Fragmentation alters stream fish community structure in dendritic ecological networks

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Abstract. Effects of fragmentation on the ecology of organisms occupying dendritic ecological networks (DENs) have recently been described through both conceptual and mathematical models, but few hypotheses have been tested in complex, real-world ecosystems. Stream fishes provide a model system for assessing effects of fragmentation on the structure of communities occurring within DENs, including how fragmentation alters metacommunity dynamics and biodiversity. A recently developed habitat-availability measure, the "dendritic connectivity index" (DCI), allows for assigning quantitative measures of connectivity in DENs regardless of network extent or complexity, and might be used to predict fish community response to fragmentation. We characterized stream fish community structure in 12 DENs in the Great Plains, USA, during periods of dynamic (summer) and muted (fall) discharge regimes to test the DCI as a predictive model of fish community response to fragmentation imposed by road crossings. Results indicated that fish communities in stream segments isolated by road crossings had reduced species richness (alpha diversity) relative to communities that maintained connectivity with the surrounding DEN during summer and fall. Furthermore, isolated communities had greater dissimilarity (beta diversity) to downstream sites not isolated by road crossings during summer and fall. Finally, dissimilarity among communities within DENs decreased as a function of increased habitat connectivity (measured using the DCI) for summer and fall, suggesting that communities within highly connected DENs tend to be more homogeneous. Our results indicate that the DCI is sensitive to community effects of fragmentation in riverscapes and might be used by managers to predict ecological responses to changes in habitat connectivity. Moreover, our findings illustrate that relating structural connectivity of riverscapes to functional connectivity among communities might aid in maintaining metacommunity dynamics and biodiversity in complex dendritic ecosystems.

Key words: conservation biology; dendritic connectivity index, DCI; dendritic ecological networks; Great Plains, USA, stream fish community structure; metacommunity theory; riverine landscapes; road-crossing fragmentation; stream fish ecology; stream fragmentation.

INTRODUCTION

Recent advances in community ecology have emphasized the relationship between ecological network structure and patterns and processes occurring within ecosystems (Brown and Swan 2010, Auerbach and Poff 2011). In particular, streams are unique in that they are constrained dendritic ecological networks (DENs) generally characterized by bifurcating branches of habitat that decrease in size and increase in number with greater distance from the base of the network (Dodds and Rothmann 2000). Examples of DENs include linear or fractal-like systems such as caves or streams with hierarchically structured patches of habitat that house multi-species communities linked by dispersal (Grant et al. 2007, Grant 2011). The framework by which multiple communities are linked by dispersal of organisms is the basis of the metacommunity concept as defined by

Leibold et al. (2004), in which environmental heterogeneity, species–environment relationships, and dispersal patterns are used to describe community assembly processes. Local community composition is dependent upon local abiotic and biotic conditions as well as on regional species pools; however, in streams the location within DENs and connectivity among network segments (patches) is an important abiotic constraint that can be a primary driver of community composition (Labonne et al. 2008, Thornbrugh and Gido 2010, Brown et al. 2011, Finn and Poff 2011). Taken together, these findings suggest spatial distribution of habitat patches and dispersal of organisms among patches (i.e., the principles of metacommunity theory; Leibold et al. 2004) aid in synthesizing complex dynamics in DENs (Brown et al. 2011). However, real-world applications of metacommunity dynamics in the context of DENs are rare (Brown et al. 2011), and existing knowledge was derived largely from theoretical models (Goldberg et al. 2010, Padgham and Webb 2010) with little empirical support (but see Falke and Fausch [2010] and Peres-Neto and

Cumming [2010]). Validating models of metacommunity dynamics in DENs with empirical data will assist in understanding how human-mediated alterations to dendritic networks threaten biodiversity as well as aid in directing conservation actions (Falke and Fausch 2010, Grant 2011).

Fragmentation of streams causes concern for the long-term persistence of species (Fagan 2002, Perkin and Gido 2011) as well as the goods and services provided by those ecosystems (Srivastava and Vellend 2005, Lecerf and Richardson 2010). Connectivity of stream networks is impacted most by the first few barriers introduced to a system, which is in contrast to most non-dendritic networks that are resistant to fragmentation caused by low numbers of barriers (Cote et al. 2009). Furthermore, simulations suggest structural modifications to streams such as changes in patch quality and accessibility are additive, causing non-interactive reductions in fish populations as patch quality and accessibility diminish (Padgham and Webb 2010). However, as noted by Padgham and Webb (2010), most analyses of DEN properties to date are theoretically modeled and potentially of limited usefulness in predicting population- or community-level responses to altered connectivity in real-world DENs (Urban et al. 2009). Models predicting metapopulation extinction risk or metacommunity dynamics in DENs are inherently simplified and generally require additional biological information (e.g., dispersal capabilities, network topology) before being applicable to real-world networks because of the complex nature of ecosystems and inability of models to incorporate all realistic parameters (Padgham and Webb 2010, Auerbach and Poff 2011, Grant 2011). Because of these issues, natural experiments that encompass a diversity of network topologies and entire communities might prove useful in predicting consequences of anthropogenic environmental modifications to complex ecosystems (Hitt and Roberts 2012).

