

# Biogeography, ecoregions, and geomorphology affect fish species composition in streams of eastern Oklahoma, USA

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**Abstract** Stream fish assemblages are structured by biogeographical, physical and biological factors acting on different spatial scales. We determined how physical factors, geomorphology and stream habitat, influenced fish species composition (presence–absence) in eastern Oklahoma, USA relative to the ecoregion and biogeographic effects previously reported. We sampled

fish assemblages and surveyed geomorphology and habitat at 107 stream sites in the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions in eastern Oklahoma. Partial canonical correspondence analyses (pCCAs) and variance partitioning showed that patterns of endemism related to drainage basins and ecoregions explained important variation in fish species composition in all streams, but stream size and local channel morphology explained more variation overall. Stream size effects were most important in explaining variability in fish species composition in both northeastern and southeastern Oklahoma streams. Local channel morphology and substrate characteristics were secondarily important. Variables typically considered important as fish habitat (aquatic vegetation, etc.) had little effect on fish species composition.

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## Introduction

Stream fish communities are structured by three sequential factors: biogeography, physical habitat, and biological interactions. Poff (1997) unified these factors in a framework describing how functional species traits allow species in the regional species pool (resulting

from biogeography) to pass through hierarchically nested habitat filters that determine which species are present at a given locality. Biotic interactions act as additional filters on local community composition.

The longitudinal profile of a stream has long provided a spatial context for stream ecology theory (Shelford 1911). Sheldon (1968) reported that species richness increased downstream in a New York stream system as a result of species additions to headwater assemblages. Horwitz (1978) found that streamflow variability changed predictably from upstream to downstream. He suggested that a decrease in streamflow variability downstream allowed additional fish species to join the species pool that consisted of those already present upstream (*sensu* Sheldon 1968). The rate of species additions reflected the temporal constancy of specific rivers. Subsequently developed stream ecology theories, such as the River Continuum Concept, emphasized longitudinally varying processes (e.g., heterotrophy versus autotrophy, energy processing and transport, physical and biological stability and diversity) and how longitudinal changes influenced fish community composition (Vannote et al. 1980). However, the predictions of the concept sometimes proved untenable when applied to regions other than those they were developed for (Minshall et al. 1985) and in river systems with anthropogenic interruptions (e.g., dams) of the continuum itself (Ward and Stanford 1983).

The influence of longitudinal processes on local habitat conditions and fish community composition varies among streams and rivers. A recent theory, the Process Domains Concept (Montgomery 1999), suggests that spatial and temporal variability in geomorphic processes (e.g., hydrology, sediment transport, woody debris recruitment) often creates homogenous zones within the river continuum, and that those zones may contrast with expectations from the River Continuum Concept. The spatial structure of these zones can strongly influence stream ecosystem structure and function and how ecosystems respond to disturbance. For example, patchy, local (i.e., reach scale) geomorphic processes, such as reach slope and bed mobility, influenced stream disturbance regimes and fish assemblage structure more than longitudinal processes in a Piedmont river drainage in the southeastern United States (Walters et al. 2003b). However, the dominance of local processes may have reflected the spatial scale of their study (see Wiens

1989). Studies focusing on a small range of stream sizes from a single river basin may show little variation in longitudinal process such that local processes dominate (Sheldon 1968; Walters et al. 2003b), whereas longitudinal processes may be more evident in studies with a larger spatial extent (Horwitz 1978).

We determined how stream size, local channel morphology, and stream habitat affected fish species composition relative to the known effects of ecoregions and biogeography in eastern Oklahoma streams. Understanding the effects of geomorphology and stream habitat is imperative given that much stream ecology theory and stream restoration principles have a geomorphic basis. Moreover, determining the magnitude of geomorphic effects relative to previously reported large-scale ecoregion differences and biogeographic effects will further reveal mechanisms influencing fish species composition and aid in conservation and management of eastern Oklahoma fishes.

## Materials and methods

### Study area

The Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions are upland regions in eastern Oklahoma (Omernik 1987; Woods et al. 2005). The Boston Mountains ecoregion in northeastern Oklahoma is a dissected mountainous plateau composed of flat-lying shale and sandstone lithology and oak-hickory forest. Annual rainfall is 112 to 130 cm and land is used mostly for logging and recreation (Woods et al. 2005). The Ozark Highlands in northeastern Oklahoma are dominated by flat-lying cherty limestone, but shale, limestone, and dolostone are present in valley bottoms. Annual precipitation is 104 to 124 cm, and land use is primarily logging, recreation, and cattle and poultry farming, including pastureland and hayfields (Rabeni and Jacobson 1993; Woods et al. 2005). The Ouachita Mountains in southeastern Oklahoma consist of folded, Paleozoic sandstone, shale, and chert. Oak-hickory-shortleaf pine forests in this region receive from 109 to 145 cm of annual rainfall. Common land uses are: logging, pastureland, hayfields, farming, and recreation (Rutherford et al. 1992; Woods et al. 2005). All Boston Mountains and Ozark Highlands streams lie within the Arkansas River basin. A few Ouachita

Mountains streams flow north into the Arkansas River, but the majority of them flow south into the Red River. Fish assemblages are known to differ among these ecoregions (Rohm et al. 1987; Howell 2001; Fisher et al. 2004), and some fish species are endemic to certain ecoregions and drainage basins in the region (Miller and Robison 2004).

