

## RESEARCH ARTICLE

# If you build it, they will go: A case study of stream fish diversity loss in an urbanizing riverscape

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## Abstract

1. Stream fish diversity is threatened by anthropogenic environmental alterations to landscapes, and successful conservation requires knowledge of the processes that degrade diversity. A primary step in identifying diversity losses is the comparison between historical and contemporary states of landscapes and fish assemblages, but uncertainty remains regarding the appropriate spatial scales of investigation.
2. Historical data collected in 1976 were paired with two years of contemporary replication (2015, 2016) to assess fish diversity change at 10 sites in Blackburn Fork, TN, USA. Analyses focused on a nested hierarchy of spatial scales, including sampling sites (fine scale), nested within stream orders (intermediate scale), nested within the entire catchment (broad scale). Diversity change between 1976 and 2015–16 was assessed using traditional diversity metrics (site scale) and rarefaction (stream-order scale), whereas spatial variation in contemporary diversity (2015–16) was assessed with nonmetric multidimensional scaling (catchment scale).
3. At the site scale, locations on the east side of Blackburn Fork and in close proximity to developed land experienced diversity loss. At the stream-order scale, the effective number of species declined in first-order streams where land development was concentrated, but no consistent species losses occurred in other stream orders. At the catchment scale, assemblages responded significantly to stream size but not land use, perhaps because diversity was already homogenized by 2015–16. Mapping 40 years of land-use change across the catchment underscored a pattern of spatial alignment between developed lands and stream fish diversity loss.
4. This study highlights the benefits of considering multiple spatial scales when assessing historical change in stream fish assemblages, and highlights stronger inference derived from historical comparisons relative to contemporary space-for-time substitutions. This framework combines recent analytical advances in rarefaction with a riverscape perspective, and can be applied to conserve streams, and their biota, in riverscapes around the world.

## KEYWORDS

aquatic biodiversity, land-use change, rarefaction, spatial scale, urban stream syndrome

## 1 | INTRODUCTION

Freshwater fish diversity in stream ecosystems is threatened by anthropogenic environmental change to natural landscapes (Closs, Krkosek, & Olden, 2016; Cooke, Paukert, & Hogan, 2012; Dudgeon et al., 2006; Vörösmarty et al., 2010); consequently, conservation of stream fish diversity is now a global concern because of the relative rarity of stream habitats and the large number of threatened species that reside within these ecosystems (Arthington, Dulvy, Gladstone, & Winfield, 2016; Lehner et al., 2011; Liermann, Nilsson, Robertson, & Ng, 2012). Directing conservation action to promote efficiency requires clear conservation goals to be established based on the historical composition of fish assemblages and landscape attributes (Bonebrake, Christensen, Boggs, & Ehrlich, 2010; Humphries & Winemiller, 2009; Matthews & Marsh-Matthews, 2017). In order to establish appropriate conservation goals, however, some knowledge of historical or presumed natural conditions is required (Hermoso, Januchowski-Hartley, & Linke, 2015; Hermoso, Linke, Januchowski-Hartley, & Kennard, 2016; Wellemeyer, Perkin, & Fore, 2018). To this end, comparisons between historical and contemporary landscape conditions and fish assemblages have become common in stream fish conservation.

Historical change among stream fish assemblages has received considerable attention (see symposium by Rinne, Hughes, & Calamuso, 2005). A commonality among approaches is the combination of historical and contemporary collections, usually made by different investigators (Miyazono & Taylor, 2015; Perkin & Bonner, 2011). Although long-term sampling of stream fish assemblages by a single investigator does occur, and the resulting datasets can be leveraged to address ecological and conservation questions (Perkin, Knorp, et al., 2017), more common approaches use known or published historical datasets paired with contemporary studies designed to replicate the historical work (Hitt & Roberts, 2012). However, combining historical and contemporary collections by different investigators to yield reliable comparisons requires knowledge of historical methods, sampling gears, and efforts (Bonar & Hubert, 2002). When methodological or gear changes are known, adjustments for these changes are possible (Patton, Rahel, & Hubert, 1998). Unfortunately, reports quantifying effort (e.g. seconds of electrofishing or number of seine hauls) are uncommon. Addressing uncertainty in effort can be accomplished by scaling species abundances to the total number of individuals captured (Bonner, Thomas, Williams, & Karges, 2005), assigning probability of occurrence among multiple collections (Gido, Dodds, & Eberle, 2010), or the process known as rarefaction (Gotelli & Colwell, 2001; Hurlbert, 1971).

Rarefaction has gained traction as a reliable method for assessing assemblage diversity change as a function of varying samples sizes, individuals encountered, or species coverage (Gotelli & Chao, 2013).

Rarefaction is routinely used on species richness and diversity metrics, including those known as Hill numbers (Hill, 1973). Hill numbers represent measures of assemblage diversity such as species richness ( $q = 0$ ), the exponential of Shannon's entropy index ( $q = 1$ ), and the inverse of Simpson's concentration index ( $q = 2$ ). Hill numbers also have advantages over other diversity indices because: (i) they have additive properties; (ii) they are expressed as 'effective number of species'; and (iii) they represent the unification of diversity and similarity properties (Chao et al., 2014). Cayuela, Gotelli, and Colwell (2015) recently extended rarefaction and Hill number diversity indices into the realm of null model hypothesis testing with the development of the ecological null hypothesis (ENH). Collectively, the emerging need for assessing historical change in stream fish assemblages and recently developed statistical methods for conducting such assessments (while controlling for differential or unmeasured effort) provide new opportunities aimed at bridging the gap between research and stream fish conservation (Fausch, Torgersen, Baxter, & Li, 2002).

Spatial heterogeneity is another factor that must be considered when historical change in stream fish assemblage structure is assessed. In streams, longitudinal zonation and spatially structured fish assemblages are well documented (Huet, 1959; Rahel & Hubert, 1991; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980), but sampling entirely through space is logistically infeasible and subsamples distributed in a manner assumed to be representative of an entire system must be used (Schlosser, 1991; Ward, 1998). Deciding which regions to sample is a challenge (Matthews, 1998) that can be addressed by viewing river ecosystems as aquatic landscapes, or 'riverscapes' (Fausch et al., 2002; Wiens, 2002). This approach relies on theoretical considerations such as hierarchy theory, in which ecosystem components are decomposed into interacting systems within a system (King, 1997). In riverscapes, scalar hierarchies using the spatial extents of study have been proposed (Frissell, Liss, Warren, & Hurley, 1986), including pools nested within reaches, nested within segments, nested within catchments (Fausch et al., 2002). Another hierarchical framework commonly applied to streams is the Strahler (1957) stream ordering system in which first-order streams flow together to form second-order streams, second-order streams flow together to form third-order streams, and so on. Through the lens of stream ordering, riverscapes can be decomposed into levels (or 'holons'; Wu, 2013), with lower levels representing small stream components and higher levels representing large stream components, and with all levels fitting together into a nested hierarchical system. Stream order has long been related to fish assemblage structure (Beecher, Dott, & Fernau, 1988; Sheldon, 1968; Whiteside & McNatt, 1972), and assessing change in fish assemblage structure in streams of a particular order is one approach to integrating spatial considerations into long-term assessments of historical change (Perkin, Gido, et al., 2017), yet few existing studies link historical change with spatially structured observations.

