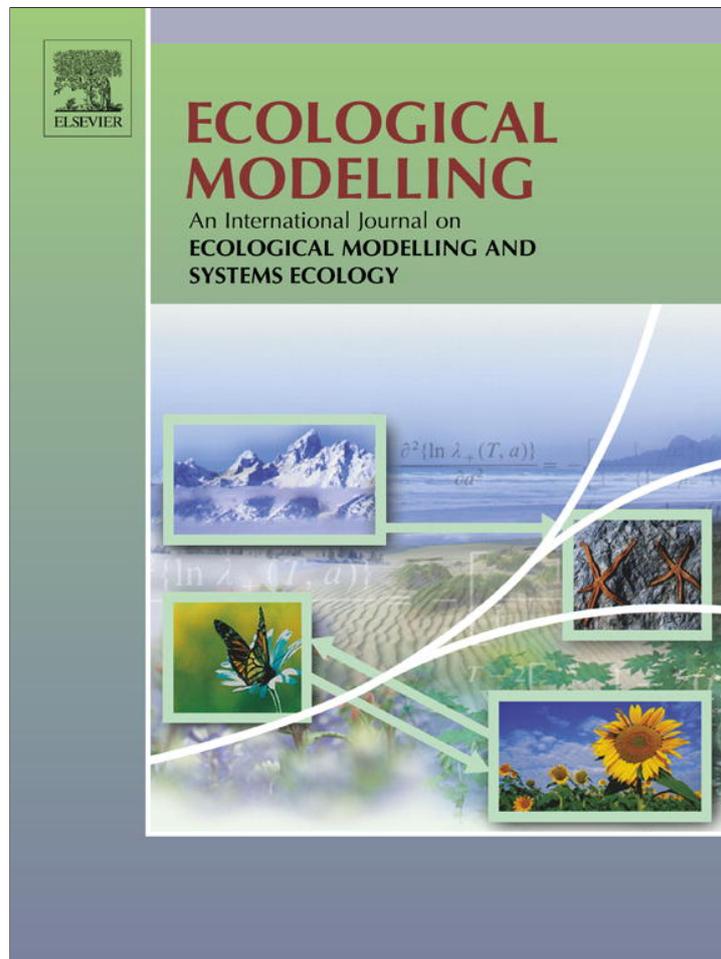


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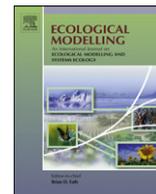
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Simulating fish dispersal in stream networks fragmented by multiple road crossings



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ARTICLE INFO

Article history:

Received 19 December 2012

Received in revised form 14 February 2013

Accepted 15 February 2013

Keywords:

Habitat fragmentation

Road-stream crossings

Dispersal affinity

Stream networks

Dendritic connectivity index, DCI

Dendritic ecological networks

ABSTRACT

Organisms inhabiting stream ecosystems are vulnerable to the effects of habitat fragmentation because of the inherent hierarchical structure of patches in riverscapes. Fragmentation caused by road-stream crossings contributes to alteration of stream organism distribution globally. We used principles of graph theory to develop three artificial riverscapes and test for network-scale changes in simulated fish dispersal caused by barriers that resembled the properties of road-stream crossings (semi-permeable; numerous within a network). Fish occupancy of nodes (habitat patches) declined in the presence of a single barrier when barrier permeability was <0.5 , and fish with high dispersal experienced greater declines in occupancy compared to fish with low dispersal. Probability of extirpation (emigration without return) from fragments was greatest for nodes that mimicked headwater stream segments. We used a network-scale measure of habitat connectivity (the dendritic connectivity index; DCI) to measure changes in occupancy across all nodes and found the DCI predicted declines in occupancy as the number of barriers in the riverscape increased. Declines in occupancy were driven by threshold responses by fish to the occurrence of small fragments (≤ 3 nodes). Our simulations identified three important properties of stream fish dispersal that are likely relevant to natural systems: (i) species dispersal affinities determine response to fragmentation; (ii) fragments that are too "small" for organism persistence drive declines in riverscape occupancy; and (iii) measurements of structural (habitat) connectivity used to draw inference on functional (population) connectivity require knowledge of organism dispersal affinity and dispersal-mediated response to barrier positioning.

