

# Hierarchy theory reveals multiscale predictors of Arkansas darter (*Etheostoma cragini*) abundance in a Great Plains riverscape

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## Funding information

Texas A&M University; National Institute of Food and Agriculture, Grant/Award Number: 1017538; Kansas Department of Wildlife, Parks, and Tourism

## Abstract

1. Landscape ecology and its emphasis on relationships between spatial heterogeneity, scale, and ecological processes can be applied to manage stream ecosystems as riverscapes. Hierarchy theory, a central tenet of riverscape ecology, allows for investigating ecological relationships between aquatic organisms and habitat by exploring the nested interactions inherent in reaches, segments, and basins. Arkansas darter *Etheostoma cragini* is a Great Plains fish endemic to the Arkansas River basin and is listed as in need of conservation in all five states within its range in North America. The aim of this study was to develop empirical models describing relationships between Arkansas darter abundance and local habitats, and identify the appropriate scale(s) for assessing and managing populations.
2. We used Arkansas darter abundance data collected from stream sample units as a fixed grain size (10<sup>2</sup> m) and compiled datasets at three hierarchical spatial extents, including reach (10<sup>3</sup> m), nested within segment (10<sup>4</sup> m), nested within basin (10<sup>5</sup> m) in southcentral Kansas. We fit generalised linear mixed models (GLMMs) to assess scale-specific relationships between Arkansas darter abundance and local habitat dimensions (stream depth and width) and heterogeneity (canopy cover, overhanging vegetation, and woody structure).
3. Habitat parameters included in best-supported GLMMs differed among extents. Variation in Arkansas darter abundance was explained by canopy cover and channel depth at the reach (54% explained) and segment (56%) extents, and stream width and depth at the basin extent (37%). Partial dependence plots from multiple regression GLMMs revealed that Arkansas darter abundance was negatively correlated with increasing channel depth across all extents, increasing canopy cover at reach and segment extents, and increasing channel width at the basin extent.
4. Our results highlight scale-specific relationships between Arkansas darter abundance and local habitats across multiple spatial extents. These findings provide direction for assessing stream fish ecology pattern-process relationships at the

appropriate spatial scales and benefit native fish conservation by highlighting the application of hierarchy theory to address management challenges.

#### KEYWORDS

conservation biology, fish ecology, landscape ecology, scaling, streams and rivers

## 1 | INTRODUCTION

Landscape ecology emphasises relationships between spatial heterogeneity, scale, and ecological processes. Central tenets of landscape ecology include consideration of the processes that create and maintain spatial heterogeneity, the influence of scale on ecological interactions, and how management of spatial heterogeneity regulates ecological processes (Turner, 1989, 2005). A major theme in landscape ecology is the application of hierarchy theory to decouple complex systems into smaller components as a means of simplifying research of whole systems (Allen & Starr, 2017; Wu, 2013). This is possible because an ecological system that operates as a true hierarchy can be characterised as a *system of systems within systems* (King, 1997). For example, foraging by herbivores occurs within a nested hierarchy in which local feeding stations are nested within larger plant community patches, and patches are in turn nested within broader landscape and regional systems (Senft et al., 1987). The principles of landscape ecology, including hierarchy theory, are applicable to stream ecosystems despite the implicit reference to *land* (Wiens, 2002). In fact, Frissell, Liss, Warren, and Hurley (1986) and Fausch, Torgersen, Baxter, and Li (2002) described the nested hierarchy of stream habitats, including microhabitats ( $10^{-1}$  to  $0$  m) nested within channel units such as pools or riffles ( $10^{1-2}$  m), nested within reaches ( $10^{2-3}$  m), nested within segments ( $10^{3-5}$  m), nested within stream systems (otherwise known as basins;  $10^{5-6}$  m). These and other studies (Labbe & Fausch, 2000) highlighted the process of viewing stream networks as *river*scape hierarchies to investigate multiscale variables that regulate organism abundance and distribution. Riverscape perspectives are increasingly applied to challenges facing conservation of biodiversity in aquatic ecosystems (Erős, O'Hanley, & Czeglédi, 2018; Fausch, 2010).

Assessing the riverscape ecology of fishes in the Great Plains, U.S.A. is of critical conservation interest because habitat diversity is commonly simplified by anthropogenic landscape alterations operating across multiple scales. Drought and flooding are natural hydrologic disturbances in the Great Plains and cause expansion and contraction of the heterogeneity and scale of riverscapes (Dodds, Gido, Whiles, Fritz, & Matthews, 2004; Stanley, Fisher, & Grimm, 1997). However, anthropogenic modifications to Great Plains riverscapes have disrupted natural patterns in spatial heterogeneity with negative consequences for ecological processes involving endemic fishes (Hoagstrom, Brooks, & Davenport, 2011). Multi-scale alterations to ecological processes result in competition with non-native species across local habitats (Gido, Schaefer, & Pigg, 2004; Labbe & Fausch, 2000), degradation of water quality across reaches (Cross,

1950), altered hydrologic regimes across segments (Costigan & Daniels, 2012), and fragmentation of hydrologic connectivity (Perkin & Gido, 2011; Worthington, Brewer, Grabowski, & Mueller, 2014) and dewatering of streams and aquifers (Perkin, Gido, Costigan, Daniels, & Johnson, 2015; Perkin, Gido, Cooper, et al., 2015; Perkin et al., 2017) across basins. These multi-scale alterations require multi-scale assessments of conservation status, particularly for regionally endemic Arkansas darter *Etheostoma craigini* (see overview by Labbe & Fausch, 2000). In the state of Colorado, Arkansas darter conservation actions now consider pool-scale habitat refuge (Smith & Fausch, 1997), reach-scale habitat connectivity (Groce, Bailey, & Fausch, 2012), and segment-scale population structure (Fitzpatrick, Crockett, & Funk, 2014). Despite abundant research in Colorado, Arkansas darter has declined locally throughout much of its range because of changes to Great Plains riverscapes (US Fish and Wildlife Service, 2016), suggesting additional research is necessary to plan conservation actions involving multi-scale environmental regulators of Arkansas darter abundance.

