

# Taxonomic and functional organization in metacommunity structure of stream-fish assemblages among and within river basins in Texas

Kryztal M. Medina Torres · Christopher L. Higgins

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**Abstract** Metacommunities are spatially structured communities linked by dispersal. They provide a connection between local community assembly and regional-level processes. One of the more widely used methods to address questions related to metacommunity concepts is those that characterize elements of metacommunity structure by quantifying aspects of coherence, species turnover, and boundary clumping. In this study, we used this approach to study the spatial ecology of freshwater fishes in Texas. Stream-fish assemblages in Texas provide an excellent opportunity to examine the patterns of metacommunity structure due to the number of drainages that empty directly into the Gulf of Mexico, which minimizes the likelihood of dispersal between basins while allowing for longitudinal movement within basins. We used fisheries data published by the Texas Parks and Wildlife Department and from the North American Water Quality Association, which consisted of 94 sampling localities distributed across 18 river basins and 11 ecoregions. To examine within-basin patterns,

we focused only on the Brazos, Colorado, and Trinity rivers because of the number of sites within each of these basins. From a taxonomic standpoint, we consistently observed Clementsian patterns regardless of whether it was among or within river basins, whereas we mostly observed Gleasonian patterns from a functional perspective. Only one functional group was found at all sites in each of the three main river basins, which consisted of invertivores with an equilibrium life-history strategy. Various bioclimatic variables were significantly correlated with metacommunity structure, but these correlations differed between taxonomic and functional organization and differed depending on which river basin was considered. The results of this study support previous findings that species composition and functional traits relate to environmental gradients, but further our understanding by providing additional evidence that species sorting processes are the dominant structuring mechanisms.

**Keywords** Connectivity · River continuum concept · Dendritic network · Spatial distributions · Warm-water streams · Life-history

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K. M. Medina Torres · C. L. Higgins (✉)  
Department of Biological Sciences, Tarleton State  
University, Stephenville, TX 76402-0100, USA  
e-mail: [higgins@tarleton.edu](mailto:higgins@tarleton.edu)

## Introduction

The field of metacommunity ecology, which focuses on sets of spatially structured communities linked by

dispersal (Leibold et al. 2004; Holyoak et al. 2005), has advanced greatly since its initial beginnings (Hanski and Gilpin 1991; Wilson 1992). In fact, metacommunity concepts have changed our perception of a community from that in which local interactions determine species coexistence to one in which a combination of local and regional factors affects community assembly (Ricklefs 2004). Traditionally, there have been four conceptual paradigms associated with the metacommunity framework; these include species sorting, mass effects, patch dynamics, and neutral models (Leibold et al. 2004). These models provide different underlying mechanisms for observed patterns and differ in the importance of environmental heterogeneity, dispersal abilities, and demographic stochasticity (Logue et al. 2011). Although neutral models may account for some empirical observations, such as compositional patterns in fish assemblages throughout the Mississippi–Missouri River System (Muneepeerakul et al. 2008; Bertuzzo et al. 2009), most metacommunities seem to coincide with the species sorting or mass effects paradigms (Logue et al. 2011). In both of these cases, heterogeneous landscapes allow for niche differentiation, but in species sorting the source–sink dynamics are not so strong that they overpower the association between functional attributes and habitat characteristics (Borthagaray et al. 2015).

One of the more widely used methods to address questions related to metacommunity concepts is those that characterize elements of metacommunity structure (EMS) by quantifying aspects of coherence, species turnover, and boundary clumping (Leibold and Mikkelsen 2002; Presley et al. 2010). Not only does this methodology identify which idealized pattern best fits empirical observations, it allows for an examination of how species composition relates to various environmental gradients (Presley et al. 2009). Some of the more common multispecies distributions have been Clementsian (Clements 1916), Gleasonian (Gleason 1926), and nested (Patterson and Atmar 1986) patterns, although checkerboard (Diamond 1975), evenly spaced (Tilman 1982), and random (Simberloff 1983) patterns are also possibilities (Leibold and Mikkelsen 2002). In addition to these six idealized patterns, there are four quasi-structures associated with this suite of analyses (quasi-Clementsian, quasi-Gleasonian, quasi-evenly spaced, and quasi-nested) depending on the degree of significance

in species turnover; each of these structures is consistent with their original theoretical underpinnings and is significantly coherent (Presley et al. 2010). Perhaps the greatest benefit of using the EMS approach is that it allows for all of these patterns to be assessed simultaneously as opposed to separately comparing each distribution against a single null model (Presley et al. 2010). This approach has been applied to both terrestrial (Presley et al. 2011; Lopez-Gonzalez et al. 2012; de la Sancha et al. 2014) and aquatic (Heino 2005; Fernandes et al. 2014; Eros et al. 2014; Schwalb et al. 2015) systems and has contributed greatly to our understanding of local community assembly and of broad-scale patterns of biodiversity (Leibold et al. 2004).

