

Beta diversity of stream fish assemblages: partitioning variation between spatial and environmental factors

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Abstract

1. Studies that analyse the structure of assemblages across relevant spatial scales can ascertain generalisable patterns and be used to guide efforts that allocate resources meant to conserve regional biodiversity. Beta diversity can shed light on the underlying factors that drive variation in assemblage structure including spatial and environmental influences. The purpose of this study was to address two questions: (1) Which is more important for the structuring of fish assemblages, spatial or environmental factors? (2) What is the dominant pattern underlying species turnover between fish assemblages, species addition (i.e. nestedness) or species replacement (i.e. spatial turnover)?
2. We examined fish beta diversity in southeastern Oklahoma by sampling 65 wadeable stream reaches and measuring 30 environmental factors at each sampling location across the Muddy Boggy River drainage. Variation in fish assemblage structure was partitioned between environmental and spatial predictors using partial redundancy analysis. Overall species turnover was calculated and separated into its two additive components of spatial turnover and nestedness to determine which of these two accounted for the most turnover across the drainage.
3. Spatial and environmental factors combined accounted for 25.5% of fish beta diversity. Environmental factors alone accounted for 20.1%, while spatial factors alone only accounted for 3.5% of the variation among assemblages.
4. Nine environmental factors were significantly related to fish beta diversity: (1) elevation; (2) stream order; (3) stream width; (4) % riffle habitat; (5) water temperature; (6) conductivity; (7) turbidity; (8) % gravel substrate and (9) current velocity.
5. Overall species turnover was driven mostly by spatial turnover rather than nestedness. This pattern was found to be the same across multiple spatial scales (entire drainage, sub-drainages, mainstems) and despite several techniques used to extract turnover coefficients.
6. These results suggest that fish assemblages—particularly in headwater streams—are structured by environmental filtering and that these assemblages tend to be compositionally distinct, rather than being nested derivatives of one another.

KEYWORDS

environmental filtering, headwater streams, nestedness, River Continuum Concept, spatial turnover

1 | INTRODUCTION

Knowledge of the processes that govern the organisation of communities across space and time is key for conserving regional biodiversity (Legendre, Borcard, & Peres-Neto, 2005; Leprieur, Olden, Lek, & Brosse, 2009; Tuomisto, Ruokolainen, & Yi-Halla, 2003). Beta diversity is the variation in local community composition within a region, i.e. differences in assemblage composition among sites, and provides a direct link between local mean richness (alpha) and regional (gamma) diversity (Whittaker, 1960, 1972). The relationship among mean local diversity, variation among local diversities and overall regional diversity is central to community ecology and conservation biology (Anderson et al., 2011; Socolar, Gilroy, Kunin, & Edwards, 2016). For a review of many measures and ways beta diversity has been used, see Tuomisto (2010a, 2010b).

Stream ecologists have proposed explanations for patterns in fish assemblage composition since at least the early 20th century (Coker, 1925; Forbes, 1907; Thompson & Hunt, 1930). A general conceptual framework for describing the structure of local fish assemblages was developed later (Smith & Powell, 1971; Tonn, 1990). This framework focused on a set of “filters” or “screens” that represent extrinsic factors at different spatial scales that are responsible for determining local fish assemblage composition. These factors fall into one of three categories: abiotic, biotic or spatial (Jackson, Peres-Neto, & Olden, 2001). Since that time, much support has developed for abiotic filters related to physical and chemical gradients, productivity and habitat size and heterogeneity (Jackson et al., 2001; Peres-Neto, 2004; Poff, 1997; Poff & Allan, 1995); biotic filters such as competition and predation (Jackson, Somers, & Harvey, 1992; Power, Matthews, & Stewart, 1985; Reserits, 1997) and spatial filters such as neutral dynamics, limitations to dispersal and spatially structured environmental characteristics (Hanski, 1999; Muneeppeerakul et al., 2008; Schlosser, 1987; Sharma, Legendre, Caceres, & Boisclair, 2011). Current work in this area is not so much concerned with what factors act on assemblage composition, but which are the most important and generalisable to most systems (Carvalho & Tejerina-Garro, 2015; Grossman, Ratjczak, Crawford, & Freeman, 1998; Jackson et al., 2001; Mouchet, Villegier, Mason, & Mouillot, 2010).

The River Continuum Concept (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980) is a general framework for describing how biological systems in catchments can be predicted based on physical and geomorphological gradients that span from headwater streams to river mouth. Headwater streams (orders 1–3) differ from medium- and large-sized rivers (order > 3) in terms of primary sources of energy input (i.e. higher terrestrial input in headwater streams versus higher autochthonous primary production in higher-order streams) (Vannote et al., 1980). And many other environmental factors are also associated with stream gradient including: habitat size, current velocity, habitat heterogeneity and temporal variability (Matthews, 1998; Schlosser, 1987 and references therein). These associations allow several predictions to be made about the assemblages of headwater streams and downstream reaches. First, downstream reaches will have higher species richness due to higher habitat heterogeneity,

volume and temporal stability (Jackson et al., 2001; Matthews, 1998; Schlosser, 1987). Second, environmental filtering should be especially prevalent in headwater streams where environmental variation is the highest (Carvalho & Tejerina-Garro, 2015; Grenouillet, Pont, & Hérissé, 2004; Ostrand & Wilde, 2002). And third, turnover in species composition between sites will be largely due to spatial turnover and not nestedness when environmental filtering is the underlying mechanism structuring assemblages (Qian, Ricklefs, & White 2005; Baselga, 2010).