Empirical models describing relationships between Arkansas darter abundance and habitat dimension and heterogeneity are necessary to inform conservation actions. Habitat dimension can be measured as stream width (m) and depth (m), whereas heterogeneity involves structures such as aquatic vegetation, canopy cover, and instream woody structure. Each of these components of habitat is regulated by hydrologic processes that link streams to terrestrial landscapes (Burcher, Valett, & Benfield, 2007; Perkin, Troia, Shaw, Gerken, & Gido, 2016). For example, terrestrial habitat transformation has disrupted historic vegetative succession regimes and allowed for woody encroachment across basins (Briggs et al., 2005), and this affects stream reaches and segments by stabilising banks, increasing stream depths, closing otherwise open canopies, and depositing instream woody structure (Fischer et al., 2010; Poff et al., 1997). Whether or not, and to what extent, these habitat changes affect Arkansas darter abundance has not been investigated (Eberle & Ernsting, 2014). Furthermore, abundance-based models are critical because conservation and restoration goals are routinely set around abundance data and descriptive models provide some expectation for the benefits associated with specific conservation actions. Depending on the nature of relationships, habitats can be manipulated to benefit fish abundances through practices such as riparian tree plantings or removals at fine scales as well as coordinated land use practices across broader scales (Kwak & Freeman, 2010). Simultaneous assessment of the appropriate habitat dimensions and heterogeneity across spatial scales will highlight the appropriate actions and spatial extents for implementing habitat preservation and

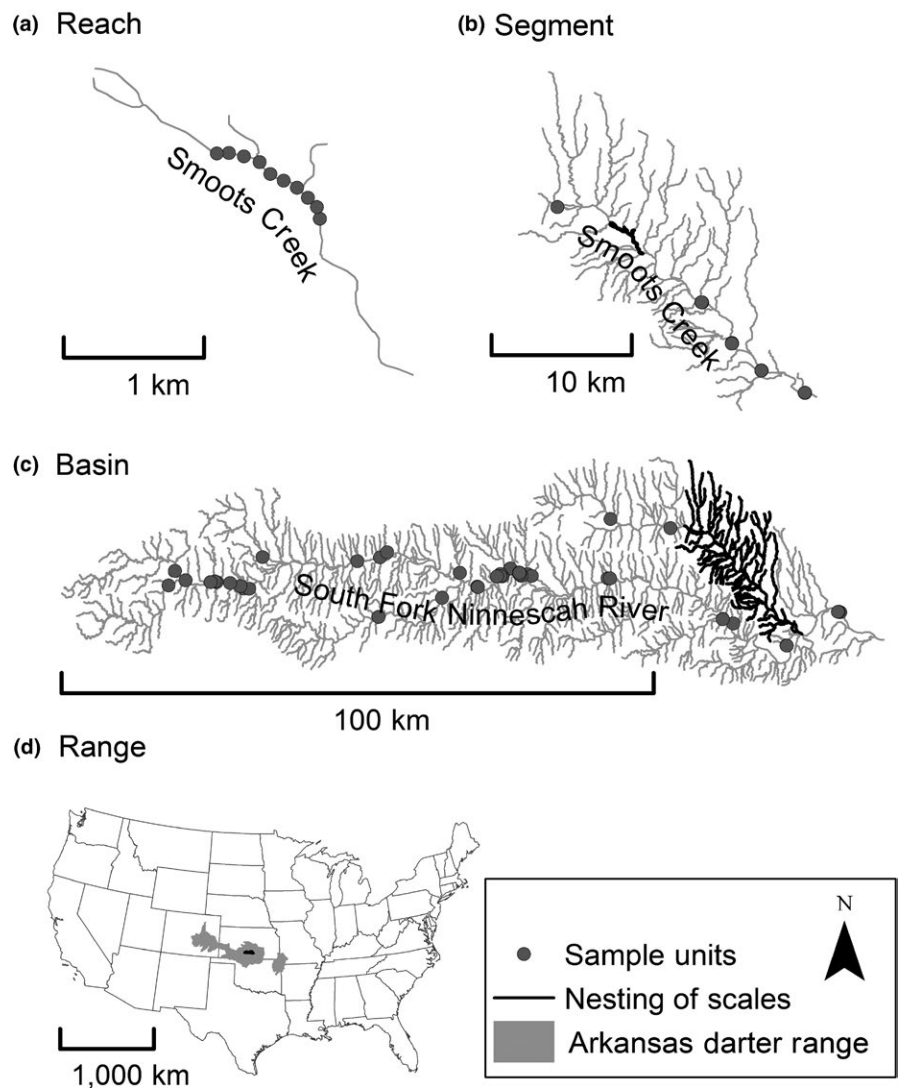
restoration to benefit conservation of Arkansas darter (Fausch et al., 2002).

The goal of this study was to evaluate environmental gradients that regulate Arkansas darter catch rate (fish/hr) across multiple spatial scales to inform conservation and management of the species. To accomplish this goal, we used principles of landscape ecology and hierarchy theory to document relationships between patterns in Arkansas darter catch rate and habitat dimension as well as heterogeneity at three nested spatial extents (reach, segment, and basin). We tested two hypotheses: (1) that ranges of values for habitat variables and Arkansas darter abundance were greater at broader spatial extents compared to finer spatial extents; and (2) that relationships between habitat and abundance would be strongest at the broadest spatial extent tested (i.e. basin). These hypotheses are based on known correlations between increases in environmental gradients and increases in the role of environmental factors in constraining fish distributions (Jackson, Peres-Neto, & Olden, 2001), and more recent evidence for greater environmental (as opposed to dispersal) effects on organisms in aquatic systems at spatial extents that approximate basins (Heino et al., 2015). Our objectives included:

(1) quantifying local habitat gradients across scales; (2) describing relationships between Arkansas darter catch rate and habitat variables across broadening spatial extents; and (3) framing multiscale interactions among environmental processes within the context of hierarchy theory.

