Prioritizing aquatic conservation areas using spatial patterns and partitioning of fish community diversity in a near-natural temperate basin

YOICHIRO KANNO[a,†], WILLIAM T. RUSS[b], CHARLES J. SUTHERLAND[a] and S. BRADFORD COOK[a,*]

[a]*Department of Biology, Tennessee Technological University, Cookeville, TN, USA*
[b]*North Carolina Wildlife Resources Commission, 645 Fish Hatchery Road, Marion, NC 28752, USA*

ABSTRACT

1. This study investigated spatial patterns and partitioning of fish community diversity in the Emory River basin, Tennessee, USA, which represents the best available biotic condition in a region characterized with high diversity and endemism. Fish community analyses were intended as one criterion for identifying aquatic conservation areas in a Habitat Conservation Plan (HCP) currently developed in the study region under the authority of the US Endangered Species Act.

2. Spatial patterns of fish community diversity were examined at 57 stream sites located in the mainstem (13 sites) and four sub-basins (a total of 44 sites) by partitioning γ diversity (total diversity) into α (within-community) and β (among-community) components in a multiplicative manner at two spatial scales. Additional analyses were conducted to assess evidence of dispersal in structuring local communities.

3. Mainstem sites were characterized with higher α diversity values relative to sub-basin sites, and γ diversity of 13 mainstem sites was comparable with that of 44 sub-basin sites. Site-level β diversity differed among sub-basins. Among-sub-basin β diversity was only modest, and one sub-basin harboured the majority of total species richness found among all sub-basins.

4. Many species had high indicator values for mainstem sites, but sub-basin sites were associated with few indicator species. Spatial autocorrelation of fish community similarity was significant within mainstem sites and sites located within two sub-basins. Catchment area explained among-site variation in species richness better than stream order, link magnitude, confluence link or downstream link. Overall, there was a lack of evidence that dispersal played an important role in shaping local fish communities in either mainstem or sub-basin sites.

5. Aquatic conservation in the study basin should focus on protecting aquatic diversity in the mainstem habitat, while a network of stream sites in the most diverse sub-basin may also be considered as aquatic conservation areas. Copyright © 2012 John Wiley & Sons, Ltd.

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INTRODUCTION

Diversity of freshwater fishes is rapidly declining globally as a result of various human activities (Jelks *et al.*, 2008; Strayer and Dudgeon, 2010).

Conservation of stream fish is challenging because they may be sensitive to even a modest degree of land disturbances within upstream basins (Stranko *et al.*, 2008; Wenger *et al.*, 2008). In addition,

streams are highly fragmented due to artificial barriers (Dynesius and Nilsson, 1994; Cote *et al.*, 2009) and non-native species are ubiquitous in stream fish communities worldwide (Rahel, 2002). As a result, few 'near-natural' basins remain in the temperate region and they possess high conservation values for aquatic diversity.

The Emory River basin, Tennessee, is an example of remaining near-natural basins in the USA. Although far from pristine, the basin is free of artificial barriers at the basin scale and fish communities are characterized by high diversity of and dominance by native species including several species of conservation concern. It represents a best available existing biotic condition in the upper Tennessee River drainage. However, it is faced with an increasing pressure from population growth and land development in the rapidly growing Cumberland Plateau region. This has triggered the development of a multi-species Cumberland Habitat Conservation Plan (HCP), a provision being prepared voluntarily by local governments at the time of writing under the authority of the US Endangered Species Act to obtain permits that allow otherwise unlawful impacts on listed and non-listed species of conservation concern. Identifying and prioritizing aquatic conservation areas was a major focus in preparing this HCP, and fish community diversity, among other criteria, was considered in this regard.

Conservation status and associated conservation efforts are often designated at the species level (e.g. the US Endangered Species Act), but community-level analyses can complement species-specific ones to improve conservation strategies (Clarke *et al.*, 2010; Paknia and Pfeiffer, 2011). Community diversity (i.e. the number of community types) is an important criterion to be considered in conservation planning, but it may be missed if conservation planning is based solely on the species-level approach (Orians, 1993; Angermeier and Winston, 1999). Community-level measures of diversity (e.g. species richness) may provide additional information because areas with high diversity often harbour more rare species (Kerr, 1997; Jetz *et al.*, 2004; Reyjol *et al.*, 2008). Indeed, community analysis may be a cost-effective approach in many instances, particularly for regions such as the south-eastern USA, where freshwater fish diversity is high (Warren and Burr, 1994; Jelks *et al.*, 2008).

Species richness and composition of stream fish communities have been studied extensively at the local habitat scale (i.e. stream reach scale; 10^1–10^2 m). Diversity of local stream fish communities (α diversity) typically increases with stream size (Angermeier and Schlosser, 1989; Rahel and Hubert, 1991). This common pattern may be explained by either a local or regional process. Stream fish ecologists have traditionally documented the importance of local habitat characteristics, and local habitat heterogeneity and volume has been attributed to higher local fish diversity in larger, more downstream sites (Gorman and Karr, 1978; Peterson and Rabeni, 2001; Cianfrani *et al.*, 2009). However, high local fish diversity may also be maintained by dispersal (immigration) to higher-order streams because they possess a higher level of spatial connectivity in the dendritic stream network (i.e. branching like a tree) (Fagan, 2002; Hitt and Angermeier, 2008). The metacommunity approach has gained recent popularity in lotic research based on the recognition that ecological processes at multiple spatial and temporal scales determine local aquatic biodiversity (Falke and Fausch, 2010; Brown *et al.*, 2011).

Little attention has been paid to the pattern of stream fish community turnover among local sites (β diversity), although it is an important component of total regional diversity (γ diversity) and can indicate community diversity directly. Jost (2007) showed that the multiplicative partitioning of diversity ($\gamma = \alpha \times \beta$) provides an ecologically meaningful definition of β diversity as the effective number of distinct communities. In other words, β diversity is a measure of uniqueness or irreplaceability of communities, and thus provides information useful for identifying 'how many community types to conserve'. Patterns of β diversity may change spatially for fish communities due to the dendritic nature of stream network habitat that mediates the importance of dispersal longitudinally. Brown *et al.* (2011) suggested that habitat heterogeneity and limited dispersal among headwater streams should lead to high β diversity, although they may have low α diversity and resulting γ diversity may be low. However, this prediction may or may not hold true for macroinvertebrate communities (Brown and Swan, 2010; Clarke *et al.*, 2010), and patterns of β diversity depend inherently on the spatial scale of study and the taxa (Soininen *et al.*, 2007; Higgins, 2010; Paknia and Pfeiffer, 2011).

