UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

BETA DIVERSITY OF STREAM FISH COMMUNITIES:

PARTITIONING VARIATION BETWEEN ABIOTIC AND SPATIAL FACTORS

A THESIS

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

Degree of

MASTER OF SCIENCE

By

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Norman, Oklahoma
2016

BETA DIVERSITY OF STREAM FISH COMMUNITIES:
PARTITIONING VARIATION BETWEEN ABIOTIC AND SPATIAL FACTORS

A THESIS APPROVED FOR THE
DEPARTMENT OF BIOLOGY

BY

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Abstract

Variation in species composition of assemblages within a region is known as beta diversity. Beta diversity contributes to regional diversity (gamma), and understanding the factors that maintain it and explain variation of it are necessary for conserving biodiversity. I examined beta diversity among stream fish communities in southeastern Oklahoma to test the hypothesis that beta diversity was driven by abiotic factors and therefore was under environmental control. I used variation partitioning via redundancy analysis to analyze the proportions of beta diversity explained by abiotic and spatial factors. I also computed total species turnover and its components of spatial turnover and nestedness, for the region and within groups. I then related turnover distance matrices to environmental and spatial distances via a Mantel approach. Environmental factors accounted for 28% of the overall beta diversity, and abiotic factors and spatial factors alone accounted for 25% and 3% respectively. Abiotic factors related to beta diversity were stream size, habitat, water quality, and position within the drainage. Overall species turnover was mostly due to spatial turnover, and much less to nestedness. Variation in overall species turnover and spatial turnover were both significantly related to variation in environment and physical distance, while nestedness was not.

Preface

This thesis has been prepared for submission to *Ecography*, and is formatted accordingly.

Introduction

To conserve biodiversity, protect individual species, and understand how ecosystems function, knowledge of the processes that govern the organization of communities across space and time is critical (Tuomisto et al. 2003; Legendre et al. 2005; Leprieur et al. 2009). Stream ecologists have a long history of explaining patterns of fish community structure in light of extrinsic factors like stream gradients, spatial scale, chemical properties, and anthropogenic impacts (Forbes 1907; Coker 1925; Thompson and Hunt 1930). By the 1970's, students of fish community ecology began to apply multivariate techniques to quantify communities and test ecological theories (Smith and Powell 1971; Smith and Fisher 1970; Matthews and Robison 1988), with emphasis on understanding why communities consist of a particular set of species (Blair 1959; MacArthur 1961).

A deterministic concept developed by Smith and Powell (1971), and further adapted and reviewed by others (Tonn 1990; Matthews 1998; Jackson et al. 2001; Ross 2013), illustrates the determination of fish community composition in space and time by extrinsic constraints. The largest possible scale includes all of the global fish fauna. This potential faunal pool passes through a series of "screens" or "filters" that operate at continuously decreasing scales and increasingly relate to the extrinsic factors of a given location (Smith and Powell 1971; Tonn 1990). The factors that constrain community composition fall into three categories: abiotic, biotic, or spatial (Jackson et al. 2001). Abiotic factors include the physical and chemical environment of a location; biotic factors relate to ecological processes such as predation, competition, and mutualism;

spatial factors relate to historical events and dispersal, which depend on the scale or scope of a study region, and create variation in the relative importance of abiotic and biotic factors (Jackson et al. 2001). For any community, these factors operate across a range of scales, and work collectively and interactively to determine local species composition (Whittaker 1956; Bray and Curtis 1957; Tuomisto et al. 1995)

Beta diversity, the variation of community composition within a region (Whittaker 1960; Whittaker 1972), is central to community ecology (Anderson et al. 2011). Alpha diversity (α) is the mean species diversity across individual communities; beta diversity (β) is the differentiation among communities; gamma diversity (γ) is the total species diversity within a region, a function of alpha and beta diversity (Whittaker 1960; Whittaker 1972). For a review of the many measures and ways of conceptualizing beta diversity see Tuomisto (2010a,b). Here I do not address "true beta diversity", (*sensu* Tuomisto 2010a) but rather community turnover and variation (Tuomisto 2010b; Anderson et al. 2011; Legendre et al. 2005), as well as compositional nestedness and non-nestedness (Simpson 1943; Lennon et al. 2013; Baselga 2010; Tuomisto 2010b).

Analyzing how beta diversity is influenced by abiotic, biotic, and spatial factors illuminates processes that structure communities over space and time, and ultimately maintain regional diversity. Beta diversity can be related to extrinsic factors by partitioning the variation between separate data sets that is related to these factors (Level II abstraction *sensu* Legendre et al. 2005; Legendre 2008). Beta diversity, in terms of overall compositional turnover, can be quantified for an entire region, or for groups within a region, to make comparisons (Baselga 2010). Overall species turnover can be partitioned into components of spatial turnover (β_{SIM} *sensu* Baselga 2010), which is conceptually associated with species replacement, and site nestedness (β_{NES} sensu Baselga 2010), associated with species addition. These two components of overall turnover are opposing factors which represent compositional distinctness (β_{SIM}) and the degree to which a site species pool is determined by, or nested within, neighboring species pools (β_{NES}). Compositional species turnover, and components, for all pair-wise site combinations also can be used to construct a distance matrix which may be related to spatial and environmental distance matrices (Level III abstraction *sensu* Legendre et al. 2005).

Spatial scale creates a trade-off between resolution (i.e., density of sampling units) and overall gradient variation (Jackson et al. 2001). The relative spatial scale of this study, which was conducted across one river basin in southern Oklahoma, USA, is intermediate compared to smaller scale studies (e.g. Smith & Powell 1971; Schlosser 1982; Grossman and Freeman 1987) and larger scale studies (Edds 1993; Marsh-Matthews & Matthews 2000; Oberdorff et al. 2001). Studies at smaller scales typically find less environmental variation, which results in a focus on micro-habitat and biotic interactions, while studies at larger scales are impacted by broad environmental gradients and are heavily influenced by spatial structuring of variation due to wider influence of historical factors and dispersal limitation (Cottenie 2005).