### 1.1 | Study area

We assessed multi-scale relationships between habitat heterogeneity and Arkansas darter abundance in the South Fork Ninescah River basin, a tributary of the Arkansas River in southcentral Kansas, U.S.A. (Figure 1). Average annual precipitation for this region is 775 mm, and average annual air temperature is 13.9°C (Houseman, Kraushar, & Rogers, 2016). The South Fork Ninescah River is a sand-bed, braided, perennial river characterised by decreasing bed slope but increasing width and depth in a downstream direction (Costigan, Daniels, Perkin, & Gido, 2014). The flow regime in the South Fork Ninescah River is unregulated, and the native fish assemblage remains largely intact despite historical losses of some species during drought periods (Perkin & Gido, 2011; Perkin, Gido, Costigan, et al.,



**FIGURE 1** Study area map illustrating multiple spatial extents at which relationships between habitat variables and Arkansas darter catch rates were tested, including (a) reach, (b) segment, and (c) basin extents. For all extents, sample units (grey circles) represent the consistent grain size at which observations of habitat and darter catch rate were made. (d) The extent of Arkansas darter range. Across all panels, black streams represent the embedded location of the next smaller spatial extent

2015). The largest tributary to the South Fork Ninescah River is a fourth-order segment of stream known as Smoots Creek. Smoots Creek flows southeast to join the South Fork Ninescah just upstream of the confluence between the South and North forks, and as typical for Great Plains streams of its size Smoots Creek is generally perennial but is subject to drying during periods of intense drought (Dodds et al., 2004). Nested within the segment of Smoots Creek is a reach of stream that flows through the 0.63 km<sup>2</sup> Gerber Reserve operated by Wichita State University. The Gerber Preserve was historically grazed by cattle, but reduced grazing and lack of active land management resulted in encroachment of native and non-native trees during recent decades (Houseman et al., 2016). In 2010, prairie restoration was initiated with managed grassland burning and tree removal, which created a gradient of woody encroachment near the upstream extent of the Gerber Preserve that transitioned to restored prairie grassland towards the middle and downstream extent of the reserve.

## 2 | METHODS

### 2.1 | Scales of investigation

We tested for relationships between Arkansas darter abundance and stream habitat parameters using a consistent (i.e. fixed) spatial grain and three spatial extents. Grain size is defined as the finest spatial resolution of study and is the scale at which observations are conducted (Wiens, 1989). We use *sample units* as our grain (*sensu* Stoddard & Hayes, 2005), defined here as a length of stream (10<sup>2</sup> m) selected based on access availability to crews and surveyed in a continuous manner to assess fish communities and habitat attributes at all spatial extents. Spatial extent is defined as the spatial dimension over which all observations are conducted (Wiens, 1989). We use three spatial extents of increasing magnitude, including reach (10<sup>3</sup> m), segment (10<sup>4</sup> m), and basin (10<sup>5</sup> m). These spatial extents, their assigned labels, and their scale magnitudes reflect those described by Frissell et al. (1986), Labbe and Fausch (2000), and Fausch et al. (2002). The reach spatial extent consisted of 10 consecutive sample units distributed longitudinally along Smoots Creek on the Wichita State University Gerber Preserve in Kingman County, KS (lat 37.6760° lon -97.9461°; Figure 1a). The segment spatial extent consisted of five sample units distributed along Smoots Creek (Figure 1b). The basin spatial extent consisted of 37 sample units distributed along the South Fork Ninescah River (Figure 1c). Each of these spatial scales encompasses a portion of the core range of Arkansas darter (Figure 1d).

We compiled fish survey data using independent datasets for each spatial extent. The reach spatial extent was sampled by the authors at the beginning of three consecutive summer months (June, July, August) during 2014 and 2015 (i.e. temporal extent of 2 years). Ten sample units were each repeatedly sampled six times for a total of 60 observations at the reach extent. The segment spatial extent was sampled by the Kansas Department of Wildlife, Parks and Tourism (KDWPT) Ecological Services Stream Survey

and Assessment Program once during the summer for five consecutive years during 2005–2009 (i.e. temporal extent of 5 years). Five sample units were each repeatedly sampled five times for a total of 25 observations at the segment extent. The basin spatial extent was sampled by the KDWPT once during summer months for 20 consecutive years during 1994–2005 (i.e. temporal extent of 20 years). Thirty-seven sample units were sampled one to nine times for a total of 97 observations at the basin extent. We did not mix datasets across spatial extents for this study, meaning that samples from the reach extent were not included in segment or basin extent analyses, and that samples from the segment extent were not included in the basin extent analysis. This scaling strategy is described in detail by Allen and Starr (2017) and involves using predefined scales, here based on previous riverscape literature (Fausch et al., 2002; Frissell et al., 1986), to investigate the manner in which ecological patterns change as scales are allowed to vary.

### 2.2 | Arkansas darter capture rate

Fish surveys included monitoring using a combination of electrofishing and seining. Detailed protocols are described in Lazorchak, Klemm, and Peck (1998) and included single-pass electrofishing of all available habitats at a sample unit in an upstream direction and seining only deeper habitats in a downstream direction. This approach is known to yield reliable estimates of fish abundances in Great Plains prairie streams and is comparable to more intensive multi-pass procedures (Bertrand, Gido, & Guy, 2006). Large streams were sampled with tote barge electrofishing and seining, while backpack electrofishing was used in small streams, and the length of time spent electrofishing or seining was recorded. All collected fishes were held at each site until they were identified to species and then released back into the habitat from which they were captured. Arkansas darter capture rate was calculated as the number of darters collected per hour of time spent sampling (i.e. fish/hr) at each sample unit. A single sample collected by the KDWPT was removed from analysis because it included a record number of Arkansas darter ( $n = 2,136$ ) and resulted in an extreme value for capture rate (2,959 fish/hr). Capture rate was then used as the response variable in model construction for each spatial extent included in this study.

### 2.3 | Local habitat data

We included measurements of local habitat dimension and heterogeneity as potential descriptors of Arkansas darter capture rate. Habitat variables were collected during the same sampling events as capture rate data and detailed methods are provided in Lazorchak et al. (1998). Briefly, habitat sampling included measurements of stream width, depth, canopy cover, instream woody structure, and bank vegetation using 10 evenly spaced transects distributed along each sample unit. At each transect, the wetted width (m) of the stream was recorded and depth (m) was measured at five points distributed evenly along the transect line. At the centre point of each

transect, a concave densiometer was used to record canopy cover by standing in the stream and facing upstream. Along each transect, the proportion of area covered by instream woody structure with a minimum diameter of 7 cm at the base (*woody structure* hereafter) and overhanging bank vegetation (*vegetation* hereafter) was visually estimated. Multiple habitat measurements collected for each sample unit were summarised by their mean, including mean depth (channel depth), mean wetted width (channel width), and mean canopy cover (% canopy).

