piscivorous trophic groups appears to support the major influence of habitat on species associations. For example, among invertivores, deep-bodied centrachids commonly found in pools were often negatively associated with small-bodied minnows common in shallow habitats. At the same time, many studies have demonstrated strong structuring effects of predation on stream communities, including some involving species negatively associated in our study (Power *et al.*, 1985; Schlosser, 1987b). Schlosser (1987b) demonstrated experimentally that habitat overlap among small fishes in shallow riffle and raceway segments resulted from the presence of predatory bass in adjacent pool habitats. Deeper-bodied centrarchids are less vulnerable to bass and other gape-limited predators, and thus are able to occupy pool habitats. Consequently, negative associations observed between invertivorous centrarchids and minnows may arise from an indirect effect resulting from habitat shifts in minnows due to predation threat by bass.

Predation has been recognized as an important structuring factor of both lake and stream fish assemblages (He & Kitchell, 1990; Brown & Moyle, 1991; Gilliam *et al.*, 1993; Rodríguez & Lewis, 1997). Most of the strongly negative associations we observed among functional groups were for predator–prey comparisons, reinforcing our interpretation of species-level co-occurrence patterns, which suggested that predation is an important structuring mechanism in these systems. Distributional patterns probably result from a combination of predator–prey interactions and habitat heterogeneity (necessary for predator-induced habitat shifts). Analyses based on functional groups separated assemblages along environmental gradients instead of geographic gradients. Habitat-selection behaviour in response to predation threat may be an important structuring factor that links various spatial scales, as demonstrated by Resetarits (2005).

Because physical habitats tend to be more predictable over time than food availability or quality, widely observed patterns in stream fish assemblages probably result from habitat associations rather than biotic interactions (Jackson *et al.*, 1992, 2001) – in these systems, capacity rules may outweigh allocation rules (*sensu* Brown, 1987). Similar to results from our taxonomic analyses, previous studies investigating the influences of abiotic factors operating at multiple spatial or temporal scales suggest that factors such as regional climate, land use, hydrology and disturbance regimes determine local fish assemblage structure, especially in variable environments

(Rahel, 1990; Tonn *et al.*, 1990; Taylor, 1996; Lohr & Fausch, 1997; Angermeier & Winston, 1998; Harding *et al.*, 1998; Marsh-Matthews & Matthews, 2000; Lamouroux *et al.*, 2002).

The differences observed between results of our taxonomic and functional analyses are not entirely surprising. If species distributions are geographically more restricted than the spatial scale of investigation, patterns derived from taxonomic analyses should be expected to result from regional faunal differences. The greater relative importance of regional factors in determining local assemblage attributes observed in earlier broad-scale studies may be an artefact of scale (Marsh-Matthews & Matthews, 2000). Similar species (e.g. congeners) may have non- or slightly overlapping distributions due to historical processes but similar ecological requirements and functions. In this manner, the assemblages in question may have similar attributes when measures other than species identity are used as the metric of investigation. For example, our taxonomic analyses separated assemblages into a geographic pattern of species distributions; however, functional analyses separated assemblages along gradients of habitat characteristics – a habitat template (Southwood, 1977).

Corresponding with earlier work, the habitat template described by our functional group analyses is strongly based on hydrological variability. Hydrological factors have been shown to play a dominant role in structuring fish assemblage traits in lotic systems (Lamouroux *et al.*, 2002). Hydrological stability is directly related to taxonomic and trophic diversity (Horwitz, 1978), with assemblages characterized by generalists in hydrologically variable sites and more specialist species in stable sites (Poff & Allan, 1995). The importance of predation in structuring local assemblages, illustrated by our assemblage structure and co-occurrence analyses, is ultimately mediated by hydrology, as large piscivores are restricted to deeper, more stable sites and prey species utilize more variable habitats as refuges from predation.

Scaling up inferences based on taxonomic and functional groups

How may inferences regarding the relative roles of local- and larger-scale factors in determining local assemblage structure derived in this study scale up to the continent or global scale? We expect the general relationship between inferences based on taxonomy and functional groups to follow the same trend at larger geographic scales. Multi-scale analyses based on species-level data should suggest a dominant role of regional-scale environmental factors or historical processes when the geographic scale of investigation is greater than the distributions of species being analysed, whatever the geographic scale. However, homogenization of regional faunas by widespread species introductions or extinction of endemic species may blur the roles played by historical factors such as colonization and speciation in shaping local assemblages (Rahel, 2000; Olden & Poff, 2003).

In contrast, multi-scale analyses based on various kinds of functional groups or guilds should sort local assemblages

according to an appropriate habitat template (Southwood, 1977; Townsend & Hildrew, 1994). Functional comparisons of stream fish assemblages from the same climatic zone as the present study should result in a habitat template similar to that described here: a dominant structuring role of hydrological variability and predation. Although the same factors may determine species richness in rivers of different climatic zones (regional net primary productivity and habitat heterogeneity; Guégan *et al.*, 1998), the importance of climatic factors in determining the functional structure of local assemblages may increase when altitude differs greatly among regions, or geographic scale is increased to include multiple climatic zones. Comparison of functional structure across climatic zones is expected to result in the addition of annual temperature extremes to the habitat template, as summer or winter temperatures may limit persistence of some functional groups among regions.