Instead, sites within catchments are generally lumped together to assess 'system-wide' or 'reach-scale' change, generally because of sample size limitations associated with analysis (Perkin & Bonner, 2016; Taylor, Millican, Roberts, & Slack, 2008). The increasing prevalence of spatial datasets (Troia & McManamay, 2016) means that future opportunities for spatially explicit comparisons will exist. Given the rise of spatially structured data (Troia & McManamay, 2017) and continued integration of landscape ecology into stream fish conservation and community ecology (Fausch et al., 2002), the development of analytical frameworks for assessing spatially structured historical change holds potential for advancing stream fish conservation (Fausch, 2010).

This study reviews historical data collected in 1976 and pairs these data with replications conducted during 2015 and 2016 to assess change in stream fish assemblage structure. This approach relies on reported historical methods and gears in the design of contemporary sampling, and accounts for unknown effort by applying recently developed null models of rarefaction (Cayuela et al., 2015). From a spatial perspective, this work leverages stream order-specific abundance data from the historical period to assess spatially structured fluxes in fish assemblage structure. The objectives of this research were: (i) to assess changes in site-specific stream fish diversity between 1976 and 2015–16; (ii) to quantify changes in the effective number of species across all sites stratified by stream order; and (iii) to use fish abundance data and landscape alteration variables from recent years to assess fish assemblage response to land-use gradients. The authors hypothesized that collections made closer together in time would be more similar than those more temporally separated. Support for this hypothesis might reflect long-term directional change. Alternatively, if assemblage structure is either consistent or unique, regardless of time, then assemblages are either in a state of long-term equilibrium or are so dynamic that change cannot be identified. The authors also hypothesized that temporal fluxes in fish assemblage structure would not be even across stream orders, and that small-order streams would be more dynamic than large-order streams. This hypothesis is grounded in principles of hierarchy theory, which state that lower levels tend to be more dynamic than higher levels (Wu, 2013).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

This study considers stream fish assemblage structure in the Blackburn Fork catchment in the Cumberland Plateau region of the south-eastern USA (Figure 1). This region is known as a global fish biodiversity hotspot, in part because of long-term climatic refugia and patterns of vicariance (Abell et al., 2008), and is characterized as a temperate forest biome situated at the southern extent of the Appalachian Mountains. Blackburn Fork is a tributary of the Roaring River, which drains north off the Cumberland Plateau and joins the Cumberland River at Cordell Hull Reservoir in north-central Tennessee. Blackburn Fork has a drainage area of 160 km<sup>2</sup>, culminates in a fourth-order

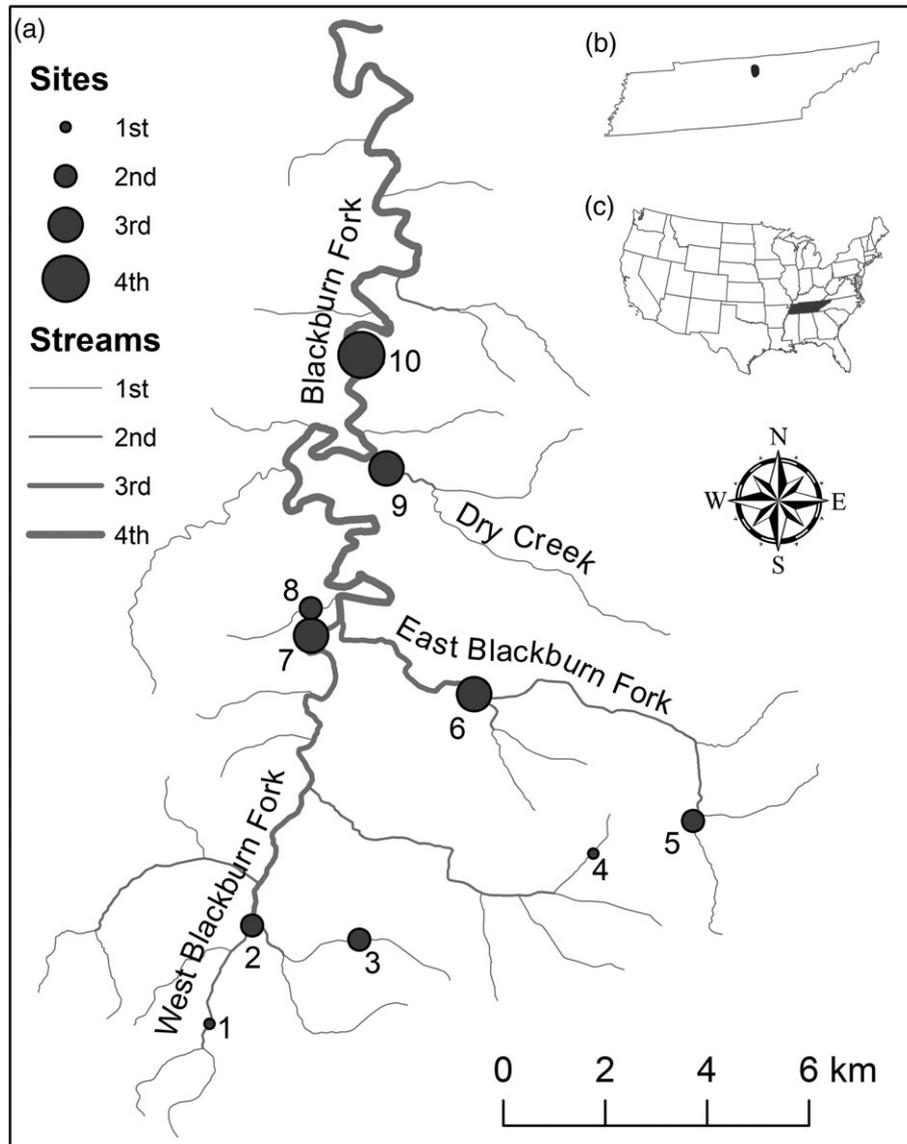
stream, and is identified as hydrologic unit code (HUC, level 12) 051301060205 in the National Hydrologic Dataset (US Environmental Protection Agency (EPA), 2012). Within Blackburn Fork, Hooper (1977) sampled 10 sites distributed across the catchment and located on streams of orders 1–4 (Figure 1a). Sites included two first-order, four second-order, three third-order, and one fourth-order stream. In both historical and contemporary periods, sampling sites were dominated by cobble and gravel substrate with a mixture of pool and riffle geomorphic units. During contemporary sampling, wetted widths and depths of streams in the Blackburn Fork ranged from 6 to 52 m and from 0.1 to 1.1 m, respectively, and canopies in smaller-order streams were generally covered (orders 1–2) and in larger-order streams (orders 3–4) they were open. See Gebhard and Perkin (2017) for further descriptions of contemporary flow and water temperature regimes in the catchment, and Hooper (1977) and Gebhard et al. (2017) for detailed descriptions of historical and contemporary fish habitats.