Differences between any two species assemblages (i.e. species turnover) can result from two very different processes. These two processes (spatial turnover and nestedness) work in different ways, but both result in overall differences in species composition between assemblages (Baselga, 2010). For example, assemblages are “nested” when the less species-rich assemblage is simply a subset of the more speciose assemblage, and this indicates an “orderly disaggregation of assemblages” potentially caused by differential extirpation and recolonisation (Baselga, 2010; Taylor & Warren, 2001). For example, such a mechanism might manifest itself as assemblages in tributary streams being simply less speciose subsets of the neighbouring assemblages in the mainstem of a river. Spatial turnover, however, is a result of species replacement among assemblages, a possible consequence of environmental filtering (Baselga, 2010; Qian, Ricklefs, & White, 2005). In this case, the tributary assemblages from the previous example would contain species not found in the neighbouring assemblages downstream. Rather than the terms “nestedness” and “spatial turnover”, much of the fish ecology literature instead uses “addition” (Jenkins & Freeman, 1972; Morin & Naiman, 1990; Sheldon, 1968) and “replacement” (Gard & Flitner, 1974; Horowitz, 1978; Matthews, 1986b) to describe the same processes respectively (Matthews, 1998).

Despite decades of investigations and resultant frameworks for generalising the patterns that structure stream assemblages, there is still contention regarding the contribution of environmental and spatial factors in structuring stream assemblages and the patterns that generally underlie species turnover—namely, species addition or species replacement. Here, we address variation between local assemblages (Anderson et al., 2011; Tuomisto, 2010b) using canonical analysis to determine how species composition is a function of environmental and spatial factors, both together and separately (Legendre, 2008; Legendre et al., 2005). In addition, we disentangle the patterns underlying species turnover using an approach developed by Baselga (2010) which has generally been used for terrestrial systems. We modify the usage of this method in order to make it more applicable to riverine networks. Using this method, one can determine the proportion of overall species turnover due to either spatial turnover or nestedness (Baselga, 2010; Lennon, Koleff, Greenwood, & Gaston, 2001; Simpson, 1943).

The purpose of this study was to address two questions: (1) Which is more important for the structuring of fish assemblages, spatial or environmental factors? (2) Is the prevailing pattern explaining species turnover between fish assemblages species addition (i.e. nestedness) or species replacement (i.e. spatial turnover)?

We examine fish beta diversity across an intermediate scale (one medium-sized river drainage including the river and surrounding tributaries) to determine the influence of environmental and spatial factors and the contribution of spatial turnover and nestedness to overall species turnover. We hypothesised that fish assemblages in the study drainage were structured non-randomly, and that structure was determined by environmental factors. We expected this pattern would be especially pronounced in headwater streams and should result in relatively more species turnover resulting from species replacement, rather than species addition.