### Stream survey

We used a geographic information system (GIS) to randomly select 175 stream sites for an inventory of fluvial geomorphology, habitat, and fishes in streams of the Boston Mountains, Ouachita Mountains, and Ozark Highlands level III ecoregions in eastern Oklahoma (Omernik 1987). Sites were allocated among the three ecoregions approximately in proportion to their areas in Oklahoma and equally distributed among stream orders 1 to 4 within each ecoregion. Forty sites were selected in the Boston Mountains and Ozark Highlands ecoregions, and 95 were selected in the Ouachita Mountains ecoregion in Oklahoma.

Watershed characteristics for each site were measured using ArcGIS 9.1 GIS software (ESRI, Redlands, California) and the National Elevation Dataset (30 m resolution; USGS 1999). Watersheds were delineated upstream of each site, and their areas and elongation ratios were measured (Morisawa 1968).

From May 2003 to August 2005 we measured channel morphology at the reach scale. A global positioning system (GPS) receiver was used to navigate to each randomly selected stream site. Stream reaches were defined as 20 times the mean channel width (Rosgen 1994). We classified channel units (e.g., riffles and pools) in each reach (Hawkins et al. 1993). Transects were surveyed across two riffles and two pools when available, with a maximum of two transects in a single channel unit. Bankfull channel width:depth ratios were calculated for transects (Arend and Bain 1999), as were entrenchment ratios (Rosgen 1994). Median particle sizes ( $D_{50}$ ) were calculated from 100 particles collected along each transect (Bain 1999). Channel unit slopes were measured individually and cumulatively represented reach slope. Sinuosity was measured as thalweg length:valley length. Width:depth ratios and median particle sizes were calculated as weighted averages based on the cumulative lengths of riffles and pools in each reach.

Instream habitat variables were estimated or measured in each channel unit. Channel units were mapped with a GPS receiver, and dimensions were measured in a GIS (Dauwalter et al. 2006). Thalweg depths were measured systematically. We visually estimated substrate distributions (modified Wentworth scale; Wolman 1954; Bain 1999). We visually estimated, and enumerated when logistically feasible, rootwads and large woody debris (10+ cm diameter, 4+ m in length) in each channel unit, and estimated the percent coverage of aquatic vegetation. Channel unit data were combined for reach estimates.

Fish species composition was estimated using snorkeling and electrofishing (Reynolds 1996; Dolloff et al. 1996). Most stream reaches were snorkeled by one to three persons depending on stream size and water clarity, and observed species were noted on a diving cuff. Five groups of species could not be identified to species while snorkeling, and were placed into species groups: redborses *Moxostoma spp.*, spotted bass *Micropterus punctulatus* and largemouth *M. salmoides* (both recorded as *M. salmoides*), lampreys *Ichthyomyzon spp.*, buffalo fishes *Ictiobus spp.*, and *Lythrurus spp.* When streams were too turbid to snorkel (visibility <1 m), they were electrofished with a Smith Root, Inc. model 15-D backpack electrofisher, or a Smith-Root 2.5 GPP model electrofisher mounted in a 3 m jon boat with a portable anode or a 4.3 m jon boat with a ring anode; a combination of electrofishing gears was sometimes used to sample all habitats. Electrofishing power density was standardized at  $1,000 \mu\text{S}\cdot\text{cm}^{-3}$ . When electrofishing, unidentified fish species were preserved in 10% formalin and later identified in the laboratory.

### Fish species associations with geomorphology and stream habitat

Using CANOCO for Windows software version 4.5 (Biometris-Plant Research International, Wageningen, The Netherlands), we performed partial canonical correspondence analysis (pCCA) to determine how fish species composition (presence-absence) was affected by drainage basins, ecoregions, geomorphology, and stream habitat in eastern Oklahoma streams. Canonical correspondence analysis is a direct gradient analysis that uses weighted averaging and a unimodal species model to explain species composition using environmental variables (ter Braak 1986). Using pCCA, variation

attributed to certain environmental variables can be factored out to focus on the variables of interest.

We used forward stepwise selection procedures and pCCA to select the geomorphic and habitat variables that best explained fish species composition in eastern Oklahoma streams. Although stepwise selection procedures were used, basin area was included in all analyses a priori as a surrogate for stream size because fish occurrences are known to change with stream size in these regions (Matthews and Robison 1998). Ecoregion and basin (Arkansas and Red River basins) variables were also included a priori because they influence species occurrences also (Rohm et al. 1987; Miller and Robison 2004). All remaining variables were entered when  $P \leq 0.05$  in a Monte Carlo permutation test with 9,999 permutations (Lepš and Šmilauer 2003). Sampling gear was included as a covariable to remove gear bias effects on species detectability. We used biplot scaling conducted on inter-species differences and down-weighted rare species in all pCCAs. We ran additional analyses for variance partitioning (Økland 2003) after