### 2.2 | Fish assemblage sampling

Fish assemblages were sampled during the autumn of 1976 by Hooper (1977) and again by the authors during the autumn of 2015 and 2016. Protocols during both historical and contemporary sampling periods included a combination of electrofishing and seining. Electrofishing was used to sample all wadeable portions of streams (<0.5 m depth) and seines were used in deeper pools (0.5–1.0 m depth) to target species not captured during electrofishing. Sampling sites ( $n = 10$ ) were bounded by geomorphic breaks (e.g. pool to riffle) that blocked fish emigration during sampling and averaged 100 m (standard deviation = 21) in length, with longer sites on larger streams. Sampling continued until reaches described by Hooper (1977) were covered and no new species were captured in subsequent electrofishing samples or seine hauls. There was no official description of effort (e.g. seconds of electrofishing or number of seine hauls) provided by Hooper (1977), so assessments of assemblage structure used relative abundances (site-specific assemblage structure) and rarefaction (stream order-specific assemblage structure). Care was taken to replicate methods during the same season (August, September, and October) at the same locations based on the timing and access site descriptions provided by Hooper (1977). All fishes collected were identified to species level and released back to the site of capture. Taxonomic statuses from Page et al. (2013) were used to update taxonomic names associated with species descriptions conducted after the initial sampling by Hooper (1977).

### 2.3 | Fine-scale, site-specific assemblage structure

Historical fish assemblage structure at each site was described using species richness ( $S$ ), diversity ( $H$ ), and evenness ( $J$ ). Species richness was the sum of species at each site. Diversity was calculated using Brillouin's index of diversity:



**FIGURE 1** Study area illustrating (a) 10 sites (circles) and streams (lines) sized in proportion to stream orders 1–4 in the Blackburn Fork catchment. Blackburn Fork is located in (b) north-central Tennessee in (c) the south-eastern USA

$$H = \frac{\ln(N!) - \sum_{i=1}^k \ln(n_i!)}{N},$$

where  $n_i$  is the number of individuals belonging to the  $i^{\text{th}}$  of  $k$  species and  $N$  is the total number of individuals in the sample (Pielou, 1975). Relative measures of  $H$  were used to calculate Pielou's evenness as:

$$J = \frac{H}{H_{\max}},$$

where  $H$  is Brillouin's index of diversity for a site and  $H_{\max}$  is the maximum value among sites. Because Hooper (1977) reported site-specific diversity metrics, but not raw abundance data by site, analyses were limited to these diversity metrics for comparison. Repeated-measures analysis of variance (rANOVA) was used to test for differences in each diversity metric ( $S$ ,  $H$ , and  $J$ ; i.e. an rANOVA

was conducted for each metric) among all three years (1976, 2015, and 2016), and when significant differences were detected using  $\alpha = 0.05$ , pairwise comparisons with a Bonferroni adjustment (i.e.  $\alpha = 0.05/3 = 0.0167$ ) were conducted. The authors concluded that there was evidence, although based on limited years of data, for long-term change if comparisons between 1976 and either 2015 or 2016 were significant, but when change between 2015 and 2016 was not. Instances where all or no comparisons were significant were interpreted as not supporting this hypothesis. The authors conducted rANOVA and pairwise contrast tests using the NLME and MULTCOMP packages in R (R Core Team, 2017), and plotted site-specific diversity metrics using scatter plots around a 1 : 1 line to illustrate relationships. Points on the 1 : 1 line in these plots represent sites with identical  $S$ ,  $H$ , or  $J$  between years, and those below or above the line represent sites where diversity indices declined or increased, respectively.

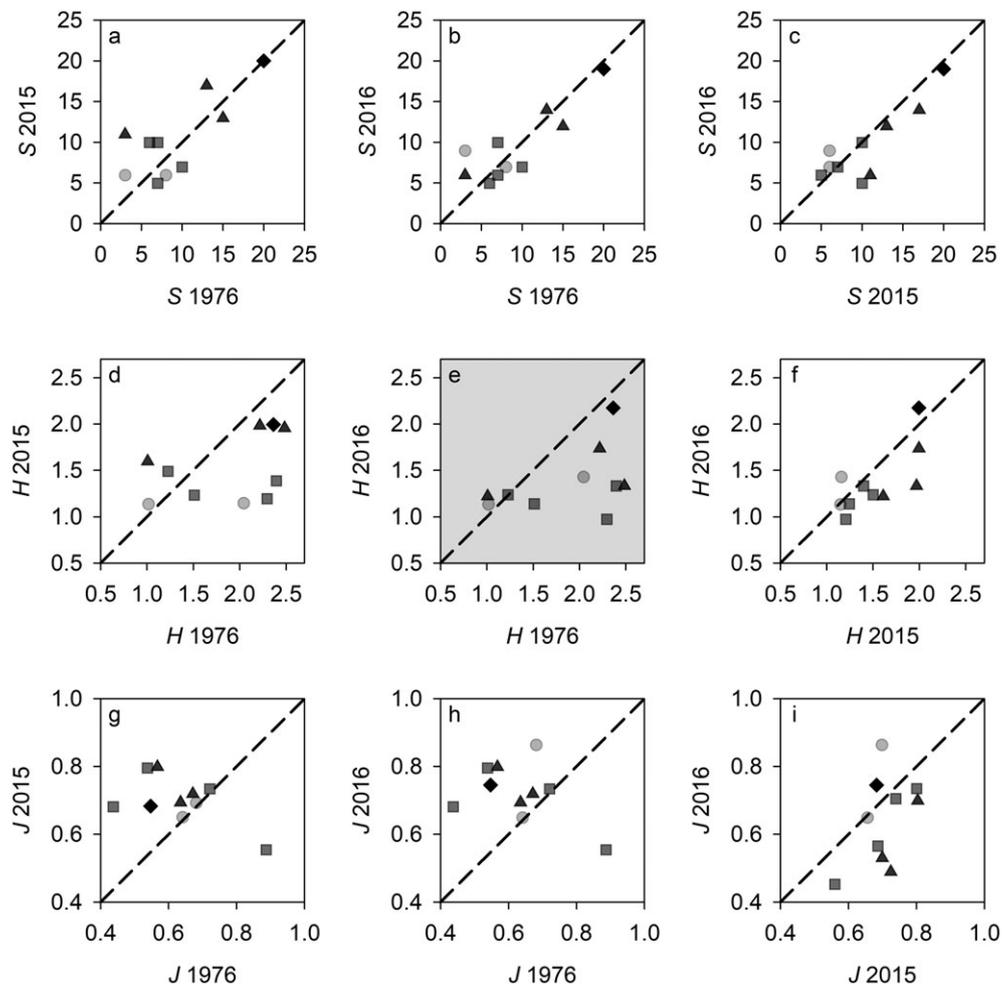
## 2.4 | Intermediate-scale, order-specific assemblage structure

Rarefaction-based null models were used to assess long-term change in fish assemblage structure for specific stream orders. Hooper (1977) provided combined abundances of all fish species captured from stream orders 1–4, but did not break down abundance data by site. Sampling data from 2015 and 2016 were compiled in a consistent manner to produce species-specific abundances by stream order for each year. Individual-based rarefaction analyses using the ENH method described by Cayuela et al., (2015) were conducted using these data. The ENH posits that two samples are drawn from a single underlying distribution of individuals, and that each sample shares similar assemblage composition, abundance, and relative abundance patterns. In the absence of change in assemblages through time, the ENH would be supported. The ENH is tested by compiling species accumulation curves using Hill Numbers ( $q = 0$ ,  $q = 1$ , and  $q = 2$ ), and comparing curves against a distribution of randomly generated

curves using  $\alpha = 0.05$  (for a conceptual overview, see Figure 2 of Cayuela et al., 2015). The authors again concluded that there was evidence for long-term change if stream order-specific accumulation curves for 1976 differed from 2015 and 2016, but when 2015 and 2016 did not differ. Species accumulation curves were constructed using the function 'rarefaction.individual' and pairwise differences in individual-based rarefaction were tested using the function 'ecoTest individual' in the RARENMTESTS package in R (Cayuela & Gotelli, 2014). There is at present no available option to adjust for experiment-wise inflation of type-1 error rate using the 'ecoTest.individual' function, although simulations conducted by Cayuela et al. (2015) show that this function inherently has a low type-1 error rate.