The purpose of the present study was to examine fish beta diversity across an intermediate scale, and to determine the importance of abiotic and spatial factors in shaping the variation of community composition. I hypothesized that fish communities in the study drainage were structured non-randomly, and that structure was determined by environmental factors. I addressed the following questions: 1) what proportion of beta diversity can be explained by spatial and abiotic factors respectively? 2) What are the most important abiotic factors? And 3) How much of the species turnover across the drainage is due to spatial turnover and how much was due to compositional nestedness?

Material and Methods

Study area

The Muddy Boggy River in southeastern Oklahoma, USA, is a major tributary to the Red River (Figure 1.) The basin is 113 km in length north to south and a maximum of 48 km wide. The basin drains 6,291 km^2, with a total of 248 river mainstem km (Pigg 1977). Rugged hills surround the basin and give way to gently rolling plains in the lower region. There are four distinct physiographic provinces: the Arbuckle Mountains to the west, the Ouachita Mountains to the northeast, the Arkoma basin in the north, and the dissected coastal plain in the south (Pigg 1977). The Muddy Boggy River is formed by the junction of Clear Boggy Creek and Muddy Boggy Creek (8-digit hydrologic unit code: 1140104 & 1140103 respectively).

Land surrounding the sampled stream reaches was typically either forested woodland (Oak, Post-oak, and Hickory), more common in the eastern side of the drainage, or pasture ranchland, more common in the western side. This rural region has little urban development, but there are many natural resource operations such as logging, coal mining, or oil and natural gas drilling. The streams are turbid, and vary from high gradient, cobble filled reaches in the headwaters to low gradient, muddy creeks or mainstems, often with much coarse woody debris, downstream. Shorelines were commonly covered in water willow (*Justicia americana*) and spike rushes (*Elocharis sp.*), while floating and submerged vegetation was observed, but less frequently.

Data collection

Two data sets representing fish community composition and environmental characteristics, separately, were generated. Between May and September 2014, fish community collections were made in 65 wadeable stream reaches throughout the Muddy Boggy River drainage (Figure 1). Locations were chosen to maximize spatial coverage and environmental gradients. These sites represent reaches spanning from the headwater streams and tributaries to the lower mainstem of Clear Boggy Creek and Muddy Boggy Creek. Fishes were collected by seining all habitats within approximately 100 m of stream reach using one or two sizes of net, depending on the width of the stream (4.57 m × 1.22 m × 4.88 mm mesh and/or 2.44 m × 1.22 m × 4.88 mm mesh). Channel and pool habitat were sampled by pulling seines downstream; riffle and edge habitat were sampled by kick-seining. Fish collecting techniques used here are described in detail by Matthews (1985). Specimens were preserved immediately in 10% formalin, identified subsequently in the laboratory.

At every sampling location I measured 30 environmental factors and logged the geographic coordinates. Measured factors included physical characteristics of the stream reach, composition of the stream reach, composition of the substrate, habitat and stream structure characters, water quality measures, and riparian characteristics (Table 1 and Appendix II). Water quality characteristics were measured using a Horiba Water Quality Monitor, model U-5000. Location coordinates were determined using a Garmin GPSmap, 60CSx. Elevation was measured using the United States Geological Survey's National Elevation Database. Stream order was assessed using the Horton-Strahler system of stream classification (Horton 1945; Strahler 1957; Kuehne 1962). The remaining factors were recorded, either as presence or absence (e.g., macrophytes) or estimated by walking through the entire reach and recording observations (e.g., percent stream composition & substrate composition) following the U.S. Forest Service and Wisconsin Department of Natural Resources guidelines for estimating stream habitat (Simonson 1993; Simonson 1994; Wang et al. 1996; Marsh-Matthews and Matthews 2000). More information regarding the measured environmental variables can be found in Appendix II.

Statistical analyses

All data analyses were performed using R 3.2.2. (R Core Team 2015) with package 'vegan' (Oksanen et al. 2016; Oksanen 2015), package 'usdm' (Naimi 2015), or package 'betapart' (Baselga et al. 2013). To reduce the environmental data set into the most meaningful set of factors, the Morisita-Horn similarity index on species abundance data (Morisita 1959; Horn 1966; Wolda 1981; Jost et al. 2011) and non-metric multidimensional scaling (NMDS; Legendre & Legendre 1998) were used to ordinate fish communities in three dimensions. 'Stress 1' with monotone regression was used to minimize stress of NMDS and assess the reliability (Kruskal 1964). Environmental variables were standardized using z-score scaling (ter Braak 1987), and fitted onto the fish community ordination using the function 'envfit'. Significance of the squared correlation coefficients (R^2) between environmental factors and NMDS axes was tested using the built in permutation procedure, with 999 permutations (Oksanen et al. 2016; Oksanen 2015). Only factors with at least one significant relationship to one of the NMDS axes were retained in further analyses. To eliminate factors with high collinearity, variance inflation factors (VIF) were calculated, and any factors with a VIF >10 were removed from the analysis (Naimi 2015; Dorman et al. 2012).

Principal Coordinates of Neighborhood Matrix (PCNM; Borcard & Legendre 2002) was used to transform a simple table of geographic coordinates into a new set of PCNM variables related to spatial structure. Relationships between PCNMs and Hellinger-transformed (Legendre and Gallagher 2001) fish community data were assessed using redundancy analysis, and significant levels were determined via permutation with 999 permutations (RDA; Rao 1964; Legendre & Legendre 1998; Oksanen 2015). Significant PCNMs were retained for use as spatial covariables for variation partitioning with redundancy analysis (RDA; Legendre & Legendre 1998; Legendre 2008). Variation partitioning was carried out to determine the proportions of beta diversity explained by environmental variables and spatial covariables (Legendre et al. 2005) (Figure 4). I again used the Hellinger transformed fish community matrix, and partitioned the variation using function ‘varpart’ in concordance with RDA and partial RDAs. Significance of the fractions of variation explained was tested using a permutation procedure with 999 permutations (Legendre 2008). From this analysis I was also able to determine which abiotic factors were significantly related to beta diversity by testing for the significance of each abiotic “term” used in a partial RDA in which spatial factors were removed, using 999 permutations.