Despite the increasing number of studies incorporating metacommunity concepts to better understand species distributions, relatively few studies have addressed them from a functional perspective (Sokol et al. 2011; Eros et al. 2012). There are several reasons why including ecological function is important when examining the patterns of metacommunity structure and broad-scale patterns of diversity. First, functional organization characterizes different aspects of community structure compared to taxonomic organization (Hoeinghaus et al. 2007; Higgins 2010). Second, functional characteristics allow comparisons to be made among broad geographic regions where communities comprise different taxa (Simberloff and Dayan 1991). For example, Lamouroux et al. (2002) observed intercontinental convergence in functional traits related to hydrogeology despite phylogenetic and historical differences in fish assemblages. Third, functional characteristics provide a means of testing theoretical expectations of changes in species traits along environmental gradients, such as those generated from habitat templates (Southwood 1977), landscape filters (Poff 1997), and the river continuum concept (Vannote et al. 1980). For example, habitat templates predict changes in reproductive traits with habitat stability, such as increasing parental care with decreased variability (Townsend and Hildrew 1994).

Freshwater ecosystems provide an ideal setting to study metacommunity concepts due to environmental differences among river basins and the dendritic nature within basins (Altermatt 2013; Heino et al. 2015a). In lentic systems, species distributions are often nested or Clementsian depending on environmental differences among watersheds and their spatial

structuring (Henriques-Silva et al. 2013) or dispersal ability with weaker dispersers being more affected by the spatial distribution of habitats than stronger dispersers (De Bie et al. 2012; Heino 2013). In lotic systems, rivers and streams provide natural ecological corridors (Rodríguez-Iturbe et al. 2009) in which fish are ideally free to move either upstream or downstream affecting metacommunity dynamics (Urban et al. 2008; Jacobson and Peres-Neto 2010; Carrara et al. 2012). In these systems, spatial distributions within basins are often consistent with Gleasonian patterns resulting from individualistic responses to linear gradients associated with longitudinal changes from headwaters to downstream reaches (Heino and Soininen 2005; Hoverman et al. 2011). Nested patterns, however, may arise in regions with strong environmental gradients associated with greater topographic relief (Cook et al. 2004) or in areas with high anthropogenic disturbance that alter the natural longitudinal profile of a river (Ibarra et al. 2005). In fact, in a recent analysis of 45 freshwater metacommunities that included both lentic and lotic systems as well as different groups of organisms (i.e., algae, bacteria, invertebrates, fishes, and macrophytes), the most common patterns were Clementsian and quasi-nested (Heino et al. 2015b).

Stream-fish assemblages in Texas provide an excellent opportunity to examine the patterns of metacommunity structure due to the number of drainages that empty directly into the Gulf of Mexico, which minimizes the likelihood of dispersal between basins while allowing for longitudinal movement within basins. The primary objective of this study was to examine the metacommunity structure of stream-fish assemblages within and among river basins from both taxonomic and functional perspectives. In Texas, among-community components are more influential in structuring the taxonomic organization of stream-fish assemblages, whereas within-community components are more important in structuring functional organization (Higgins 2010). This suggests that functional organization should change little from basin to basin (low beta diversity), whereas taxonomic organization should change considerably (high beta diversity). Among basins, we expect to find Gleasonian structure in functional organization resulting from idiosyncratic responses to minor changes in environmental conditions and Clementsian structure in taxonomic organization due to biogeographic constraints