2 | METHODS

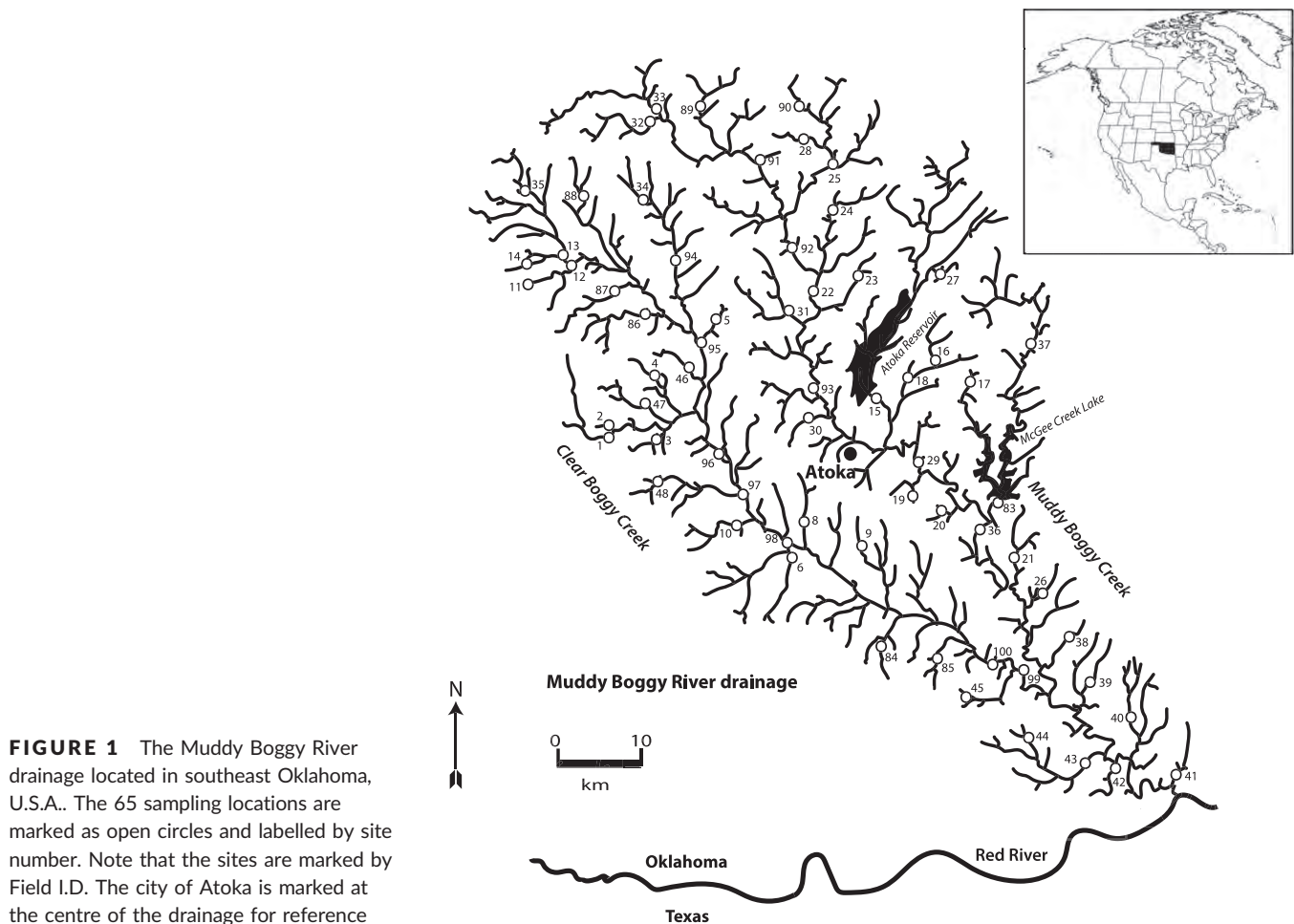
2.1 | Study area

The Muddy Boggy River in southeastern Oklahoma, U.S.A., is a major tributary to the Red River (Figure 1). The basin is 113-km-long north to south and a maximum of 48 km wide, draining 6,291 km². The main channel of the Muddy Boggy runs a total of 248 fluvial kilometers (Pigg, 1977). The Muddy Boggy River is formed by the junction of Clear Boggy Creek and Muddy Boggy Creek, which divide the mid and upper portions of the river into two distinct sub-drainages (8-digit hydrologic unit code: 1140104 & 1140103 respectively). Land surrounding the sampled stream reaches was typically

forested woodland, more common in the eastern side of the drainage, or pasture–ranchland, more common in the western side. The streams were turbid, and varied from high gradient, cobble filled reaches in the headwaters to low gradient, muddy tributaries or mainstems, often with much large woody debris, downstream. Shorelines or shallows were commonly covered in water willow (*Jussiaea americana*) and spike rushes (*Elocharis* sp.). Floating and submerged vegetation was observed, but less frequently.

2.2 | Data collection

Between May and September 2014, we made fish collections in 65 wadeable stream reaches throughout the Muddy Boggy River drainage (Figure 1). These sites represent reaches from headwater streams and tributaries to the lower mainstem of Clear Boggy Creek and Muddy Boggy Creek. Collections spanned from relatively wet to relatively dry seasons, but all collections were made at times when streams were wadeable and effort was not impaired by high water conditions. Collecting effort was standardised by seining all discernable habitats within 100 m of stream reach for 1 hr and using one or two lengths 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 (1986a). Specimens were preserved immediately in 10% formalin and identified to species subsequently in the laboratory. Specimens are archived in the Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma.

At every sampling location we measured 30 environmental factors and logged the geographic coordinates. 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). Water quality characteristics were measured using a Horiba Water Quality Monitor, model U-5000 (Alvin, Texas, U.S.A.). Geographic coordinates were determined using a Garmin GPSmap, 60CSx (Olathe, Kansas, U.S.A.). 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). 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. per cent stream composition and

TABLE 1 Descriptive statistics of environmental factors measured at each sampling location

Environmental variables	Median	Min.	Max.	Mean	St. Dev.
Elevation (m)	185.10	131.80	280.70	185.07	29.46
Stream width (m)	7.00	3.00	20.00	7.78	3.20
Maximum depth (cm)	120.00	30.00	220.00	122.29	51.57
% Pool habitat	20.00	0.00	100.00	27.54	21.03
% Riffle habitat	20.00	0.00	60.00	21.38	17.71
% Channel habitat	50.00	0.00	100.00	44.45	25.89
% Backwater habitat	10.00	0.00	30.00	6.63	6.55
Water temperature (°C)	23.98	16.70	30.16	23.74	3.36
Dissolved oxygen (mg/L)	9.07	3.20	13.10	8.84	2.37
pH	7.30	5.64	7.81	7.13	0.51
Conductivity (µS/cm)	0.25	0.06	0.57	0.25	0.11
Turbidity (NTU)	49.50	4.00	294.00	73.40	66.86
% Mud substrate	40.00	0.00	90.00	36.62	25.66
% Sand substrate	10.00	0.00	90.00	21.54	24.57
% Gravel substrate	10.00	0.00	80.00	17.85	19.98
% Cobble substrate	15.00	0.00	100.00	21.38	21.77
% Bedrock substrate	0.00	0.00	30.00	2.62	6.74
% Canopy Cover	60.00	10.00	90.00	50.08	25.02
Bank incision (m)	3.00	0.00	8.00	3.05	1.60
	First order	Second order	Third order	Fourth order	Fifth order
Stream order	13	29	11	10	2
	(0 cm/s)	(1–15 cm/s)	(16–30 cm/s)	(>30 cm/s)	
Current velocity	6	28	23	8	
	Clear Boggy	Muddy Boggy			
Drainage	31	34			
	Yes	No			
Adventitious stream	13	52			
Mainstem (river)	15	50			
Tributary (creek)	50	15			
	Absent	Present			
Riparian pasture	28	37			
Riparian woodland	19	46			
Attached algae	46	19			
In-stream macrophytes	23	42			
Boulders	41	24			
Coarse woody debris	12	53			

substrate composition) following the U.S. Forest Service and Wisconsin Department of Natural Resources guidelines for estimating stream habitat (Marsh-Matthews & Matthews, 2000; Simonson, 1993; Simonson, Lyons, & Kanehl, 1994; Wang, Simonson, & Lyons, 1996). Measurements of stream width and depth were taken at the widest and deepest section, respectively. Per cent habitat was estimated by walking along the stream reach after sampling and recording the types and relative proportions of habitats present (e.g. pool, riffle, channel, backwater). The same procedure was repeated for per cent substrate.