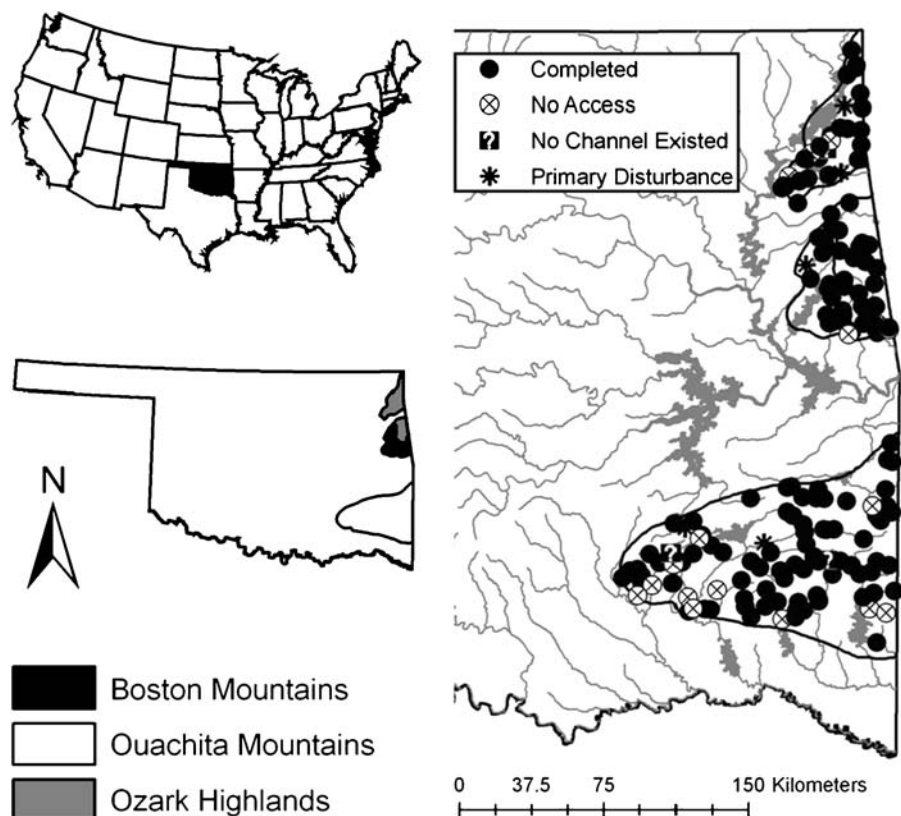
important geomorphic and stream habitat variables were selected.

## Results

### Stream survey

We surveyed fluvial geomorphic features, stream habitat, and stream fishes at 107 of the 175 selected stream sites in the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions. Seventeen stream sites were inaccessible or access was denied by landowners. Four streams had primary channel disturbances (e.g., gravel mining, concrete channels) and were not sampled, and no definable channel was found at three sites. Nineteen streams were dry. Trained personnel were not available to snorkel and identify fish species at 20 sites, and no fish were observed at four. Presence–absence data on fishes were collected at 107 stream sites (Fig. 1); 23 sites in the Boston Mountains, 64 in the Ouachita Mountains, and 20 in

**Fig. 1** Locations of randomly selected stream sites used for an inventory of fluvial geomorphology, stream habitat, and stream fishes in eastern Oklahoma, of which presence–absence of fish species was estimated at 107



the Ozark Highlands. Seventeen sites in the Ouachita Mountains, 3.9 to 54.6 m mean channel width, were electrofished because water clarity prohibited effective snorkeling. Streams among ecoregions differed mostly in substrate and some channel morphology characteristics (Table 1).

We observed 59 fish species total during stream surveys (Appendix 1). Thirty-four species were observed at 23 stream sites in the Boston Mountains. When fish were present, richness ranged from 3 to 20 (mean=10.0). In the Ozark Highlands, 42 species were observed at 20 stream sites, and richness ranged from 1 to 26 (mean 12.0). In the Ouachita Mountains, 41 species were observed at 64 sites; richness ranged from 1 to 18 (mean=7.6). Richness was 51 and 39 in the Arkansas and Red River basins, respectively. Twenty species were observed only in the Arkansas River basin and eight were observed only in the Red River basin.

Fish species associations with geomorphology and stream habitat

Fish species composition was explained by several factors. In addition to the known effects of ecoregion, drainage basin, and basin area on fish species composition, width:depth ratio ( $p=0.001$ ), slope ( $p=0.002$ ), large woody debris density ( $p=0.009$ ), sinuosity ( $p=0.021$ ), and  $D_{50}$  ( $p=0.030$ ) also explained

fish species composition in all streams. Variance inflation factors showed no redundancy among variables. Entrenchment ratio was not tested for its effect because very few sites had ratios  $<2.2$ , the maximum measured. Axis 1 explained 42.0% of the species-environment correlation, whereas axes 2 and 3 explained 21.9 and 9.5%, respectively (Table 2). Axis 1 reflected patterns of endemism in species composition (Fig. 2). The ecoregion and drainage basin centroids both aligned with axis 1. Several species were correlated with the northeastern ecoregions and Arkansas River basin (distance between species optima and variable centroids). The northern hog sucker *Hypentelium nigricans* and banded sculpin *Cottus carolinae* are endemic to the Boston Mountains and Ozark Highlands ecoregions in the Arkansas River basin (Miller and Robison 2004), and short distances between their optima and ecoregion centroids reflected this. The southern redbelly dace *Phoxinus erythrogaster* also does not occur in the Ouachita Mountains and was strongly associated with northeastern ecoregions. Substrate size was correlated with ecoregions and basins (direction of vector in relation to centroids) and reflected generally larger substrates in southeastern Oklahoma streams. The degree of parallelism between basin area and channel slope vectors suggested negative correlation and both aligned with axis 2. This axis reflected the influence of stream size and local channel morphology on fish

**Table 1** Summary (mean±1 SD) of geomorphology and habitat from streams in the Boston Mountains ( $n=23$ ), Ouachita Mountains ( $n=64$ ), Ozark Highlands ( $n=20$ ), Oklahoma