To assess overall compositional turnover throughout the drainage, and to derive components of spatial turnover and nestedness, I used package ‘betapart’ (Baselga 2010; Baselga et al. 2013). Using species presence-absence data, I calculated total turnover (β_{SOR}) and its two components: spatial turnover (β_{SIM}) and nestedness (β_{NES}) for the entire drainage, for Clear Boggy Creek and Muddy Boggy Creek drainages separately, and for mainstem sites of Clear Boggy Creek and Muddy Boggy Creek separately using the function ‘beta.multi’(Baselga 2010; Baselga et al. 2013). For comparing groups with different sample sizes, ‘beta.sample’ was used to randomly generate 100 sub-samples of equal size for the two groups (Baselga 2010). Finally, I analyzed the relationships between variation in compositional turnover and ecological and spatial distances using compositional turnover distance matrices, via function ‘beta.pair’, and environmental and spatial distance matrices, using a Mantel approach (Legendre et al. 2005). Environmental distances were calculated using Euclidean distance based on retained abiotic factors, and spatial distance matrices were generated using Euclidean distance based on latitude and longitude.

Results

Fish community sampling across 65 sites in the Muddy Boggy drainage yielded 59 species and 2 hybrids belonging to 13 families, all of which were native to the drainage (Table 2). Species richness ranged from 3 to 22 species per site, and mean richness was 11.3 species per site. The most diverse families were Cyprinidae, Centrarchidae, and Percidae with 20, 11, and 9 species respectively. The families Sciaenidae, Atherinopsidae, Poeciliidae, Aphredoderidae, Fundulidae, Esocidae, and Clupeidae were represented by only 1 species each (Table 2). The four most widespread fish families throughout the drainage, determined by the proportion of sites in which they occurred, were: Centrarchidae (100%), Cyprinidae (95%), Poeciliidae (83%), and Percidae (72%) (Table 3). These four families also contributed heavily to typical fish community composition, with the average proportion of individuals in a given community being 56% Cyprinidae, 18% Centrarchidae, 15% Poeciliidae, and 6 % Percidae (Table 3).

The most widespread, generalist species throughout the drainage, that occurred at half or more of all locations, included *Gambusia affinis* (85% of sites), *Lepomis megalotis* (83%), *Lepomis macrochirus* (70%), *Etheostoma radiosum* (55%), *Lythrurus umbratilis* (55%), *Cyprinella lutrensis* (50%), and *Micropterus salmoides* (45%). Hybrids, along with 17 other species occurred in 3 or fewer samples (marked with * in Table 2), and were not included in subsequent analysis (Sály et al. 2011). In addition, two *Lepisosteus* species were considered as one in the analysis because most individuals were young-of-year and too small to identify to species. The two *Campostoma* species were also considered as one species in the analysis because they are allopatric species with non-overlapping distributions in the drainage. I assumed these species are functionally equivalent, and did not want this spatial artifact to influence the analysis. This will underestimate the spatial component of variation of beta diversity.

Fish communities were ordinated in 3-dimensional non-metric multidimensional space, which resulted in an acceptable stress1 (i.e. reliability) equal to 0.164 (Kruskal 1964). The abiotic environmental data set was reduced from 30 total factors to 21 meaningful variables by fitting environmental vectors onto dimensions of the NMDS (Figure 2) and retaining only factors with at least one significant relationship to fish community ordination (Table 4). I examined variance inflation factors of the remaining variables for issues of collinearity and found only the spatial variables had VIFs > 7.0 and only one had a VIF > 10.0 (longitude = 11.7). Longitude and latitude were removed from the overall data set to create a separate spatial data set composed of only these coordinates, which reduced all VIFs < 5.0 .

Principal coordinates of neighborhood matrix (PCNM), was computed using the spatial data and a determined threshold of 30, and produced 44 principal coordinate axes related to spatial structure of the sites. Only two of these axes (PCNM3, $F=2.045$ $p = 0.041$; & PCNM13, $F = 2.122$ $p = 0.037$) were significantly related to fish community composition, and retained as two variables of spatial structure. Variation partitioning determined that the spatial (PCNMs) and abiotic factors combined explained 28% (Adj.$R^2 = 0.284$, $p = 0.001$) of the variation in community composition.

The measured abiotic factors alone explained 24% of the variation (Adj. R^2 = 0.244, p = 0.001), the spatial factors alone accounted for 3% of the variation (Adj. R^2 = 0.031, p = 0.02), and the interaction between spatial and abiotic explained approximately 1% of the variation (Adj. R^2 = 0.009)(Table 5). Ten abiotic factors were significant: 1) elevation; 2) drainage ; 3) stream order (only first, second, and third order were significant); 4) maximum width ; 5) maximum depth ; 6) percent riffle ; 7) dissolved oxygen; 8) turbidity; 9) current speed (only medium current was significant), and 10) percent gravel (all p-values < 0.05, Figure 5).

Overall species turnover (β_{SOR}) was due more to spatial turnover (β_{SIM}) than to nestedness (β_{NES}). Over the entire drainage beta coefficients were β_{SOR} = 0.95; β_{SIM} = 0.93; β_{NES} = 0.02, suggesting that spatial turnover alone is responsible for approximately 98% of overall turnover in species composition. This pattern was similar even when dividing the drainage between Clear Boggy drainage (β_{SOR} = 0.91; β_{SIM} = 0.87; β_{NES} = 0.04) or Muddy Boggy drainage (B_{SOR} = 0.90; β_{SIM} = 0.86; β_{NES} = 0.04) though nestedness increases from about 2% across the entire drainage to about 5% viewed in that manner. When analyses were limited to Clear and Muddy Boggy mainstems (7 sites sampled from each) there was a difference in the proportions in Clear Boggy (β_{SOR} = 0.68 ; β_{SIM} = 0.64 ; β_{NES} = 0.04) and Muddy Boggy (β_{SOR} = 0.68 ; β_{SIM} = 0.57 ; β_{NES} = 0.11). Species turnover in the Clear Boggy main channel was similar to that over the rest of the drainage (~95% spatial turnover & 5% nestedness) while the Muddy Boggy main channel has more nestedness (84% spatial turnover & 16% nestedness).