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1. Introduction

Habitat fragmentation and loss threaten global biodiversity and cause concern for the long-term persistence of numerous organisms (Dudgeon et al., 2006; Lindenmayer and Fischer, 2006). However, the manner in which organisms respond to landscape-scale changes in habitat availability is mediated by structural properties of the habitats required for species persistence (Grant et al., 2007). For example, many terrestrial organisms interact with lattice networks of habitat patches arranged so that multiple dispersal routes exist between any two patches, whereas organisms inhabiting dendritic networks characterized by hierarchically arranged branches of habitat tend to have limited access to many patches even in the absence of fragmentation (Labonne et al., 2008; Cote et al., 2009; Padgham and Webb, 2010; Neeson et al., 2012). Consequently, organisms inhabiting dendritic land-

scapes such as streams tend to respond strongly to fragmentation (Fagan, 2002).

Stream fragmentation is associated with range reductions and local extinctions of fish species on a global scale. Anthropogenic barriers to fish movement include large and small dams as well as road crossings over small tributaries (Morita and Yamamoto, 2002; Alexandre and Almeida, 2010; Lehner et al., 2011). Road networks that overlap with stream networks present a global form of anthropogenic fragmentation to stream ecosystems and disrupt fish dispersal (Forman and Alexander, 1998; O'Hanley, 2011). Unlike large dams, structures that allow water to flow under or over roads that are characterized by rapid drops in elevation at their outflow (referred to as *perching*) represent semi-permeable barriers to dispersal with fluxes in permeability associated with stream flow (Norman et al., 2009; Nislow et al., 2011). Perched road crossings are common features on contemporary landscapes, far outnumbering dams, and partially blocking fish passage at 53–97% of crossings within a single watershed (Gibson et al., 2005; Poplar-Jeffers et al., 2009).

The manner in which fish respond to fragmentation is mediated by their dispersal ability or behavior, and fish that tend to disperse

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over greater distances tend to respond more strongly to fragmentation (Pépin et al., 2012). Given that fish dispersal can vary widely within a community (e.g., Albanese et al., 2008) and that fish dispersal can change with age or size (e.g., Skalski and Gilliam, 2000), the potential for fish to interact with barriers distributed throughout a watershed can also vary depending on the spatial scale of the network used by fish (Schlosser, 1991). Consequently, network-scale measures of habitat connectivity that incorporate the impacts of multiple barriers are emerging as a central theme in freshwater fish conservation (i.e., riverscape approaches sensu Fausch et al., 2002) with significant potential for developing robust predictions of fish response to fragmentation across a range of spatial scales (Bourne et al., 2011; Erős et al., 2011; Perkin and Gido, 2012).

Network-scale measures of habitat connectivity that identify particular barriers contributing most to fragmentation of riverine landscapes or riverscapes (hereafter *riverscape* and *network* are used interchangeably) and attenuated habitat availability can be used to guide conservation or management actions (Fausch et al., 2002). Multiple approaches for quantifying habitat availability have recently been developed (see reviews: Fullerton et al., 2010; Kemp and O'Hanley, 2010) and include prioritizing barriers for remediation based on barrier permeability and maximizing fragment sizes (i.e., portion of a network isolated by one or more barriers; Cote et al., 2009) or maximizing the size of the single largest stream fragment in a riverscape (O'Hanley, 2011). Approaches targeting particular fragment sizes or maximizing fragment size in general seem most appropriate for enhancing the conservation of stream fish given reported relationships between species richness or population viability and stream fragment length (Bain and Wine, 2010; Perkin and Gido, 2011). Among recently developed measures involving fragment size is the *dendritic connectivity index* (DCI; Cote et al., 2009), which considers the fraction of stream network length isolated by a barrier (i.e., fragment) and computes the weighted average probability of movement within (permeability = 1) and among (permeability < 1) all fragments; among-fragment movement probability is dependent on the number and assigned permeability of individual barriers in the network (see Cote et al., 2009 for additional details). The DCI is a quantitative measure of connectivity that can be assigned to stream networks regardless of their overall size or the number of barriers present and allows for differing spatial scales while addressing the interactions among multiple barriers and the associated responses by fish (Fullerton et al., 2010; Bourne et al., 2011; Erős et al., 2012; Perkin and Gido, 2012).