Variable	Boston Mountains		Ouachita Mountains		Ozark Highlands	
	Mean	SD	Mean	SD	Mean	SD
Basin area (km <sup>2</sup> )	127.9	167.8	70.0	91.4	184.4	235.8
Channel width (m)	22.1	12.6	16.6	9.4	21.8	14.1
$D_{50}$ (mm)	37.6	19.0	78.3	69.3	27.4	7.5
Elongation ratio	0.57	0.09	0.52	0.14	0.50	0.11
Large woody debris density (#/m <sup>2</sup> )	0.003	0.008	0.003	0.005	0.003	0.003
Mean thalweg depth (m)	0.30	0.15	0.39	0.21	0.42	0.18
% Bedrock	20.9	25.5	11.2	16.7	8.7	17.9
% Pool	61.5	25.9	87.9	16.9	65.2	24.7
% Silt-Clay	4.2	7.6	7.5	10.5	4.9	5.9
% Vegetation	1.3	2.2	7.9	10.8	3.9	4.9
Rootwad density (#/m <sup>2</sup> )	0.004	0.008	0.006	0.010	0.008	0.013
Sinuosity	1.13	0.13	1.19	0.28	1.17	0.22
Slope	0.007	0.006	0.006	0.007	0.005	0.004
Width:depth ratio	23.5	7.9	17.2	6.4	25.3	11.9

**Table 2** Cumulative percent variance of species data and species-environment data explained by axes from pCCAs of fish species (presence–absence) and drainage basins, ecoregions, geomorphology and stream habitat from 107 eastern Oklahoma streams

Region/Variance component	Axis 1	Axis 2	Axis 3	Axis 4
All regions				
Species data	10.3	15.7	18.0	19.9
Species-environment data	42.0	63.9	73.4	81.4
Northeast				
Species data	11.3	15.6	18.7	20.9
Species-environment data	53.9	74.8	89.5	100.0
Southeast				
Species data	6.9	9.2	11.2	21.2
Species-environment data	62.0	82.1	100.0	

species composition (Fig. 2). The southern redbelly dace most often occurred in small, high gradient streams, whereas the banded darter *Etheostoma zonale*, smallmouth bass *Micropterus dolomieu*, and logperch *Percina caprodes* were found in larger, low gradient streams. The Boston Mountains and Ozark Highlands centroids separated along axis 3, a sinuosity gradient (sinuosity vector parallel to axis 3). Examples of species correlated with this gradient were banded sculpin and western mosquitofish *Gambusia affinis* in Ozark Highland streams.

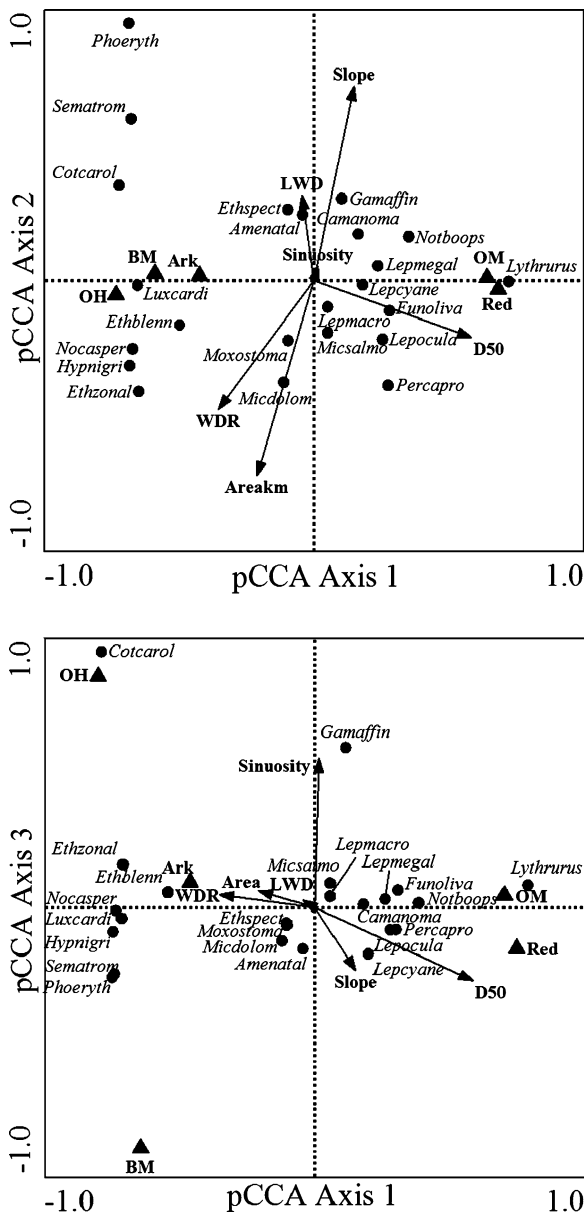
Variance partitioning showed geomorphology to collectively explain the most variation in fish species composition in eastern Oklahoma streams, but only after effects of ecoregion and drainage basin were accounted for (Table 3). Not surprisingly, there was some indistinguishable variation between ecoregions and drainage basins (i.e., their intersection) because the Ouachita Mountains ecoregion is primarily represented by the Red River drainage. Variation was also indistinguishable between geomorphology and ecoregions because some geomorphology was unique to ecoregions.

As a result of the strong differences between northeastern and southeastern Oklahoma streams, we conducted additional analyses to assess the influences of geomorphology and stream habitat within each region. Forward stepwise selection of variables was again used as explained above. Selection of environmental variables for northeastern streams was done in a pCCA with data from both ecoregions but with ecoregion as a covariable. Variable selection for Ouachita Mountains streams was done in a pCCA in which drainage basin and gear type were included as covariables. Again, basin area was included a priori in

both analyses due to its known effect on species composition.