Finally, overall species turnover (β_{sor}) and spatial turnover (β_{sim}) were both related to the multivariate environmental distance between sites as well as spatial distance, while the nestedness component (β_{nes}) was not. A Mantel test showed β_{sor} between sites was significantly related to the multivariate environmental distance between sites ($r = 0.303$, $p = 0.0001$), as was β_{sim} ($r = 0.290$, $p = 0.0001$). β_{nes} was not significantly related to environmental distance ($r = {}^{-}0.080$, $p = 0.911$). Similarly, β_{sor} between sites was significantly related to the physical spatial distance between sites ($r = 0.330$, $p = 0.0001$), as was β_{sim} ($r = 0.331$, $p = 0.0001$), while β_{nes} between sites was not ($r = {}^{-}0.110$, $p = 0.990$). Multivariate environmental distance and physical distance were significantly related, $R^2 = 0.163$, $p < 0.00001$ (Figure 6).

Discussion

The results of this study supported the environmental control hypothesis for fish community organization, as measured environmental variation explained almost 30% of variation in stream fish beta diversity, and abiotic factors alone explained much more variation than spatial factors alone. The major abiotic influences of beta diversity were related to stream size, habitat, water quality, and position within the drainage. In addition, overall species turnover was maintained mostly by spatial turnover, and only minimally by nestedness. Finally, variation in overall species turnover and spatial turnover were both significantly related to variation in environment and physical distance, which was not surprising given that difference in environment significantly increased with increasing physical distance between sites.

Abiotic factors better explained fish beta diversity than spatial factors, as corroborated by other studies of stream fish assemblages at similar scales (Sály et al. 2011; Godinho et al. 2000; Magalhaes et al. 2002). In all three of these studies, abiotic factors explained more variation in fish community composition than spatial factors, the amount of variation explained by abiotic factors ranged from 18 to 36%, and similar abiotic factors were found to be most meaningful including: elevation, stream order, depth, and width. Despite differences in fish collecting techniques and differences in some of the abiotic factors measured, similar patterns emerged in these three European studies. Unexplained variation was high in my study, and that is typical for studies of this kind as well. Unexplained variation is likely due to biotic interactions, dispersal, and unmeasured abiotic factors (Legendre 2008).

The abiotic factors associated most strongly with fish beta diversity in this study were comparable to those found by Matthews and Robison (1988). Results of that study came from 2323 collections over a 20 year period across the state of Arkansas, USA. Those authors found 10 environmental variables that associated strongly with variation in fish community composition, which was quantified using detrended correspondence analysis. Seven of the factors corroborated by our study included: elevation, longitude, latitude, turbidity, substrate, width, and geology. The other 3 factors they found to be important were mean January temperature, mean July temperature, and frost-free days. Those factors were not measured here because I did not expect substantial spatial variation in temperature given the size of the Muddy Boggy drainage.

Overall species turnover was influenced most by spatial turnover rather than nestedness. This indicated high diversity sites were not the major driver of diversity throughout the drainage, but rather it was the variation in species between sites and the compositional distinctness of individual communities throughout the drainage that enhanced gamma diversity. This compositional distinctness was created by changes in environment over distance which drove species turnover. The environment and habitat within this drainage can be highly variable. As the distance between sites increased so to did the difference in their overall environmental qualities, however, sometimes even nearby sites can vary substantially much in overall environmental conditions (Figure 5).

Studies addressing beta diversity and compositional turnover across different spatial and temporal scales are the key to understanding how alpha, or mean species diversity, is related to gamma, or regional diversity. It is necessary to understand the importance of scale, and its effects on the outcome of such studies. Identifying factors associated with beta diversity will allow managers to develop plans aimed at both maintaining local diversity, and enhancing regional diversity. The high degree of spatial turnover compared to nestedness within this drainage means that sites are often compositionally distinct in terms of the local fish species. This means that conservation efforts cannot focus solely on protecting habitats with the highest diversity, but must consider the drainage as a whole. Future studies should address this pattern across other drainages and over a range of scales.

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Appendix I

Table 1. Thirty environmental factors measured at each of the 65 locations where fish communities were collected. See Appendix II for specific details.

Environmental Factors	
Physical reach characteristics	Water Quality
Elevation	Water temperature
Maximum stream width	Dissolved oxygen (DO)
Maximum stream depth	pH
Stream order	Conductivity
Creek or mainstem	Turbidity
Adventitious or not	
Current speed	
Drainage	Substrate Composition
	Percent mud
Stream composition	Percent sand
Percent pool	Percent gravel
Percent riffle	Percent cobble
Percent channel	Percent bedrock
Percent backwater	
Riparian Characteristics	Habitat and Stream Structure
Bank incision	Attached algae
Percent canopy cover	Macrophytes
Riparian pasture	Large boulders
Riparian woodland	Coarse woody debris (CWD)

Table 2. Fish families and species found across the study drainage. Species noted with an asterisk were not included in analyses because they occurred in fewer than 5% or 3 of the total sites.

Fish species by family		
Lepisosteidae	**Catostomidae**	**Centrarchidae**
Lepisosteus oculatus	*Carpiodes carpio* *	*Lepomis cyanellus*
Lepisosteus osseus	*Ictiobus bubalus* *	*Lepomis gulosus*
	Minytrema melanops	*Lepomis humilis*
Clupeidae	*Moxostoma duquesnei* *	*Lepomis macrochirus*
Dorosoma cepedianum *	*Moxostoma erythrurum*	*Lepomis megalotis*
		Lepomis microlophus
Cyprinidae	**Ictaluridae**	*Lepomis* hybrids *
Campostoma anomalum	*Ameiurus melas*	*Micropterus punctulatus*
Campostoma spadiceum	*Ameiurus natalis* *	*Micropterus salmoides*
Chrosomus erythrogaster *	*Ictalurus punctatus*	*Pomoxis annularis*
Cyprinella lutrensis	*Noturus gyrinus*	*Pomoxis nigromaculatus* *
Cyprinella venusta	*Noturus nocturnus*	
Cyprinella whipplei	*Pylodictis olivaris* *	
Hybopsis amnis *		**Percidae**
Luxilus chrysocephalus *	**Esocidae**	*Etheostoma chlorosomum*
Lythrurus umbratilis	*Esox americanus* *	*Etheostoma fusiforme* *
Notemigonus crysoleucas		*Etheostoma gracile*
Notropis atrocaudalis		*Etheostoma parvipinne* *
Notropis boops	**Fundulidae**	*Etheostoma radiosum*
Notropis buchanani	*Fundulus notatus*	*Etheostoma spectabile*
Notropis stramineus		*Percina copelandi* *
Notropis suttkusi	**Aphredoderidae**	*Percina phoxocephala*
Notropis volucellus *	*Aphredoderus sayanus* *	*Percina sciera*
Phenacobius mirabilis		
Pimephales notatus	**Poeciliidae**	**Sciaenidae**
Pimephales promelas	*Gambusia affinis*	*Aplodinotus grunniens* *
Pimephales vigilax		
C. venusta X C. lutrensis *	**Atherinopsidae**	
	Labidesthes sicculus	