2.3 | Variation partitioning

All data analyses were performed using R 3.2.2. (R Development Core Team, 2015) with package “vegan” (Oksanen, 2015; Oksanen et al., 2016), package “usdm” (Naimi, 2015) or package “betapart” (Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2013), and ArcGIS 10.2. (Esri, Houston, Texas, U.S.A.). Four total datasets were used—two representing fish assemblages as either species abundance or species presence/absence, one representing environmental factors at each sampling location, and one representing geographic position as latitude and longitude and fluvial distance between sites.

We reduced the 30 factor environmental dataset via environmental fitting prior to variation partitioning. Only factors with a significant correlation with assemblage ordination were retained for subsequent analysis. The Morisita-Horn similarity index on species abundance data (Morisita, 1959; Horn 1966; Wolda, 1981; Jost, Chao, & Chazdon, 2011) and non-metric multidimensional scaling (NMDS; Legendre & Legendre, 1998) were first used to ordinate fish assemblages in three dimensions. The “stress1” with monotone regression was used to minimise stress of NMDS and assess the reliability of the ordination (Kruskal, 1964). The 30 environmental factors were standardised using z-score scaling (Ter Braak, 1987), and fitted onto the ordination using the function “envfit”. Significance of the squared correlation coefficients (R^2) between environmental vectors and NMDS axes (assemblage structure) was tested using the built-in permutation procedure, with 9,999 randomisations (Oksanen, 2015; Oksanen et al., 2016). Only factors with one or more significant relationships to NMDS were retained in further analyses. To eliminate factors with high collinearity, variance inflation factors (VIF) were calculated, and any factor with a $VIF > 5$ was removed from the analysis (Dorman et al., 2012; Naimi, 2015).

The geographic dataset was created by first constructing a matrix of fluvial distance between all pairs of sites using the Network Analysis extension in ArcGIS (Grönroos et al., 2013). This matrix was transformed into a rectangular matrix suitable for canonical analysis using Principal Coordinates of Neighborhood Matrix (PCNM; Borcard & Legendre, 2002). Relationships between principal coordinates and Hellinger-transformed fish assemblage data (Legendre & Gallagher, 2001) were assessed using redundancy analysis, and significant levels were determined via permutation with 9,999 randomisations (RDA; Rao, 1964; Legendre & Legendre, 1998; Oksanen, 2015). Significant principal coordinates were retained for use as spatial covariables for

variation partitioning (RDA; Legendre & Legendre, 1998; Legendre, 2008).

Variation in assemblage structure (beta diversity) explained by the extrinsic datasets was partitioned between the reduced environmental dataset and the spatial principal coordinates dataset using redundancy analysis (Legendre et al., 2005). We again used the Hellinger-transformed fish assembly matrix, and partitioned the variation using function “varpart” (Oksanen et al., 2016). Significance of the fractions of variation explained was tested using a permutation procedure with 9,999 randomisations (Legendre, 2008; Oksanen et al., 2016). In addition to partitioning variation between environmental datasets, we were also able to determine which individual environmental factors were significantly related to beta diversity by testing for the significance of each individual term from RDA using permutation with 9,999 randomisations (Oksanen et al., 2016).

2.4 | Calculating the additive components of turnover

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 two additive components: (1) spatial turnover (β_{sim} *sensu* Baselga, 2010), which is conceptually associated with species replacement; and (2) nestedness (β_{nes} *sensu* Baselga, 2010), akin to species addition. These two components of overall turnover are opposing factors which represent either compositional distinctness (β_{sim}), or the degree to which a site species pool is determined by, or nested within, a neighbouring species pools (β_{nes}). Both spatial turnover and nestedness contribute to overall compositional difference between assemblages ($\beta_{sor} = \beta_{sim} + \beta_{nes}$).

To assess overall species turnover throughout the drainage, we used package “betapart” (Baselga, 2010; Baselga et al., 2013). Using species presence-absence data, we calculated total species turnover (β_{sor}) and its two additive components: spatial turnover (β_{sim}) and nestedness (β_{nes}). Turnover coefficients were calculated separately for three spatial scales starting with the entire drainage ($n = 65$), Clear Boggy Creek ($n = 31$) and Muddy Boggy Creek ($n = 34$) drainages separately, and mainstem sites of Clear Boggy Creek ($n = 8$) and Muddy Boggy Creek ($n = 7$). Three different methods were used to calculate turnover coefficients. The first method “beta.multi” calculates each pairwise beta coefficient between all possible site combinations and finds the mean of each beta coefficient. The second method “beta.sample” takes a random sub-sample of the total number of sites and repeats this process a specified number of times before it finds the mean of all three beta coefficients across iterations. In this case we chose a sub-sample size of $n = 7$ because this was the smallest sample size of our three spatial scales and we repeated this procedure 9,999 times. The sampling procedure of beta.sample allows for comparison of groups that differ in sample size (Baselga, 2010) and is most appropriate for comparing coefficients among the spatial scales in our analysis that differ in the

number of samples. For the third and final method, which we refer to as "beta.pair", we incorporated a modified version of "beta.pair-wise" (Baselga, 2010) that creates a matrix of pairwise beta coefficients. Instead of comparing every single pair of sampling locations, we extracted only the beta coefficients for pairs of nearest neighbouring sites (by fluvial distance) and found the mean for each beta coefficient.