## 2.4 | Data analyses

We compared univariate gradients in environmental variables and Arkansas darter capture rates across scales using probability density functions to test our first hypothesis that gradients increase with spatial extent. Probability density functions are particularly useful for assessing distributions when non-normal distributions are expected and do not require binning data. We used the *sm.density.compare* function from the *sm* package in R (R Core Team, 2016) with 10,000 bootstrapped samples to test equality of data distributions for vegetation, stream depth, woody structure, canopy cover, and stream width across reach, segment, and basin extents (Bowman & Azzalini, 2014). We also assessed differences in time spent sampling (i.e. electrofishing and seining, measured in s) and Arkansas darter capture rates (fish/hr) across extents. We first conducted three-way tests of equality for each variable, and if significant differences occurred ( $p < 0.05$ ,  $\alpha = 0.05$ ), we assessed pairwise differences across scales (i.e. three pairwise possibilities) based on overlapping confidence intervals. The three-way test was a permuted test of equality across density estimates grouped by spatial extent, and 95% confidence intervals provided by the function *sm.density.compare* allowed for assessing pairwise differences when the permuted test was significant. We illustrated variable distributions using density kernels and asterisks to summarise *post hoc* pairwise comparisons.

Prior to model fitting and hypothesis testing, we assessed the presence of autocorrelation and correlation among habitat variables. We tested for spatial autocorrelation among variables measured at the finest spatial extent (reach) because measurements taken close together in space are more likely to correlate (Legendre, 1993). Autocorrelation functions applied using the *acf* in R illustrated the absence of spatial autocorrelation for all parameters except channel width (Supporting Information Figure S1). Significant negative spatial autocorrelation among widths occurred only during a single visit and only at a single distance (Supporting Information Figure S1). Given these patterns, we proceeded with statistical analyses without incorporating adjustments for spatial autocorrelation. Next, we assessed pairwise correlations among habitat variables using the *corrplot* function in R (Wei & Simko, 2017). This initial test revealed some level of correlation among habitat variables (Supporting Information Figure S2), indicating that any subsequent modelling should include consideration of multicollinearity (Mansfield &

Helms, 1982) and rely on model selection methods that avoid issues of multicollinearity (Graham, 2003).

We fit generalised linear mixed models (GLMMs) and used model selection to quantify relationships between Arkansas darter capture rate and local habitat parameters at reach, segment, and basin extents to test our second hypothesis that models fit at broader extents describe more variation. For each extent independently, we built 16 competing models with Arkansas darter catch rate as the response variable and intercept-only, channel depth (m), channel width (m), canopy cover (proportion), woody cover (proportion), vegetation cover (proportion), and all possible two-way combinations of these variables as predictors (Table 1). We did not include more complex models (e.g. 3–5-term models) because samples sizes were insufficient. For each model, we used repeated visits (site visit) to sample units through time as a random variable, allowed intercepts and slopes to vary randomly, employed a Poisson error distribution, and z-score transformed all predictor variables to better approximate normal distributions. We fit GLMMs using the *glmer* function from the *lme4* package in R and compared models using Akaike information criterion adjusted for small sample size (AICc) using the *sem.model.fits* function from the *piecewiseSEM* package (Lefcheck, 2015). We assessed model fit using marginal  $R^2$  value described by Nakagawa and Schielzeth (2013) because this value describes the variance explained by fixed factors in the model (i.e. pure environmental effects). We illustrated scale-specific relationships between Arkansas darter capture rate and habitat parameters included in best-supported models using partial dependence plots and the *sjp.glmer* function from the *sjPlot* package (Lüdtke, 2017). Finally, although AICc model selection involving all possible subsets of variables is an accepted method for avoiding issues of multicollinearity (Graham, 2003), we assessed multicollinearity in best-supported models using condition number (K) and variance inflation factor (VIF) as described in detail by Alin (2010). As general principles, multicollinearity is not considered problematic at  $K < 5$  and  $VIF < 10$  (Alin, 2010). All statistics were conducted in R version 3.3.2 (R Core Team, 2016).

## 3 | RESULTS

Gradients for predictor variables, sampling effort, and Arkansas darter catch rate varied with spatial extent, but ranges of only channel width increased as hypothesised. Environmental variables and Arkansas darter capture rates were collected during a total of 182 sampling occasions. Distributions of observed values for vegetation coverage differed among extents (probability density test,  $p < 0.01$ ) and attenuated with increased spatial extent (Figure 2a), while stream depth ( $p = 0.09$ ) and woody structure ( $p = 0.11$ ) distributions were consistent among extents (Figure 2b,c). Canopy cover differed among extents ( $p < 0.01$ ) but was similar between segment and basin extents (Figure 2d). Stream widths differed among all three extents ( $p < 0.01$ ; Figure 2e). Time spent sampling increased with spatial extent ( $p < 0.01$ ; Figure 2f); however, Arkansas darter capture rates

**TABLE 1** Scales and structures for generalised linear mixed models selected at reach ( $n = 60$  observations), segment ( $n = 25$ ), and basin ( $n = 97$ ) extents illustrating  $AIC_c$ ,  $\Delta AIC_c$ , Akaike weights, and  $r$ -square values for models used to describe relationships between local habitat and Arkansas darter capture rate in the South Fork Ninescah River, KS, U.S.A