Community analyses can also shed light on the processes responsible for the observed patterns, particularly the role of dispersal. Dispersal may be difficult to quantify in the field especially at the basin scale, but it may be inferred from spatial patterns of

fish community composition. The correlation between fish diversity and variables related to stream position within a basin (e.g. confluence and downstream link) is frequently considered evidence of fish dispersal (Osborne and Wiley, 1992; Smith and Kraft, 2005; Hitt and Angermeier, 2008), and spatial autocorrelation analysis may quantify the degree of dispersal within a metacommunity (Grenouillet et al., 2008; Brown and Swan, 2010). Diversity partitioning of stream fish communities, combined with these additional analyses, has rarely been studied. We believe that the lack of research is partly because only a limited opportunity exists to study spatial patterns of fish community diversity in a near-natural river basin, especially in the temperate region.

This study investigated spatial patterns and partitioning of fish community diversity in the Emory River basin, Tennessee, USA, to help prioritize aquatic conservation areas in the Cumberland HCP. Fish community data were analysed to assess (1) longitudinal patterns and partitioning of fish community diversity and (2) evidence of dispersal affecting fish community diversity and composition. The HCP has embraced the use of best available scientific information, and understanding spatial patterns of fish community diversity could inform the process greatly.

METHODS

Study area

This study was conducted at 57 stream sites located in the Emory River basin, Tennessee, USA (Figure 1). The basin is located in the Cumberland Plateau and the Cumberland Mountains regions. The study basin covers an area of approximately 2250 km^2 and drains into Watts Bar Lake (Figure 1). Regional geological formations are composed of Pennsylvanian-age conglomerate, sandstone, siltstone, and shale covered by mostly well-drained, acidic soils of low fertility. The basin is predominantly forested (68.9%) along with agriculture (10.8%), urban development (7.6%), and coal mining (nine active mines and five active quarries) based on the 2006 National Land Cover Data (http://www.epa.gov/mrlc/nlcd-2006.html). Importantly, the study area has a significant aquatic conservation value in the region. A number of endemic and rare aquatic species are known in the Emory River basin, including four mussel species that are federally listed as endangered

(turgid blossom *Epioblasma turgidula*, fine-rayed pigtoe *Fusconaia cuneolus*, Alabama lampmussel *Lampsilis virescens*, and purple bean *Villosa perpurpurea*) and one fish species that is federally listed as threatened (spotfin chub *Erimonax monachus*). The study area contains characteristic natural areas represented by the Obed Wild and Scenic River, Catoosa Wildlife Management Area, and Frozen Head State Park (Figure 1). Although signs of human impacts are not uncommon, the Emory River basin is a valuable remnant of what free-flowing rivers in the upper Tennessee River drainage historically represented. No man-made barriers are known to occur between any pair of the 57 study sites, although water supply reservoirs do exist at the very headwaters of the Emory River basin, which are located around the City of Crossville (Figure 1).

Fifty-seven stream sites were selected based on accessibility, ability for effective sampling, presence of representative habitat types (i.e. pools, runs, and riffles), and spatial representation within the study basin. They were classified as either mainstem or sub-basin sites, and the latter were further divided into Clear, Daddys, Emory and Obed sub-basin sites (Figure 1). There is no obvious way of grouping stream sites when they are distributed in a spatially continuous manner, but the catchment sizes of mainstem sites exceeded 300 km^2 in this study (Table 1). Of the four sub-basins, Emory Sub-basin was the least disturbed overall as represented by high percentage values of forest and low values of impervious cover within upstream catchments of study sites (Table 1). The Daddys and Obed sub-basins were the two most disturbed in the study area, although sites in these sub-basins were not highly disturbed in an absolute sense; the median value of impervious cover within the upstream catchment was still 1.9% in Daddys and 2.4% in Obed (Table 1). Other catchment-scale and local-scale habitat characteristics are summarized in Table 1.

Fish sampling

Fish were sampled using electrofishing at 57 stream sites (200 m section at each site) (Figure 1). Each site was sampled once in 2004 or 2005 primarily during summer (May–October). A single-pass electrofishing was conducted with AC backpack electrofishing units powered by a Honda EX-350 portable generator. Block nets were not used because previous studies had shown that use of block nets was not required to obtain a representative sample of fish
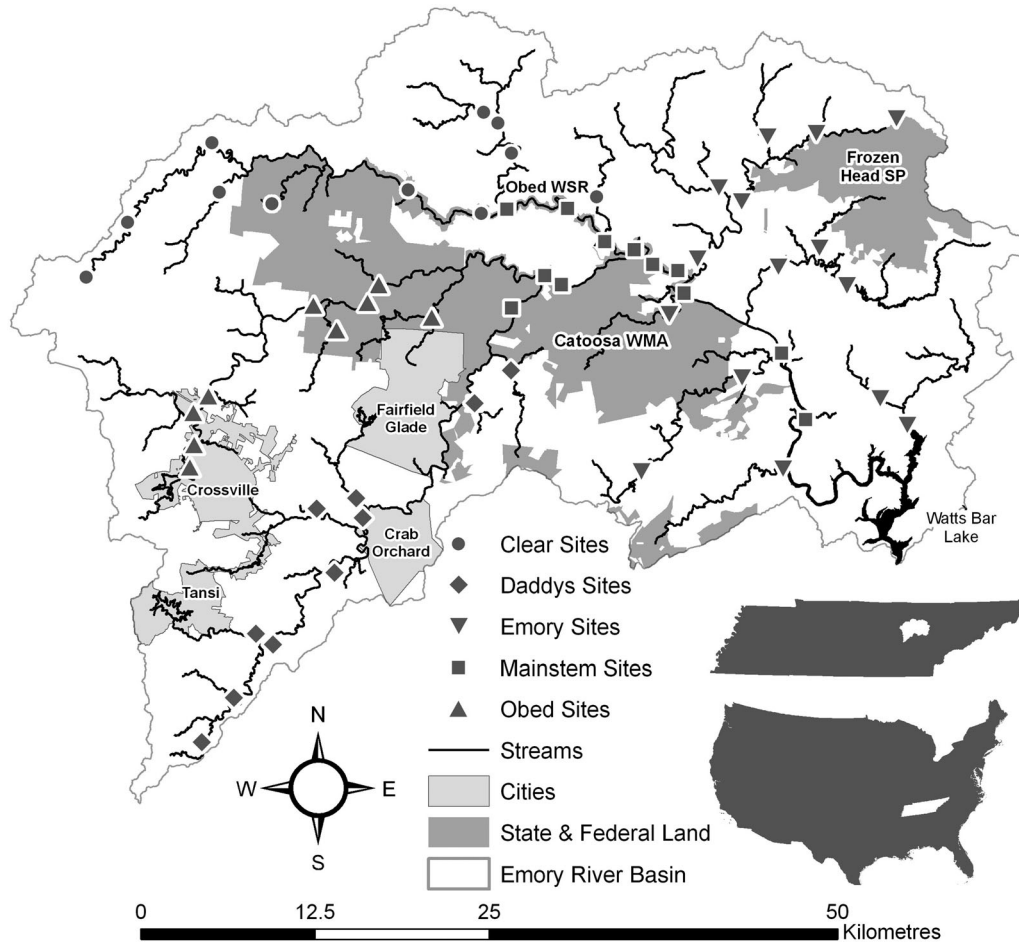
Figure 1. Map of 57 study sites in the Emory River basin located in Tennessee, USA. Spatial locations of some study sites were jittered for visual clarification.