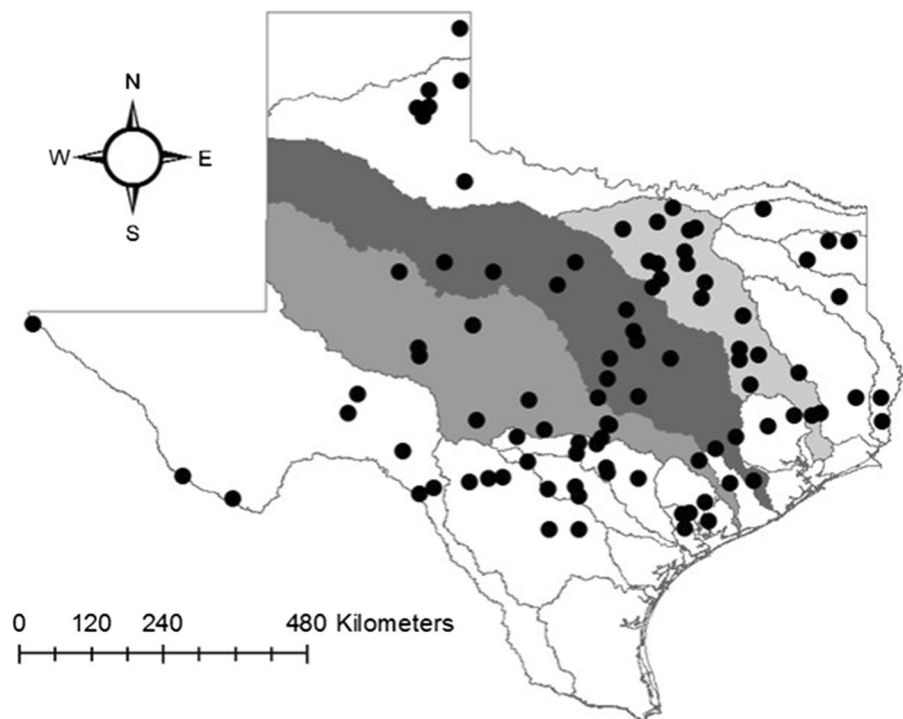
on local patterns of endemism. Within basins, we expect to find nested distributions in both functional and taxonomic organization resulting from breaks in connectivity from headwaters to downstream reaches and potential anthropogenic disturbances along the way. The secondary objective was to examine environmental correlates associated with metacommunity structure as they related to climatic, connectivity, and geographic factors. We hypothesized that various combinations of temperature and precipitation would be important drivers of metacommunity structure due to environmental differences among basins, and we also hypothesized that longitude, elevation, and connectivity would be important in structuring metacommunities within particular river basins.

## Methods

### Fish assemblage data

We used fisheries data from a report published by the Texas Parks and Wildlife Department (TPWD) on the regionalization of indices of biotic integrity for Texas streams (Linam et al. 2002) and bioassessment data from the North American Water Quality Association (NAWQA). The TPWD data contained information on fish assemblages from 62 sites across Texas and have been used in previous studies (e.g., Higgins and Strauss 2008; Higgins 2010). The NAWQA data contained bioassessment data (biological community and physical habitat data) from 2288 fish assemblages in stream ecosystems across the nation sampled by USGS scientists (<https://aquatic.biodata.usgs.gov>); these data provided an additional 32 sampling localities in Texas that were not provided by TPWD ( $N = 94$  sites across Texas; Fig. 1). Combined, the sampling localities were distributed across 18 river basins (Brazos, Brazos–Colorado, Canadian, Colorado, Colorado–Lavaca, Cypress Creek, Guadalupe, Lavaca, Lavaca–Guadalupe, Neches, Nueces, Red River, Rio Grande, Sabine, San Antonio, San Jacinto, Sulfur, and Trinity river basins) and 11 ecoregions (Central Great Plains, Central Oklahoma–Texas Plains, Chihuahuan Desert, East Central Texas Plains, Edwards Plateau, South Central Plains, Southern Texas Plains, Southwestern Tablelands, Texas Blackland Prairies, Western Gulf Coastal Plain, and Western High Plains).

**Fig. 1** Map showing the location of the 94 sampling localities included in the study as they relate to various river basins across Texas. The three main river basins are represented by a different *shade of gray*: Brazos River Basin is *dark gray*, Colorado River Basin is *medium gray*, and Trinity River Basin is *light gray*



The 94 sites were sampled over the course of 23 years (1988–2009). In some cases, certain localities were sampled multiple times. For these sites, we averaged species abundance and rounded up to the nearest whole number. For example, if only one individual was collected across three sampling times, we rounded 0.33–1 to indicate that one individual was indeed collected at that location. This methodology incorporated as much data as possible while ensuring that each location contributed the same amount of information to overall metacommunity structure. However, not all river basins had the same number of sites. For example, the Canadian River only had one sampling locality, whereas the Trinity River had 21 sampling localities. Therefore, we focused only on three river basins that contained more than 10 sampling localities when looking at within-basin patterns; these included the Brazos River (17 sites), Colorado River (12 sites), and Trinity River (21 sites).

#### Formation of functional groups

We characterized the functional organization of stream-fish assemblages using the same classification scheme as Hoeinghaus et al. (2007) and Higgins

(2010) in their assessment of local versus regional determinants of taxonomic and functional organization of stream-fish assemblages in Texas. Their functional groupings were based on dietary regimen and life-history strategies (Winemiller 1995), which characterizes different aspects of assemblage structure rather than taxonomic organization by distinguishing among groups of fishes with similar evolutionary adaptations, ecological niches, and population dynamics (Winemiller 2005). The life-history strategies were based on the triangular model (opportunistic, periodic, and equilibrium) proposed to explain evolutionary adaptations to particular environmental factors relative to generation time (Winemiller and Rose 1992). Species that utilize opportunistic strategies have short generation times, produce lots of offspring per reproductive effort, are small in size, and show little parental investment. Species that use periodic strategies have long generation times, moderate reproductive effort, large body size, high batch fecundity, and little parental investment per offspring. Species that have an equilibrium life-history strategy have moderate generation times, low reproductive effort, variable body size, low batch fecundity, and high investment in offspring. These various strategies are associated with

different environmental factors (e.g., biotic interactions, environmental disturbance, and resource stability) and are rooted in  $r$ - $K$  selection (Pianka 1970; Winemiller 2005).