Table 3. The thirteen fish families found across the darinage. The two left hand columns represent the proportion of total individuals belonging to that family in the average community (mean) and also the highest proportion of individuals belonging to that family in any community (maximum). The right hand columns represent each family's distribution across the drainge with the number of sites in which the family occurred, the proportion of sites in which the family occurred, and the number of sites in which the family was the most numerically dominant family.

	community composition		occurrence across drainage		
Family	**Mean**	**Maximum**	**Occurred**	**Percent**	**Times Most Numerous**
Centrarchidae	17.92%	78.57%	65	100.0%	8
Cyprinidae	56.32%	97.03%	62	95.4%	46
Poeciliidae	15.22%	85.71%	54	83.1%	9
Percidae	5.54%	38.86%	47	72.3%	1
Ictaluridae	1.22%	14.29%	25	38.5%	0
Atherinopsidae	2.13%	22.38%	24	36.9%	1
Catostomidae	0.88%	22.33%	15	23.1%	0
Lepisosteidae	0.14%	2.98%	7	10.8%	0
Fundulidae	0.27%	8.11%	7	10.8%	0
Aphredoderidae	0.17%	8.00%	3	4.6%	0
Clupeidae	0.07%	4.17%	2	3.1%	0
Esocidae	0.13%	7.14%	2	3.1%	0
Sciaenidae	0.00%	0.21%	1	1.5%	0

Table 4. Results of the environmental fit analysis are shown below. Environmental vectors were fitted on each of the 3 two-dimensional plots from the non-metric multidimensional scaling ordination. Factors are ordered by the number of significant relationships with NMDS axes. Factors without a significant relationship were not retained in further analysis (factors 24 – 30).

	Factor	**NMDS 1&2**	**NMDS 1&3**	**NMDS 2&3**
1	Elevation	0.001	0.029	0.017
2	Maximum width	0.004	0.004	0.003
3	Percent canopy	0.007	0.002	0.027
4	Drainage	N.S.	0.024	0.004
5	Stream order	0.001	0.001	N.S.
6	Creek or mainstem	0.001	0.001	N.S.
7	Maximum depth	N.S.	0.006	0.001
8	Percent riffle	0.008	N.S.	0.001
9	Percent backwater	0.014	N.S.	0.032
10	Dissolved oxygen (DO)	0.012	N.S.	0.010
11	pH	N.S.	0.013	0.037
12	Conductivity	0.015	N.S.	0.017
13	Current speed	0.002	0.002	N.S.
14	Percent gravel	0.001	N.S.	0.001
15	Macrophytes	N.S.	0.001	0.003
16	Bank incision	0.001	0.001	N.S.
17	Percent pool	N.S.	N.S.	0.029
18	Turbidity	0.014	N.S.	N.S.
19	Percent cobble	N.S.	0.019	N.S.
20	Percent bedrock	0.022	N.S.	N.S.
21	Boulders	N.S.	0.021	N.S.
22	Percent channel	N.S.	N.S.	N.S.
23	Water temperature	N.S.	N.S.	N.S.
24	Adventitious	N.S.	N.S.	N.S.
25	Percent mud	N.S.	N.S.	N.S.
26	Percent sand	N.S.	N.S.	N.S.
27	Algae	N.S.	N.S.	N.S.
28	Coarse woody debris (CWD)	N.S.	N.S.	N.S.
29	Pasture	N.S.	N.S.	N.S.
30	Woodland	N.S.	N.S.	N.S.

Table 5. Results of the variation partitioning analysis reveals the amount of variance in the community composition data table **Y** explained by abiotic **X** and spatial **W** explanatory factors.

Partitions	D.f.	R squared	Adj. R squared	p - value
[a + b] = X	26	0.557	0.253	0.001
[b + c] = W	2	0.071	0.041	0.002
[a + b + c] = X + W	28	0.597	0.284	0.001
Individual Fractions				
[a] = X | W	26		0.244	0.001
[b]	0		0.009	NA
[c] = W | X	2		0.031	0.02
[d] = Residuals			0.716	NA

Figure 1.

The Muddy Boggy River drainage. The 65 sampling locations are marked as open circles and labeled by site number. Note that the sites are not consecutively numbered, e.g., the 65th site is labeled 100. This is because the site labels represent collection numbers and some collections were made in other drainages following the 48th collection in this drainage, but they resume with 83rd overall collection. For orientation, some of the larger towns are marked as black circles, and reservoirs are outlined in black.

Figure 2.

Fish communities at 65 sampling locations ordinated with non-metric multidimensional scaling based on Morisita-Horn similarity index. Stress1 = 0.164.

Figure 3.

This illustrates the environmental fitting analysis, in which environmental vectors were related to the 3 axes of the NMDS that represent fish community variation, or beta diversity. This figure shows only axis 1 and 2 of the NMDS, but the relationships with axis 3 were considered also.

Figure 4.

Adapted from Legendre et al. 2005, this figure shows how the total amount of variation in the fish community data table **Y** is partitioned between the abiotic facors **X** and the spatial data **W**. The smaller fractions of the variation are [a] = pure abiotic; [b] = interaction between abiotic and spatial; [c] = pure spatial; [d] = unexplained variation.