3 | RESULTS

The distance between any two neighbouring sampling locations in the drainage varied from 7.58 to 41.37 fluvial km with a mean equal to 13.93 ± 7.58 km. Descriptive statistics of the 30 environmental factors measured at each sampling location are shown in Table 1. The sampled streams varied from first-order to fifth-order streams (First order = 13; Second order = 29; Third order = 11; Fourth order = 10; Fifth order = 2). Therefore, the majority of sampled streams ($n = 53$) were considered headwater streams (Vannote et al., 1980). Means and variances of standardised environmental variables were grouped between headwater and mainstem streams and compared using *t*-test and Levene's test. Headwater streams differed significantly from mainstem streams with regards to mean environmental measures including: maximum width, maximum depth, pH, turbidity and % cobble substrate (Table 2). In addition, environmental variables between these two groups showed significant differences in the amount of variance in measures that included:

elevation, % sand substrate, % gravel substrate and % bedrock substrate (Table 2).

Fish assemblage sampling across the Muddy Boggy drainage yielded 58 species and 2 hybrids belonging to 13 families, all of which were native to the drainage (Table 3). Of these species, 39 were found in mainstem sampling locations and 5 were unique to these areas, while 55 species were found in headwater sampling locations and 21 species were unique to these locations. Species richness ranged from 3 to 22 species per site. Mean richness was 11.3 species per location across the drainage; 13.83 species for mainstem locations and 10.72 species for headwater locations. The four most widespread fish families throughout the drainage and the proportion of sites in which they occurred were as follows: Centrarchidae (100%), Cyprinidae (95%), Poeciliidae (83%) and Percidae (72%). These four families also contributed heavily to typical fish assemblage composition, with the average proportion of individuals in a given assembly being 56% Cyprinidae, 18% Centrarchidae, 15% Poeciliidae and 6% Percidae. The two *Lepisosteus* species were considered as one in the analyses because most individuals sampled were young-of-year and too small to accurately identify to species.

Fish assemblages were ordinated using NMDS, which resulted in an acceptable stress1 (i.e. reliability) equal to 0.164. Environmental fitting showed 19 of the 30 environmental factors were significantly related to fish assembly ordination. These factors were as follows: elevation; stream order; tributary or mainstem; maximum width; % riffle habitat; water temperature; dissolved oxygen; conductivity; turbidity; current velocity; % sand substrate; % gravel substrate;

TABLE 2 Descriptive statistics of environmental variables grouped by headwater stream and mainstem sampling location. Results comparing the variance (Leven's Test) and means (*t*-test) between headwater and mainstem groups shown in the right hand columns. Marginally significant *p*-values denoted (*). Significant *p*-values ($\alpha = .01$) denoted (**)

	Headwater ($n = 53$)		Mainstem ($n = 12$)		Levene's Test		t-test		
	Mean	SE	Mean	SE	F	p	t	df	p
Elevation (m)	188.78	4.24	168.66	3.97	6.384	.014*	2.200	63	.031
Maximum width (m)	7.23	0.38	10.25	1.09	3.819	.055	-3.157	63	.002**
Maximum depth (cm)	113.94	6.26	159.17	17.90	1.986	.164	-2.897	63	.005**
% Pool	26.51	2.83	32.08	6.67	0.588	.446	-0.827	63	.411
% Riffle	21.13	2.44	22.50	5.24	0.002	.965	-0.240	63	.811
% Channel	46.49	3.48	35.42	7.96	0.016	.899	1.346	63	.183
% Backwater	5.87	0.90	10.00	1.63	3.822	.055	-2.012	63	.048
Water Temp. (°C)	23.32	0.47	25.60	0.64	1.678	.200	-2.196	63	.032
Dissolved Oxygen (mg/L)	8.93	0.33	8.43	0.69	0.140	.709	0.664	63	.509
pH	7.23	0.06	6.68	0.17	3.793	.056	3.669	63	.001**
Conductivity (μ S/cm)	0.24	0.01	0.30	0.03	0.091	.763	-1.740	63	.087
Turbidity (NTU)	59.17	7.37	136.26	24.36	5.278	.025	-4.008	63	<.001**
% Mud	35.00	3.48	43.75	7.81	0.094	.760	-1.068	63	.290
% Sand	23.40	3.61	13.33	3.55	7.308	.009**	1.288	63	.203
% Gravel	20.38	2.90	6.67	1.88	11.397	.001**	2.211	63	.031
% Cobble	18.02	2.85	36.25	6.00	0.051	.821	-2.751	63	.008**
% Bedrock	3.21	1.01	0.00	0.00	12.197	.001**	1.504	63	.138

TABLE 3 Fish species collected in the Muddy Boggy River drainage

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

% cobble substrate; % bedrock substrate; macrophytes; boulders; bank incision; % canopy and pasture riparian zone (all relationships significant at $p < .05$). Variation inflation factors for stream order and tributary/mainstem variables were correlated ($VIF > 5.0$). Therefore, we retained only stream order and removed tributary/mainstem from subsequent analyses. After removing this variable, all VIFs were < 4.0 .