communities (Simmonson and Lyons, 1995; Edwards *et al.*, 2003). Electrofishing was conducted in wadeable habitats following a zigzag pattern while moving upstream, ensuring that all habitat types were sampled. The number of electrofishing units used depended on mean stream width (i.e. < 10 m = 1 unit, 10–20 m = 2 units, and > 20 m = 3 units). At larger sites, additional sampling effort was expended with seine hauls in wadeable large pools or electrofishing downstream into a seine. All individuals captured were identified, enumerated, and released alive at the site of capture.

Data analysis

Both native and non-native species were included in the subsequent community-level analyses. This was an appropriate approach owing to the dominance of native species in the study basin (see Results), and the inclusion of non-native species should have negligible influence on the outcome of the analyses.

Total fish diversity (γ), as measured by species richness and Shannon diversity, was partitioned into within-community (α) and among-community (β) components using a multiplicative decomposition method (i.e. $\gamma = \alpha \times \beta$) (Jost, 2007). Jost (2007) showed that conventional diversity indices fail to produce ecologically meaningful interpretation of β diversity, and proposed to use 'numbers equivalents' of conventional diversity indices. Specifically, while species richness did not require transformation, Shannon entropy (the conventional Shannon–Wiener index) was converted by taking its exponential (i.e. $\exp(-\sum_{i=1}^{S} p_i \ln p_i)$, where S is the number of species and p is proportional abundance for species i). Importantly, β diversity calculated by this multiplicative partitioning method can be interpreted as the effective number of distinct communities in the group (Jost, 2007). In this paper, diversity partitioning based on species richness is referred to as S_α, S_β, and S_γ, and that based on Shannon diversity is referred to as D_α, D_β, and D_γ.

Table 1. Habitat summary of 57 study sites. Median (range) values are shown by each group of sites

	Mainstem	Clear sub-basin	Daddys sub-basin	Emory sub-basin	Obed sub-basin
Number of sites	13	11	9	15	9
Catchment characteristics					
Catchment area (km^2)	855 (362–1958)	49 (16–232)	44 (13–240)	52 (11–239)	46 (18–267)
Stream order[‡]	5 (4–6)	3 (1–4)	3 (2–4)	3 (1–4)	3 (2–4)
Link magnitude[‡]	182 (72–426)	8 (1–43)	11 (2–56)	12 (1–45)	10 (4–57)
Confluence link[‡]	25 (12–36)	39 (27–55)	52 (33–61)	25 (3–39)	38 (32–53)
Downstream link[‡]	183 (73–428)	9 (3–5)	23 (5–99)	23 (2–443)	27 (5–62)
% forest within catchment[*]	64 (56–84)	66 (51–75)	53 (43–88)	82 (70–98)	51 (37–90)
% impervious within catchment[*]	1.7 (1.1-2.2)	1.4 (1.1–1.8)	1.9 (1.1–3.2)	1.2 (1.0–2.0)	2.4 (1.0–5.7)
Local site characteristics					
Mean width (m)[†]	25.0 (19.6–42.3)	9.7 (5.1–15.2)	10.6 (4.5–16.5)	10.8 (6.3–21.5)	12.5 (5.8–25.7)
Mean depth (cm)[†]	57.7 (48.9–82.6)	41.0 (14.3–51.2)	35.7 (20.4–53.7)	40.0 (15.3–53.6)	35.5 (12.8–55.5)
Site gradient[†]	1.3 (0.6–1.9)	0.7 (0.2–1.1)	0.5 (0.2–1.0)	0.7 (0.3–1.9)	0.6 (0.4–1.2)
Temperature (°C)[†]	23.5 (16.9–27.7)	19.1 (15.8–25.3)	20.5 (17.4–21.9)	21.5 (16.2–25.3)	19.3 (17.2–22.8)
pH[†]	7.6 (6.8–8.5)	7.0 (6.5–7.6)	7.7 (7.1–8.0)	7.0 (6.5–8.0)	7.7 (7.2–8.0)
Conductivity (µS)[†]	88.3 (38.1–112.0)	46.7 (23.0–82.8)	72.7 (47.5–115.2)	99.9 (37.7–295.9)	120.2 (26.3–221.5)
Turbidity (NTU)[†]	1.3 (0.8–5.0)	2.2 (0.8–4.9)	4.1 (2.1–15.1)	2.9 (0.5–8.8)	4.4 (1.5–5.9)

[‡]Calculated based on the Environmental Protection Agency's Reach File Version 3.0.
[*]Calculated based on the 2006 National Land Cover Data.
[†]Measured in the field at the time of fish sampling.