Habitat-availability measures that relate structural landscape connectivity to functional connectivity among metapopulations or metacommunities within DENs allow for testing the effects of fragmentation on the ecology of organisms inhabiting complex ecosystems. *Structural connectivity* is defined as the adjacency or proximity of patches within a landscape and is a measure of the degree to which patches are connected without regard to organism behavior or interpretation of the landscape (Taylor et al. 1993). Alternatively, *functional connectivity* is conceptually defined as the degree to which a landscape impedes or facilitates movement of organisms among patches (Bélisle 2005). The *dendritic connectivity index* (DCI) developed by Cote et al. (2009) measures structural connectivity of riverine landscapes regardless of the spatial extent or complexity of networks. The DCI considers stream networks as branching lines of continuous habitat in which the absence of barriers yields a DCI value of 100. As barriers are introduced, the number, placement, and permeability of barriers are considered so that the DCI value of a given system declines from 100, and the rate of decline can vary depending upon life history attributes of the stream organisms being considered (i.e., diadromous, moving between freshwater and marine systems; potamodromous, migrating within freshwater systems; Cote et al. 2009). Permeability of barriers is of concern because most stream obstacles do not completely thwart organism dispersal, that is, structures are considered semi-permeable. For example, Norman et al. (2009) found fish passage at road crossings that exhibited rapid drops in elevation at their outflow, commonly known as "perching," was limited to periods of storm runoff when elevated discharges caused water levels to inundate perches. Alexandre and Almeida (2010) found changes in habitat caused by a series of perched crossings resulted in spatially segregated fish communities associated with each crossing so that upstream sites generally had fewer native species, and Nislow et al. (2011) showed that species richness in stream segments upstream of perched crossings was reduced by as much as half the number of fishes occurring immediately downstream. These examples illustrate the negative effects of fragmentation on the availability of habitat to fishes in stream networks and the capacity of semi-permeable barriers to mimic larger obstacles (e.g., impoundments; Winston et al. 1991, Luttrell et al. 1999) in disrupting dispersal pathways of fishes (Alexandre and Almeida 2010). However, such examples lack network-scale analysis of barriers (i.e., the cumulative effect of multiple barriers occurring within a network) and do not allow predictive ability regarding ecological responses to fragmentation across riverine landscapes (Fausch et al. 2002). Consequently, examining the performance of habitat-availability indices such as the DCI is now a key area of research required for further significant progress in our understanding of the relationship between network structure and community ecology (Erős et al. 2012).

In this study, we use dendritic stream networks and stream fish community samples taken throughout these networks to test for changes in community assembly associated with fragmentation of DENs caused by road crossings. Perched road crossings present semi-permeable barriers characterized by rapid elevation changes or channelized sections with swift current velocities that selectively exclude fishes with slow critical swimming speeds (Leavy and Bonner 2009), limited leaping ability (Ficke et al. 2011), or are otherwise disinclined to pass culverts (Alexandre and Almeida 2010). Barriers to fish movement invoked by road crossings was the impetus for development of the DCI (Cote et al. 2009), and to our knowledge we present the first empirical assessment of the DCI associated with biodiversity patterns in stream fish communities. We show that fragmented communities exhibit lower species richness and increased dissimilarity to communities that maintain connectivity with the surrounding DEN using geo-

referenced data for perched road crossings, DENs composed of second- and third-order streams, and stream fish community data collected from multiple points within 12 replicates of DENs. Furthermore, we show that dissimilarity among communities (an indirect measure of interrupted functional connectivity) within DENs is negatively correlated with structural connectivity measured using the DCI.

MATERIALS AND METHODS

Dendritic ecological networks (DENs) and fragmentation

We evaluated the distribution and topology of stream DENs using a version of the U.S. Geological Survey National Hydrography Dataset (NHD; *available onlne*)[2] modified for the Kansas Aquatic Gap program (Oaks et al. 2005). We selected DENs composed of second- and third-order streams defined using the Strahler (1957) classification system because our primary interest was fragmentation imposed by perched road crossings that occur most frequently within these stream classes (Appendix A). Within each DEN we sampled stream fish communities at three locations designated as (1) a third-order stream site from which fish species were expected to disperse upstream ("source" sites), (2) an unfragmented second-order stream site with no instream barriers that would thwart dispersal from the third-order site ("unfragmented" sites), or (3) a fragmented second-order stream site separated from the source site by at least one perched road crossing ("fragmented" sites) (Fig. 1a; Appendix B). Stream organisms—especially fishes—can disperse upstream into adjacent streams during reproductive seasons and such dispersal has implications for local community assembly (Schlosser 1987, Hitt and Angermeier 2006, Grant 2011). For each DEN, unfragmented and fragmented second-order stream sampling locations were placed so that distances from the source sampling site were approximately equal. For replication, we selected three DENs composed of streams in close proximity to control for variation in abiotic parameters such as land use and precipitation as well as biotic parameters such as regional species pools (Fig. 1b). We then selected four 8-digit USGS hydrologic unit codes (HUCs) in the eastern portion of Kansas (Lower Big Blue, 10270205; Middle Kansas, 10270102; Lower Cottonwood, 11070203; Upper Verdigris, 11070101) that generally correspond with the Flint Hills Ecoregion where uplands are grazed by cattle and river valleys are row-crop agriculture (Fig. 1c, d). Because of the relatively small size of watersheds included in this study (third-order catchments) and proximity of sampling sites (<10 km apart), land-use changes were not expected to influence unfragmented and fragmented sampling sites differently within DENs.

We initially used the geographic information systems (GIS) layer produced by the Kansas Department of Transportation (KDOT) for the abundance and distribution of road crossings potentially characterized by perched outflows capable of blocking fish dispersal. We then used a GIS approach to select three DENs in close proximity with similar topologies (i.e., number of bifurcations) and variation in number and placement of perched road crossings. We estimated average stream width (m) observed during fish community sampling (see *Fish community sampling*, below) as a measure of patch size. During field sampling we surveyed all crossings to ensure perches existed. When perches (if present) were inundated by water and therefore did not constitute a barrier to fish dispersal, we removed the barrier from our GIS database. We also evaluated stream corridors by walking sections between sampling sites and inquiring with local landowners, to ensure the absence of natural barriers that might confound connectivity measures. To our knowledge no natural barriers to dispersal were present in the study DENs. Because of discrepancies between perched crossings in the initial KDOT GIS layer and those identified during field sampling, the number of unfragmented and fragmented sites was not always balanced within each DEN, although both classifications existed within each HUC (Appendix C).