PCNM analysis of the stream distance between sites resulted in 42 principal coordinates of spatial structure. Three of these coordinates (PCNM1, $F = 2.39$, $p = .012$; PCNM9, $F = 1.97$, $p = .031$; and PCNM28, $F = 2.14$, $p = .019$) were significantly related to fish assemblage composition, via redundancy analysis, and retained as spatial covariables. Variation partitioning showed that the spatial (PCNMs) and environmental factors combined explained 25.5% of the variation in fish assemblage composition (Adj. $R^2 = .2554$, $F = 1.844$, $p < .001$). The measured environmental factors alone explained 20.1% of the variation (Adj. $R^2 = .2012$, $F = 1.716$, $p < .001$), the spatial factors alone accounted for 3.5% of the variation (Adj. $R^2 = .0350$, $F = 1.643$, $p = .011$) and the interaction

between spatial and environmental explained approximately 2% of the variation (Adj. $R^2 = .0192$) (Figure 2).

Nine of the environmental factors were significantly related to fish beta diversity including: (1) elevation ($F = 3.134$, $p = .0014$); (2) stream order (first order, $F = 3.614$, $p = .0003$; second order, $F = 3.505$, $p = .0002$; third order $F = 2.948$, $p = .0025$); (3) maximum width ($F = 3.058$, $p = .0021$); (4) % riffle ($F = 2.763$, $p = .0036$); (5) water temperature ($F = 2.520$, $p = .0079$); (6) conductivity ($F = 1.894$, $p = .0397$); (7) turbidity ($F = 2.203$, $p = .0158$); (8) % gravel ($F = 1.831$, $p = .0465$) and (9) current velocity (medium current, $F = 2.050$, $p = .0271$) (Figure 3).

The analysis of species turnover (β_{sor}) showed that spatial turnover (β_{sim}) contributes more to overall turnover than nestedness (β_{nes}) despite the method used (multi, sample or pair) or the scale of the group analysed (entire drainage, sub-drainages and mainstems). Over the entire drainage beta coefficients from nearest neighbour comparisons (beta.pair) were $\beta_{sor} = 0.552$; $\beta_{sim} = 0.445$; $\beta_{nes} = 0.107$, suggesting that spatial turnover alone was responsible for approximately 81% of overall turnover of species composition,

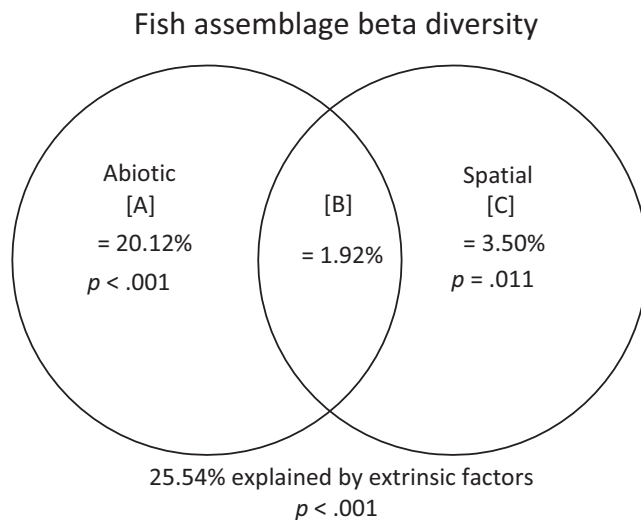


FIGURE 2 This diagram shows the results of the variation partitioning analysis. The rectangular area represents all of the variation in fish assemblage composition, and within that area, the circles represent the portions explained by environmental factors, spatial factors and the interaction between the two

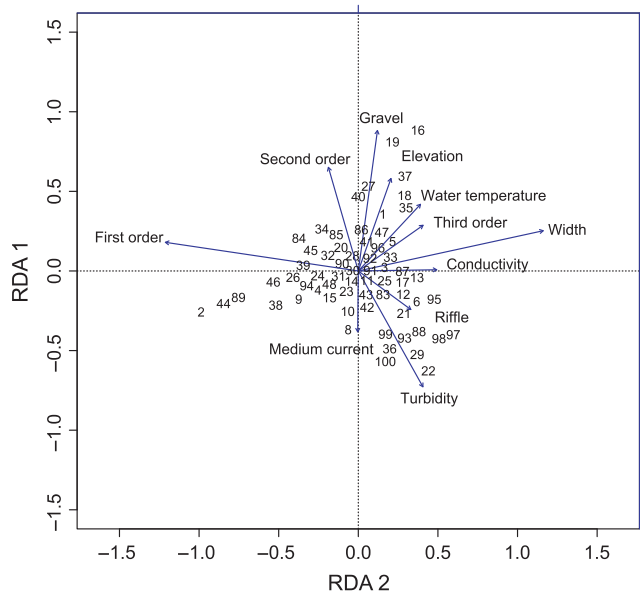


FIGURE 3 Ordination of the results of RDA of 65 fish assemblages and environmental factors. Only the factors which were significantly related to beta diversity are shown on the plot above. Individual assemblages are denoted by field number. Vector arrows are labelled with the corresponding environmental factor, and the length of the arrows indicates the relative strength of the relationship between that factor and assemblage structure