The specific functional groups used in this study were herbivore–periodic (h–p), invertivore–equilibrium (i–e), invertivore–opportunistic (i–o), invertivore–opportunistic/equilibrium (i–oe), invertivore–opportunistic/periodic (i–op), invertivore–periodic (i–p), omnivore–equilibrium (o–e), omnivore–equilibrium/periodic (o–ep), omnivore–opportunistic (o–o), omnivore–opportunistic/periodic (o–op), omnivore–periodic (o–p), piscivore–equilibrium (p–e), piscivore–equilibrium/periodic (p–ep), piscivore–opportunistic/equilibrium (p–oe), and piscivore–periodic (p–p). Following Hoeinghaus et al. (2007) and Higgins (2010), individuals of each species were classified into a single functional group. For the species classifications not found in the previous papers, we used the trophic classification provided in Linam et al. (2002) and information provided in Winemiller (1992) and Winemiller and Rose (1992) for life-history strategies.

#### Elements of metacommunity structure

We analyzed coherence, turnover, and boundary clumping to determine which idealized pattern (Leibold and Mikkelsen 2002) or quasi-structure (Presley et al. 2010) best fits empirical observations. First, data matrices were ordinated via reciprocal averaging, which arranged sites based on similarities in species composition and arranged species based on similarities in spatial distribution (Gauch 1982; Leibold and Mikkelsen 2002). Coherence was assessed statistically by comparing the number of embedded absences in the ordinated matrix to a null distribution. If the number of embedded absences was not significantly different from chance expectations, then a preponderance of species did not respond to the same environmental gradient and metacommunity structure was considered to be consistent with random patterns. Significantly more embedded absences than expected (i.e., negative coherence) was indicative of a checkerboard pattern. Significantly fewer embedded absences than expected was indicative of positive coherence and required further evaluation of range turnover and boundary clumping to distinguish among 12 possible coherent structures (Presley et al. 2010).

Turnover was assessed by counting the number of replacements along the latent gradient and comparing the empirical value to a null distribution (Leibold and Mikkelsen 2002). Fewer replacements than expected was consistent with nested distributions, whereas more replacements than expected required analysis of boundary clumping to differentiate among evenly spaced, Gleasonian, or Clementsian distributions (Leibold and Mikkelsen 2002). Quasi-structures have turnover indistinguishable from that expected by chance, but have structures consistent with the conceptual underpinning of Clementsian, evenly spaced, Gleasonian, or nested distributions (Presley et al. 2010). Analysis of boundary clumping can also distinguish among three types of nested structure (Presley et al. 2010). Boundary clumping was quantified using Morisita's index and statistically evaluated via a  $\chi^2$  goodness-of-fit test that compared the observed distribution to an expected equiprobable distribution of range boundaries. Additional details about analyses of EMS are available elsewhere (Leibold and Mikkelsen 2002; Presley et al. 2009, 2010). All analyses of EMS were conducted with algorithms written in MATLAB 7.5 (script files available at <http://faculty.tarleton.edu/higgins/metacommunity-structure.html>).

#### Characterization of environmental factors

We used bioclimatic data downloadable from the WorldClim Web site ([www.worldclim.org](http://www.worldclim.org)) to capture spatial variation in environmental conditions derived from monthly temperature and rainfall values (Hijmans et al. 2005). The bioclimatic factors were Bio1 = mean annual temperature, Bio2 = mean diurnal range (mean of monthly (maximum temp – minimum temp)), Bio3 = isothermality (Bio2/Bio7) ( $\times 100$ ), Bio4 = temperature seasonality (standard deviation  $\times 100$ ), Bio5 = maximum temperature of warmest month, Bio6 = minimum temperature of coldest month, Bio7 = annual temperature range (Bio5–Bio6), Bio8 = mean temperature of wettest quarter, Bio9 = mean temperature of driest quarter, Bio10 = mean temperature of warmest quarter, Bio11 = mean temperature of coldest quarter, Bio12 = annual precipitation, Bio13 = precipitation of wettest month, Bio14 = precipitation of driest month, Bio15 = precipitation seasonality (coefficient of variation), Bio16 = precipitation of wettest quarter, Bio17 = precipitation of driest quarter,



Bio18 = precipitation of warmest quarter, and Bio19 = precipitation of coldest quarter. Because dispersal is so important in the mechanistic process of community assembly (Jacobson and Peres-Neto 2010), we used data from the National Inventory of Dams (<http://geo.usace.army.mil/pgis/f?p=397:1:0>) to obtain geographic coordinates of various-sized dams across Texas. Using this data, we quantified the number of dams within a 25 km radius for each of the sampling localities. Dams have dramatic and obvious effects on the natural connectivity within basins (Van Looy et al. 2014). To examine potential effects of geographic location, we also included elevation, latitude, and longitude as potential spatial factors.