Modeling approaches for testing relationships between fish population persistence and stream network properties allow for assessing the utility of new connectivity measures with relatively few data requirements. Riverscape models have recently illustrated the relative effects of habitat accessibility versus quality on simulated fish distributions (Padgham and Webb, 2010), effects of network structure and organism movement bias (upstream or downstream) on metapopulation persistence (Grant, 2011), and the effect of network structure on species-specific responses to the distribution of habitats (Neeson et al., 2011, 2012). In the context of habitat fragmentation, similar riverscape models can be combined with principles of graph theory to test network-scale relationships between habitat connectivity and population persistence (Urban and Keitt, 2001; Lookingbill et al., 2010). In particular, stream networks based on realistic riverscapes can be generated using a neutral landscape model approach (e.g., With, 1997; Gardner and Urban, 2007) and combined with individual-based (Neeson et al., 2011) or transition-matrix-based (Padgham and Webb, 2010) dispersal models to simulate fish interaction with riverscape features. By simulating fragmentation, relationships between structural connectivity (i.e., physical relations among nodes) and functional connectivity (i.e., the manner in which the riverscape impedes or

facilitates movement of individuals or populations) can reveal the utility of network-scale measures of habitat connectivity (Taylor et al., 1993; Urban and Keitt, 2001; Zetterberg et al., 2010; Rayfield et al., 2011). Whereas such approaches are well developed in terrestrial settings (e.g., Andersson and Bodin, 2009), examining the performance of patch-based graphic approaches as well as network-scale habitat availability measures in freshwater ecosystems requires additional research (Grant et al., 2007; Erős et al., 2012).

The goal of this study was to evaluate how network-scale dispersal and occupancy by fish responded to habitat fragmentation using a patch-based graphic modeling approach. Specific objectives were to: (i) develop alternative stream networks that resembled the architecture of real-world riverscapes using patch-based graphs; (ii) evaluate responses in simulated fish dispersal to the presence of simulated road-stream crossings across a range of network architectures, fish dispersal abilities, and barrier number and permeability values; and (iii) assess whether habitat availability measured at the network scale using the DCI is useful for predicting fish response to changes in connectivity.

2. Methods

In this study we used graph theory to visualize a stream network as a series of linked nodes and used simulated fish dispersal to test relationships between habitat connectivity and fish population distributions measured at the scale of stream networks (Fig. 1). The processes are fully described below, but here we provide a brief overview. We first developed three riverscapes that resembled realistic hierarchical structuring of habitat patches in stream networks using nodes (habitat patches) and edges (dispersal corridors). Second, we simulated fish dispersal for relatively high and low dispersal (i.e., “high” dispersal was approximately twice as much as “low”) using a transition matrix approach to track network-scale occupancy of nodes in the absence of fragmentation (i.e., a neutral condition; sensu With, 1997). We began by assuming all nodes were initially occupied by an equal portion of a population and used a Markovian random walk model to represent movement of fish throughout each riverscape. Third, we fragmented riverscapes by randomly placing up to five barriers with various permeability values (0.5, 0.05, and 0.00; where 1 is completely passable and 0 is impassable) among links and recorded the percent of nodes occupied after sufficient iterations to achieve model convergence in the neutral case. Finally, we calculated the DCI for all barrier insertions as a measure of network-scale habitat connectivity and explored mechanistic factors involved with the observed relationships between the DCI and riverscape occupancy.

2.1. Development of riverscapes

We adopted the approach of generating distributions of nodes in theoretical riverscapes based on topological patterns of stream channel networks observed in nature (Kirchner, 1993). To begin, we used 15 nodes that represent stream segments (i.e., the section of stream between two confluences; Neeson et al., 2011) based on previous analyses of stream networks (Fagan, 2002). Nodes were then arranged using Horton's Laws regarding stream channel network architecture (Horton, 1945; Labonne et al., 2008). Horton's Laws describe patterns in the number and size of stream segments according to Strahler's (1957) ordering system, in which the smallest of headwater stream channels are first-order stream segments, two first-order segments meet to form a second-order stream segment, two second-order segments meet to form a third-order stream segment, and so on. The first of Horton's Laws is the