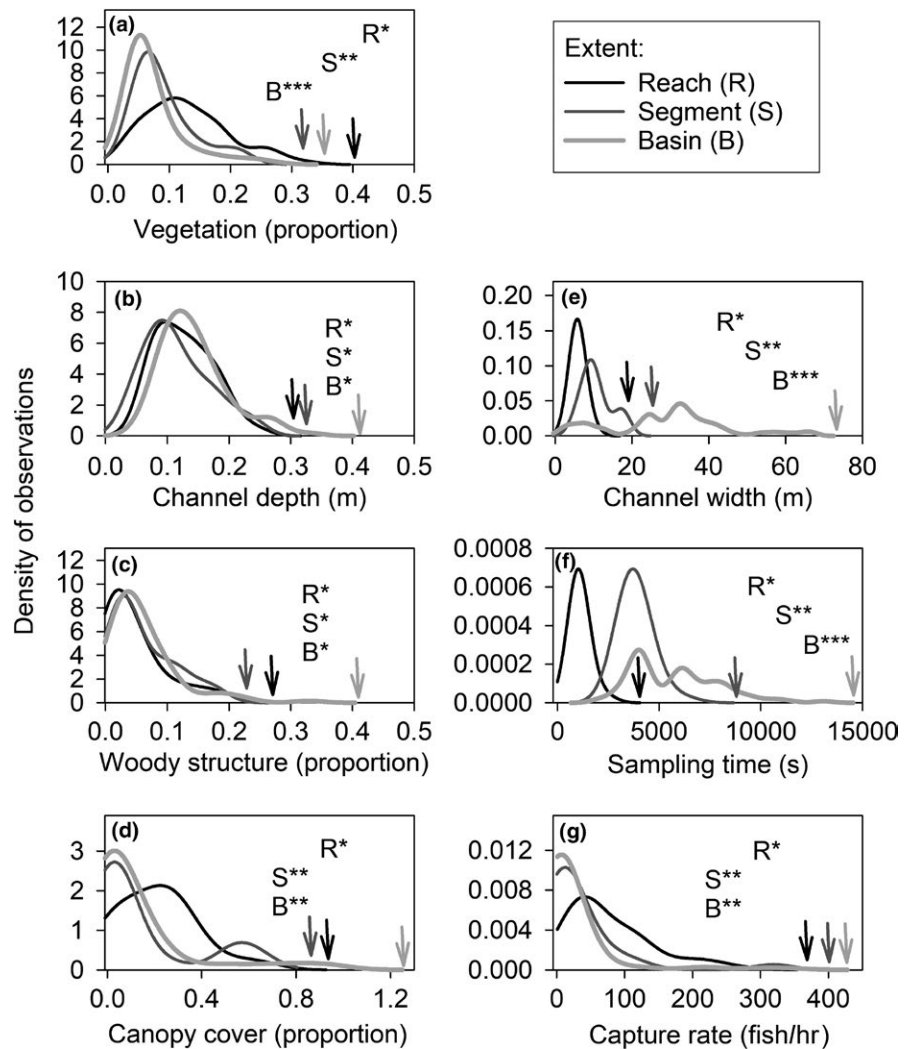
Scale and model structure	$AIC_c$	$\Delta AIC_c$	$w_i$	$R^2$
<b>Reach</b>				
1 + D + C + (1 + D + C SV)	1,675.9	0.0	0.999	0.54
1 + D + WS + (1 + D + WS SV)	1,725.0	49.1	<0.001	0.50
1 + WS + C + (1 + WS + C SV)	1,915.7	239.8	<0.001	0.28
1 + W + C + (1 + W + C SV)	1,945.8	269.9	<0.001	0.40
1 + D + V + (1 + D + V SV)	2,054.1	378.2	<0.001	0.51
1 + W + WS + (1 + W + WS SV)	2,064.3	388.4	<0.001	0.29
1 + D + W + (1 + D + W SV)	2,072.3	396.4	<0.001	0.38
1 + V + C + (1 + V + C SV)	2,090.6	414.7	<0.001	0.44
1 + WS + V + (1 + WS + V SV)	2,100.6	424.7	<0.001	0.28
1 + C + (1 + C SV)	2,122.0	446.1	<0.001	0.44
1 + WS + (1 + WS SV)	2,136.7	460.8	<0.001	0.34
1 + D + (1 + D SV)	2,272.3	596.4	<0.001	0.49
1 + W + V + (1 + W + V SV)	2,385.9	710.0	<0.001	0.15
1 + W + (1 + W SV)	2,572.1	896.2	<0.001	0.11
1 + V + (1 + V SV)	2,676.5	1,000.6	<0.001	0.00
1 + (1 SV)	2,734.9	1,059.0	<0.001	0.00
<b>Segment</b>				
1 + D + C + (1 + D + C SV)	388.7	0.0	0.999	0.56
1 + D + W + (1 + D + W SV)	402.2	13.5	<0.001	0.45
1 + W + C + (1 + W + C SV)	410.2	21.5	<0.001	0.64
1 + W + WS + (1 + W + WS SV)	448.3	59.6	<0.001	0.65
1 + W + V + (1 + W + V SV)	464.7	76.0	<0.001	0.62
1 + D + V + (1 + D + V SV)	470.2	81.5	<0.001	0.59
1 + D + WS + (1 + D + WS SV)	499.1	110.4	<0.001	0.69
1 + D + (1 + D SV)	568.8	180.2	<0.001	0.65
1 + V + C + (1 + V + C SV)	695.5	306.8	<0.001	0.34
1 + WS + C + (1 + WS + C SV)	768.9	380.2	<0.001	0.33
1 + W + (1 + W SV)	823.3	434.7	<0.001	0.49
1 + WS + V + (1 + WS + V SV)	831.0	442.3	<0.001	0.25
1 + V + (1 + V SV)	895.1	506.5	<0.001	0.38
1 + C + (1 + C SV)	909.4	520.7	<0.001	0.40
1 + WS + (1 + WS SV)	911.7	523.0	<0.001	0.32
1 + (1 SV)	1,134.7	746.0	<0.001	0.00
<b>Basin</b>				
1 + D + W + (1 + D + W SV)	2,539.12	0.00	0.999	0.37
1 + W + WS + (1 + W + WS SV)	2,881.52	342.40	<0.001	0.13
1 + WS + C + (1 + WS + C SV)	2,970.48	431.36	<0.001	0.00
1 + W + V + (1 + W + V SV)	2,985.39	446.27	<0.001	0.09
1 + W + C + (1 + W + C SV)	3,047.79	508.66	<0.001	0.20
1 + W + (1 + W SV)	3,276.51	737.38	<0.001	0.40
1 + D + C + (1 + D + C SV)	3,673.22	1,134.10	<0.001	0.02
1 + V + C + (1 + V + C SV)	4,167.67	1,628.54	<0.001	0.06

(Continues)

**TABLE 1** (Continued)

Scale and model structure	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	R <sup>2</sup>
1 + D + V + (1 + D + V SV)	4,391.63	1,852.50	<0.001	0.01
1 + C + (1 + C SV)	4,580.19	2,041.07	<0.001	0.02
1 + D + WS + (1 + D + WS SV)	4,681.14	2,142.01	<0.001	0.00
1 + WS + V + (1 + WS + V SV)	4,805.10	2,265.98	<0.001	0.04
1 + D + (1 + D SV)	4,876.42	2,337.30	<0.001	0.00
1 + V + (1 + V SV)	5,123.35	2,584.22	<0.001	0.02
1 + WS + (1 + WS SV)	5,698.78	3,159.66	<0.001	0.04
1 + (1 SV)	5,872.30	3,333.17	<0.001	0.00

Model parameters include intercept (1), depth (D), width (W), vegetation (V), woody structure (WS), canopy cover (C), and site visit (SV—a random variable representing repeated visits).