We used a regression tree approach to determine which of the 23 environmental variables contributed most to metacommunity structure. Regression trees explain a variation in response variables by repeatedly splitting the data into homogeneous groups using combinations of explanatory variables (De'ath and Fabricius 2000). Statistically, regression trees are useful in situations in which the effects of the predictor variables are nonadditive and when interaction terms are not multiplicative (Urban 2002). That is, there is no assumption that the underlying relationships between independent and dependent variables are linear, that they follow a specific nonlinear link function, or that they are monotonic in nature. Thus, regression trees represent alternatives to several traditional statistical techniques, such as multiple regression, generalized linear models, and discriminant function analysis (Loh 2011). Not to mention, results are intuitive and visually appealing.

## Results

Patterns of taxonomic organization were all consistent with Clementsian distributions regardless of whether it was across Texas (among basins) or within a particular river basin; in fact, this was true for both the primary and secondary axis of variation (Table 1). Patterns of functional organization were mostly consistent with Gleasonian or quasi-Gleasonian distributions (Table 2). The only discrepancies were along the primary axis when all sites were combined (Clementsian) and along the secondary axis when sites from just the Trinity River Basin were analyzed separately (quasi-Clementsian). In all cases, we

observed positive coherence in which there was statistically fewer embedded absences than expected by chance given the constraints of the null model, indicating that a majority of the species are indeed responding similar to the same environmental gradient.

In regard to ecological traits, only one functional group was consistently found at all sites in each of the three main river basins (Fig. 2). This group consisted of invertivores with an equilibrium life history (pirate perch *Aphredoderus sayanus*; flier *Centrarchus macropterus*; Rio Grande cichlid *Herichthys cyanoguttatus*; redbreast sunfish *Lepomis auritus*; bluegill *Lepomis macrochirus*; dollar sunfish *Lepomis marginatus*; longear sunfish *Lepomis megalotis*; redear sunfish *Lepomis microlophus*; spotted sunfish *Lepomis punctatus*; bantam sunfish *Lepomis symmetricus*). Each of the three main river basins included in our study also had one other functional group that was found at all sites within that particular basin. In the Brazos River, this additional functional group consisted of omnivores with periodic life-history strategies (river carpsucker *Carpionodes carpio*; common carp *Cyprinus carpio*; roundnose minnow *Dionda episcopa*; gizzard shad *Dorosoma cepedianum*; creek chubsucker *Erimyzon oblongus*; lake chubsucker *Erimyzon sucetta*; cypress minnow *Hybognathus hayi*; Mississippi silvery minnow *Hybognathus nuchalis*; plains minnow *Hybognathus placitus*; smallmouth buffalo *Ictiobus bubalus*). In the Colorado River, the additional group consisted of invertivores with an opportunistic/periodic life history (plateau shiner *Cyprinella lepida*; red shiner *Cyprinella lutrensis*; Proserpine shiner *Cyprinella prosperpina*; blacktail shiner *Cyprinella venusta*; striped shiner *Luxilus chrysocephalus*; ribbon shiner *Lythrurus fumeus*; red-fin shiner *Lythrurus umbratilis*; speckled chub *Macrhybopsis aestivalis*; golden shiner *Notemigonus crysoleucas*; Texas shiner *Notropis amabilis*; Red River shiner *Notropis bairdi*; Tamaulipas shiner *Notropis braytoni*; ironcolor shiner *Notropis chalybaeus*; Chihuahua shiner *Notropis chihuahua*; sand shiner *Notropis stramineus*; weed shiner *Notropis texanus*; mimic shiner *Notropis volucellus*; pugnose minnow *Opsopoeodus emiliae*; bullhead minnow *Pimephales vigilax*). In the Trinity River, the additional group consisted of piscivores with an equilibrium/periodic life history (blue catfish *Ictalurus furcatus*; flathead catfish *Pylodictis olivaris*;

**Table 1** Results of analyses of coherence, turnover, and clumping for taxonomic organization of metacommunity structure