and only 19% was accounted for by nestedness. The pattern was similar when the drainage was divided into sub-drainages: species turnover in Clear Boggy drainage = 76% spatial turnover and 24% nestedness ($\beta_{\text{sor}} = 0.571$; $\beta_{\text{sim}} = 0.435$; $\beta_{\text{nes}} = 0.135$) and species turnover in Muddy Boggy drainage = 85% spatial turnover and 15% nestedness ($\beta_{\text{sor}} = 0.535$; $\beta_{\text{sim}} = 0.454$; $\beta_{\text{nes}} = 0.081$). And again

when the analysis was restricted to the smallest scale of only main-stem sites (Clear Boggy $n = 8$ and Muddy Boggy $n = 7$) similar proportions of spatial turnover and nestedness were observed: species turnover in Clear Boggy mainstems = 75% spatial turnover and 25% nestedness ($\beta_{\text{sor}} = 0.349$; $\beta_{\text{sim}} = 0.260$; $\beta_{\text{nes}} = 0.089$) and spatial turnover in Muddy Boggy mainstems = 76% spatial turnover and 24% nestedness ($\beta_{\text{sor}} = 0.414$; $\beta_{\text{sim}} = 0.314$; $\beta_{\text{nes}} = 0.100$). Table 4 shows the complete results of the species turnover analyses.

4 | DISCUSSION

The results of this study supported the hypothesis of environmental filtering as a significant force in structuring fish species assemblages. Spatial and environmental variables combined accounted for almost 26% of the variation in species composition between assemblages, and abiotic factors alone accounted for much more of the variation than spatial factors. In addition, overall species turnover was largely a result of spatial turnover (i.e. species replacement), and only minimally related to nestedness (i.e. species addition).

The relationship between environmental factors and assemblage composition should become stronger when there is more variation in those factors—which is the case in headwater streams (Carvalho & Tejerina-Garro, 2015; Grenouillet et al., 2004; Ostrand & Wilde, 2002). Ostrand and Wilde (2002) supported this prediction in the Brazos River, Texas, and they found the headwater streams to be a “mosaic of interspersed habitats” which contributed to more variation and higher compositional distinctness of these assemblages. Grenouillet et al. (2004) echoed support as well by finding stronger environmental control of local species richness in upstream regions. Carvalho and Tejerina-Garro (2015) found functional diversity of fish assemblages to be strongly related to environmental variables in headwater streams, while the relationship was less clear for rivers.

Environmental factors are often better than spatial factors for explaining fish beta diversity, as has been shown in other studies of stream fish assemblages at similar scales (Godinho, Ferreira, & Santos, 2000; Magalhaes, Batalha, & Collares-Pereira, 2002; Sály, Takács, Kiss, Bíró, & Erős, 2011). In all three of those studies environmental factors explained more variation in fish assemblage composition than spatial factors. The amount of variation explained by environmental factors ranged from 18% to 36%, and similar factors were found to be most meaningful including: elevation, stream order, depth and stream width. Despite differences in fish collecting techniques and differences in some of the factors measured, similar patterns emerged in these three European studies. The opposite pattern (i.e. spatial factors being as important or more important than environmental factors) has been observed (e.g. Stewart-Koster et al., 2007). We should expect more studies to result in a stronger environmental influence since most studies of stream fish assemblages take place at small-to-intermediate spatial scales (Jackson et al., 2001; Nakagawa, 2014), while spatial factors should become more important as spatial scale increases (Jackson et al., 2001).

TABLE 4 Results of species turnover analysis using package “betapart”. Three spatial scales are shown: Overall drainage, Clear Boggy and Muddy Boggy drainages separately, and Clear Boggy and Muddy Boggy Mainstem sites separately. Within each spatial scale, three methods were used to estimate overall turnover (β_{sor}) and its components of spatial turnover (β_{sim}) and nestedness (β_{nes}). “Beta.multi” compares each assemblage to all others to determine the mean of each turnover measure. “Beta.sample” chooses seven sites at random and calculates mean measures of turnover and then repeats this process 10,000 times. “Beta.pair” generates turnover matrices for each measure and mean measures were calculated by only considering turnover between each site and its closest neighbouring site (by fluvial distance)

	β_{sor}	β_{sim}	β_{nes}
Overall Drainage (n = 65)			
beta.multi	0.955	0.932 (98%)	0.023 (2%)
beta.sample	0.763	0.672 (88%)	0.091 (12%)
beta.pair	0.552	0.445 (81%)	0.107 (19%)
Clear Boggy Drainage (n = 31)			
beta.multi	0.911	0.855 (94%)	0.056 (6%)
beta.sample	0.750	0.627 (84%)	0.123 (16%)
beta.pair	0.571	0.435 (76%)	0.135 (24%)
Muddy Boggy Drainage (n = 34)			
beta.multi	0.915	0.879 (96%)	0.0361 (4%)
beta.sample	0.739	0.656 (89%)	0.083 (11%)
beta.pair	0.535	0.454 (85%)	0.0811 (15%)
Clear Boggy Mainstem (n = 8)			
beta.multi	0.713	0.644 (90%)	0.069 (10%)
beta.sample	0.690	0.618 (90%)	0.072 (10%)
beta.pair	0.349	0.260 (75%)	0.089 (25%)
Muddy Boggy Mainstem (n = 7)			
beta.multi	0.677	0.565 (83%)	0.112 (17%)
beta.sample	0.677	0.565 (83%)	0.112 (17%)
beta.pair	0.414	0.314 (76%)	0.100 (24%)