## 2.5 | Broad-scale, contemporary spatial patterns

Spatial patterns in contemporary assemblage structure were assessed using multivariate statistical methods. Raw abundance data for each site were available for contemporary, but not historical, collections,



**FIGURE 2** Comparison of temporal changes in species richness ( $S$ ; a–c), diversity ( $H$ ; d–f), and evenness ( $J$ ; g–i) between 1976 and 2015 (left column), 1976 and 2016 (centre column), and 2015 and 2016 (right column). Sampling sites are represented by shapes that indicate stream order ( $\circ$ , first order;  $\square$ , second order;  $\triangle$ , third order;  $\diamond$ , fourth order). Dashed lines represent the 1 : 1 relationship (i.e. no temporal change), with points falling above and below the 1 : 1 line representing gains and losses, respectively, in  $S$ ,  $H$ , and  $J$ . Boxes with grey shaded backgrounds represent significant differences (see text)

so analysis was limited to collections made during 2015 and 2016. Abundance data for each site were fourth-root transformed to down-weight the influence of abundant taxa and analysed using nonmetric multidimensional scaling (NMDS), based on Bray-Curtis distance, and plotted in two dimensions. This approach allows for displaying latent assemblage gradients along two dimensions without omitting higher-dimension information and provides a measure of stress associated with two-dimensional display (Kruskal, 1964). The significance of correlations between assemblage structure and landscape variables was assessed using the 'envfit' function from the VEGAN package (Oksanen et al., 2018) and tested for significance using 999 permutations. Landscape variables included stream order and upstream drainage area downloaded from the National Hydrography Dataset (EPA, 2012), as well as the percentage of catchment area covered by forest, developed, and cultivated lands using data from the 2011 National Land Cover Dataset (Homer et al., 2015). Environmental variables were overlain on the NMDS plot of sites and a surface representing stream order was added to the plot of species scores using the 'ordisurf' function to illustrate the spatial zonation of contemporary fish assemblage structure along a stream-order gradient. All analyses were conducted in R 3.4.3 (R Core Team, 2017).

## 2.6 | Mapping changes in composition

Historical change was illustrated in a spatially explicit manner by mapping site-specific assemblage structure indices for 1976 and 2016 over land uses for each period. Results (see below) suggested that  $H$  differed through time, and thus  $H$  patterns were plotted for 1976 and 2016. Diversity change maps were overlain onto maps of land development change because terrestrial land development is an agent of change for fish assemblages, including contributing to the loss of fish diversity (Perkin, Troia, Shaw, Gerken, & Gido, 2016; Wang et al., 2003). Historical land use for the years 1974 and 2012 were acquired from Falcone (2015). Although these years do not exactly match fish assemblage sampling years (1974 versus 1976; 2012 versus 2016), these data do represent antecedent conditions at the time of sampling.

## 3 | RESULTS

Thirty-one species were collected across all sites and years of sampling (Table 1). Collections throughout Blackburn Fork during 1976 yielded 25 species, collections during 2015 yielded 29 species, and collections during 2016 yielded 28 species. Twenty-four species occurred in all three years, and common carp (*Cyprinus carpio* (Linnaeus, 1758)) occurred in historical but not contemporary collections. Chestnut lamprey (*Ichthyomyzon castaneus* (Girard, 1958)), black redhorse (*Moxostoma duquesnei* (Lesueur, 1817)), western mosquitofish (*Gambusia affinis* (Baird and Girard, 1853)), warmouth (*Lepomis gulosus* (Cuvier and Valenciennes, 1829)), redear sunfish (*Lepomis microlophus* (Günther, 1859)), and greenside darter

(*Etheostoma blennioides* (Rafinesque, 1819)) occurred in contemporary but not historical collections. The total incidence of species by stream order across all sampling locations and times was 14 in first-order, 17 in second-order, 17 in third-order, and 26 in fourth-order streams.

### 3.1 | Fine-scale patterns

Assemblage composition metrics revealed some evidence of change through time. Species richness ( $S$ ) did not differ among any sampling periods ( $F_{2,18} = 0.85$ ,  $P = 0.367$ ; Figure 2a-c). Diversity ( $H$ ) differed among sampling periods ( $F_{2,18} = 5.25$ ,  $P = 0.016$ ), and pairwise comparisons with Bonferroni adjustment showed no difference between 1976 and 2015 ( $Z = -2.22$ ,  $P = 0.079$ ), a significant reduction between 1976 and 2016 ( $Z = -3.15$ ,  $P = 0.004$ ), and no difference between 2015 and 2016 ( $Z = -0.93$ ,  $P = 0.999$ ). Differences in  $H$  between historical and contemporary periods were associated with reduced diversity at some sites but not others (Figure 2d-e), whereas comparisons between 2015 and 2016 fell along the 1 : 1 line (Figure 2f). Evenness ( $J$ ) did not differ among sampling periods ( $F_{2,18} = 1.19$ ,  $P = 0.326$ ), although the site that was historically the most even (site 3) was the least even during recent samples (Figure 2g-i).

### 3.2 | Intermediate-scale patterns

Rarified Hill numbers revealed temporal change in fish assemblage structure for some, but not all, stream orders. First-order streams supported our hypothesis for long-term change, including differences among historical and contemporary samples, but no differences between contemporary samples (Table 2). In general, species richness accumulated fastest over a gradient of number of individuals sampled in 1976 (Figure 3a), and exponential Shannon (Figure 3b) and inverse Simpson indices accumulated faster and plateaued at higher effective numbers of species in 1976 compared with contemporary sampling (Figure 3c). The remaining stream orders illustrated non-directional change in the effective number of species, including second-order (Figure 3d-f), third-order (Figure 3g-i), and fourth-order (Figure 3j-l) streams.