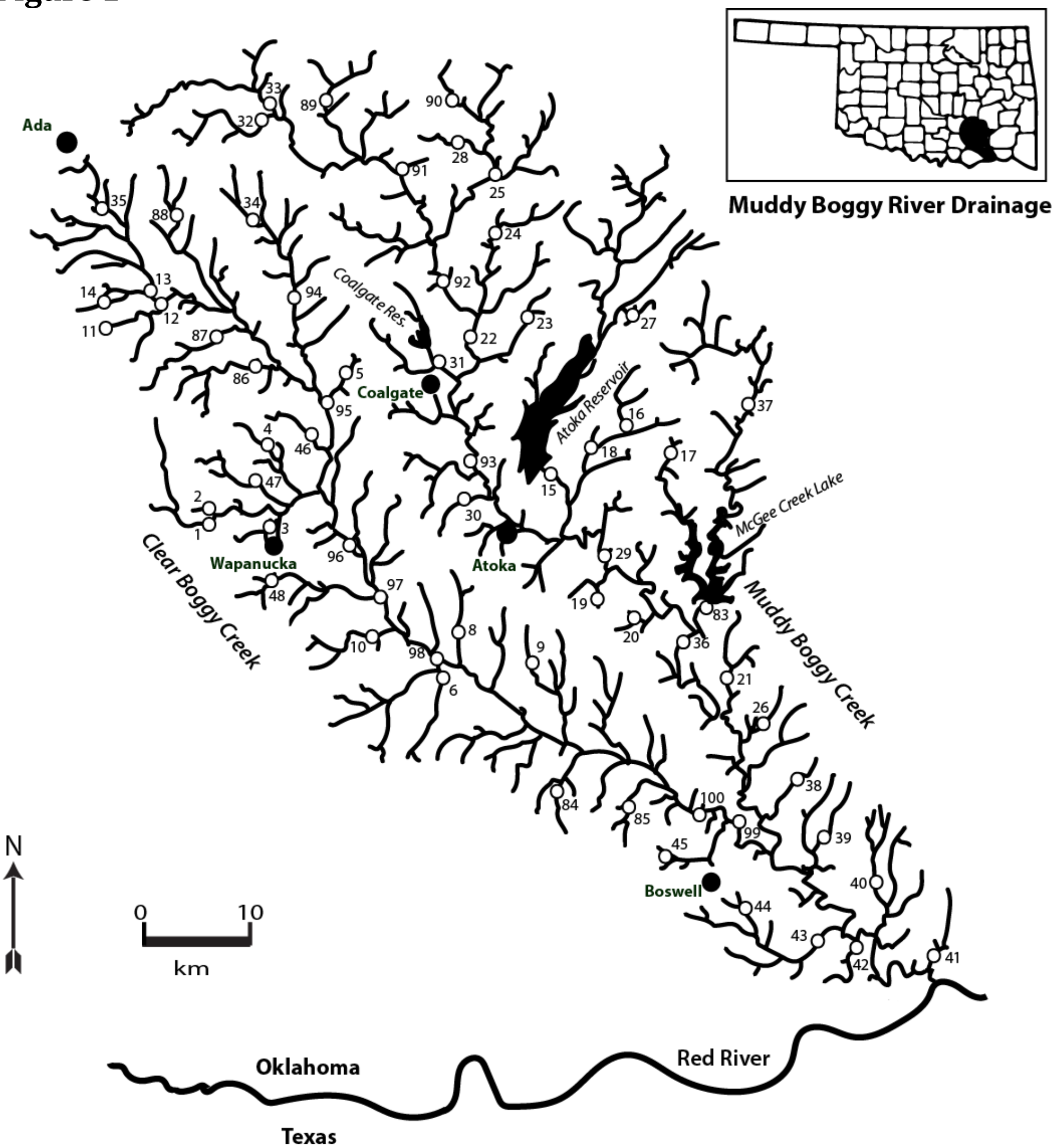
Figure 5.

The final RDA biplot from the variation partitioning step of the analysis. This figure illustrates the abiotic factors that were significantly related to variation in fish community structure.

Figure 6.

This figure illustrates the relationship between multivariate environmental distance (i.e., a Euclidean distance matrix based on all abiotic factors) and spatial distance (i.e., a Euclidean distance matrix based on latitude and longitude).

Figure 1



Muddy Boggy River Drainage
Ada
Coalgate
Coalgate Res.
Atoka Reservoir
Atoka
Wapanucka
McGee Creek Lake
Clear Boggy Creek
Muddy Boggy Creek
Boswell
N
0
10
km
Oklahoma
Texas
Red River