Diversity partitioning was calculated at two spatial scales. First, S_γ and D_γ were calculated for a group of mainstem sites and each group of the four sub-basin sites; D_γ was based on the mean relative abundance across sites within the habitat group (i.e. equal weights were given among sites). Mean species richness and mean of an exponential of Shannon entropy per site represented S_α and D_α, respectively, and β diversity was calculated by $S_\beta = S_\gamma/S_\alpha$, and $D_\beta = D_\gamma/D_\alpha$. Second, diversity partitioning of the four sub-basins was conducted in order to quantify community uniqueness of each sub-basin. At this spatial scale, S_γ was the total number of species among sub-basins, and D_γ was based on the mean relative abundance across sub-basins. S_α was the mean species richness per sub-basin, and D_α was the mean of an exponential of Shannon entropy per sub-basin. Again, $S_\beta = S_\gamma/S_\alpha$, and $D_\beta = D_\gamma/D_\alpha$ at the sub-basin scale as well. Because values of β diversity depend upon the number of samples within a group (Jost, 2007) and the number of sites differed among the mainstem and sub-basin groups, species accumulation curves were constructed for each group of sites in order to assess whether S_β and D_β were influenced by sampling effort. Species accumulation curves were derived from 200 randomizations of stream site sampling order without replacement in EstimateS (Colwell, 2005).

Indicator species analysis was used for assessing species' association with the mainstem versus sub-basin sites in order to identify the contribution of individual species to the community diversity pattern. The analysis is based on two measures related to the association of species to a group of sites (Dufrene and Legendre, 1997). Relative mean abundance measures uniqueness of a species to a particular group of sites, and relative frequency measures how ubiquitous that species is among samples of that particular group. For species i in site group j, relative mean abundance = Nindividuals$_{ij}$ / Nindividuals$_i$, where Nindividuals$_{ij}$ is the mean number of individuals of species i across sites of group j, and Nindiviauls$_i$ is the sum of the mean numbers of individuals of species i over all groups. Relative frequency is expressed as Nsites$_{ij}$ / Nsites$_j$, where Nsites$_{ij}$ is the number of sites in group j, in which species i is present, and Nsites$_j$ is the total number of sites in the group j. Indicator values are then calculated as (relative mean abundance) × (relative frequency) × 100. The indicator value ranges from 0% (no affinity of a species to a group of sites) to 100% (perfect affinity); the maximum indicator value is obtained when a species is found in all sites within a group but absent from all other group(s). Two independent analyses of indicator values were performed because indicator values depend on how study sites are clustered into groups. Specifically, one analysis was based on two groups (13 mainstem sites versus 44 sub-basin sites), and the other analysis further divided the sub-basin sites into four groups (11 Clear sites, 9 Daddys sites, 15 Emory sites, and 9 Obed sites). The group for which each species had the highest indicator value was identified and its significance (P-value < 0.05) was calculated with 1000 random permutations of the original data (i.e. the null model was random distributions of individuals among

sites). Indicator species analysis was conducted using the labdsv package in R (R Development Core Team, 2011).

Effect of stream size and position on species richness was examined with a generalized linear regression model (GLM). The Poisson model was used because the response variable (i.e. species richness) took on positive integer values. Catchment size, stream order, link magnitude (number of first-order streams within the upstream catchment), confluence link (number of confluences downstream from each stream reach), and downstream link (link magnitude of the next downstream confluence) were calculated for each stream site (Smith and Kraft, 2005) based on the US Environmental Protection Agency's Reach File Version 3.0 (http://www.epa.gov/waters/doc/rfnsdr. html). All covariates, except stream order and confluence link, were log-transformed to improve linearity. The GLM using each of the covariates as a predictor was fitted, and support for models was assessed using Akaike's Information Criterion corrected for small sample size (AIC_c); smaller AIC_c values indicated better model fit (Burnham and Anderson, 2002).

Spatial autocorrelation analysis was performed on fish communities within the mainstem sites and each group of sub-basin sites. This analysis complemented indicator species analysis by examining distance-mediated changes in fish communities within the clusters of sites determined a priori. Waterway distance following stream channel networks was calculated between all pairs of stream sites within each group, using the Network Analysis Toolbox in the ArcGIS version 9.3. Community distance between site pairs was quantified with the Bray–Curtis dissimilarity index (Bray and Curtis, 1957) based on relative abundance (labdsv package in R). Indices based on species presence and absence (e.g. Sorensen dissimilarity index) were not used because stream fish community data have an abundance of singletons and doubletons (Kanno *et al.*, 2009), and relative abundance should more accurately reflect ecological distances among samples. The presence of spatial autocorrelation was assessed using a simple linear regression and a local polynomial regression ('loess' function in R) between the Bray–Curtis dissimilarity index and waterway distance.

RESULTS

In total, 11 415 individuals from 52 fish species were collected in the 57 study sites (Appendix 1). Fish communities were dominated by those native to the Emory River basin, except that five non-native species were observed (golden shiner *Notemigonus crysoleucas*, redeye bass *Micropterus coosae*, redbreast sunfish *Lepomis auritus*, western mosquitofish *Gambusia affinis*, and yellow perch *Perca flavescens*). Based on total abundance, the five most common species were largescale stoneroller *Campostoma oligolepis* (2666 individuals), whitetail shiner *Cyprinella galactura* (989 individuals), telescope shiner *Notropis telescopus* (802 individuals), warpaint shiner *Luxilus coccogenis* (757 individuals), and Tennessee shiner *Notropis leuciodus* (686 individuals). Several rare species were collected including the federally threatened spotfin chub, and species of regional conservation concern (tangerine darter *Percina aurantiaca*, longhead darter *Percina macrocephala*, and olive darter *Percina squamata*). Overall, the characteristics of the observed fish communities reaffirmed the high aquatic conservation value of the study basin.