We quantified connectivity at the DEN scale using the DCI. Networks were defined as third-order streams and all second-order tributaries, including tributaries that were not sampled for fish community data, but excluding all first-order streams because most were dry during the year. In all cases, the downstream limit of DENs was the confluence with a fourth-order or larger stream. Barriers consisted of all perched road crossings that existed within DENs and were uniformly assigned a permeability value of 0.5 (where 0 = impassable and 1 = completely passable). Although permeability of crossings might be a function of perch height and local hydrologic regimes (Norman et al. 2009, Bourne et al. 2011), we used a value of 0.5 because Cote et al. (2009) found that the DCI yields informative structural connectivity measures even in the absence of specific permeability values for each barrier and because we generally encountered box culverts with perched outflows as barriers (low-head dams were absent from DENs included in our study system and only one corrugated crossing, which also exhibited perching, was observed). We used the potadromous component of the DCI (DCI$_p$) that assumes fishes are not obligated to disperse beyond the lowest levels of DENs (i.e., long-distance migrations to the ocean, Cote et al. 2009). This approach includes dividing the total stream network length (measured in stream kilometers) into sections isolated by barriers, then computing a weighted average of connectivity within (permeability = 1) and among (permeability = 0.5) all sections so that greater DCI values correspond with isolation of a smaller fraction of the riverscape (see Cote et al. [2009] and Bourne et al. [2011]
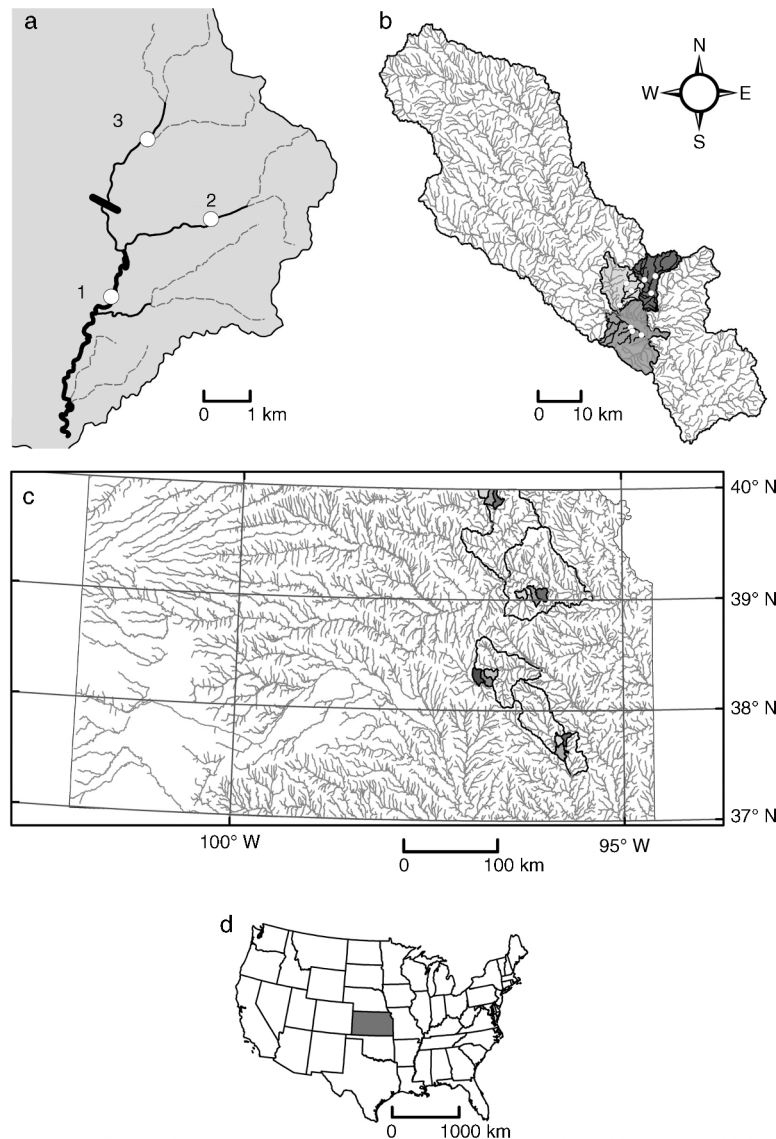
FIG. 1. Examples of our sampling sites in Kansas (USA), and their relation to U.S. Geological Survey (USGS) Hydrologic Unit Codes (HUCs, which are drainage areas delineated to nest in a multi-level, hierarchical drainage system). (a) Little Sandy Creek dendritic ecological network (DEN) composed of a third-order stream and second-order tributaries (first-order streams are shown as dashed lines) with three fish sampling sites (white circles): (1) a source community in a third-order stream, (2) an unfragmented community in a second-order stream, and (3) a fragmented community in a second-order stream isolated by a perched road crossing (short thick black line). (b, c) Examples of USGS HUCs of two sizes: the smaller 14-digit HUCs are specific areas (polygons) that fit within larger 8-digit HUCs (polygons). (b) Streams, fish sampling sites, and 14-digit HUCs associated with three DENs within the Upper Verdigris 8-digit HUC (USGS no. 11070101). (c) Distribution of four 8-digit USGS HUCs (black-outlined polygons) in which three DENs were sampled; 14-digit HUCs associated with DENs are shown (shaded polygons). (d) Kansas is located in the central contiguous United States. See Appendix B for detailed illustrations of 12 DENs included in the study.

for detailed calculation methods). All DCI calculations were conducted in statistical program R version 2.12.1 (R Development Core Team 2012) using source code obtained from David Cote (Parks Canada staff).

Fish community sampling

Stream fish communities were sampled during summer and fall of 2010. Summer sampling was conducted during May and June when Great Plains prairie stream discharges are characterized by flashy pulses with potential to inundate road-crossing perches, whereas fall sampling was conducted during September and October when prairie streams typically have muted hydrographs with few pulses (Dodds et al. 2004). At each site, a combination of single-pass electrofishing (Smith-Root LR-24 backpack electrofisher; Smith-Root, Vancouver, Washington, USA) and seining (4.6 × 1.8 m, 3.2-mm mesh) was conducted for 150–300 m of stream following

the standardized methods of McMahon et al. (1996) to obtain representative samples of communities within stream reaches. All fishes collected were identified to species, enumerated, and released in the case of large-bodied specimens or retained for laboratory identification in the case of small-bodied specimens. In the field, length and width of habitats sampled were measured to calculate area sampled and estimate fish densities. Each site was visited twice (once during each season) with the exception of sites that dried during the fall and were not sampled a second time ($n = 4$, Appendix C). We also visited road crossings within each DEN and surveyed perch heights (cm) using standard survey equipment to verify presence of barriers included in the KDOT GIS layer. Based on the occurrence of perched road crossings (heights, 4–102 cm) within DENs, we determined that our summer collections included 12 source, 13 unfragmented, and 13 fragmented communities and fall collections included 12 source, 12 unfragmented, and 10 fragmented communities. The 72 total samples retained excluded four sites (one unfragmented and three fragmented) that dried during fall and a single site that was dominated by groundwater discharge surfacing upstream of the sampling area, which contributed to notably cooler water temperatures, narrow channel widths, and reduced species richness relative to surrounding streams.