### 3.3 | Broad-scale patterns

Ordination of assemblage structure using NMDS illustrated the spatial segregation of sites and species along stream size and land-cover gradients (Table 3>). The two-dimensional stress value was 0.09, indicating that sites are well represented in two dimensions (Figure 4). The first NMDS axis represents a gradient of sites from upstream (positive along NMDS 1) to downstream (negative along NMDS 1), whereas the second axis represents a gradient of sites with forested (positive along NMDS 2) versus developed (negative along NMDS 2) catchments (Figure 4a). Along these gradients, fish

**TABLE 1** Fish family, genus and species, species code, and encounters by stream order during 1976, 2015, and 2016 (1, first order; 2, second order; 3, third order; 4, fourth order), and species scores along nonmetric multidimensional scaling (NMDS) axis 1 and axis 2 (see Figure 4) for fishes sampled in Blackburn Fork, TN

Species	Code	1976	2015	2016	NMDS 1	NMDS 2
Petryomyzontidae						
<i>Ichthyomyzon castaneus</i>	ictcas	-	4	-	-1.69	0.32
Cyprinidae						
<i>Camptostoma anomalum</i>	camano	1,2,3,4	1,2,3,4	1,2,3,4	-0.19	-0.01
<i>Chrosomus erythrogaster</i>	chrery	1,2,3	2,3	2,3	0.55	0.5
<i>Cyprinella galactura</i>	cypgal	4	3,4	4	-1.46	0.31
<i>Cyprinus carpio</i>	cypcar	4	-	-	-	-
<i>Notropis telescopus</i>	nottel	4	3,4	4	-1.4	0.34
<i>Pimephales notatus</i>	pimnot	1,2,3,4	4	4	-1.17	-0.01
<i>Luxilus chrysocephalus</i>	luxchr	2,3,4	2,3,4	3,4	-0.75	0.08
<i>Lythrurus fasciolaris</i>	lytfas	2,3,4	4	2,3,4	-0.88	-0.09
<i>Rhinichthys atratulus</i>	rhiart	1,2,3,4	1,2,3	1,2,3	0.24	0.25
<i>Semotilus atromaculatus</i>	sematr	1,2,3,4	1,2,3	1,2,3	0.32	0
Catostomidae						
<i>Hypentelium nigricans</i>	hypnig	2,3,4	2,3,4	1,2,3,4	-0.6	-0.03
<i>Moxostoma duquesnei</i>	moxduq	-	4	4	-1.74	0.12
Ictaluridae						
<i>Noturus flavus</i>	notfla	4	4	4	-1.73	0.13
Fundulidae						
<i>Fundulus catenatus</i>	funcat	1,3,4	4	3,4	-1.07	-0.05
Poeciliidae						
<i>Gambusia affinis</i>	gamaff	-	-	1,2	0.11	-0.84
Cottidae						
<i>Cottus carolinae</i>	cotcar	2,3,4	2,3,4	1,2,3,4	-0.36	0.03
Centrarchidae						
<i>Ambloplites rupestris</i>	ambrup	2,3,4	2,3,4	2,3,4	-0.7	-0.23
<i>Lepomis cyanellus</i>	lepcya	1,2,3	1,2,3,4	1,2,3	0.32	0.03
<i>Lepomis gulosus</i>	lepgul	-	2	-	0.95	-0.05
<i>Lepomis macrochirus</i>	lepmac	2,3,4	1,2,3	1,3	0.29	-0.2
<i>Lepomis megalotis</i>	lepmeg	4	4	4	-1.44	0.05
<i>Lepomis microlophus</i>	lepmic	-	2	1	0.93	-0.79
<i>Micropterus dolomieu</i>	micdol	4	4	4	-1.73	0.14
<i>Micropterus salmoides</i>	micsal	4	1,2	1,2,4	0.08	-0.62
Percidae						
<i>Etheostoma blennioides</i>	ethble	-	4	4	-1.72	0.17
<i>Etheostoma caeruleum</i>	ethcae	4	4	4	-1.73	0.14
<i>Etheostoma flabellare</i>	ethfla	1,3	2,3	2,3	-0.28	-0.34
<i>Etheostoma lawrencei</i>	ethlaw	1,2,3,4	1,2,3	1,2,3	0.3	-0.2
<i>Etheostoma rufilineatum</i>	ethruf	4	4	4	-1.73	0.15
<i>Etheostoma simoterum</i>	ethsim	4	4	4	-1.73	0.16

species segregate by stream order (Figure 4b). Stream order ( $r^2 = 0.76$ ,  $P < 0.001$ ) and drainage area ( $r^2 = 0.82$ ,  $P < 0.001$ ) were significantly correlated with assemblage structure, whereas forest

( $r^2 = 0.24$ ,  $P = 0.079$ ), developed ( $r^2 = 0.13$ ,  $P = 0.325$ ), and cultivated ( $r^2 < 0.01$ ,  $P = 0.958$ ) land cover were not significantly correlated with assemblage structure.

**TABLE 2** Results from individual-based tests of the ecological null hypothesis (Cayuela et al., 2015) using Hill numbers 0 (species richness), 1 (exponential Shannon), and 2 (inverse Simpson) in three-way contrasts among 1976, 2015, and 2016 for first-, second-, third-, and fourth-order streams in Blackburn Fork, TN. Statistical values ( $Z$ ) and  $P$  values ( $P$ ) set in bold denote significant contrasts

Hill number	Contrast	First-order	Second-order	Third-order	Fourth-order
0	1976 vs 2015	$Z = 1050.3$ $P = 0.005$	$Z = 628.9$ $P = 0.005$	$Z = 6359.0$ $P = 0.005$	$Z = 402.1$ $P = 0.375$
0	1976 vs 2016	$Z = 1213.3$ $P = 0.005$	$Z = 752.0$ $P = 0.005$	$Z = 4911.6$ $P = 0.005$	$Z = 63.9$ $P = 0.005$
0	2015 vs 2016	$Z = 261.4$ $P = 0.265$	$Z = 628.7$ $P = 0.005$	$Z = 1534.4$ $P = 0.005$	$Z = 373.1$ $P = 0.325$
1	1976 vs 2015	$Z = 764.8$ $P = 0.005$	$Z = 173.6$ $P = 0.130$	$Z = 2160.7$ $P = 0.005$	$Z = 1071.2$ $P = 0.005$
1	1976 vs 2016	$Z = 771.8$ $P = 0.005$	$Z = 123.5$ $P = 0.275$	$Z = 1123.3$ $P = 0.005$	$Z = 677.8$ $P = 0.005$
1	2015 vs 2016	$Z = 6.7$ $P = 0.935$	$Z = 412.6$ $P = 0.010$	$Z = 1344.5$ $P = 0.005$	$Z = 252.8$ $P = 0.005$
2	1976 vs 2015	$Z = 749.8$ $P = 0.005$	$Z = 40.8$ $P = 0.755$	$Z = 1773.3$ $P = 0.005$	$Z = 1433.9$ $P = 0.005$
2	1976 vs 2016	$Z = 741.9$ $P = 0.005$	$Z = 336.76$ $P = 0.005$	$Z = 1108.4$ $P = 0.005$	$Z = 890.6$ $P = 0.005$
2	2015 vs 2016	$Z = 14.9$ $P = 0.81$	$Z = 517.1$ $P = 0.005$	$Z = 1385.2$ $P = 0.005$	$Z = 422.4$ $P = 0.005$