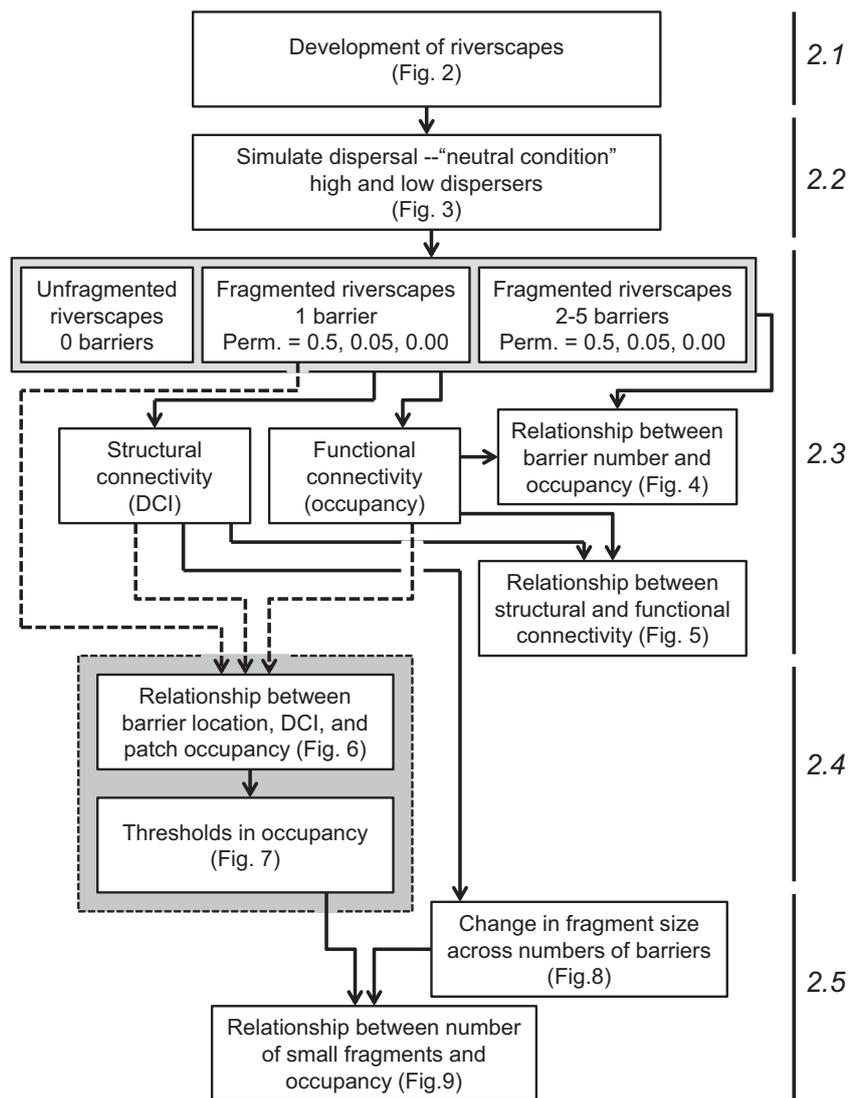


Fig. 1. Flow chart of operations used to test relationships between fish distributions and fragmentation in simulated riverscapes. Section 2 associated with steps is given to the right and figures associated with outputs are listed. Gray boxes represent the combination of multiple steps to obtain an output. “Perm.” refers to barrier permeability (where 1 is completely passable and 0 is impassible); DCI is the *dendritic connectivity index* described by Cote et al. (2009).

bifurcation ratio (R_B), which describes the number of streams of a particular order in a network:

$$R_B = \frac{N_w}{N_{w+1}} \quad (1)$$

where N_w is the number of streams of order w . The R_B ranges from three to five among natural stream channel networks and exhibited a modal value of roughly four in simulations conducted by Kirchner (1993). Horton also developed the length ratio (R_L), which describes the distribution of stream lengths in a network:

$$R_L = \frac{L_w}{L_{w-1}} \quad (2)$$

where L_w is the mean length for streams of order w . The R_L ranges from 1.5 to 3 among natural stream channel networks and exhibited a modal value of roughly two during simulations conducted by Kirchner (1993). Stream channel networks also exhibit random patterns in elongation or compaction, described as the relative amount of stream between the most upstream headwater and the outlet of the network (Kirchner, 1993). Although recent studies suggest other measures of network structure are useful when constructing large networks (e.g., network diameter; Neeson et al., 2011),

here we focus on the R_B and R_L for characterizing channel structure because of the small size of networks generated (i.e., only 15 nodes) and use of Horton’s Laws in similar studies of network connectivity (Labonne et al., 2008).