In analysis of northeastern streams, reach slope ( $p=0.001$ ), width:depth ratio ( $p=0.001$ ), and  $D_{50}$  ( $p=0.032$ ) were entered during forward stepwise procedures. Axis 1 explained 53.9% of the species-environment correlation (Table 2), and represented a notable stream size gradient whereby there was nearly a direct, inverse relationship between basin area and reach slope (Fig. 3). Southern redbelly dace were associated with small, higher gradient streams, and rock bass *Ambloplites rupestris*, redborses *Moxostoma* spp., logperch, and banded darters were associated with larger, lower gradient streams. Axis 2 explained 20.9% of the species-correlation (Table 2), and represented a substrate-size gradient with southern redbelly dace associated with smaller substrates and multiple species with larger substrates. Larger variation in substrate size among sites in the Boston Mountains appeared to influence this gradient (Fig. 3). The ubiquitous green sunfish *Lepomis cyanellus* was not strongly associated with any factor.

There also were stream size and substrate gradients in the Ouachita Mountains.  $D_{50}$  ( $p=0.009$ ) and slope ( $p=0.017$ ) were entered during the forward stepwise selection of variables. Axis 1 explained 62.0% of the species-environment correlation and represented stream size effects (Table 2, Fig. 4), whereas axis 2 explained 20.1% of the species-environment correlation and reflected a reach slope gradient that was not correlated with stream size. Southeastern Oklahoma streams lack an indicative headwater stream species, although several species were associated with larger streams. Again, green sunfish was not strongly associated with any factor.



**Fig. 2** Biplots of pCCA axes 1 and 2 (top) and pCCA axes 1 and 3 (bottom). Biplots of fish species and basin area, channel width:depth ratio, median particle size (D<sub>50</sub>), reach slope, and large woody debris density summarize the differences in fish species composition in streams of the Boston Mountains, Ouachita Mountains and Ozark Highlands ecoregions and Red and Arkansas River basins in eastern Oklahoma. Species having weights greater than 5% are displayed. Species codes represent genus for species groupings, or the first three letters of genus and first five of species

## Discussion

Several factors associated with different spatial scales influenced fish species presence, and hence composition, in upland streams of eastern Oklahoma. Historical biogeography and resulting endemism explained an important component of variation in fish species composition in the region. Collectively, however, the geomorphic factors of stream size and local reach morphology explained more variation overall. And although woody debris was selected by stepwise procedures in one analysis, its effect on fish species composition was small relative to other factors, and it was unimportant in separate regional analyses. Other fish habitat variables did not explain the presence or absence of fishes.

Historical biogeography and resulting endemism explained important variation in fish species presence. Many fish species were found only in streams of the Arkansas River or Red River basins, confirming well-known distributional patterns of Oklahoma fishes (Miller and Robison 2004). These patterns also corresponded to ecoregions, as the Ouachita Mountains in southeastern Oklahoma consist primarily of streams in the Red River basin. However, Ouachita Mountains streams within the Arkansas River basin south of the Arkansas River mainstem lacked some species found only north of the mainstem in Ozark Highlands and Boston Mountains streams. This likely led to ecoregions explaining more variation in fish species composition than did basins, although much variation was indistinguishable between the two.

Although some ecoregion effects were not separable from basins, ecoregions themselves explained more variation in fish species composition than did drainage basins. Ozark Highlands streams are clear, cool, and spring-fed as a result of a cherty-limestone geology and karst topography. Boston Mountains streams are also less turbid than those in the Ouachita Mountains. Large-scale properties associated with ecoregions cause regional streams to have unique physicochemical properties and corresponding habitat irrespective of channel form and stream size (Woods et al. 2005). However, some streams cross ecoregion boundaries and may be more indicative of upstream than downstream ecoregions because of unidirectional water and sediment routing processes. Streams crossing ecoregion boundaries may further blur boundaries that are already best described as ‘complex’ (Omernik

**Table 3** Variance in fish species composition (presence–absence) attributable to ecoregions, drainage basins, geomorphic variables, or variance shared in the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions in eastern Oklahoma

Factor	Number of variables	$\sum$ canonical eigenvalues	% of variance	Mean % per variable
Geomorphology	6	0.232	44.4	7.4
Ecoregions	1	0.134	25.6	25.6
Basins	1	0.028	5.4	5.4
Geomorph $\cap$ Ecoregions	7	0.014	2.7	0.4
Geomorph $\cap$ Basins	7	0.004	0.8	0.1
Ecoregions $\cap$ Basins	2	0.039	7.5	3.7
Geomorph $\cap$ Ecoregions $\cap$ Basins	8	0.072	13.8	1.7
Sum		0.523		