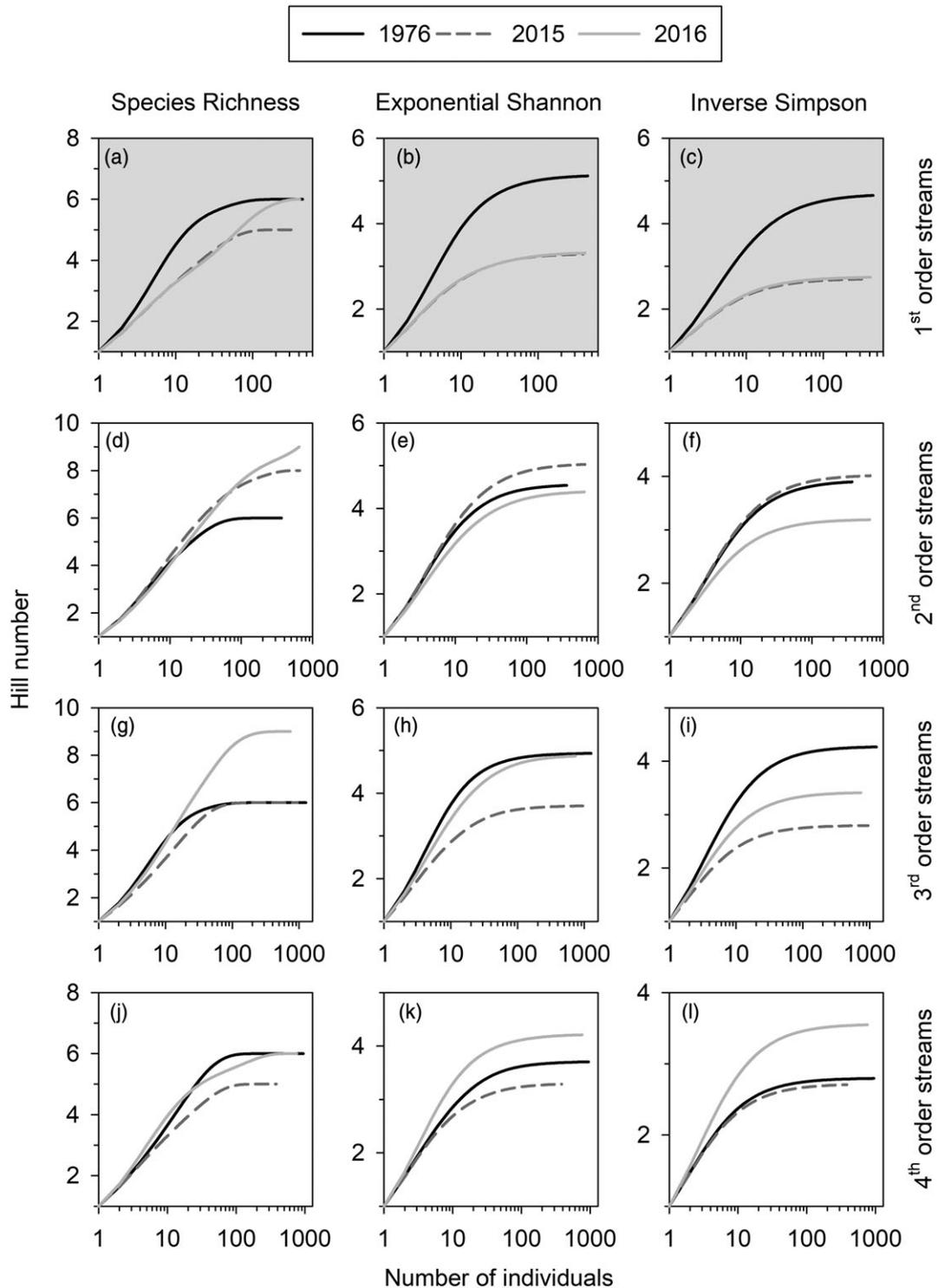
Mapping site-specific changes in  $H$  to the Blackburn Fork riverscape was effective for illustrating patterns detected by pairwise diversity comparisons, stream-order rarefaction, and contemporary spatial structuring. Diversity measured in 1976 was greatest at sites located further away from highly developed lands near the city of Cookeville, TN (Figure 5a). Spatial variation in  $H$  during 2016 shows that the greatest reductions in  $H$  occurred at sites surrounded by lands developed between 1976 and 2016 (Figure 5b). Across the riverscape, land development was most prominent in upstream reaches draining into first-order streams, the same hierarchical level identified as undergoing long-term change in the rarefaction analysis. Furthermore, sites falling in catchments with high urban (and consequently little forest) land cover were the same sites with low diversity indices. Notably, the site that maintained the greatest diversity in 2016 was the site with the lowest level of developed land in its catchment.

#### 4 | DISCUSSION

This study highlights the benefits of considering multiple spatial scales when analysing historical change in the structure of stream fish assemblages. When viewed together and from a landscape perspective integrating land cover patterns, the work revealed an emergent property of declining stream fish diversity across a gradient of increasingly developed land. The analytical framework applied here is grounded in scale and hierarchy theory and provides ecologically relevant guidance for multi-scale strategic conservation planning.

Conservation approaches targeting fine-scale implementations such as land acquisitions might target the preservation of the intact and diverse fish assemblage at site 8. Intermediate-scale implementations, such as the installation of riparian buffers and channel restorations, might focus on first-order streams where ecological degradation is most obvious. Broad-scale implementations such as Native Fish Conservation Areas (Williams et al., 2011) might be established for Blackburn Fork if fishes and their habitats as they occur throughout the entire catchment are the targets of conservation. These approaches collectively promote efficiency because proactive conservation implemented before species extirpation avoids the extensive planning and resource investment necessary for successful species reintroduction (e.g. Malone et al., 2018). Similar multi-scale analyses can be applied to other systems, regardless of their location, size, or the complexity of their fish assemblages, to advance the conservation of stream fishes in altered riverscapes on a global scale (Hermoso, Pantus, et al., 2015).

The ensemble approach applied here identified consistent and inconsistent themes in fish assemblage structure across spatial and temporal scales of investigation. The lowest-resolution data included a list of species that occurred in the catchment during each year of sampling. Based solely on the catchment-wide occurrence of species among years 1976, 2015, and 2016 (shown in Table 1), species richness in Blackburn Fork increased over the long term. Inconsistent with this theme of increasing richness was evidence of temporal beta diversity, including the absence of common carp in contemporary samples, but new occurrences of greenside darter, chestnut lamprey, black redhorse, redear sunfish, and western mosquitofish. The absence of



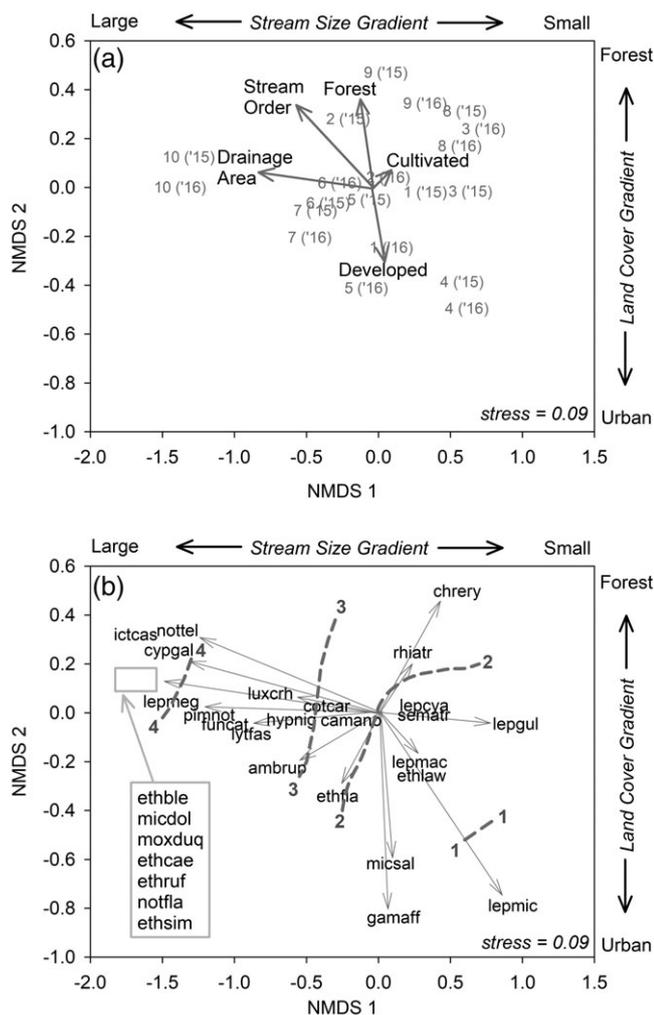
**FIGURE 3** Species accumulation curves based on individual-based rarefaction for Hill numbers  $q = 0$  (species richness; left column),  $q = 1$  (exponential Shannon; centre column), and  $q = 2$  (inverse Simpson; right column) by stream orders 1 (a–c), 2 (d–f), 3 (g–i), and 4 (j–l), illustrating collections from years 1976 (black solid line), 2015 (grey dashed line), and 2016 (grey solid line) in Blackburn Fork, TN. The x-axis is shown on a log scale and the y-axis scales differ among panels. Boxes with grey shaded backgrounds represent significant differences between 1976 and 2015–16 (see Table 2)