Figure 2

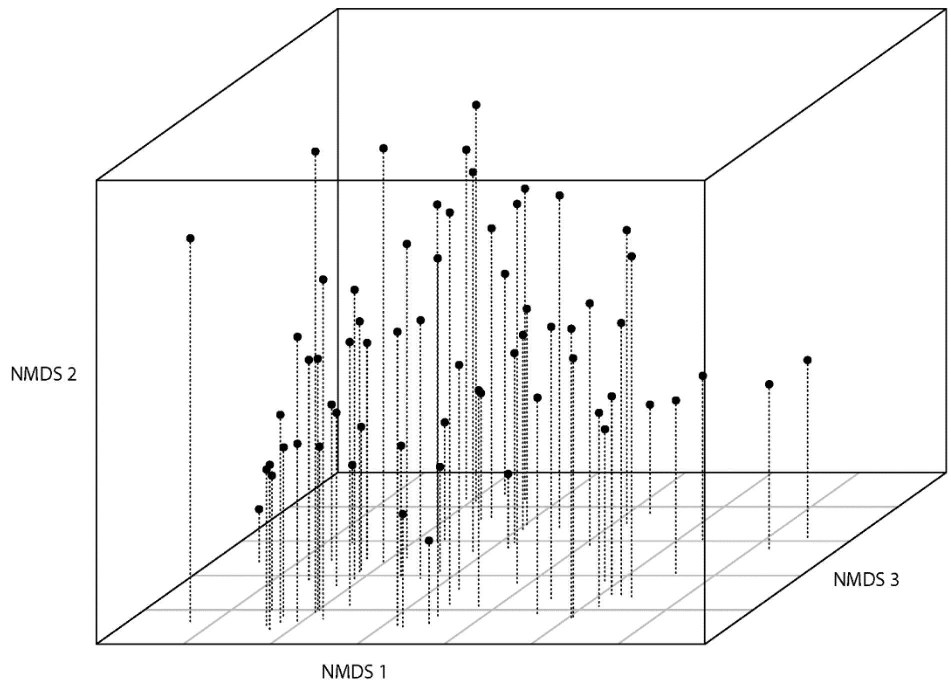


Figure 3

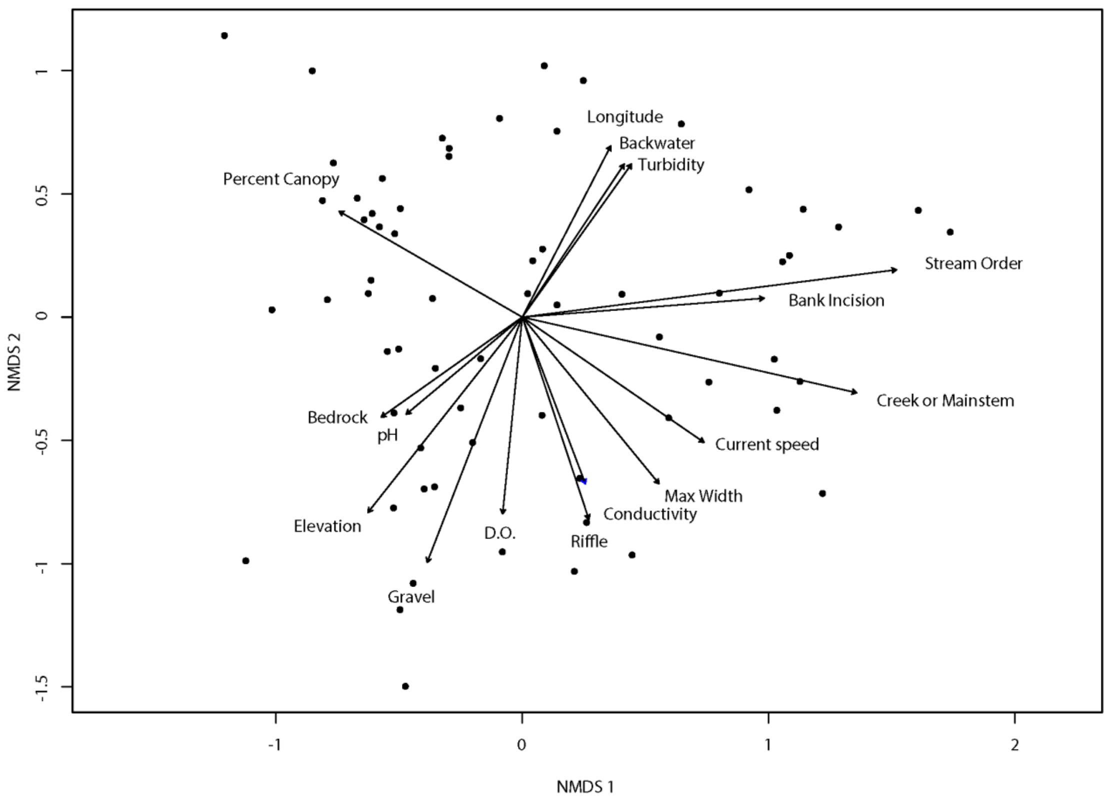
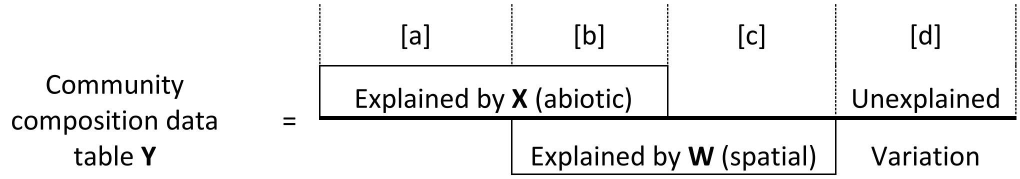
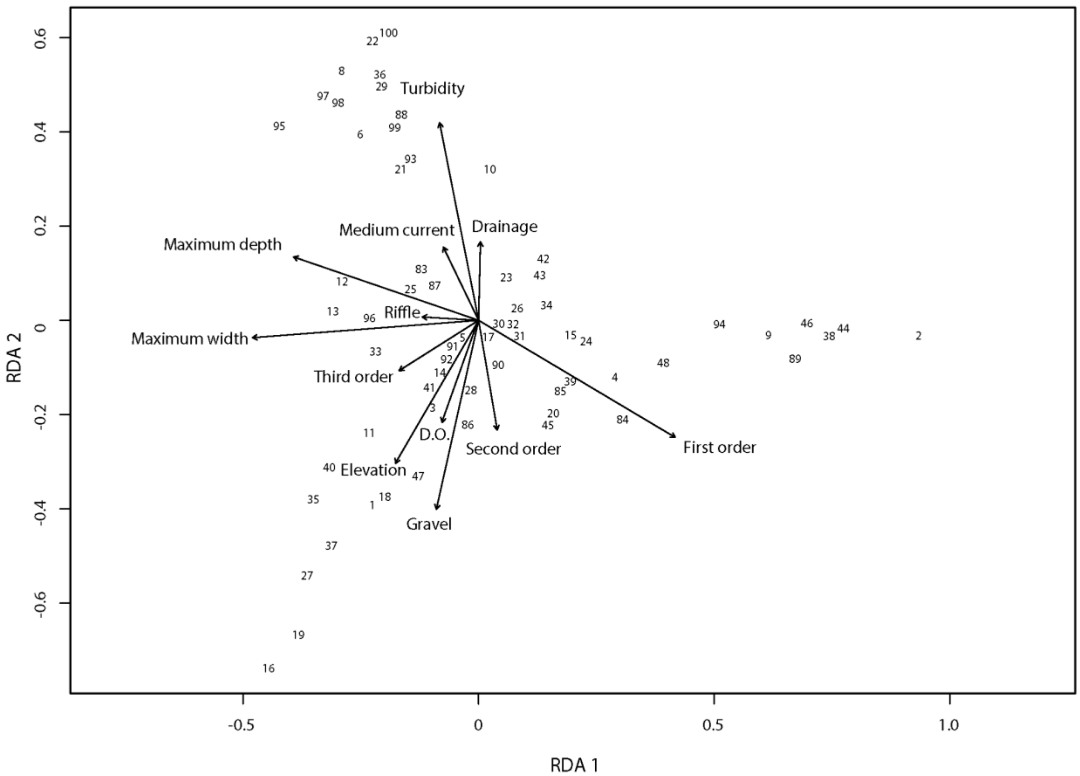