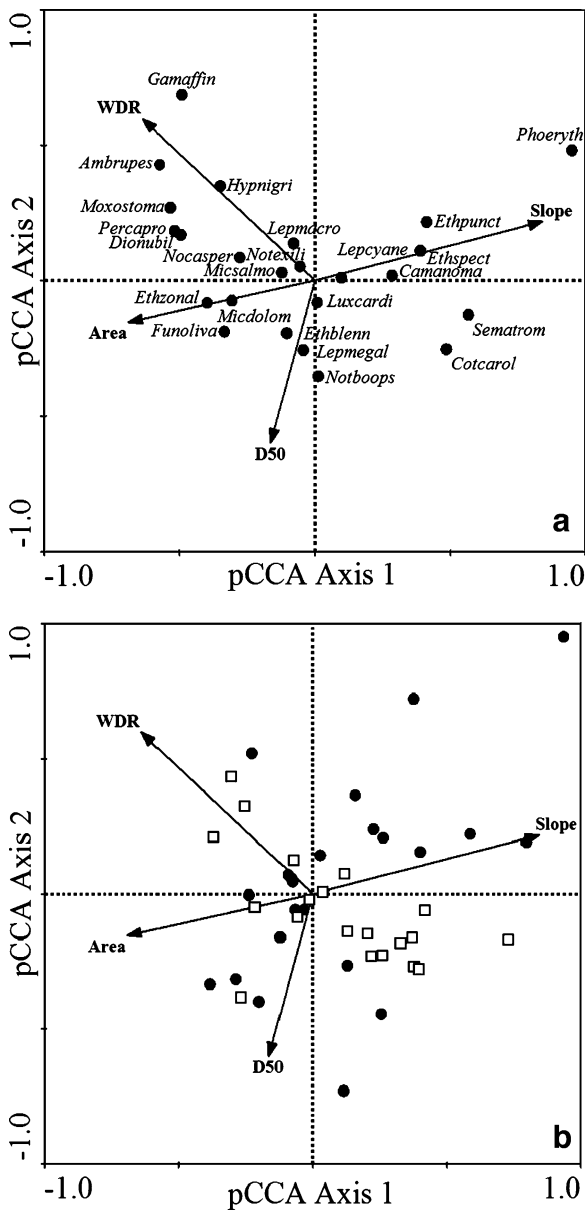
2004) and may be why some ecoregion boundaries have recently been redefined in the region (Woods et al. 2005). These boundary effects have been noted in Mid-Atlantic Highlands streams that cross ecoregion boundaries (McCormick et al. 2000), and may make it difficult to assess stream and fish assemblage patterns in smaller level IV ecoregions. The sporadic occurrence and low detectability of rare species endemic to ecoregions and drainage basins, as well as not sampling the downstream extent of regional rivers where some additional endemics may occur, might have led to a slight underestimate of the importance of both ecoregions and drainage basins in explaining fish species composition.

Some variation in fish species composition in eastern Oklahoma streams was indistinguishable between geomorphology and ecoregions. This shared variation reflected differences in geomorphology (including rates of change with stream size for some variables) among ecoregions (Splinter 2006). Previously reported differences in fish assemblages among ecoregions may have reflected, to some degree, unmeasured differences in local channel morphology among ecoregions (Rohm et al. 1987; Matthews and Robison 1988).

Despite the prevalence of biogeography and large-scale effects, geomorphology collectively explained more variation in fish species composition overall. Placing species into groups may have masked the effects of some geomorphic variables on those species, underestimating the total variance explained. However, important relationships between geomorphology and fish species composition were still revealed. Longitudinal processes related to stream size were most important. These stream size effects were reflected by the presence of southern redbelly

dace, a notable headwater species, in small streams in northeastern Oklahoma. Interestingly, Ouachita Mountains streams showed strong stream size effects on species composition despite the fact that it has no species indicative of small headwater streams. This effect likely resulted from the many species that were only observed in larger streams. These effects of stream size on species composition and richness have been reported previously for these regions (Matthews and Robison 1998; Dauwalter et al. 2003; Dauwalter and Jackson 2004; Tejan 2004).

Reach morphology also influenced fish species composition. Stream slope was important, but differentially so among regions. It was directly but negatively correlated with basin area in northeastern Oklahoma streams. However, it had a weak, negative relationship with basin area in the Ouachita Mountains, suggesting at least some local, reach-scale influence on stream gradient; for example, some reaches of small streams were in the mountains and others were in floodplains of larger regional streams and rivers. Species like the Ouachita Mountain shiner *Lythrurus snelsoni* have been reported to occur in lower gradient reaches of higher elevation streams in the Ouachita Mountains (Taylor and Lienesch 1995). High gradient stream reaches are typically less turbid and have less siltation that is detrimental to many fishes residing in these upland streams (Dauwalter et al. 2003; Dauwalter and Jackson 2004). Substrate size ( $D_{50}$ ) was also important. In northeastern Oklahoma streams it was relatively independent of basin area, and reflected spatial variability in sediment dynamics within the stream-size continuum. Ouachita Mountains streams typically had larger substrates. Substrate size showed a weak, positive correlation with basin area in southeastern streams. Variability in substrate

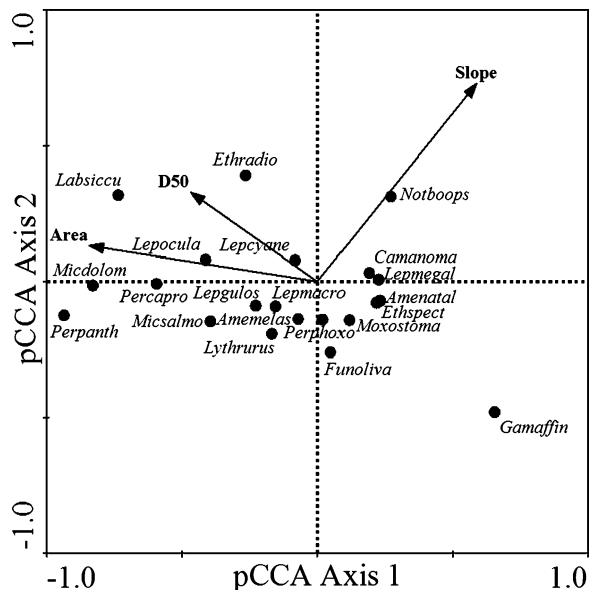


**Fig. 3** pCCA biplots of fish species (a) and basin area, reach slope, channel width:depth ratio, and median particle size ( $D_{50}$ ) summarizing differences in fish species composition along stream size and local geomorphic gradients in Boston Mountains (filled circles) and Ozark Highlands (open squares) streams. Species having weights greater than 5% are displayed. Species codes represent genus for species groupings, or the first three letters of genus and first five of species

size was much higher in Ouachita Mountains streams and explained the presence of species that typically are found in large streams that have larger substrates, such as the leopard darter *Percina pantherina*. Width:

depth ratio only explained fish species composition in northeastern streams where it was somewhat positively correlated with stream size. Larger width:depth ratios typically indicate more alluvial, less stable stream channels (Rosgen 1994). Apparently these local stream conditions were favorable to some fishes. For example, channel instability may ensure that at least some local woody debris recruitment occurs and creates habitat for species that associate with woody cover (e.g., rock bass).