Longitudinal patterns in fish species richness and assemblage structure are well documented (Matthews, 1998). Stream order was one of the most significant factors for explaining fish beta diversity in this study, as it has been in others (e.g. Matthews, 1986b; Naiman, Melillo, Lock, Ford, & Reice, 1987). It has been noted that stream order is merely a human classification and of little importance to fish (Grenouillet et al., 2004; Matthews, 1998). Hughes & Omerik (1983) argue for incorporating more variables associated with stream order instead of using it directly. In this study, the nine variables most significantly related to fish beta diversity including: elevation, stream width, per cent riffle, water temperature, conductivity, turbidity, gravel substrate and current velocity are all expected to be associated with the upstream–downstream (i.e. longitudinal) gradient (Vannote et al., 1980; Schlosser 1991; Matthews, 1998).

Although it is by definition difficult to explain residual variation, it is possible to speculate about the underlying factors. This study focused solely on environmental and spatial factors and explained

approximately 26% of the spatial variation in assemblage composition, while the remaining residual variation was about 74%. Variation left unexplained by analyses that partition variation among environmental factors is typically high in studies of this kind (Legendre, 2008; Sály et al., 2011). This is likely due to a combination of biotic interactions, dispersal dynamics and unmeasured environmental factors (Legendre, 2008).

In this study, overall species turnover was influenced more by spatial turnover than by nestedness, meaning that species replacement, rather than species addition along a longitudinal continuum, was responsible for the pattern of species turnover across the Muddy Boggy Drainage. Local assemblages tended to be compositionally distinct from one another, rather than low diversity sites being less rich collections of species present in high diversity sites. This indicated that 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 assemblages throughout the drainage—but particularly in headwater areas—that enhanced gamma (regional) diversity.

This pattern in species turnover across the drainage that results in assemblages being compositionally distinct from neighbouring assemblages can be the result of either discontinuities in the connection between habitat, the prevalence of environmental filters, or both (Gard & Flitner, 1974; Horowitz, 1978; McNeely, 1986; Tramer & Rogers, 1973). Discontinuities in habitat can occur due to variation in discharge, for example, spring rains bring higher discharge in the Muddy Boggy River drainage, followed by drought in late summer. Headwater streams should be affected more by this cycle than mainstems, which maintain a more consistent seasonal flow throughout the year (Horowitz, 1978). In addition, the habitat among stream reaches was highly variable. Abrupt changes in depth, substrate and stream composition from site to site were typical, and these changes could occur even between sites relatively close together. These factors can make dispersal among assemblages difficult, and ultimately result in assemblages across space being compositionally distinct from one another rather than sharing all of their species.

Nestedness has been shown to be a predominant pattern of turnover between fish communities in other cases (e.g. Baselga, 2010; Taylor & Warren, 2001). Taylor and Warren (2001) found nestedness to be the result of differential extinction and colonisation rates between upstream and downstream areas. Because extirpation rates of populations found in upstream reaches were higher, due to higher variation in flow and smaller stream size, those reaches were often colonised by populations from the more speciose and stable downstream reaches. This results in a strong signal of nestedness, as the upstream populations are nested within the downstream populations (Taylor & Warren, 2001). However, the results of this study suggest that environmental filtering, rather than differential extinction and colonisation, is the primary driver of variation in assemblage composition between upstream and downstream regions. The highest levels of nestedness we found occurred between sites along the mainstem of the drainage.

We used several approaches to calculate overall species turnover and its two additive components: spatial turnover and nestedness (Baselga, 2010) (Table 4). All three methods are similar in that they show a consistent pattern of proportionately higher spatial turnover compared to nestedness. However, these three methods differ in the magnitude of the resultant turnover (Table 4). “Beta.multi” (Baselga, 2010) results in the highest turnover because all site comparisons are used to calculate the overall value. While this approach makes sense for two-dimensional terrestrial systems, it may overestimate turnover for a dendritic stream network, where sites are separated by much more fluvial distance than “straight-line” distance. “Beta.sample” differs from “beta.multi” in that it takes a random subsample of turnover values and finds the mean of a set number of iterations, and while the beta coefficients resulting from this analysis are lower than those from “beta.multi”, they still may be an overestimate for stream networks. Our modified version, which we call “beta.pair”, extracts only the beta coefficients between sites that are nearest neighbours by fluvial distance to calculate the mean coefficients of overall turnover, spatial turnover and nestedness. As a result, turnover coefficients calculated by this technique were much lower than either “beta.multi” or “beta.sample”.

Future studies should address beta diversity and compositional turnover across different spatial and temporal scales to understand how local diversity is related to regional diversity across continents and the globe. 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 environmental managers to develop plans aimed at maintaining local diversity while also enhancing regional diversity. Patterns of species turnover across space can be valuable for developing efficient management plans that make the most of limited resources. 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. Although higher stream orders had higher mean diversity, and the highest diversity sites occurred further downstream, many species were endemic to assemblages in headwater streams. Thus, fish conservation efforts should not be focused solely on protecting habitats with the highest diversity, but should instead consider a variety of habitat types across a region if the goal is to maintain regional diversity.

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