Diversity partitioning

Analysis of diversity partitioning revealed a few notable patterns (Table 2). First, local site-level S_α and D_α were higher at the mainstem sites, compared with sites located in sub-basins (ANOVA: F-value = 8.19, P-value < 0.001 for S_α; F-value = 4.83, P-value = 0.002 for D_α). For example,

Table 2. Partitioning of fish community diversity for species richness and Shannon diversity

	Species richness	Shannon diversity
Mainstem (13 sites)		
α (sites)	19.31	9.65
β (sites)	2.07	1.70
γ	40.00	16.35
Sub-basin (44 sites)		
Clear sub-basin (11 sites)		
α (sites)	11.09	5.75
β (sites)	1.98	1.97
γ	22.00	11.33
Daddys sub-basin (9 sites)		
α (sites)	11.00	6.33
β (sites)	2.00	1.72
γ	22.00	10.88
Emory sub-basin (15 sites)		
α (sites)	12.67	6.12
β (sites)	3.08	2.52
γ	39.00	15.43
Obed sub-basin (9 sites)		
α (sites)	9.67	5.24
β (sites)	2.59	2.38
γ	25.00	12.49
All sub-basins (4 sub-basins)		
α (sub-basins)	27.00	12.53
β (sub-basins)	1.63	1.38
γ	44.00	17.26

S_α among mainstem sites (19.31) exceeded S_α among Emory sub-basin sites (12.67), which had the highest S_α value among the four sub-basins. Second, site-level S_α and D_α values were comparable among the four sub-basins (ANOVA: F-value = 0.84, P-value = 0.48 for S_α; F-value = 0.20, P-value = 0.89 for D_α), but site-level β values differed, particularly for S_β. As a result, S_γ values ranged from 22 total species for Clear and Daddys sub-basins to 39 total species for Emory Sub-basin. Third, γ diversity among 13 mainstem sites was comparable with that among 44 sub-basin sites. A total of 40 species were collected in 13 mainstem sites versus a total of 44 species in 44 sub-basin sites, and D_γ was 16.35 for the mainstem sites compared with 17.26 for the sub-basin sites. Fish communities were not highly distinct among the four sub-basins (S_β = 1.63 and D_β = 1.38); it should be noted that maximum values of S_β and D_β would be four if each sub-basin harboured a completely unique fish community.

Species accumulation curves differed between the mainstem and sub-basin groups, and also among the sub-basins (Figure 2). The Emory sub-basin had a higher rate of species accumulation with increasing number of stream sites, relative to other three sub-basins. Notably, this pattern was observed despite the comparable mean site-level species richness among sub-basins (Table 2). This observation confirmed that the high site-level β values for the Emory sub-basin were not an artifact of more sampling effort (more sites) in this sub-basin.

Indicator species analysis

A number of species were associated with the mainstem sites, while few were associated with sub-basin
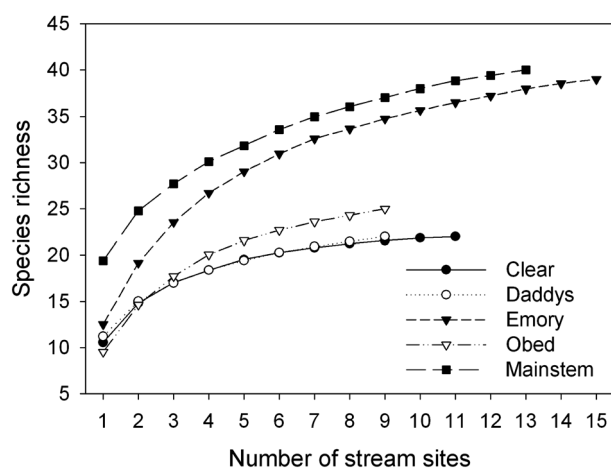

Figure 2. Species accumulation curves in the mainstem and four sub-basins. Mean number of species richness derived from 200 randomizations is shown at each number of stream sites.

sites (Table 3). Several species had high indicator values (> 60%) for the mainstem sites. Tangerine darter had the highest indicator values for the mainstem sites. The federally threatened spotfin chub was also associated with mainstem sites. The high number of indicator species for the mainstem sites meant that many species, including some species of concern, were generally confined to the mainstem but were commonly observed among the mainstem sites.

For sub-basin sites, creek chub *Semotilus atromaculatus* was the only species with a statistically significant indicator value when mainstem sites were compared with a group of all sub-basin sites (Table 3). This suggested that this species was widespread among sub-basin sites, but not common in the mainsteam sites. When each sub-basin was used in indicator species analysis, one to four species had statistically significant indicator values for each sub-basin (Table 3).

Effect of stream size and position on species richness

Covariates related to stream size and position were highly correlated with each other (Spearman's rank correlation $r_s > |0.51|$, P-value < 0.001). Of the five covariates, catchment area (AIC_c = 312.64) explained among-site variation in species richness better than downstream link (AIC_c = 317.02), link magnitude (AIC_c = 318.10), stream order (AIC_c = 330.36) or confluence link (AIC_c = 357.80). The difference in AIC_c values (ΔAIC_c) exceeding 2 is typically considered evidence of support for the better candidate model (i.e. the one with smaller AIC_c value) (Burnham and Anderson, 2002); therefore, catchment area had support as the most influential habitat covariate related to stream size and position.

Spatial autocorrelation analysis

Simple linear regression identified statistically significant spatial autocorrelation among mainstem sites (r_s = 0.44, P < 0.001), Daddys sub-basin sites (r_s = 0.53, P = 0.001), and Obed sub-basin sites (r_s = 0.36, P = 0.033) (Figure 3). Spatial arrangements of the stream sites were rather linear in these groups of sites, indicative of a longitudinal biotic gradient (Figure 1). In contrast, significant spatial autocorrelation was not confirmed based on simple linear regression for Clear sub-basin sites (r_s = 0.11, P = 0.443) and Emory sub-basin sites (r_s = 0.10, P = 0.322) (Figure 3); stream sites in these sub-basins were located in a set of smaller drainages flowing into the Emory River mainstem (Figure 1). Interestingly,

Table 3. Summary of two indicator species analyses. Indicator values shown are statistically significant (P-value < 0.05) with 1000 random permutations