We constructed three riverscapes represented as patch-based graphs (Erős et al., 2012) so that nodes were arranged in a manner consistent with bifurcating stream networks that conform to Horton’s Laws of stream channel networks but varied in their relative compactness (i.e., R_B within 3–5, R_L within 1.5–3; Kirchner, 1993; Grant et al., 2007). For simplicity, we assumed all nodes were of equal size and quality (homogeneous node resolution), but differed in their spatial arrangement in a manner consistent with the topology of third-order stream channel networks. Riverscapes included in this study were characterized by $R_B=4$ (calculated using N_w = number first-order streams), $R_L = 1.5$ (calculated using L_w = length of third-order stream), and relatively compact (Fig. 2; riverscape A); $R_B = 3.5$, $R_L = 2$, and intermediate compaction (Fig. 2; riverscape B); and $R_B = 3$, $R_L = 2.5$, and relatively elongated (Fig. 2; riverscape C). Whereas alternative architectures were possible within the constraints listed above, as a starting point we conducted analyses on only these three networks (sensu Fagan, 2002). These theoretical riverscapes constitute constrained networks that mimic

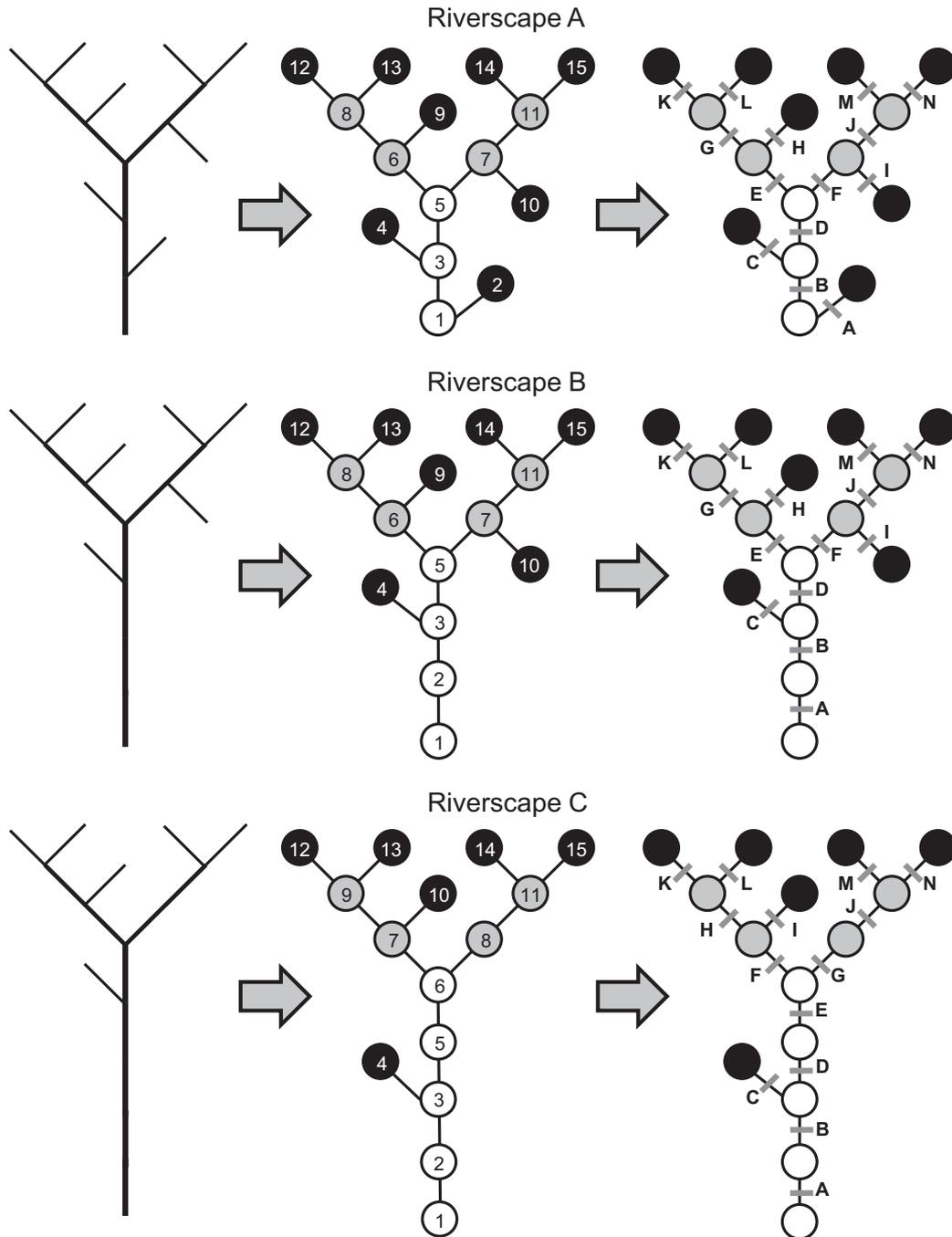


Fig. 2. Simulated riverscapes included in study. Proceeding from left to right stream sections between confluences were converted to nodes (numbered circles) linked by dispersal pathways (lines; see description by Erős et al., 2012) on which barriers were randomly placed (lettered bars). Nodes are illustrated as first-order stream segments (black circles), second-order stream segments (gray circles), and third-order stream segments (white circles) according to Strahler's (1957) stream ordering system.