Community composition within and among dendritic ecological networks

We evaluated differences in community composition among unfragmented and fragmented sampling sites using distance matrices (Bray and Curtis 1957) as a measure of beta diversity (i.e., biodiversity changeover between sites; greater distance indicates greater beta diversity) and species richness as a measure of alpha diversity (i.e., biodiversity at a single site). Proportional densities (i.e., density of each species/density of all species encountered) were calculated (no. fish/m^2) for species within each community and imported into the statistical program Primer 6 (Primer-E, Ivybridge, UK). Because densities of common and rare species varied by two orders of magnitude, we fourth-root-transformed data before analyzing to reduce skewness of distributions (Somerfield et al. 1995). We then used the transformed data and the resemblance function in Primer 6 to construct a nonmetric Bray-Curtis distance matrix among all communities sampled. We developed pair-wise measures of dissimilarity for all source and unfragmented or fragmented comparisons by multiplying distance measures by 100 to yield values between 0 (no dissimilarity) and 100 (completely dissimilar). Because habitat isolation and size tend to align along general gradients associated with stream fish community composition (Angermeier and Schlosser 1989, Lonzarich et al. 1998), we tested for differences in distance between unfragmented and fragmented communities from source communities as well as stream size (width in meters). For each potentially confounding effect we used linear regression to test for

either isolation by distance (stream distance vs. dissimilarity between sites) or a species–area relationship (stream width vs. species richness at each site). We then directly compared stream distances from source sites for unfragmented and fragmented sites using a two-tailed t test ($\alpha = 0.05$) and stream widths among source, unfragmented, and fragmented sites using a single-factor ANOVA ($\alpha = 0.05$), followed by Fisher's least significant difference (LSD) multiple comparisons. We hypothesized that communities occurring upstream of perched crossings (fragmented sites) would show increased dissimilarity to source sites (greater beta diversity) as well as lower species richness (attenuated alpha diversity) relative to unfragmented sites because of reduced dispersal through perched crossings. We then tested for differences in dissimilarity and species richness between unfragmented and fragmented sites using a two-tailed t test and ANOVA.

We assessed the relationship between structural and functional connectivity to evaluate the effects of fragmentation on metacommunity structure in DENs. We measured structural connectivity at the scale of DENs and deemed patches isolated when perched road crossings occurred using the spatially implicit DCI to produce quantitative measures of connectivity for each DEN. We estimated functional connectivity as the degree of dissimilarity among communities. Thus, increased connectivity throughout the riverscape would contribute to high faunal similarity and low beta diversity (assuming organisms are moving optimally; Bélisle 2005). We hypothesized that reduced structural connectivity would cause a reduction in functional connectivity among communities because of the lack of alternative routes within stream DENs (Grant et al. 2007). To test this hypothesis we evaluated the relationship between structural and functional connectivity using linear regression and plotting mean dissimilarity among all pair-wise comparisons within a DEN as a function of the DCI. We then considered how structural connectivity related to functional connectivity among HUCs by evaluating the coefficient of determination among DCI values and mean dissimilarity values for all 12 DENs included in the study.

RESULTS

Stream fish community structure in dendritic ecological networks (DENs)

Stream fish community collections produced 47 species representing 30 genera and 11 families (Appendix D). Gamma diversity measured across DENs and seasons was 19 in the Lower Big Blue HUC, 25 in the Middle Kansas HUC, 22 in the Lower Cottonwood HUC, and 30 in the Upper Verdigris HUC, and alpha diversity (species richnesss) at sampling sites was generally similar during summer and fall (Appendix C). Among all sites, drainage distance from source sampling sites was on average 5.68 ± 2.23 km (mean ± SD) for unfragmented sites, 5.88 ± 2.20 km for fragmented sites, and distance distributions did not

significantly differ ($t = 0.23$, df = 24, $P = 0.82$). Third-order stream sites had widths ranging from 3.9 to 8.5 m, whereas second-order sites ranged from 2.2 to 6.2 m for unfragmented sites and from 1.5 to 6.2 m for fragmented sites. Whereas widths differed among second- and third-order streams (ANOVA; $F_{2,69} = 22.88$, $P < 0.01$), post hoc Fisher's LSD comparisons indicated unfragmented and fragmented sites had similar widths ($P = 0.78$). Sites exhibited a general reduction in stream width from summer to fall (paired t test; $t = 5.86$, df = 33, $P < 0.01$) as discharges declined and four second-order sites dried entirely (Appendix C).

Community response to fragmentation

Regression analysis of drainage distance (km) between source-unfragmented or source-fragmented sites as the independent variable and dissimilarity between communities as the dependent variable indicated no isolation by distance at the spatial extent of our study (Fig. 2). There was no relationship between drainage distance (km) and dissimilarity during summer ($n = 26$ sites, $F_{1,25} = 0.32$, $r^2 = 0.02$, $P = 0.57$) or fall ($n = 22$ sites, $F_{1,21} = 0.86$, $r^2 = 0.04$, $P = 0.36$). However, dissimilarity was on average 15% lower for source-unfragmented community comparisons relative to source-fragmented community comparisons during summer ($t = 3.22$, df = 24, $P < 0.01$; Fig. 2a) and 14% lower during fall ($t = 2.18$, df = 20, $P = 0.04$; Fig. 2b), indicating significantly greater similarity among source-unfragmented communities.