Mainstem and a group of sub-basins			Mainstem and four sub-basins		
Group	Species	Indicator values	Group	Species	Indicator values
Mainstem	Tangerine darter	93.5	Mainstem	Tangerine darter	79.4
	Smallmouth bass	87.0		Spotfin chub	67.1
	River chub	83.5		Smallmouth bass	63.7
	Redline darter	80.9		Tennessee shiner	57.8
	Greenside darter	78.7		Spotfin shiner	56.2
	Telescope shiner	75.4		Telescope shiner	54.8
	Spotfin chub	73.3		Redline darter	52.9
	Rock bass	66.2		River chub	52.0
	Spotfin shiner	66.0		Longear sunfish	50.2
	Whitetail shiner	65.9		Greenside darter	48.7
	Longear sunfish	61.8		Wounded darter	38.5
	Tennessee shiner	60.2		Rock bass	34.3
	Warpaint shiner	58.9		Snubnose darter	32.3
	Wounded darter	38.5		Flathead catfish	31.6
	Snubnose darter	36.1		Mimic shiner	30.1
	Flathead catfish	35.8		Silver shiner	23.1
	Mimic shiner	30.5			
	Silver shiner	23.1			
Sub-basins	Creek chub	56.8	Clear sub-basin	Black bullhead	27.3
			Daddys sub-basin	Black darter	74.2
			Emory sub-basin	Striped shiner	63.5
				Stripetail darter	53.3
				Logperch	35.4
				Sand shiner	31.9
			Obed sub-basin	Green sunfish	49.5
				Redeye bass**	33.3

**Fish species not native to the study basin.

community dissimilarity showed a dome-shaped pattern to waterway distance in these sub-basins (Figure 3), meaning that fish communities were most dissimilar at the intermediate geographic distances.

DISCUSSION

This study represented a unique effort to assess spatial patterns and partitioning of fish community diversity in a near-natural basin of high conservation value in south-eastern USA, a region which harbours aquatic biodiversity disproportionately in North America (Warren and Burr, 1994; Jelks et al., 2008). The presence of several rare species of conservation concern and dominance of fish communities by native species reaffirmed the high conservation value of the study area. This study also advances general understanding of diversity patterns in the dendritic habitat network, which is shown to have characteristic properties of connectivity distinct from the two-dimensional terrestrial habitat (Fagan, 2002; Brown et al., 2011).

Community diversity among the mainstem sites

The mainstem habitat was evidently characterized with high α and γ diversity in the Emory River

basin. This was an expected result; a downstream increase in stream fish diversity is a commonly observed pattern (Angermeier and Schlosser, 1989; Rahel and Hubert, 1991). A few rare stream fish species were found almost exclusively in the mainstem sites, as shown by high indicator species values. Tangerine darter, the species with the highest indicator values to the mainstem sites, is deemed in need of management in Tennessee. Another notable species is spotfin chub, which is federally listed as threatened and considered to be endangered in three states that contain remaining populations. This species is clearly restricted to the mainstem habitat in the study area; in fact, local abundance generally increases downstream among stream sites in which this species occurs in the study area (Kanno et al., 2012).

High site-level α diversity resulted in high γ diversity in the mainstem habitat (40 species from 13 sites), which was comparable with γ diversity of all sub-basin sites (44 species from 44 sites). Interestingly, the Emory sub-basin possessed γ diversity (39 species from 15 sites) that was similar to the mainstem habitat. In this sub-basin, it was high β diversity, rather than high α diversity, that contributed much to total diversity. In fact, the species accumulation curve of the Emory sub-basin (lower α and higher β diversity) was rather similar to that of the mainstem (higher α and lower β diversity). This comparison
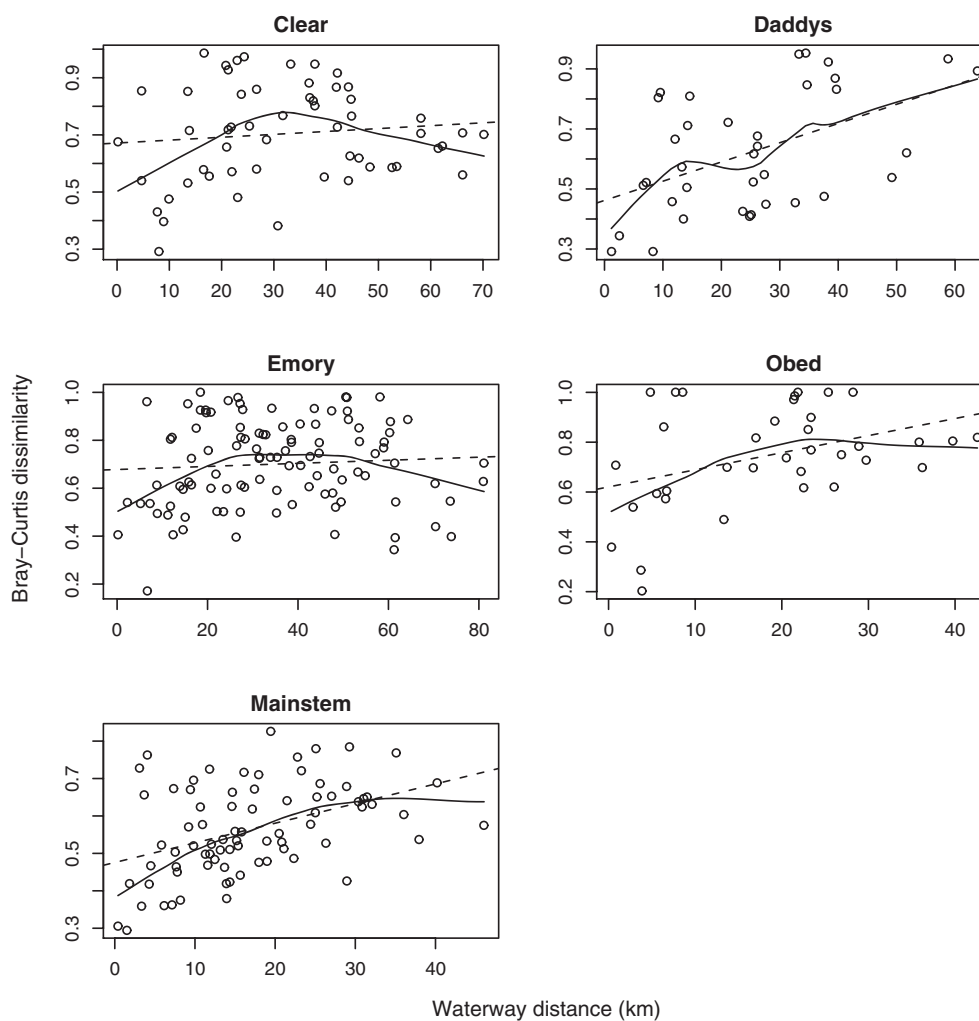
Figure 3. Spatial autocorrelation analysis based on relative abundance (Bray–Curtis dissimilarity) and waterway distance in the mainstem and four sub-basins. Dashed lines represent fit from simple linear regression and solid lines represent fit from polynomial regression. Note that the range of the x-axis varies among panels.

showed from interesting empirical data that a group of mainstem sites and another of tributary sites may have similar total fish community diversity, although relative contributions of α and β components differ between them.