Axis of variation	Texas (all)	Brazos River	Colorado River	Trinity River
<b>Primary axis</b>				
Coherence				
Observed absences	5210	218	127	628
Expected absences	7973	361	196	855
<i>P</i> value	<0.001	<0.001	<0.001	<0.001
Turnover				
Observed replacements	887,509	3942	2310	22,086
Expected replacements	543,200	2239	1723	13,745
<i>P</i> value	<0.001	<0.001	0.031	<0.001
Clumping				
Morisita's indices	2.33	1.56	1.58	2.28
<i>P</i> value	<0.001	<0.001	<0.001	<0.001
Best-fit patterns	Clementsian	Clementsian	Clementsian	Clementsian
<b>Secondary axis</b>				
Coherence				
Observed absences	4664	248	136	607
Expected absences	8049	382	208	877
<i>P</i> value	<0.001	<0.001	<0.001	<0.001
Turnover				
Observed replacements	815,209	3468	1903	25,771
Expected replacements	568,730	2907	1435	20,957
<i>P</i> value	<0.001	0.177	0.023	0.023
Clumping				
Morisita's indices	2.85	1.52	1.51	1.73
<i>P</i> value	<0.001	<0.001	<0.001	<0.001
Best-fit patterns	Clementsian	Quasi-Clementsian	Clementsian	Clementsian

smallmouth bass *Micropterus dolomieu*; spotted bass *Micropterus punctulatus*; largemouth bass *Micropterus salmoides*; Guadalupe bass *Micropterus treculii*; black crappie *Pomoxis nigromaculatus*; white crappie *Pomoxis annularis*).

Across the state, the environmental components important in determining metacommunity structure were based on a combination of spatial and climatic factors (Appendix A of supplementary material). In terms of taxonomic organization, these factors included latitude, longitude, the number of ams within 25 km of sampling localities, annual temperature range, mean temperature of driest quarter, mean annual precipitation, and precipitation seasonality. In terms of functional organization, these factors included latitude, elevation, the number of dams, mean annual temperature, mean diurnal range, isothermality, temperature seasonality, maximum

temperature of warmest month, mean temperature of wettest quarter, mean temperature of driest quarter, mean annual precipitation, and precipitation seasonality. Metacommunity structure within the Brazos River Basin (Appendix B of supplementary material) was based on spatial factors (longitude—functional and taxonomic organization) and climatic conditions associated with both temperature (temperature seasonality, mean temperature of wettest quarter, and mean temperature of warmest quarter—functional organization only) and precipitation (mean annual precipitation and mean precipitation of wettest month—taxonomic organization only). Metacommunity structure within the Colorado River Basin (Appendix C of supplementary material) was based on climatic conditions associated with temperature only for both functional (mean annual temperature and isothermality) and taxonomic (isothermality and mean

**Table 2** Results of analyses of coherence, turnover, and clumping for functional organization of metacommunity structure

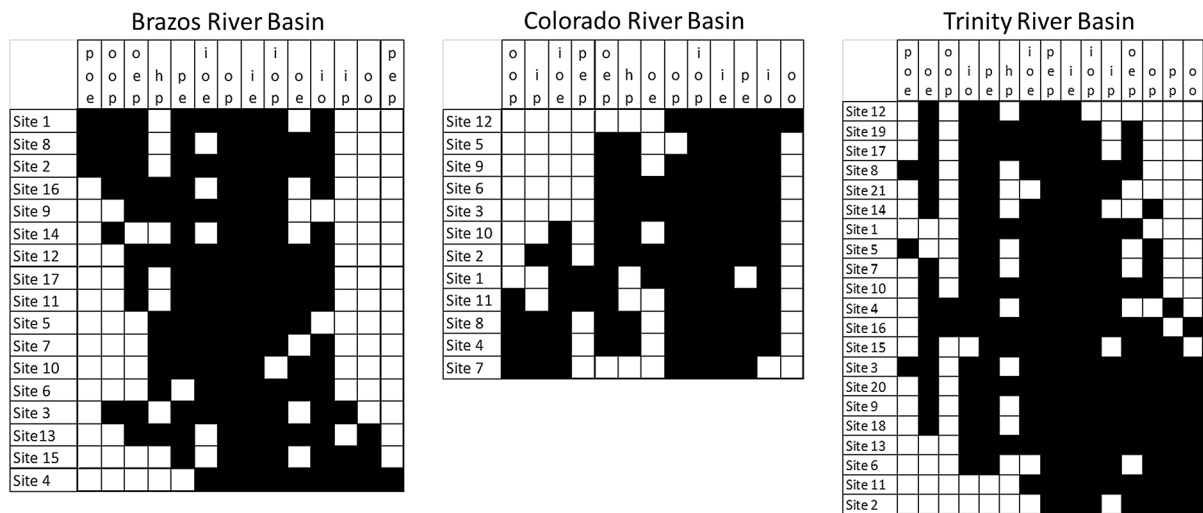
Axis of variation	Texas (all)	Brazos River	Colorado River	Trinity River
Primary axis				
Coherence				
Observed absences	417	37	20	53
Expected absences	536	71	36	79
<i>P</i> value	<0.001	<0.001	<0.001	<0.001
Turnover				
Observed replacements	4177	344	142	486
Expected replacements	492	101	111	270
<i>P</i> value	<0.001	<0.001	0.521	0.130
Clumping				
Morisita's indices	4.6	1.67	0.909	1.12
<i>P</i> value	<0.001	0.153	0.466	0.340
Best-fit patterns	Clementsian	Gleasonian	Quasi-Gleasonian	Quasi-Gleasonian
Secondary axis				
Coherence				
Observed absences	401	44	19	60
Expected absences	544	78	41	86
<i>P</i> value	<0.001	<0.001	<0.001	<0.001
Turnover				
Observed replacements	4343	274	210	216
Expected replacements	2216	191	94	98
<i>P</i> value	0.125	0.249	0.008	0.055
Clumping				
Morisita's indices	1.75	0.909	1.27	2.71
<i>P</i> value	0.211	0.474	0.229	0.037
Best-fit patterns	Quasi-Gleasonian	Quasi-Gleasonian	Gleasonian	Quasi-Clementsian