common carp from contemporary sampling might have been an artefact of a fish barrier on Roaring River that was installed in 1976, and was effective at blocking the immigration of this species (Bulow, Webb, Crumby, & Quisenberry, 1988). The occurrence of chestnut

lamprey, black redhorse, and greenside darter in only the contemporary sampling, and in the largest stream sampled, might have been related to detection efficiency. Sampling efficiency declines with increasing stream size (Erős, 2017), and the levels of effort in historical

**TABLE 3** Sampling site identification number (see Figure 1 for locations), latitude, longitude, stream order (Strahler, 1957), drainage area (km<sup>2</sup>), and percentage of catchment with forested, cultivated, and developed land cover for 2011 (data from Homer et al., 2015)

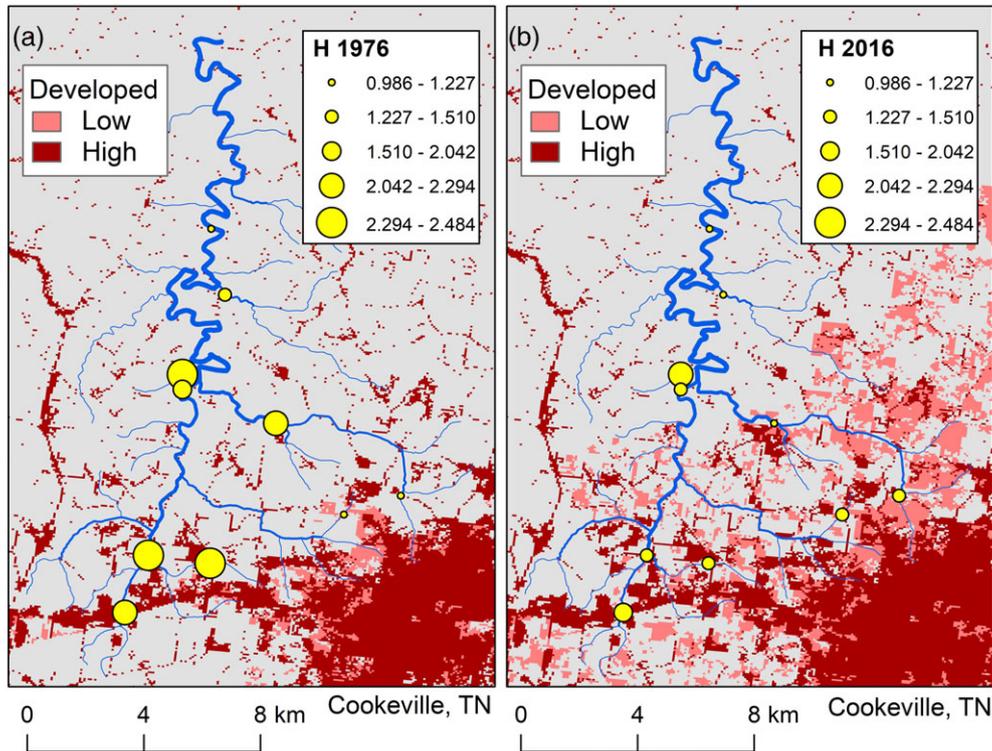
Site ID	Latitude	Longitude	Stream order	Drainage area	% Forested	% Cultivated	% Developed
1	36.1717	-85.5923	1	8.1	17	57	25
2	36.1893	-85.5850	2	11	13	60	25
3	36.1869	-85.5659	2	4	18	29	52
4	36.2019	-85.5247	1	2	22	55	23
5	36.2077	-85.5071	2	7	26	8	66
6	36.2300	-85.5457	3	31	36	37	25
7	36.2405	-85.5745	3	62	21	53	24
8	36.2451	-85.5745	2	2	28	61	10
9	36.2697	-85.5614	3	13	51	33	13
10	36.2900	-85.5656	4	137	34	44	21



**FIGURE 4** Nonmetric multidimensional scaling (NMDS) plot of (a) site and (b) species scores for collections made during 2015 and 2016 at 10 sites in Blackburn Fork, TN. (a) Sites are labelled by their identification number (Figure 1), with the year of collection noted in parentheses (2015 = 15; 2016 = 16); vectors for catchment attributes are overlain (Table 3). (b) Species scores (see Table 1 for codes) are overlain with stream orders (dashed lines: 1, first order; 2, second order; 3, third order; 4, fourth order) to illustrate species associations

and contemporary sampling might have been insufficient to detect the occurrence of all of the species that were actually present. Conversely, the occurrence of redear sunfish and western mosquitofish in the contemporary sampling only, and in smaller streams where sampling is more efficient, was probably related to urbanization. Both species had strong loadings for sites with high urban land development (sites 4 and 5), and these two sites were the only two that indicated a slight increase in diversity between 1976 and 2016. Previous work suggests that urbanization-based habitat modifications promote invasion by western mosquitofish (Pyke, 2008) and sunfishes like redear sunfish (Scott & Helfman, 2001). Consequently, these invasions contributed to a counter-intuitive increase in diversity at two sites during a period of diversity loss across all other sites. At the other end of the land-use gradient, southern redbelly dace (*Chrosomus erythrogaster* (Rafinesque, 1820)) and blacknose dace (*Rhinichthys atratulus* (Hermann, 1804)) were most abundant at the site with the greatest fish diversity across all time periods and the lowest level of urban development. Both of these species have shown sensitivity to urban land development in other regions (Fraker, Snodgrass, & Morgan, 2002; Long & Schorr, 2005; Perkin et al., 2016). From this case study it is clear that broad-scale and catchment-wide assessments of assemblage change do not capture finer-scale or spatially structured changes, and multi-scale investigations stand a better chance of identifying the most appropriate spatial scales for assessing assemblage and species status (Fausch et al., 2002). Notably, when the basin was decomposed into stream-order levels, evidence for long-term change emerged among first-order streams, including a decline in the effective number of species. Had only broad-scale data been used, these patterns in diversity loss might not have been detected.