the spatial scale at which dispersal and fragmentation are known to influence fish community composition (i.e., third-order stream networks; Hitt and Angermeier, 2008; Perkin and Gido, 2012).

2.2. Dispersal model description

Our model depicted riverscapes as constrained networks (sensu Padgham and Webb, 2010) defined by 15 nodes. Edges defined the dendritic topology of nodes and describe each as headwater, confluence, second- or third-order channel unit, or the base of the network (Fig. 2, middle column). We assumed directional variability among links (i.e., heterogeneous link resolution)

consistent with a patch-base graphic model type II from Erős et al. (2012).

Dispersal among nodes (i.e., link resolution) was constrained by discrete transition probabilities that defined the ability of fish to move to adjacent reaches in upstream (*u*) and downstream (*d*) directions (Fig. 3a). We again followed the conceptual framework of Padgham and Webb (2010) that emphasizes that such connectivities are generally involved in landscape-scale measures of species movement (Bélisle, 2005) and habitat connectivity (Cote et al., 2009). However, the model differed from that of Padgham and Webb (2010) in that perceptual range of fish was limited to only immediately adjacent nodes rather than network-scale knowledge

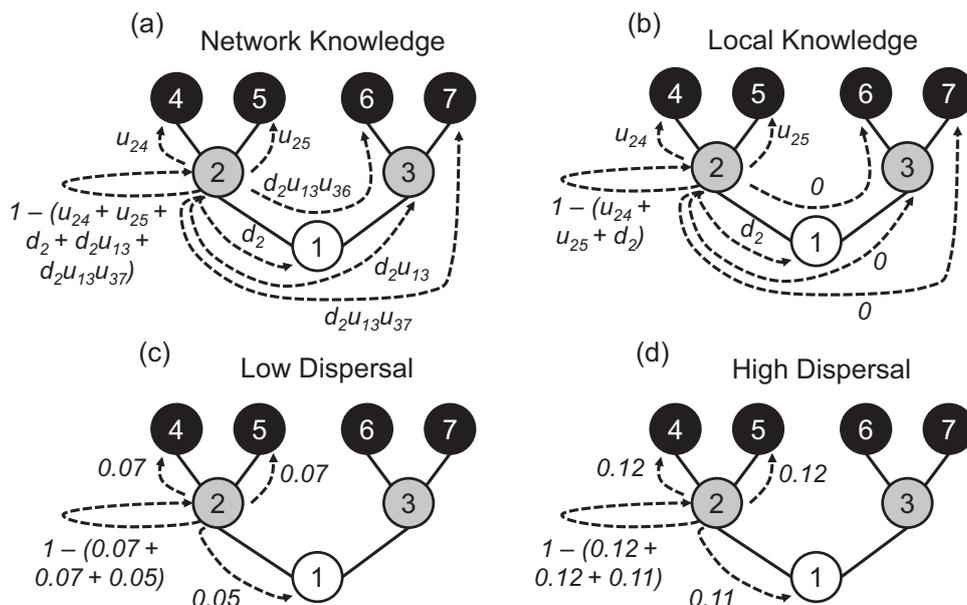


Fig. 3. Basis for calculation of transition probabilities for network (a) versus local (b) knowledge of riverscapes as well as applied probabilities (invoking local knowledge) for low (c) and high (d) dispersing fish.