temperature of wettest month) organization. Metacommunity structure within the Trinity River Basin (Appendix D of supplementary material) was based on spatial factors (elevation—functional and taxonomic organization) and climatic conditions associated with both temperature (mean diurnal range and mean temperature of coldest quarter—functional organization; mean diurnal range and maximum temperature of warmest month—taxonomic organization) and precipitation (mean annual precipitation—functional organization; precipitation seasonality—taxonomic organization). Minimum temperature of coldest month, precipitation of driest month, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter were not found to be structuring factors for any of the metacommunity analyses.

## Discussion

The results of this study clearly indicate that the patterns of metacommunity structure differ between taxonomic and functional perspectives. Based on taxonomic organization, we consistently observed Clementsian patterns regardless of whether the emphasis was among or within particular river basins. While we expected to see Clementsian patterns among basins as a consequence of disrupt changes in species composition resulting from biogeographic and environmental differences among basins, we did not expect to find these patterns within a basin where there should be more of a continual gradient in physical conditions. In these cases, we expected to find Gleasonian or nested distributions depending on the strength of environmental gradients (Cook et al. 2004)





**Fig. 2** Ordinated data matrices based on functional organization for each of the three focal river basins. Sites are numbered according to their geographic position with *smaller numbers* representing locations at lower latitudes (*downstream*) and *higher numbers* representing higher latitudes (*upstream*). Acronyms for functional groups are herbivore–periodic (h–p), invertivore–equilibrium (i–e), invertivore–opportunistic (i–o),

invertivore–opportunistic/equilibrium (i–oe), invertivore–opportunistic/periodic (i–op), invertivore–periodic (i–p), omnivore–equilibrium (o–e), omnivore–equilibrium/periodic (o–ep), omnivore–opportunistic (o–o), omnivore–opportunistic/periodic (o–op), omnivore–periodic (o–p), piscivore–equilibrium (p–e), piscivore–equilibrium/periodic (p–ep), piscivore–opportunistic/equilibrium (p–oe), and piscivore–periodic (p–p)

or degree of zonation (Ibarra et al. 2005). Perhaps spatial connectivity resulting from ephemeral stream systems or the presence of over 2337 dams within 25 km of our sampling localities, both of which prevent normal upstream–downstream movement of migratory fishes, had an impact on these distributional patterns. We did, however, find Gleasonian patterns when examining functional organization of metacommunity structure within river basins according to both the primary and secondary axis of variation.

In the early 1900s, researchers were trying to understand the variation in plant communities along environmental gradients, and two major models emerged to account for observed patterns of vegetative change. Clements (1916) suggested that communities were discrete entities, with a distinct species composition coinciding with species replacement as groups align along the environmental gradient. Another characteristic of the communities' organization described by Clements is that these communities experienced discrete changes over time and these changes culminated in a stable climax community. Gleason (1926) argued that species are distributed idiosyncratically along environmental gradients. That is, in a Gleasonian gradient, the boundaries of the

communities are randomly distributed, unlike the clumped nature associated with a Clementsian gradient (Presley et al. 2010). Our results show that these historic models of species distributions are still prevalent 100 years later and can be applied to different taxonomic groupings, various dimensions of biodiversity, and aquatic or terrestrial ecosystems. These results also provide documentation that niche-based processes, such as species sorting and mass effect paradigms, are a dominant structuring mechanism in freshwater systems in Texas.