Regression analysis of stream width (m) as the independent variable and species richness as the dependent variable indicated a species–area relationship at the spatial extent of our study (Fig. 3). There was a positive relationship between stream width (m) and alpha diversity (species richness) in source and unfragmented sampling sites for summer ($n = 26$ sites, $F_{1,23} = 5.51$, $r^2 = 0.19$, $P = 0.03$) and fall ($n = 25$ sites, $F_{1,22} = 5.23$, $r^2 = 0.19$, $P = 0.03$). Fragmented sites were excluded from regression analysis because of the potential for confounding effects of barriers on alpha diversity. During summer, species richness was 14.2 ± 3.6 species (mean ± SD) for source, 10.5 ± 2.5 for unfragmented, and 8.1 ± 3.5 for fragmented sampling sites, and richness values differed significantly among sampling site types (ANOVA; $F_{2,35} = 11.22$, $P < 0.01$). During fall, species richness was 13.6 ± 2.8 species for source, 10.8 ± 2.7 for unfragmented, and 7 ± 4.1 for fragmented sampling sites, and richness values differed significantly among sampling site types (ANOVA; $F_{2,31} = 11.60$, $P < 0.01$). Despite similarities in stream width between unfragmented and fragmented sites, mean species richness was significantly greater in unfragmented relative to fragmented sites during summer (Fisher's LSD, $P < 0.05$; Fig. 3a) and fall (Fisher's LSD, $P < 0.05$; Fig. 3b).

Variability in alpha and beta diversity among stream fish communities at unfragmented and fragmented
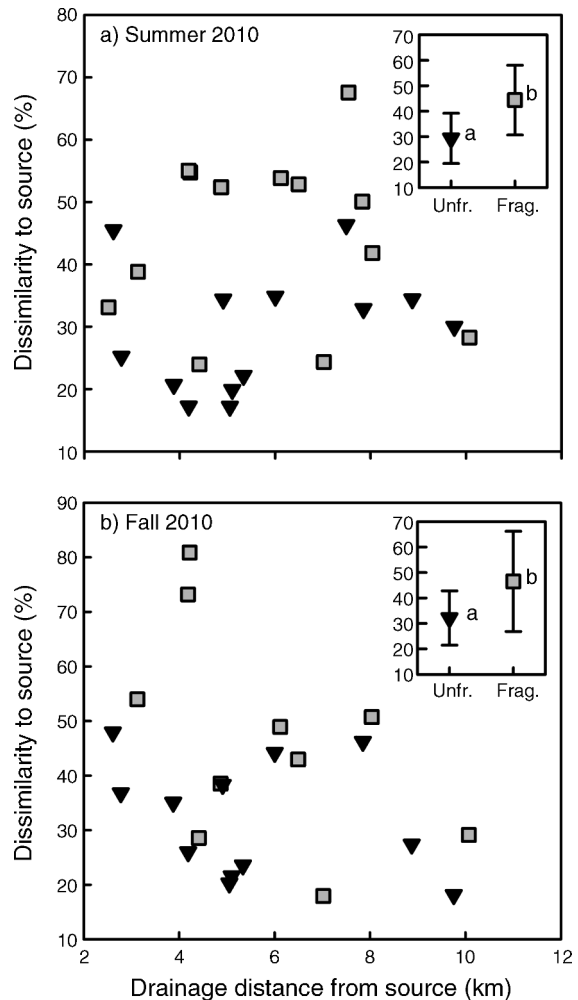

FIG. 2. Relationship between drainage distance from source sampling sites and dissimilarity to source sampling site communities for second-order stream fish communities sampled in Kansas (USA) streams during (a) summer and (b) fall of 2010. Inserts illustrate mean (±SD) dissimilarity among source-unfragmented (Unfr.; black triangles) vs. source-fragmented (Frag.; gray boxes) sampling sites for summer and fall; different lowercase letters next to symbols indicate differences in dissimilarity between unfragmented and fragmented sites detected during t-test analysis ($P < 0.05$).

second-order stream sites was associated with patterns in species occurrences. Sixteen species occurred in approximately equal numbers of unfragmented and fragmented streams, including seven in family Cyprinidae, three in Ictaluridae, four in Centrarchidae, and one in Percidae (Appendix D). Five species from different families (Fundulidae, Poeciliidae, Atherinidae, Centrarchidae, and Percidae) occurred in a greater number of fragmented streams. Fifteen species had reduced occurrences or were absent altogether in fragmented streams, including seven in the family Cyprinidae, two in Catostomidae, one in Ictaluridae, two in Centrarchidae, and three in Percidae. Commonly occurring species
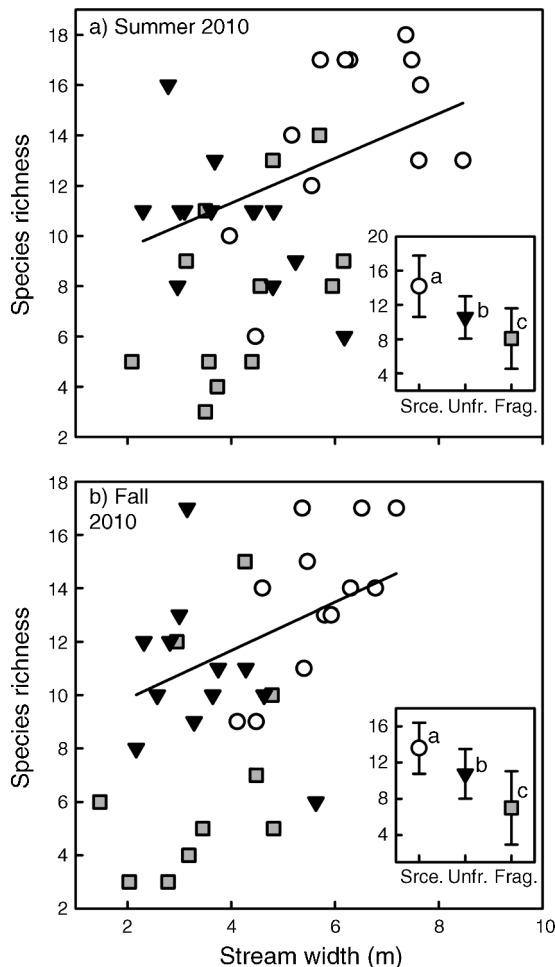
FIG. 3. Relationship between stream width and species richness among Great Plains stream fish communities in Kansas (USA) sampled during (a) summer and (b) fall of 2010. Insets illustrate mean (±SD) species richness according to third-order source (Srce., white circles), second-order unfragmented (Unfr., black triangles), and second-order fragmented (Frag., gray boxes) sampling sites; different lowercase letters next to symbols indicate significant differences in species richness detected during analysis of variance and post-hoc testing ($P < 0.05$). Regression models illustrate the relationship between stream width and species richness for source and unfragmented sampling sites to avoid confounding effects of barriers among fragmented sampling sites.