Surprisingly, variables typically considered instream habitat explained little or no variation in fish species composition in eastern Oklahoma streams. Large woody debris was selected during stepwise procedures in analysis of all streams only, but was not strongly related to primary ordination axes that explained fish species composition. Its effect also was not evident in separate analyses of regional streams. Stream habitat has long been considered a dominant factor in structuring fish communities (Gorman and Karr 1978), and the lack of explanatory power of habitat variables likely reflected our use of presence–absence data instead of abundance. Our analyses suggested that certain large- and reach-scale factors determine species presence



**Fig. 4** pCCA biplot of fish species and basin area, median particle size ( $D_{50}$ ), and reach slope summarizing differences in fish species composition along stream size and local geomorphic gradients in Ouachita Mountains streams. Species having weights greater than 5% are displayed. Species codes represent genus for species groupings, or the first three letters of genus and first five of species

within the region. However, other studies from these regions have suggested that stream habitat (Bart 1989; Taylor 2000; Peterson and Rabeni 2001; Wilkinson and Edds 2001) and biotic interactions (Harvey 1991; Taylor 1996) are important in structuring fish assemblages. When considered together, these studies suggest that species within the regional species pools have traits that allow them to pass through nested hierarchical habitat filters at the basin and reach scales (*sensu* Poff 1997). These filters determine fish assemblage composition at the reach scale, and their abundances (that we did not measure) are then primarily affected by local habitat and interactions with other biota.

Both stream size and local channel morphology affected fish species composition and suggest that both the River Continuum Concept and Process Domains Concept apply to eastern Oklahoma streams. Beyond the effects of biogeography and endemism related to both drainage basins and ecoregions, stream size explained an important component of variation in fish species composition in all analyses. This suggests that concomitant changes in the stream environment with stream size, and related to the River Continuum Concept (Vannote et al. 1980), were the primary factors in structuring fish species composition within regions. Channel morphology and substrate size within reaches were conditions that influenced the presence of fish species at the reach scale. These local-scale effects were sometimes independent of stream size, and suggest that spatial variability in geomorphic processes exists within the longitudinal continuum of these streams and were of secondary importance. This spatial variability is the focal point of the Process Domains Concept (Montgomery 1999). However, it is unknown whether these local effects on species composition independent of stream size were related to changes in valley morphology, underlying geology, bedrock outcroppings, or tributaries (Montgomery 1999; Poole 2002; Benda et al. 2004).

The spatial and temporal distribution of natural or anthropogenic disturbances within channel networks can impart specific impacts on local geomorphic processes. This can lead to habitat patches that disrupt the longitudinal processes of rivers. Floods, fires, and debris flows are spatially and temporally explicit natural disturbances that affect local geomorphic processes, especially at tributary junctions (Benda et al. 2004). We did not document specific anthropogenic disturbances that might have resulted in

changes in channel morphology or substrates, but land use changes alter the hydrology and sediment regimes that can change channel form and sediment inputs (Marston et al. 2003; Walters et al. 2003a). Pastureland dominates the landscape in northeastern Oklahoma (Balkenbush and Fisher 2001; Fisher et al. 2004), but a legacy of previous logging activity may still be impacting geomorphic processes in certain watersheds (Rabeni and Jacobson 1993; Harding et al. 1998). Silviculture activity has and continues to dominate the landscape in the Ouachita Mountains in southeastern Oklahoma (Rutherford et al. 1992; Balkenbush and Fisher 2001). Gravel mining and removal of riparian vegetation, which occurs in the Ozark Highlands and Boston Mountains ecoregions, can cause local bank instability and result in wider, less sinuous channels having higher slopes (Rosgen 1994). Such changes in channel morphology adversely affect stream habitat and sensitive fish species (Brown et al. 1998). Understanding variability in hydrology, geomorphology, and disturbance history (e.g., landslides, floods, land use) is important in understanding processes affecting fish habitat (Montgomery and Bolton 2003), and this is why geomorphic evaluations are at the forefront of stream restoration practices and need to be considered in fish conservation efforts (Rosgen 1996; Chessman et al. 2006).

Fish species composition in eastern Oklahoma streams reflected known regional biogeography and varied longitudinally and with local channel morphology. Consequently, historical and large-scale factors dictate the regional species pool, but geomorphic processes determine which of those fish species are found locally within a stream reach. Accordingly, changes in geomorphic processes should lead to predictable changes in stream habitat and the presence of selected fish species. Application of watershed or local restoration principles that restore geomorphic processes and channel morphology should produce specific responses from the fish community if individual species are available for recolonization. However, quantifying exactly how each species will respond to geomorphic change remains unknown, and should be the focus of future research in streams of eastern Oklahoma and similar regions.

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**Appendix 1**

Fish species by Boston Mountains (BM), Ouachita Mountains (OM), and Ozark Highlands (OH) eco-regions and Arkansas (AR) and Red (RR) River basins observed during snorkeling surveys of eastern Oklahoma streams. Nomenclature adopted from Miller and Robison (2004).