Our study characterized spatial distributions for 116 species of freshwater fishes across 94 different localities in Texas with cyprinids and centrarchids being the most widely distributed. In another study on the distribution of freshwater fishes in Texas, Anderson et al. (1995) compared fishery surveys conducted by Clark Hubbs in 1953 to surveys conducted in 1986 (33 years later). They analyzed data from 129 sampling localities distributed across 10 drainages, namely the Brazos, Colorado, Guadalupe, Neches, Nueces, Red, Rio Grande, Sabine, San Antonio, and Trinity river basins. Their results revealed a reduction in the distribution of lotic-adapted, specialist species (e.g., percids) and an increase in tolerant species (e.g.,

sunfishes) that can more effectively respond to environmental disturbances (Anderson et al. 1995). This increase could account for the fact that we observed the invertivore–equilibrium functional group, which was comprised primarily of sunfishes, at all localities in the Brazos, Colorado, and Trinity river basins. Although each river had an additional functional group found at all locations within that basin, they differed among basins. However, they all contained ecological traits that included some combination of a periodic life-history strategy, which is typically associated with increasing predictability in spatiotemporal variability in resources and mortality factors (Wine-miller 2005). Despite the potential for increased predictability, all three river basins exhibited the patterns of metacommunity structure consistent with Gleasonian distributions; this suggests that functional groups and associated ecological traits had randomly distributed boundaries.

The river continuum concept (RCC) is a model that describes the changes in physical characteristics of lotic systems from headwaters to downstream reaches (Vannote et al. 1980) as well as the patterns of biodiversity that should result from such changes (Schlosser 1982). The RCC was one of the first attempts to provide testable hypotheses in regard to changes in species composition and functional groups along resulting environmental gradients (Tornwall et al. 2015). In fact, longitudinal zonation in species composition and diversity, from headwaters to downstream reaches, is one of the most frequently described patterns for freshwater fish (Schlosser 1982; Oberdorff et al. 1993; Ostrand and Wilde 2002; Habit et al. 2007). However, most of these studies simply document fewer species upstream and more species downstream with no real connection to metacommunity concepts. The results of our study support the RCC by showing that species composition and functional traits relate to environmental gradients from headwaters to downstream reaches, but further our understanding by identifying the patterns of metacommunity structure both among and within river basins.

Another important factor that could play a role in producing the patterns of metacommunity structure in dendritic systems (i.e., river networks) is connectivity (Altermatt 2013; Borthagaray et al. 2015). Connectivity is a key factor in freshwater ecology regardless of whether it is in lentic (Cottenie et al. 2003; Hortal

et al. 2014; Guimaraes et al. 2014) or lotic (Perkin and Gido 2012; Heino et al. 2015a; Fernandes et al. 2014) systems. Within this context, a combination of biogeographic, ecological, and evolutionary processes interacts to produce the spatial structuring associated with metacommunities (Leibold et al. 2010). Although highly vagile organisms (e.g., some insect groups) may be less constrained by dispersal in dendritic systems, other groups of organisms (e.g., amphibians and fishes) may be more constrained by hierarchical nature of rivers and streams (De Bie et al. 2012). Of course, the degree to which connectivity influences metacommunity structure may change over time. For example, Fernandes et al. (2014) examined the metacommunity structure of fish in the Pantanal floodplain system in South America and found a nested pattern at the beginning of the flood season when species co-occurrence was important, but changed to a quasi-Clementsian pattern by the end of the wet season when environmental factors took over. In addition to seasonal differences in environmental conditions affecting the patterns of species composition, the presence of non-native species may also alter metacommunity structure by distributing themselves throughout the riverscape (Eros et al. 2014). Regardless, dispersal ability and the degree of connectivity continue to be implicated as important drivers of metacommunity structure among and within freshwater systems.

Spatial, temperature, and precipitation factors all influenced metacommunity structure to some degree. At the largest spatial scale (i.e., across the entire state of Texas), all three were important structuring components. The easternmost river basin, the Trinity River Basin, receives the most rainfall of the three main basins included in this study. In this basin, temperature and spatial factors were also important. The westernmost river basin, the Colorado River Basin, receives the least amount of precipitation. In this basin, temperature was the only environmental factor influential in metacommunity structure. The structure within the Brazos River Basin, on the other hand, is based on all three types of environmental components although the relative influence is dependent on which dimension of biodiversity is considered. In 2007, Hoeinghaus et al. conducted a broad-scale study on stream-fish assemblages across Texas and found that they are structured by a combination of local and regional factors;

Hoeinghaus et al. (2007) also documented the differences between taxonomic and functional organization regarding the relative influence of local versus regional factors. Significant coherence both among and within river basins suggests that stream fish respond similar to latent environmental gradients giving support for niche-based mechanisms, such as species sorting and mass effect models. Other niche-based studies of stream-fish assemblages in Texas found that niche apportionment plays a fundamental role in structuring taxonomic and functional components of fish diversity (Higgins and Strauss 2008). However, fish diversity is partitioned differently between functional and taxonomic organization with among-community components contributing more to taxonomic diversity and within-community components to the primary factor influencing functional organization (Higgins 2010). Although the relative influence of spatial and climatic factors varied within and among river basins, there was always a significant coherence, indicating that a majority of the species responded similar to latent environmental gradients and that these gradients were strong enough to affect metacommunity dynamics.

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