(occurred in >30 of 72 collections) that indicated approximately equal occurrences in unfragmented and fragmented streams included central stoneroller (*Campostoma anomalum*), redfin shiner (*Lythrurus umbratilis*), bluntnose minnow (*Pimephales notatus*), creek chub (*Semotilus atromaculatus*), black bullhead (*Ameiurus melas*), green sunfish (*Lepomis cyanellus*), bluegill sunfish (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and orangethroat darter (*Etheostoma spectabile*). Intermediately common species (occurred in >15 of 72 collections) that indicated absence or reduced

occurrence at fragmented sites included red shiner (*Cyprinella lutrensis*), common shiner (*Luxilus cornutus*), sand shiner (*Notropis stramineus*), suckermouth minnow (*Phenacobius mirabilis*), fathead minnow (*Pimephales promelas*), white sucker (*Catostomus commersonii*), slender madtom (*Noturus exilis*), longear sunfish (*Lepomis megalotis*), and orangespotted sunfish (*Lepomis humilis*).

Community composition and connectivity at the scale of dendritic ecological networks

Regression analysis predicting beta diversity among sites within DENs as a function of DCI indicated a relationship between structural and functional connectivity (Fig. 4). Mean dissimilarity among sites decreased
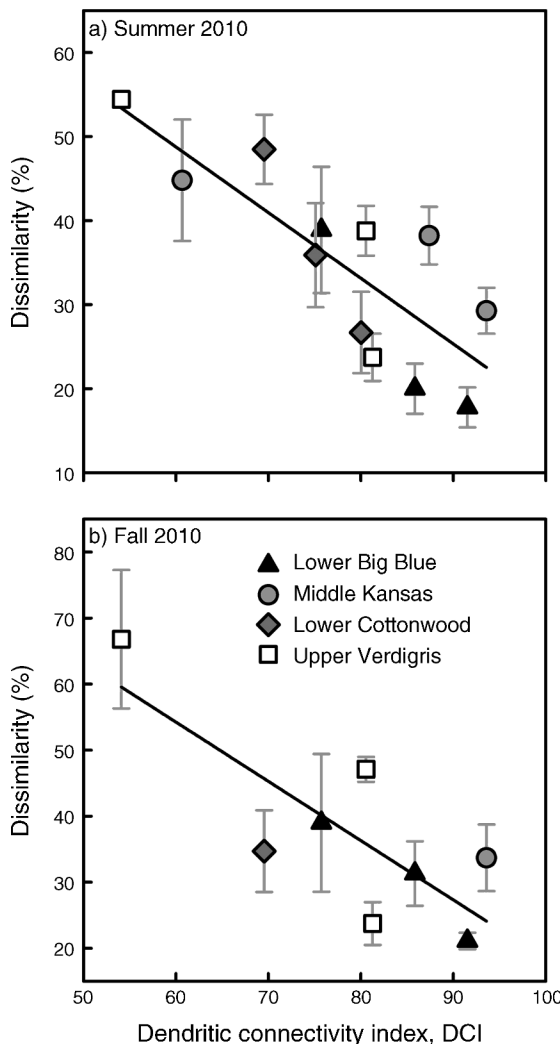

FIG. 4. Relationship between the dendritic connectivity index (DCI) and mean (±SD) dissimilarity among stream fish community sampling sites within dendritic ecological networks (DENs) in Kansas (USA) sampled during (a) summer and (b) fall of 2010. The drying of sites and subsequent exclusion of associated DENs reduced sample size during the fall.

as DCI increased among DENs for summer ($n = 12$ networks, $F_{1,10} = 19.05$, $r^2 = 0.66$, $P < 0.01$; Fig. 4a) and fall ($n = 8$ networks, $F_{1,6} = 10.09$, $r^2 = 0.63$, $P = 0.02$; Fig. 4b). Sites that were not sampled during fall were in the Middle Kansas (two sites in the Dry Creek DEN, one site in the Mulberry Creek DEN) and Lower Cottonwood (one site in the Bruno Creek DEN, one site in the Coyne Creek DEN) 8-digit HUCs, and these DENs were removed from regression analysis for fall. Although pair-wise comparisons could still be conducted for the remaining sites within excluded DENs, mean dissimilarity values might be skewed because contributions from communities at dried sites no longer existed. Following removal of DENs in which sites dried, the relationship between DCI and dissimilarity was driven largely by the small DCI value for the Snake Creek DEN in the Upper Verdigris 8-digit HUC. Consequently, we tested the relationship between DCI and all available measures of dissimilarity for fall, acknowledging seasonal patterns in dissimilarity for four DENs were likely confounded by extirpated communities from dried sites, and we still detected a relationship ($n = 12$, $F_{1,10} = 5.15$, $r^2 = 0.34$, $P = 0.04$).

DISCUSSION

Our findings empirically show that structural connectivity influences community structure of stream fishes at both local and network scales. We found communities in fragmented stream sections had reduced alpha diversity (lower species richness) as well as increased beta diversity (greater dissimilarity) compared to communities that maintained connectivity with the surrounding dendritic ecological network (DEN). These patterns were not explained by isolation because of drainage distance or variation in second-order stream patch size, rather community disparity coincided with occurrence of barriers that impeded dispersal routes. We also found that structural connectivity measured at the scale of DENs using the dendritic connectivity index (DCI; Cote et al. 2009) predicted reduced dissimilarity among communities, presumably because of increased dispersal and colonization of second-order streams, and consequently augmented alpha diversity in less fragmented DENs. Our findings support network connectivity as a mediator of ecological processes occurring within complex dendritic ecosystems and promote the need for improved connectivity to enhance conservation of metacommunity dynamics and biodiversity in DENs.