Longitude
Backwater
Turbidity
Percent Canopy
Stream Order
Bank Incision
Creek or Mainstem
Bedrock
pH
Current speed
Max Width
Conductivity
Elevation
D.O.
Riffle
Gravel
NMDS 2
NMDS 1
1
0.5
0
-0.5
-1
-1.5
-1
0
1
2

Figure 4



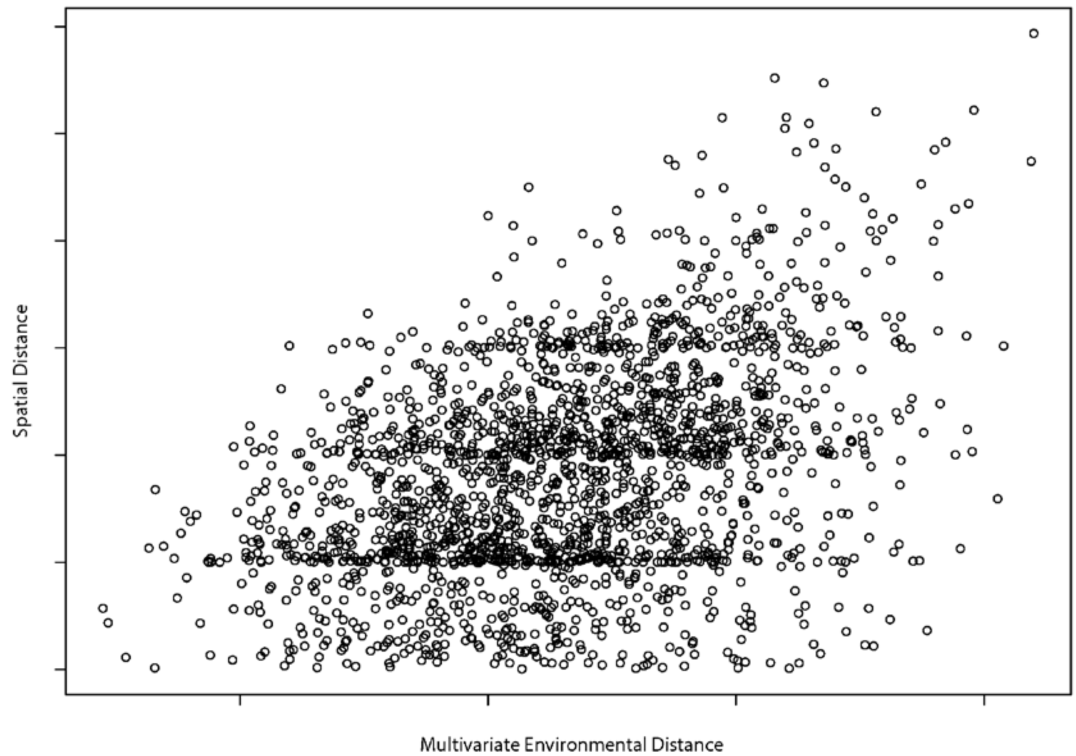
[a]
[b]
[c]
[d]
Community composition data table Y
=
Explained by X (abiotic)
Unexplained
Explained by W (spatial)
Variation

Figure 5



Turbidity
Drainage
Medium current
Maximum depth
Riffle
Maximum width
Third order
D.O.
Elevation
Gravel
Second order
First order
RDA 1
RDA 2

Figure 6



Appendix II

Quantitative Variables

<u>Physical Reach Characteristics</u>

Latitude	coordinates indicating position North or South
Longitude	coordinates indicating position East or West
Elevation	meters above sea level
Maximum Reach Width	maximum width of the sampled stream reach
Maximum Reach Depth	maximum depth of the sampled stream reach

<u>Stream Composition</u>

Percent Pool	proportion of pool habitat in the stream reach
Percent Riffle	proportion of riffle habitat in the stream reach
Percent Channel	proportion of channel habitat in the stream reach
Percent Backwater	proportion of backwater habitat in the stream reach

<u>Water Quality</u>

Water Temperature	surface water temperature in degrees Celsius
Dissolved Oxygen	dissolved oxygen below the surface of the water (mg/mL)
pH	pH of the water (0 to 14 pH scale)
Conductivity	conductivity of the water (micro S/cm)
Turbidity	amount of dissolved solids affecting water clarity (NTUs)

<u>Substrate Composition</u>

Percent Mud	proportion of stream bed substrate composed of mud
Percent Sand	proportion of stream bed substrate composed of sand
Percent Gravel	proportion of stream bed substrate composed of gravel
Percent Cobble	proportion of stream bed substrate composed of cobble
Percent Bedrock	proportion of stream bed substrate composed of bedrock

<u>Riparian Characteristics</u>

Bank Incision	height in meters of bank erosion
Percent Canopy	proportion of sampled stream shaded by tree canopy

Categorical Variables

Physical Reach Characteristics

Stream Order	score (1 to 5) based on stream size and position in drainage network
Current Speed	categorized as none, low, medium, fast
Drainage	either Clear Boggy or Muddy Boggy Creek
Creek or Main stem	designates whether a site was on a tributary creek or on a main stem section of Clear Boggy or Muddy Boggy Creek
Adventitious stream	Streams draining directly into streams 3 times the size in terms of stream order.

Habitat and Stream Structure

Attached Algae	presence or absence of filamentous algae
Macrophytes	presence or absence of aquatic vegetation
Large Boulders	presence of large rocks and/or boulders
Coarse Woody Debris (CWD)	presence or absence of woody structure in the stream bed

Riparian Characteristics

Riparian Pasture	presence or absence of pasture land along the stream bank
Riparian Woodland	presence or absence of woodland along the stream bank