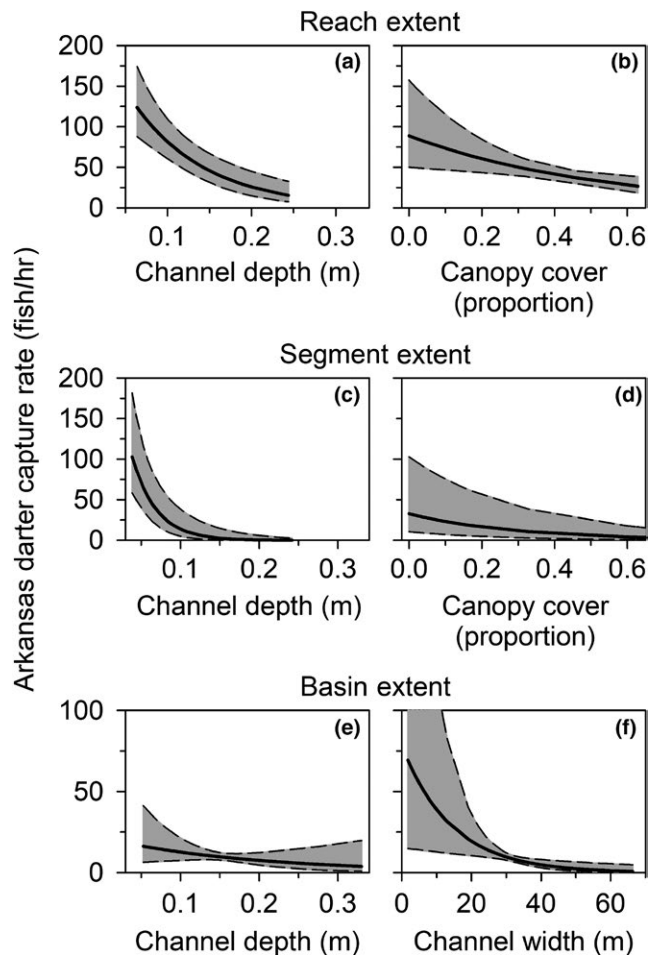


**FIGURE 2** Probability density functions illustrating extent-specific distributions of observations for (a) proportion of area with overhanging vegetation (vegetation), (b) channel depth, (c) proportion of area with woody structure (woody structure), (d) proportion of area with canopy cover (canopy cover), (e) channel width, (f) sampling time, and (g) Arkansas darter capture rate. Extent symbols (reach = R, segment = S, basin = B) with matching numbers of asterisks have similar density distributions (i.e. not significantly different) and arrows of corresponding colours mark maximum observed values

were greatest at the reach extent ( $p < 0.01$ ), where sample time was least (Figure 2g).

Relationships between habitat variables and Arkansas darter capture rate differed among spatial extents, but model fit did not increase with spatial extent as hypothesised. At the reach extent, 54% of variation in Arkansas darter catch rate was explained by channel

depth and canopy cover, there was strong support for this model above all others based on AIC<sub>c</sub> and w<sub>i</sub> values (Table 1), and multicollinearity was not present ( $K = 1.011$ ;  $VIF = 1.026$ ). Reach-scale Arkansas darter capture rate was negatively correlated with channel depth (Figure 3a) and canopy cover (Figure 3b). At the segment extent, 56% of variation in Arkansas darter capture rate was explained



**FIGURE 3** Partial dependence plots from generalised linear mixed models fit to Arkansas darter catch rate (fish/hr) at reach, segment, and basin extents. Panels illustrate estimates (solid lines) and 95% confidence intervals (dashed lines and grey shades) for partial dependence of Arkansas darter catch rate on (a) channel depth and (b) canopy cover at the reach extent, (c) channel depth and (d) canopy cover at the segment extent, and (e) channel depth and (f) channel width at the basin extent

by channel depth and canopy cover, there was strong support for this model (Table 1), and multicollinearity was not present ( $K = 1.261$ ;  $VIF = 1.026$ ). Segment-scale Arkansas darter capture rate was negatively correlated with channel depth (Figure 3c) and canopy cover (Figure 3d). At the basin extent, 37% of variation in Arkansas darter capture rate was explained by channel depth and width, there was strong support of this model (Table 1), and multicollinearity was not present ( $K = 1.543$ ;  $VIF = 1.433$ ). Basin-scale Arkansas darter capture rate was negatively correlated with channel depth (Figure 3e) and channel width (Figure 3f).