Family/Species	Common name	Ecoregion			Basin	
		BM	OM	OH	AR	RR
<b>Petromyzontidae</b>						
<i>Ichthyomyzon</i> spp.	lampreys		x	x	x	x
<b>Lepisosteidae</b>						
<i>Lepisosteus oculatus</i>	spotted gar	x	x	x	x	x
<i>Lepisosteus osseus</i>	longnose gar		x	x	x	x
<b>Clupeidae</b>						
<i>Dorosoma cepedianum</i>	gizzard shad		x	x	x	x
<b>Cyprinidae</b>						
<i>Campostoma anomalum</i>	central stoneroller	x	x	x	x	x
<i>Cyprinella lutrensis</i>	red shiner		x		x	
<i>Cyprinella whipplei</i>	steelcolor shiner	x	x	x	x	x
<i>Cyprinus carpio</i>	common carp		x	x	x	x
<i>Dionda nubila</i>	Ozark minnow	x		x	x	
<i>Luxilus cardinalis</i>	cardinal shiner	x		x	x	
<i>Lythrurus</i> spp.	lythrurus shiners		x		x	x
<i>Nocomis asper</i>	redspot chub	x		x	x	
<i>Notropis boops</i>	bigeye shiner	x	x	x	x	x
<i>Phoxinus phoxinus</i>	southern redbelly dace	x		x	x	
<i>Pimephales</i>	bluntnose	x		x	x	x

Family/Species	Common name	Ecoregion			Basin	
		BM	OM	OH	AR	RR
<i>notatus</i>	minnow					
<i>Semotilus atromaculatus</i>	creek chub	x		x	x	
<b>Catostomidae</b>						
<i>Catostomus commersoni</i>	white sucker	x	x	x	x	x
<i>Ictiobus</i> spp.	buffalos			x	x	
<i>Hypentelium nigricans</i>	northern hogsucker	x		x	x	
<i>Minytrema melanops</i>	spotted sucker			x	x	
<i>Moxostoma</i> spp.	redhorses	x	x	x	x	x
<b>Ictaluridae</b>						
<i>Ameiurus melas</i>	black bullhead	x	x		x	x
<i>Ameiurus natalis</i>	yellow bullhead	x	x	x	x	x
<i>Ictalurus punctatus</i>	channel catfish			x	x	x
<i>Noturus exilis</i>	slender madtom	x	x	x	x	
<i>Noturus nocturnus</i>	freckled madtom		x			x
<i>Pygodictis olivaris</i>	flathead catfish			x		x
<b>Esocidae</b>						
<i>Esox americanus</i>	redfin pickerel			x		x
<b>Salmonidae</b>						
<i>Oncorhynchus mykiss</i>	rainbow trout			x	x	
<b>Aphredoderidae</b>						
<i>Aphredoderus sayanus</i> <sup>1</sup>	pirate perch			x		x
<b>Fundulidae</b>						
<i>Fundulus catenatus</i>	northern studfish			x	x	
<i>Fundulus olivaceus</i>	blackspotted topminnow	x	x	x	x	x
<b>Poeciliidae</b>						
<i>Gambusia affinis</i>	western mosquitofish	x	x	x	x	x
<b>Atherinopsidae</b>						
<i>Labidesthes sicculus</i>	brook silverside	x	x		x	x
<b>Cottidae</b>						
<i>Cottus carolinae</i>	banded sculpin	x		x	x	
<b>Centrarchidae</b>						
<i>Ambloplites rupestris</i>	rock bass	x		x	x	
<i>Lepomis cyanellus</i>	green sunfish	x	x	x	x	x
<i>Lepomis gulosus</i>	warmouth			x	x	x
<i>Lepomis humilis</i>	orangespotted sunfish			x		x

Family/Species	Common name	Ecoregion			Basin	
		BM	OM	OH	AR	RR
<i>Lepomis macrochirus</i>	bluegill	x	x	x	x	x
<i>Lepomis megalotis</i>	longear sunfish	x	x	x	x	x
<i>Lepomis microlophus</i>	redecor sunfish	x	x	x	x	x
<i>Micropterus dolomieu</i>	smallmouth bass	x	x	x	x	x
<i>Micropterus salmoides</i> <sup>2</sup>	largemouth bass	x	x	x	x	x
<i>Pomoxis annularis</i>	white crappie	x	x	x	x	x
<i>Pomoxis nigromaculatus</i>	black crappie			x	x	
Percidae						
<i>Etheostoma blennioides</i>	greenside darter	x	x	x	x	x
<i>Etheostoma flabellare</i>	fantail darter	x	x		x	
<i>Etheostoma punctulatum</i>	stippled darter	x		x	x	
<i>Etheostoma radiosum</i>	orangebelly darter		x			x
<i>Etheostoma spectabile</i>	orangethroat darter	x	x	x	x	x
<i>Etheostoma whipplei</i>	redfin darter		x		x	
<i>Etheostoma zonale</i>	banded darter	x		x	x	
<i>Percina caprodes</i>	logperch	x	x	x	x	x
<i>Percina copelandi</i>	channel darter		x			x
<i>Percina maculata</i>	blackside darter		x		x	x
<i>Percina pantherina</i>	leopard darter		x			x
<i>Percina phoxocephala</i>	slenderhead darter		x		x	x
Sciaenidae						
<i>Aplodinotus grunniens</i>	freshwater drum			x	x	

<sup>1</sup> Only collected in stream sites that were electrofished.

<sup>2</sup> Included spotted bass *Micropterus punctulatus*.

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