Metacommunity response to fragmentation in dendritic ecological networks

Altered dispersal routes in an upstream direction, or toward the extremities of DENs, have direct implications for metacommunity dynamics. Brown and Swan (2010) suggested dispersal among headwater streams is generally low for aquatic organisms confined to within-branch movement, but rates of dispersal increase with proximity to the base of dendritic stream networks.

Thus, metacommunities in headwater reaches are structured by species-sorting processes (i.e., species occupy patches of highest suitability), whereas the influence of mass-effects (i.e., strong dispersal among all species allows for persistence even in poorly suited patches) increases with proximity to the base of the network (see Leibold et al. [2004] for further details of metacommunity paradigms). In the context of stream-dwelling fish communities, second- and third-order streams likely occur within the transitional zone between strong species sorting in first-order headwater streams and mass-effect-dominated dynamics in third-order and greater streams (Hitt and Angermeier 2006). We found evidence that species associated with small streams (as classified by Goldstein and Meador [2004]) showed little response to fragmentation in our study system (e.g., redfin shiner, southern redbelly dace *Phoxinus erythrogaster*, creek chub, western mosquitofish *Gambusia affinis*, and orangethroat darter) whereas other species characteristic of a range of stream sizes, including small-bodied and early maturing cyprinids (e.g., red shiner, sand shiner, and suckermouth minnow) exhibited reduced occurrence or were absent altogether from fragmented streams (Appendix D). These observations are consistent with previous findings that suggest early maturing fishes with small body size disperse upstream from larger adjacent streams to colonize communities in second- and third-order streams (Schlosser 1987, Hitt and Angermeier 2006). For example, we detected an absence of stream species such as sand shiner but relatively little change in occurrence of generalist species such as creek chub, bluntnose minnow, and green sunfish in fragmented communities (Goldstein and Meador 2004), which reflect findings by Falke and Gido (2006) among streams isolated by impounded water upstream of large reservoirs. We also found a general reduction of red shiner and an absence of Topeka shiner *Notropis topeka* in fragmented streams, two species known to be extirpated from fragmented streams because of reduced dispersal (Adams et al. 2000, Matthews and Marsh-Matthews 2007, Franssen 2011). Spatial extent over which stream fish complete their life history varies (Schlosser 1991), and can range from dispersal on scales ranging from 10–100 m (Fletcher et al. 2004) to hundreds of kilometers (Perkin and Gido 2011). Although existence of obligate potamodromy among many Great Plains small-bodied fishes is poorly studied, thwarted dispersal and attenuated mass effects caused by instream obstructions generally explain reduced alpha diversity and increased beta diversity among fragmented communities in prairie streams (Winston et al. 1991, Perkin and Gido 2011).

Metacommunities fragmented by barriers distributed throughout DENs become isolated communities in which dispersal linkages to processes operating at regional scales are severed and local composition is determined largely by local drivers (Angermeier and Winston 1998, Mathews and Robison 1998). Existing

theoretical models have linked small and isolated populations or communities within DENs to reduced population size and increased extinction risk among organisms (Labonne et al. 2008, Padgham and Webb 2010, Grant 2011), a pattern consistent with our findings. Fishes dependent upon processes occurring at broader spatial scales (e.g., cyprinids, catostomids) were either absent or occurred at low abundances within fragmented communities and support reduced dispersal as the primary cause for altered community composition in fragmented stream reaches. On the other hand, species characteristic of smaller headwater reaches indicated little response to fragmentation and occurred in nearly equal numbers of unfragmented and fragmented communities. These differential levels of persistence are likely related to functional or life-history attributes of fishes, which might allow for persistence of certain guilds through a suite of mechanisms (e.g., competition, predation, or suitability of available resources). In the absence of dispersal, isolated communities likely diverged from communities that maintained connectivity with the surrounding DEN because of biological (e.g., predation or competition) or non-biological (e.g., desiccation of streams) processes. Matthews and Marsh-Matthews (2006) found seven initially identical isolated mesocosm fish communities diverged over the course of approximately one year despite control of abiotic factors (e.g., water availability, habitat mosaics), suggesting biological interactions might be contributing to stream fish community structure. Disrupted connectivity between second- and third-order streams might also thwart predator–prey transitions among stream sizes during periods of hydrologic stability when biotic interactions are expected to contribute largely to community composition (Creed 2006). Lastly, we observed drying among three fragmented communities included in this study to the extent that all fish were completely extirpated, suggesting influence of abiotic factors cannot be ruled out in natural settings such as Great Plains streams that commonly endure harsh fluctuations in hydrology (Dodds et al. 2004). Although dispersal for a diversity of fish species is negatively affected by the presence of perched culverts at road crossings (Norman et al. 2009, Alexandre and Almeida 2010, Nislow et al. 2011), altered ecological interactions and occurrence of abiotic processes within fragmented communities likely contributed, in part, to variability in community composition and patterns in biodiversity.

Structural connectivity predicts functional connectivity in dendritic ecological networks

We can think of at least three reasons for the strong relationship we observed between DCI and community dissimilarity within DENs, each of which are not necessarily mutually exclusive. First, dispersal corridors are singular and linear in stream networks and disruption to structural connectivity eliminates routes for organisms confined to within-branch movement