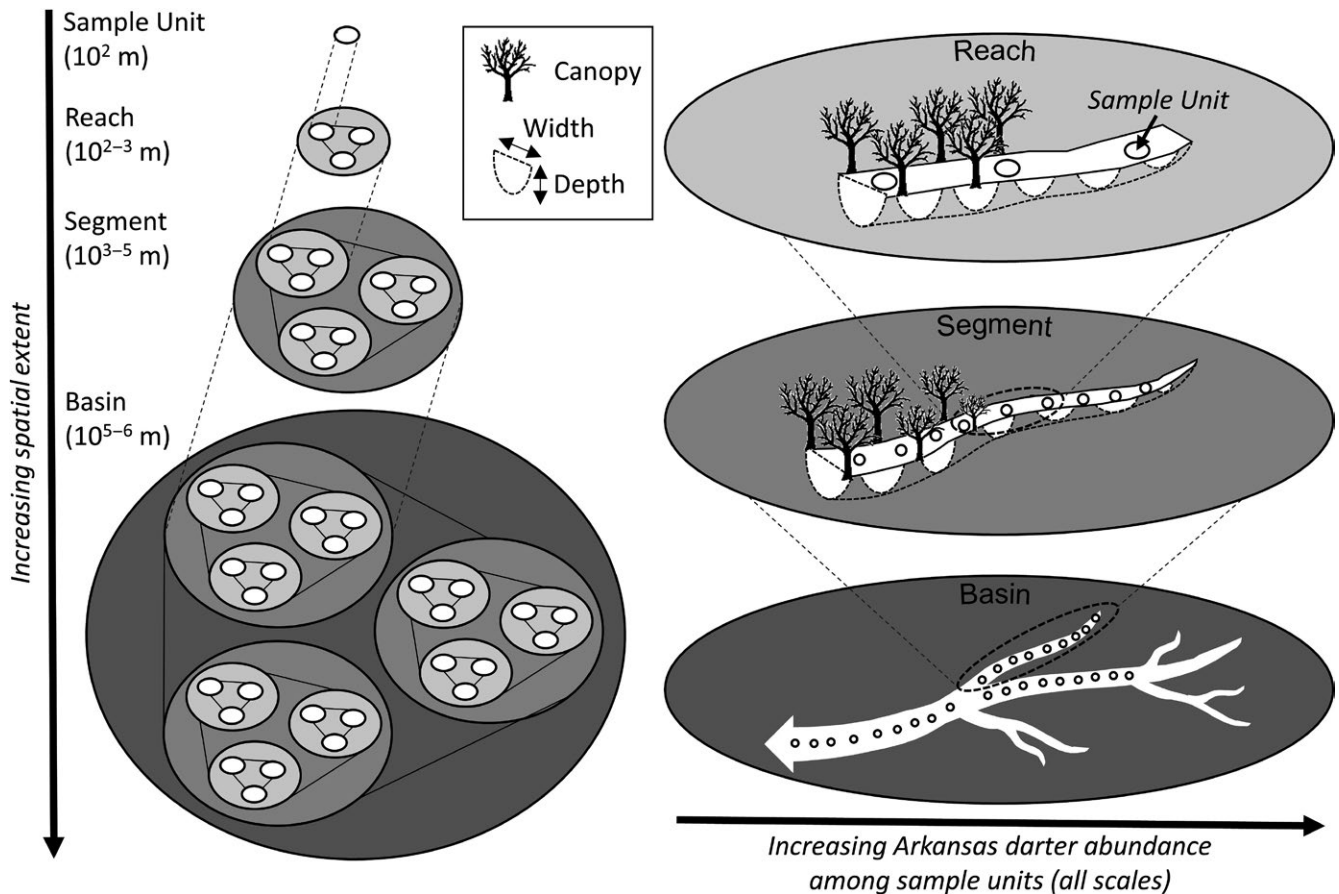
## 4 | DISCUSSION

Fausch et al. (2002) suggested that taking a continuous view of stream habitats across riverscapes was the best approach to bridging the gap between research and conservation of stream fishes.

Application of hierarchy theory as a means of decomposing complex systems into interacting parts or *systems of systems within systems* is a critical step in establishing continuous views of complex ecosystems such as riverscapes (King, 1997; Simon, 1962). Conceptually, this entails nesting multiple sample units within reaches, reaches within segments, and segments within basins (Figure 4, left column). Viewing Arkansas darter habitat associations through the lens of hierarchy theory means basins such as the South Fork Ninnescah River can be decomposed into stream segments such as Smoots Creek, and segments of Smoots Creek can be decomposed into reaches such as the one flowing through the Gerber Reserve (Figure 4, right column). In our empirical example, reach-scale distribution of sample units along gradients of channel depth and canopy cover revealed strong correlations between these local habitat parameters and Arkansas darter abundance. Increasing the spatial extent of investigation to the broader segment of Smoots Creek did not modify observed variation (i.e. gradient length) for channel depths, although less canopy cover was present among sample units based on probability density analyses. However, both channel depth and canopy cover were retained as descriptors of local abundance across the segment and explained a consistent amount of variation in catch rate compared to the reach extent. Scaling-up to the basin lengthened the gradient of stream widths observed during sampling, but channel depths remained consistent among extents, and measurements of habitat dimension (i.e. width and depth) emerged as correlates of Arkansas darter catch rate. These multiscale findings illustrate the application of hierarchy theory to gain greater insight into the ecology and conservation of Arkansas darter.

Scale is the *central problem in biology* because of uncertainty in how information is transferred among differing grains and extents (Levin, 1992). We hypothesised that increasing extent would be accompanied by increases in gradient lengths for habitat variables because of inclusion of rarer habitats at broader extents. We found that scaling between reach, segment, and basin extents resulted in increasingly broader gradients only for channel width and depth, and among these, only channel width distributions differed significantly. This pattern reflects the widely documented hierarchical structure of stream channels as detailed by Horton (1945) and Strahler (1957). Patterns for other habitat variables, including vegetative cover, woody structure, and canopy cover, had no consistent scaling pattern. However, these habitat variables tended to be correlated with each other. For example, canopy cover and woody structure were strongly correlated ( $r > 0.55$ ) across all spatial extents, and these correlations are probably the result of landscape processes that structure these habitat features. Flow pulses maintain channel cross-sectional areas (depth and width) through the processes of sediment deposition and erosion, but woody encroachment can alter deposition–erosion dynamics and contribute to deeper channels among stream segments with riparian forests (Trimble, 1997). Trees that exist as a consequence of woody encroachment ultimately provide canopy cover and, after death, are deposited into streams to create instream woody structure (Costigan, Daniels, & Dodds, 2015). Thus, although woody encroachment is a long-term





**FIGURE 4** Conceptual diagram illustrating application of nested hierarchy theory to Arkansas darter habitat associations. On the left, hierarchy theory is conceptually shown as nested circles of increasing size and shading intensity to represent habitat units of increasing spatial extent, including sample unit (white) as the spatial grain size nested within reach (light grey) nested within segment (medium grey) nested within basin (dark grey) spatial extents. On the right, the hierarchy of Arkansas darter habitat associations is shown using the same progression of colour shades and spatial scales. Scale-specific descriptors of Arkansas darter abundance identified during modelling are shown as streams with gradients in canopy cover and depth for both reach and segment extents and width and depth for the basin extent. Across all spatial extents, Arkansas darter abundance measured at sample units increases from left to right, or as canopies open and streams become shallower at reach and segment extents and as streams narrow and become shallower at the basin extent

change in landscape pattern, the geomorphic processes that interact with woody encroachment structure instream habitats in a manner that does not scale consistently with spatial extent.