Evaluation of fish assemblage organization models

Several models have been developed to predict freshwater fish assemblage attributes in both lotic and lentic habitats (reviewed by Jackson *et al.*, 2001). Schlosser (1987a) developed a longitudinal gradient model for warm-water stream systems similar to one described by Zalewski & Naiman (1984) for different types of riverine fish communities. In both models, assemblages in stable or predictable environments are regulated by biotic interactions, whereas assemblages in unstable environments are viewed as products of colonization/extinction dynamics. Another influential theory describes the role of factors representing multiple geographic scales on the structure of local assemblages as a series of environmental filters, such that the local community is composed of only those species from the larger species pool that are able to persist through all filters. Originally developed by Smith & Powell (1971), the filter model was later adopted and modified by Jackson & Harvey (1989) and Tonn (1990) to incorporate biotic interactions such as predation, and by Poff (1997) to incorporate species traits.

Results from our taxonomic (species-level) analyses suggest that historical and environmental factors act in a hierarchical manner to produce the local assemblage. Compositional similarity of regional species pools follows a geographic pattern. This pattern suggests that regional environmental factors and historical processes such as speciation and dispersal strongly affect local assemblages. In our assemblage structure analyses, regional environmental factors such as climate patterns explained most of the variation, with local-scale factors accounting for within-sub-basin differences. At the regional scale, species exhibited non-random co-occurrence patterns, and strong negative associations among species within sub-basins suggested sorting according to hydrological stability. These species-level results fit well with the original environmental filter model of Smith & Powell (1971).

Analyses based on functional groups, on the other hand, separated sites into habitat types differing in terms of stability

and predation pressure, irrespective of sub-basin. Although assemblages were sampled in some of the most arid, as well as the wettest, regions of Texas, a geographic trend was not observed for regional composition, assemblage structure or co-occurrence of functional groups. Regional and local-scale environmental factors were found to have approximately equal influence on local assemblage structure. Deeper, more stable sites in our study were characterized by piscivore-dominated assemblages, whereas variable riffle or headwater sites were composed of generalist or opportunistic functional groups. Functional group co-occurrence patterns suggested an important structuring effect of predation mediated by habitat type at the local scale. These results correspond with models developed by Horwitz (1978) and especially Poff & Allan (1995) and Schlosser (1987a). The filter-type models modified to incorporate biotic interactions and species traits (Jackson & Harvey, 1989; Poff, 1997) may be interpreted to suggest a dominant effect of large-scale processes (filters) and thus fit only marginally with our functional group results.

Ultimately, the applicability of the above models depends on the question to be addressed. The original filter-type models are suitable when addressing biogeographic trends in species composition, whereas assessment or prediction of assemblage-level responses to species introductions or habitat degradation, such as alteration of hydrological regimes, probably requires a functional group approach. When dealing with applied problems of species introductions, for example, the assemblage organization models of Poff & Allan (1995) and Schlosser (1987a) may be more appropriate, as functional composition and diversity in combination with key habitat factors may affect the susceptibility of an ecosystem to invasion, and may be used to predict which species will be extirpated (Moyle & Light, 1996; Olden *et al.*, 2004, 2006).

CONCLUSIONS

The awareness that local assemblages are shaped by factors at multiple spatial and temporal scales has improved our understanding of community organization and our ability to predict community traits such as species richness (Ricklefs, 2004). In the present study, we used taxonomic and functional group analyses in a multi-scale approach to compare patterns of local stream fish assemblage structure. What do taxonomic and functional analyses tell us about the organization of stream fish assemblages? Analyses based on taxonomy reveal species-distribution patterns, whereas analyses using functional groups separate assemblages according to a habitat template. Large-scale processes shape the pool of species that potentially may occur in a local assemblage, thereby strongly influencing local assemblage structure. However, general functional responses to the environment and habitat-specific assemblages occurred regardless of the taxonomic history of the constituent species. Analyses of various kinds of functional groups can provide opportunities to infer ecological responses to environmental variation, and may therefore provide a more fruitful avenue for developing

and testing general ecological theories of community organization across biogeographic scales.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online from http://www.Blackwell-Synergy.com:

Appendix S1 Summary statistics of local environmental variables.

Appendix S2 Summary statistics of regional environmental variables.

Appendix S3 Species functional group classifications.

Appendix S4 Pairwise comparisons of species co-occurrences.

Appendix S5 Adjusted scores of species pairwise co-occurrences.

Appendix S6 Pairwise comparisons of functional group co-occurrences.

Appendix S7 Adjusted scores of functional group pairwise co-occurrences.

BIOSKETCHES

David Hoeinghaus conducts research on fish ecology, aquatic community and ecosystem ecology, and food webs of freshwater and estuarine ecosystems. Of particular interest are determinants of community organization, and community-level responses to anthropogenic impacts and habitat restoration.

Kirk Winemiller conducts research on fish ecology, food webs of river and coastal ecosystems, evolutionary ecology and ichthyology. He is interested in the manner in which alternative life-history strategies influence population and community dynamics, the influence of stochastic and deterministic processes on community organization, and the influence of species on food web patterns and dynamics.

Jenny Birnbaum has conducted research on the influence of woody cover density on fish and benthic macroinvertebrate assemblages in central Texas streams. She currently works for the Mystic River Watershed Association in Massachusetts as the Mystic Monitoring Network Director, which entails coordinating volunteer water quality monitors, managing data, and communicating results to various environmental entities.

Editor: Robert McDowall