Dispersal is considered to exert an important influence on the composition of mainstem communities in the dendritic stream network habitat (Brown and Swan, 2010). However, a strong effect of dispersal on the mainstem fish communities was not detected in this current study. It was primarily the presence of mainstem-obligate species, but not dispersal of headwater species into mainstem sites, that characterized local communities. In addition, significant spatial autocorrelation was found among mainstem sites, which was almost linearly arranged along the mainstem habitat (Figure 1). If dispersal had been ubiquitous and strong, no significant spatial autocorrelation should be expected at the spatial scale of investigation (i.e. 10^1 km along a connected

habitat). In other words, high rates of dispersal should have 'swamped' local habitat influences that are expected to exist longitudinally (Vannote et al., 1980; Poff, 1997). Inference of limited dispersal among mainstem sites is inconclusive from this study alone and some individuals of resident (non-migratory) stream fish may infrequently exhibit long-range dispersal (Skalski and Gilliam, 2000; Fausch et al., 2002), but results suggest that the mainstem metacommunity might be best described to follow the 'species-sorting' perspective, which suggests that local environmental factors are more important than dispersal in structuring local community composition (Leibold et al., 2004).

Community diversity among the sub-basin sites

Sub-basin sites were generally characterized with low site-level α diversity, but site-level β diversity was higher in the Emory sub-basin than in the other

three sub-basins. As a result, γ diversity of the Emory sub-basin was higher than that of other sub-basins despite having similar site-level α values. Perhaps, high site-level β diversity in the Emory sub-basin might be partly explained by its stream network pattern. Stream sites in other sub-basins, particularly Obed and Daddys sub-basins, were located along the stream channel in a rather linear manner (Figure 1). However, the Emory sub-basin was composed of a subset of smaller drainages that emptied into the Emory River mainstem. High β diversity may have resulted from habitat heterogeneity within Emory sub-basin sites, or isolation of fish communities among the smaller drainages if the mainstem habitat acted effectively as a movement barrier caused by poor habitat suitability or geographical distance for headwater species.

The characteristic network pattern of the Emory sub-basin, and to a lesser extent of the Clear sub-basin, may also explain results of spatial autocorrelation analysis. Fish community dissimilarity increased with waterway distance in Daddys sub-basin, Obed sub-basin and mainstem habitat. However, patterns were different for Clear and Emory sub-basins, in which community dissimilarity showed a unimodal relationship with waterway distance. In the stream network system, the greatest geographic separation may occur between two points located at the most upstream areas of spatially disjunct drainages. Low community dissimilarity at the greatest geographic distances observed in Clear and Emory sub-basins generally indicates that upstream sites share similar fish communities even though they are located further apart from each other in different parts of sub-drainages. Spatial autocorrelation analysis has been used to assess the relative importance of dispersal in metacommunity analysis of stream communities (Grenouillet *et al.*, 2008; Brown and Swan, 2010). However, the interpretation of such analysis may not be straightforward and needs to carefully incorporate stream network pattern.

Fish communities were only modestly distinct among sub-basins, as represented by relatively low sub-basin-level β diversity. This result was not surprising given the spatial scale and configuration of the study sites; longitudinal variation in fish communities within sub-basins was large, compared with variation among spatially adjacent sub-basins located within a large single basin. We do not think the fish community similarity among sub-basins is

due to high rates of dispersal among them, although more detailed studies are required to substantiate such a hypothesis (e.g. genetic analysis of movement patterns for headwater species).

Similar to the mainstem habitat, dispersal appears to be a limited factor that shapes fish communities in sub-basin sites, a hypothesis proposed by earlier work (Fagan, 2002; Brown and Swan, 2010). Stream size, as represented by catchment size, was the most important covariate that explained variation in among-site species richness in this study. This was an interesting result because previous studies found that accounting for stream size and position would explain fish community diversity better than stream size alone (Osborne and Wiley, 1992; Smith and Kraft, 2005; Hitt and Angermeier, 2008). These studies considered that such a spatial pattern resulted from immigration of fish from mainstem to tributary sites. The finding that many species were confined to the mainstem sites (i.e. high indicator values) despite connectivity to sub-basin sites suggested that local habitat characteristics of sub-basin sites may filter out mainstem species in the study catchment. Finally, significant spatial autocorrelation in Daddys and Obed sub-basins are also indicative of limited dispersal. Taken together, the 'species-sorting' perspective appears to be the best paradigm for sub-basin metacommunities as well (Leibold *et al.*, 2004).

Conservation implications

Conservation actions frequently need to be taken based on the best available scientific information. The Cumberland HCP being developed in the study area at the time of writing aims to protect 23 terrestrial (e.g. bats and birds) and aquatic (e.g. fish, mussels and crayfish) species by suggesting species-specific conservation measures. Analyses of fish community diversity patterns and partitioning here was intended to complement efforts to identify and prioritize aquatic conservation areas in the Cumberland HCP; more restrictive conservation measures and mitigation efforts are being proposed in these areas. Below, the utility of fish community analyses are discussed with regards to the Cumberland HCP.