Spatial context dependences associated with long-term change in stream fish assemblage structure might be evaluated by applying the principles of hierarchy theory. The early foundations of hierarchy theory emphasized a theoretical framework or point of view (Simon, 1962) rather than what now might be considered an 'efficient theory' in ecology (Marquet et al., 2014). In the context of riverscapes, the nested hierarchy of stream orders is a well-defined



**FIGURE 5** Change in stream fish assemblage diversity ( $H$ ) and land development between (a) 1976 and (b) 2016. Circles are sized in proportion to stream fish diversity measured in (a) 1976 and (b) 2016, and low (light red) and high (dark red) levels of developed lands are shown for (a) 1974 and (b) 2012 (land-use data from Falcone, 2015)

framework for measuring the interacting components of a broader network. For example, Perkin, Gido, et al. (2017) used order-specific occurrences of stream fishes to assess components of Great Plains catchments undergoing long-term change associated with groundwater depletion. In that study, stream orders and their fish inhabitants reacted differentially to changes in water availability, despite being linked by hydrological connectivity (Pringle, 2003). These patterns illustrate the ‘near-decomposability’ (*sensu* Simon, 1977) of riverscapes, in that rates of change within stream orders were more consistent than among stream orders. In the context of Blackburn Fork, decomposing the catchment by stream orders to assess long-term patterns in assemblage structure revealed change in first, but not other, stream orders. Given that headwater streams are tightly coupled with terrestrial land-cover changes through cascading processes (Burcher, Valett, & Benfield, 2007), extensive terrestrial landscape change as documented here for Blackburn Fork might be expected to affect headwater streams. However, other threats to freshwater ecosystems (Dudgeon et al., 2006) have spatial contexts associated with their effects on stream fishes. An efficient approach to highlighting these pattern–process relationships is decomposing riverscapes using nested hierarchies (Allan, Erickson, & Fay, 1997). Examples include habitat fragmentation by road crossings afflicting streams of orders 1–3 (Perkin & Gido, 2012), flow regime alteration by dams afflicting streams of order 3–7 (Poff, Olden, Merritt, & Pepin, 2007), the probability of non-native fish invasions increasing with stream order (Schade & Bonar, 2005), and water quality degradation increasing with stream order (Buck, Niyogi, & Townsend,

2004). Although past work has demonstrated that faunal breaks in stream fish assemblages are not correlated with stream order (Matthews, 1986), recent assessments suggest that metrics based on hierarchical stream classifications (e.g. link magnitude) are strong predictors of fish assemblage structure across basin and sub-basin scales (Troia & Gido, 2013), and that spatial context matters in assessing fish assemblage response to anthropogenic alterations (Erős, O’Hanley, & Czeglédi, 2018).

Assessments of historical change in stream fish assemblage structure might benefit from new perspectives and analytical tools. Natural experiments of long-term ecological change generally suffer from a lack of experimental controls (Diamond, 1983), and the same is true for many assessments of change in stream fish assemblages (Rinne et al., 2005); however, the assessment of multiple sites across gradients of species compositional change can provide insight across gradients of environmental alteration (Wang et al., 2008). The increasingly prevalent use of rarefaction analysis in assessments of long-term changes in stream fish assemblages (e.g. Gido et al., 2010; Miyazono & Taylor, 2015; Quinn & Kwak, 2003; Tucker et al., 2018) could benefit from multi-scale approaches that decompose riverscapes into finer components of space. This point is relevant because anthropogenic alterations to riverscapes are not uniform through space or time (Allan, 2004). In the case of Blackburn Fork, fish diversity measured as  $H$  was maintained to the greatest extent at the site that experienced the least amount of urban development in its catchment (site 8). A reduced diversity at sites with heavily developed catchments is consistent with the concept of ‘urban stream syndrome’, in which water and pollutants

delivered to streams through urban drainage networks degrade the physical, chemical, and biological status of streams (Walsh et al., 2005). Despite increasing global investigations into urban stream syndrome (Booth, Roy, Smith, & Capps, 2016), diagnosing symptoms that manifest as fish assemblage response to urban stream syndrome can be challenging when the spatial distribution of sampling sites is not considered (Kollaus, Behen, Heard, Hardy, & Bonner, 2015). This is one reason why analyses of multiple spatial scales organized into hierarchical frameworks are successful at identifying ecological change (Fausch et al., 2002; Labbe & Fausch, 2000). In addition, our analysis of the spatial effect of land use on contemporary fish assemblage structure did not show a significant relationship between land use and fish assemblages (NMDS results). This suggested that space-for-time substitutions can be invalid for assessing ecological responses to urbanization and supports the value of historical land-use data for assessing patterns in biodiversity change (Harding, Benfield, Bolstad, Helfman, & Jones, 1998). Implementing multiple scales of resolution into assemblage change with multiple Hill numbers is an effective method for measuring spatial and temporal changes in assemblage structure (Cayuela et al., 2015), and can be combined with functional trait data to assess potential mechanisms that might be contributing to observed assemblage change (Crumby, Webb, Bulow, & Cathey, 1990; Hoeinghaus, Winemiller, & Birnbaum, 2007). Our approach here suggests that combining a riverscape perspective with new rarefaction-based analyses is a promising avenue for identifying the spatiotemporal extents of change in stream fish assemblages.

The framework presented here has implications for stream fish diversity conservation in other regions of the world. This study focused on a fish biodiversity hotspot characterized by a large number of species in need of conservation (Warren et al., 2000), but similar hotspots exist elsewhere (Abell et al., 2008) and conservation initiatives are not limited to such hotspots (Dauwalter, Sanderson, Williams, & Sedell, 2011). Emerging conservation strategies focus on proactive, catchment-scale management and protection to minimize human perturbations for the long-term preservation of native fish assemblages (Saunders, Meeuwig, & Vincent, 2002; Williams et al., 2011). Long-term ecological research (LTER) is critical for understanding the drivers and consequences of change for stream fish assemblages in multiple regions (Matthews & Marsh-Matthews, 2017), but LTER programmes characterized by time-series collection of data over long periods are rare for many regions (Magurran et al., 2010). Instead, snapshots of assemblage structure tend to be available, perhaps as interval or rotational monitoring programmes such as those used by many state and federal natural resource agencies (EPA, 2013). Nevertheless, data are most commonly available as single sampling events covering multiple sites (Hooper, 1977; Roth, Allan, & Erickson, 1996). Although past studies have grouped sites together for analyses, the use of rarefaction approaches to assess site-specific changes might be more useful for conservation planning, given that threats to freshwater diversity are not consistent through space or time (Strayer & Dudgeon, 2010). Assessments of land-use change before species are extirpated can be useful for preserving remaining diversity,

and when coupled with life-history traits can help to identify which species or habitats are most vulnerable to the particular threats (e.g. urbanization or fragmentation) within a system (Perkin, Knorp, et al., 2017). Moreover, these analyses could highlight areas that are intact and require preservation, compared with areas that might be priorities for restoration to meet human needs, while maintaining ecological integrity (Dudgeon et al., 2006; Hermoso, Pantus, et al., 2015). Multi-scale analytical approaches such as the one developed here allow the diagnosis of intact versus degraded areas that may otherwise be masked when using larger spatial units. Implementing such frameworks to a greater extent holds promise for promoting the preservation of local and regional stream fish diversity in riverscapes around the world.

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