(Grant et al. 2007). Functional connectivity must then be reduced given the strong dependency of fishes on aquatic corridors for dispersal (Padgham and Webb 2010). Secondly, the occurrence of strong mass effects within streams at the spatial extent of our study would lead to a disruption of community mixing within and among non-headwater streams caused by perched culverts at road crossings. In fragmented sections, biological (e.g., competition, predation) and non-biological (e.g., local extinctions during desiccations) processes might be altered because fishes are not able to mix with other sections. This pattern would explain the greater levels of community disparity we observed in highly fragmented DENs relative to DENs with greater connectivity, and perhaps would contribute to incremental increases in similarity among communities as connectivity increased. Finally, perched culverts included in this study were constructed during the 1950s-1980s according to dates stamped on the structures (J. Perkin, *personal observation*) and fish communities might have responded to the presence of culverts well before our study was conducted given the resiliency of Great Plains stream communities (Dodds et al. 2004). Inundation of perches during summer high flows likely allowed for temporary dispersal of fishes into perennial second-order streams (Bouska and Paukert 2009, Norman et al. 2009), but given that prairie stream fishes are generally resistant to downstream displacement during floods (Franssen et al. 2006) communities in upstream segments might have been resistant to colonization (Hitt and Roberts 2012). Although evidence exists for stream fish communities being invadable (Angermeier and Winston 1998), colonization of upstream reaches is generally lower relative to downstream reaches (Gotelli and Taylor 1999). By this account, community similarity and functional connectivity among stream segments might be rigid despite ephemeral increases in structural connectivity caused by flood pulses. Regardless of the mechanism, our findings promote the use of the DCI as a habitat-availability measure with potential for significant contribution toward understanding ecological processes in fragmented riverscapes (Erős et al. 2012).

Fragmentation and conservation of biodiversity in dendritic ecological networks

Habitat loss and fragmentation are primary threats to aquatic biodiversity and action is required to conserve rare and declining organisms that increasingly constitute the majority of biodiversity in stream networks on a global scale (Nilsson et al. 2005, Dudgeon et al. 2006, Jelks et al. 2008, Cote et al. 2009). Building evidence suggests alterations to connectivity have ecological and evolutionary consequences for aquatic communities (Falke and Gido 2006, Franssen 2011; this study) and network connectivity in DENs is emerging as a central theme in conserving biodiversity (Erős et al. 2011, 2012). Examples of diminished connectivity negatively affecting freshwater biodiversity exist for regions around the

world (Morita and Yamamoto 2002, Alexandre and Almeida 2010, Fullerton et al. 2010), and illustrate the critical need for synthesizing the effects of fragmentation in stream DENs regardless of topology or spatial scale (Fausch et al. 2002, Erős et al. 2012). In particular, intermediate spatial scales incorporating stream reaches or segments ranging from 10^2 to 10^4 m have been largely ignored in the context of stream fish conservation research. According to Fausch et al. (2002), these are the scales at which anthropogenic alterations to streams most strongly conflict with the life history needs of stream-dwelling fishes. We found evidence for fragmentation of DENs contributing to altered community composition among Great Plains stream fishes at the spatial scale of our study (10^2–10^4 m), illustrating the utility of the DCI for researching stream mosaics at ecologically meaningful scales (sensu Fausch et al. 2002). Cote et al. (2009) suggested the DCI could be applied to networks as large as the entire Mississippi drainage basin or as small as a single tributary reach, which allows for directly addressing the challenge of variability in network topology when assessing connectivity across spatial scales (Fullerton et al. 2010). An advantage of applying the DCI to measure habitat connectivity over the spatial extent of a species' life span is the scale-independent nature of networks that can be modeled as well as the improved ability to incorporate species-specific dispersal capabilities with regard to barrier permeability.

Our understanding of long-term responses among stream organisms to fragmentation of dendritic stream networks is temporally limited. Assemblage-level responses to fragmentation of large rivers on time scales of 30–60 years suggest time-lag effects on demography of stream-dwelling organisms might cause prolonged responses to current levels of fragmentation (Taylor et al. 2008, Perkin and Bonner 2011), which might constitute extinction debts in many systems (Tilman et al. 1994, Strayer et al. 2004). Prioritizing barriers for remediation based on contemporary responses to fragmentation might attenuate long-term ecological effects caused by reduced connectivity, and a diversity of approaches have been developed to measure connectivity in stream networks (Fullerton et al. 2010). Our findings suggest relating functional connectivity of stream fish communities in DENs to structural connectivity measured with minimal biological data (here, the DCI with uniform barrier permeability of 0.5) might be a fruitful approach to prioritizing specific barriers for remediation in order to achieve desired connectivity of metapopulations or communities (sensu Cote et al. 2009). However, to ensure remediation approaches reach maximum potential improvement to connectivity, additional detail pertaining to barrier permeability is needed before prioritization (Bourne et al. 2011). Similarly, predictive scenarios for reducing connectivity to control spread of invasive species (Jackson and Pringle 2010) might also be applied to network management in order to assess the role of connectivity in mediating ecological processes at relevant spatial scales in complex, dendritic ecosystems.

CONCLUSIONS

Stream fragmentation imposed by semi-permeable barriers is a global pattern contributing to the reduced abundance and distribution of stream organisms and constitutes a major environmental problem. Mitigation approaches for developing improved fish passage structures in place of perched or otherwise impermeable obstacles indicate success in terms of allowing local improvements to organism dispersal. Cost–benefit analysis and prioritization of barriers that yield maximum gains in structural connectivity is now possible with advances in habitat-availability measures such as the dendritic connectivity index (DCI; Cote et al. 2009). However, evaluating benefits of improved structural connectivity requires some ability to predict potential ecological outcomes before action is taken, such as the potential for increased dispersal of organisms throughout stream networks. Our findings suggest that improvements to structural connectivity are likely to equal associated improvements in the abundance and distribution of organisms confined to within-stream dispersal (e.g., fishes).

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SUPPLEMENTAL MATERIAL

Appendix A

A figure illustrating the relative frequency of stream orders and distribution of road crossings within the USGS eight-digit hydrologic unit codes for four streams in Kansas, USA (*Ecological Archives* A022-117-A1).

Appendix B

A figure showing 12 Great Plains, USA, dendritic ecological networks with locations of perched road crossings and fish collections as well as Dendritic Connectivity Index values for each network (*Ecological Archives* A022-117-A2).

Appendix C

A table summarizing data for sampling sites in each dendritic ecological network, listing connectivity status, species richness, and stream widths (*Ecological Archives* A022-117-A3).

Appendix D

A table presenting information about fish species collected during summer and fall, as well as occurrence of each species in unfragmented and fragmented streams (*Ecological Archives* A022-117-A4).