High γ diversity and the presence of species of conservation concern make the mainstem habitat disproportionately important for conservation in the Emory River basin. It is worth mentioning that obligate riverine species have historically suffered out of proportion because of the construction of

mainstem reservoirs in the upper Tennessee River drainage, as well as other regions globally (Benke, 1990; Dynesius and Nilsson, 1994). Thus, existing near-natural rivers such as Emory River bear an exceptional conservation value. In addition, the list of fish species collected at the mainstem sites in this study does not capture all species present in the sites. Ecological surveys can rarely detect all species that are present at survey sites, and we consider that incomplete detection was more likely to occur at the mainstem sites than at the sub-basin sites. A smaller proportion of the available habitats were effectively sampled by the fish survey methods used (i.e. backpack electrofishing and seines) at the mainstem sites. In fact, additional snorkelling and shoreline visual surveys conducted at some mainstem sites confirmed the presence of additional species including freshwater drum *Aplodinotus grunniens*, longnose gar *Lepisosteus osseus*, and ashy darter *Etheostoma cinereum* (W.T. Russ, unpublished data); the last species is listed as threatened in Tennessee. Therefore, the issue of incomplete detection further underscores species diversity at the mainstem sites and makes them even more important from a conservation perspective.

Consequently, the mainstem segment of the Emory River and its riparian zone are being proposed as important aquatic conservation areas in the Cumberland HCP. A noteworthy point is that extensive upstream segments and their associated riparian areas are also considered aquatic conservation areas in this HCP because of longitudinal connectivity and influence of stream habitats (Vannote *et al.*, 1980). This was important in the Cumberland HCP because the largest population growth and related land development is expected to occur further upstream around the City of Crossville and Fairfield Glade (Figure 1). The spatial extent of downstream influence of human activities is difficult to quantify, but protection of aquatic diversity in the mainstem habitat evidently requires spatially extensive application of conservation measures at the basin scale (e.g. protection of riparian areas and stormwater management).

A particularly useful attribute of community-level analyses stems from the interpretation of β diversity as the effective number of distinct communities (Jost, 2007). In this study, sub-basin-level S_β was 1.63 and D_β was 1.38 out of a potential maximum value of 4 (i.e. four sub-basins). The low sub-basin-level β diversity suggests that fish communities are not highly distinct between four sub-basins. In this case,

a sensible conservation approach is to focus on one (or two) sub-basins but provide extensive conservation measures for them. Because the Emory sub-basin harboured most of the species richness found among sub-basin sites (40 out of 44 species), the stream network in this basin is also proposed for aquatic conservation areas. In regional conservation planning like the Cumberland HCP, we consider that β diversity can provide some scientific basis for deciding how much habitat needs to be conserved, whereas α and γ may primarily indicate where priority areas exist.

Community-level analyses also provide useful information when distributions of species of conservation concern are apparently clustered in a particular locale or habitat type. In this study, species of the highest conservation priorities (e.g. spotfin chub, tangerine darter) were confined to the mainstem habitat. If regional conservation planning had been based solely on individual species, fish community patterns within and among sub-basins would not have been documented. Yet, streams encompass a range of physical and biological gradient longitudinally (Vannote *et al.*, 1980), and conserving a representative component of landscapes and habitats is an important principle of conservation planning (Noss *et al.*, 1999). Community analyses may also facilitate planning efforts when distributional and other ecological information on individual species is lacking (Clarke *et al.*, 2010; Paknia and Pfeiffer, 2011). Thus, community analyses complement, but do not replace, species-level analyses in conservation planning efforts.

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APPENDIX 1

LIST OF FISH SPECIES AND THEIR OCCURRENCE IN THE 57 STUDY SITES IN THE EMORY RIVER BASIN. SPECIES ARE LISTED ALPHABETICALLY BY SCIENTIFIC NAME

Scientific name	Common name	Number of individuals observed	Number of sites observed
Ambloplites rupestris	Rock bass	416	38
Ameiurus melas	Black bullhead	3	3
Ameiurus natalis	Yellow bullhead	16	11
Campostoma oligolepis	Largescale stoneroller	2666	53
Catostomus commersonnii	White sucker	9	2
Cottus carolinae	Banded sculpin	4	1
Cyprinella galactura	Whitetail shiner	989	40
Cyprinella spiloptera	Spotfin shiner	146	16
Dorosoma cepedianum	Gizzard shad	28	2
Erimonax monachus	Spotfin chub	62	12
Etheostoma blennioides	Greenside darter	391	34
Etheostoma camurum	Bluebreast darter	43	2
Etheostoma duryi	Black darter	80	8
Etheostoma jessiae	Blueside darter	6	1
Etheostoma kennicotti	Stripetail darter	80	8
Etheostoma rufilineatum	Redline darter	532	31
Etheostoma simoterum	Snubnose darter	33	7
Etheostoma vulneratum	Wounded darter	11	5
Gambusia affinis[**]	Western mosquitofish	19	1
Hypentelium nigricans	Northern hogsucker	324	44
Lepomis auritus[**]	Redbreast sunfish	517	44
Lepomis cyanellus	Green sunfish	327	38
Lepomis gulosus	Warmouth	25	10
Lepomis macrochirus	Bluegill	258	42
Lepomis megalotis	Longear sunfish	97	20
Lepomis microlophus	Redear sunfish	25	2
Luxilus chrysocephalus	Striped shiner	291	14
Luxilus coccogenis	Warpaint shiner	757	31
Lythrurus ardens	Rosefin shiner	226	11
Micropterus coosae[**]	Redeye bass	31	3
Micropterus dolomieu	Smallmouth bass	134	31
Micropterus punctulatus	Spotted bass	17	9
Micropterus salmoides	Largemouth bass	36	15
Moxostoma erythrurum	Golden redhorse	2	2
Moxostoma sp.	Redhorse sp.	10	1
Nocomis micropogan	River chub	366	27
Notemigonus crysoleucas[**]	Golden shiner	1	1
Notropis leuciodus	Tennessee shiner	686	10
Notropis photogenis	Silver shiner	8	3
Notropis stramineus	Sand shiner	90	10
Notropis telescopus	Telescope shiner	802	22
Notropis volucellus	Mimic shiner	113	5
Perca flavescens[**]	Yellow perch	4	4
Percina aurantiaca	Tangerine darter	146	21
Percina caprodes	Logperch	74	10

(*Continues*)

Continued

Scientific name	Common name	Number of individuals observed	Number of sites observed
Percina evides	Gilt darter	1	1
Percina macrocephala	Longhead darter	7	1
Percina squamata	Olive darter	3	3
Pimephales notatus	Bluntnose minnow	19	3
Pylodictis olivaris	Flathead catfish	10	6
Rhinichthys atratulus	Blacknose dace	51	5
Semotilus atromaculatus	Creek chub	423	25

** Species that are not native to the study basin.