There was no evidence to support our second hypothesis regarding increase in model fit at the basin extent. Our data suggest that Arkansas darter occupy shallow and narrow *headwater* streams, and locations of the reach and segment extents included in this study overlapped with headwater streams. Scaling up to the basin extent resulted in the inclusion of other reaches and segments that existed outside of areas Arkansas darter is able or willing to disperse. This suggests a trade-off between local environmental effects influencing abundance at finer spatial scales and dispersal limitations influencing occurrence at broader spatial scales. Heino et al. (2015) reviewed the effect of spatial extent on relative influences of environmental and dispersal processes in regulating aquatic organism distributions and found that environmental effects (considered here) begin to diminish while dispersal effects (not considered here) increase with greater spatial extent, and these process switch in their

dominance at approximately the basin spatial extent. The most comprehensive study of Arkansas darter ecology supports such a trade-off, including correlates of occurrence (spawning habitat, predation) at broad spatial extents (catchments or basins) and correlates of abundance (individual and population growth rates) at fine spatial extents (reaches and segments; Labbe & Fausch, 2000). This trade-off is potentially related to the *space-time correspondence principle*, which states increases in the spatial scale of ecological processes are accompanied by increases in temporal scale (Wu, 2013). In hierarchy theory, dynamics of lower levels are predicted to occur at a faster pace than higher levels (Allen & Starr, 2017), and population growth (an abundance factor) is a faster process than population establishment (an occurrence factor). Future research might investigate these processes at the scales identified in this work, including experimental manipulations of habitat heterogeneity (e.g. instream structure manipulations; Höjesjö, Gunve, Bohlin, & Johnsson, 2015) or simulations in population growth rates tested under a range of abiotic conditions (e.g. hydrologic connectivity; Jaeger, Olden, & Pelland, 2014).

Despite significant relationships between habitat variables and Arkansas darter capture rates, limitations to our study should be considered. First, our samples were acquired over several years and collected by different groups, which can introduce variation caused by differences in sampling effort. Nevertheless, historical data are critical in assessing population stability over broad spatiotemporal extents and this caveat can be addressed (Patton, Rahel, & Hubert, 1998). We tested for variability of sampling effort through space and time and accounted for differences by using catch rate rather than absolute numbers captured. Second, although woody structure and stream depth are known to influence sampling efficiency for other species (Rosenberger & Dunham, 2005), the distributions of these variables were consistent across extents in our study and therefore were unlikely to systematically influence cross-scale comparisons of capture rate. Third, our analysis utilised multiple spatial extents combined with a fixed grain size to assess multiscale influences on capture rate (i.e. *focus on scale* as described by Allen & Starr, 2017), but there was no spatial replication of reaches, segments, or basins. Similar approaches employing a fixed grain size are commonly used to control for fine-scale (i.e. sample unit in our case) variation in observational bias (Barton et al., 2013), and the temporal replication included in our models (rather than spatial replication) provides indication of the generality of patterns as in other studies (Labbe & Fausch, 2000). Finally, each of our GLMMs contained some unexplained variation, suggesting other factors not measured during our study or more complex models at least partly correlate with Arkansas darter capture rate (e.g. water temperature, Smith & Fausch, 1997) and could be included in future hierarchical assessments (Quist, Rahel, & Hubert, 2005). Our study provides direction for the spatial scales at which other parameters might be explored in future work, including measurements of habitat dimensions at broader scales and measures of habitat heterogeneity at finer scales.

Anthropogenic alterations to Great Plains riverscapes operate across spatiotemporal scales to threaten Arkansas darter, and our work suggests that hierarchy theory can inform conservation actions. Groundwater depletion across basins over the past century has reduced the abundance and distribution of the small streams that support Arkansas darter (Eberle & Ernsting, 2014; Fitzpatrick et al., 2014; Steward & Allen, 2016). Groundwater is increasingly consumed by the expanding human population and densities of phreatophytes that render water inaccessible to fishes (Garbrecht, Van Liew, & Brown, 2004; Perkin et al., 2017). Our analyses suggest that this simultaneous drying and shading of headwater streams creates habitats that constrain Arkansas darter abundance. Consequently, maintenance of surface-groundwater connections should be a conservation priority to maintain base flow conditions and avoid extirpation of fishes dependent upon groundwater outflows (Falke et al., 2011). Maintaining aquifers that support surface flow will become increasingly difficult under a changing climatic regime, and Arkansas darter range constrictions caused by aquifer depletion have already occurred (Eberle & Stark, 2000; Perkin et al., 2017). At finer scales, woody encroachment across segments and reaches has increased depths of small stream channels, deposition of woody structure,

and canopy cover (Briggs et al., 2005; Huxman et al., 2005). Riparian corridors should be managed for native landscape buffers, including the removal of trees where prairie landscapes exist or have been re-established (e.g. the Gerber Reserve) to ensure open canopy and prairie floodplain characteristics persist; however, trade-offs between benefits and consequences of riparian buffers in agriculturally altered landscapes must be addressed (Briggs et al., 2005; Fischer et al., 2010). At fine scales such as reaches, habitat size gradients (e.g. channel depth) should be maintained so that mixtures of shallow, deep, wide, and narrow habitats allow for persistence of a diversity of fishes requiring differing habitat dimensions (Troia & Gido, 2013, 2014). The long-term persistence of Arkansas darter populations in Kansas (Gido, Dodds, & Eberle, 2010) suggests protection of existing riverscape conditions is critical, and our application of hierarchy theory provides direction for the habitat features and scales that should be targeted to enhance conservation of Arkansas darter.

## ACKNOWLEDGMENTS

We thank Wichita State University for allowing access to the Gerber Reserve as well as Kansas State University and the KDWP for logistical support. Sampling assistance was provided by Wichita State University student E. (Dudeck) Engasser, KSU students T. Davis, C. Pennock, M. Waters, R. Weber, and B. Wellemeyer, KDWP Fishery Division staff J. Mounts and crew, KDWP Ecological Services staff J. Conley and crew, and many others. A. Gebhard and two anonymous reviewers provided helpful feedback during manuscript preparation. This manuscript is contribution 28 of the Wichita State University Ninescah Biological Station. Support for J.S.P. was provided by Texas A&M University and by the USDA National Institute of Food and Agriculture, HATCH Project 1017538.

## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Wellemeyer JC, Perkin JS, Jameson ML, Costigan KH, Waters R. Hierarchy theory reveals multiscale predictors of Arkansas darter (*Etheostoma cragini*) abundance in a Great Plains riverscape. *Freshw Biol.* 2019;00:1–12. <https://doi.org/10.1111/fwb.13252>