(Fig. 3b). Local knowledge is likely more biologically relevant for organisms forming dispersal decisions in the absence of enhanced perception of entire networks (e.g., olfactory cues from distant upstream nodes; Neeson et al., 2011). Because dispersal ability of organisms can influence their response to fragmentation, and high dispersing organisms generally respond more strongly than low dispersers (e.g., Funk et al., 2005; Pépino et al., 2012), the model included two levels of dispersal. We began with transition probability values based on mark-recapture rates for stream fish documented by Norman et al. (2009). Mean weekly transition probabilities for movement from one stream segment to the immediately adjacent segment in upstream (u) and downstream (d) directions were calculated across study sites for benthic (“low” dispersal, $u = 0.07$; $d = 0.05$; Fig. 3c) and water column (“high” dispersal, $u = 0.12$, $d = 0.11$; Fig. 3d) fish (see Norman et al., 2009). These values resulted in an upstream movement bias for both high and low dispersal, which is consistent with previously reported patterns of organism dispersal in ecological networks (Grant, 2011). We assumed initial occupation of each node (Fagan, 2002) by an even portion of the population (i.e., $1/15$) and used a Markovian random walk model based on a transition matrix (Padgham and Webb, 2010) to simulate iterative time steps of transition probabilities (Ching and Ng, 2006). This approach resulted in biased random movements (i.e., a biased random walk) among nodes so that the decision regarding dispersal in the subsequent iteration depended on the current distribution among nodes and occurred independently of the decision in the previous iteration (Codling et al., 2008). We used a context-depend number of iterations ($n = 156$) based on model convergence in the neutral case (i.e., no barriers present) for both high and low dispersal and replicated scenarios 1000 times for each of the three riverscapes.

2.3. Fragmentation of riverscapes

We simulated fragmentation of riverscapes by inserting up to five semi-permeable barriers at randomly assigned locations. Previous assessments of fish passage through perched road crossings suggest permeability values are generally less than or equal to 0.5 (Bourne et al., 2011; Anderson et al., 2012), thus we used a range of permeability values (i.e., 0.5, 0.05, and 0.00) in our simulation of

fragmentation to assess how barrier permeability influenced connectivity measures. Furthermore, although permeability values are rarely equal among barriers within a network (e.g., Anderson et al., 2012), we assumed uniform permeability within each simulation to gain a better understanding of the importance of barrier location (and consequently fragment size) without confounding effects of variability in permeability. To simulate fragmentation, we began with addition of a single barrier randomly placed at one of 14 possible locations in each riverscape (labeled A–N in Fig. 2) and replicated this process 1000 times for each barrier permeability value (i.e., 0.5, 0.05, and 0.00). Next, we inserted barriers at two randomly selected locations and repeated the previous process, followed by insertion of three, four and five barriers so that two or more barriers were never placed on the same link. To estimate functional connectivity, we began with the addition of a single barrier and multiplied barrier permeability (0.5, 0.05, or 0.00) by the upstream transition probability for the corresponding location in the transition matrix. This process resulted in the probability of transition through a fragmented node in an upstream direction being reduced according to the permeability of the newly inserted barrier; while movement in a downstream direction remained unaltered (assuming fish were capable of downstream dispersal over perches). We estimated network-scale functional connectivity by considering each node as occupied or unoccupied, where occupied nodes contained at least 1% of the population after 156 iterations and unoccupied nodes contained <1%. For cases in which <1% of the population persisted within a node, we use the term “extirpation”, but we stress that our approach does not involve any measure of demography or population dynamics. Here, the term extirpation exclusively describes emigration without return to the node. The sum of all occupied nodes divided by the total number of nodes in the riverscape (i.e., 15) was then multiplied by 100 to estimate percent of riverscape occupied.

To estimate structural connectivity, we used the potamodromous component of the DCI (as opposed to the anadromous component; see Cote et al., 2009). Calculation of the DCI involves dividing stream networks into fragments separated by barriers and characterized by known longitudinal lengths, then calculating the probability of fish movement between all fragments in the network. Here we use the term *fragment* to define the total number of stream

nodes (segments) that remain connected after barrier addition (i.e., fragments are made up of connected nodes). The DCI is calculated as:

$$DCI = \sum_{i=1}^n \sum_{j=1}^n c_{ij} \frac{l_i}{L} \frac{l_j}{L} \times 100 \quad (3)$$

where l is the length of fragments i and j , c_{ij} is the connectivity between fragments i and j , and L is the length of all the segments in the network (Cote et al., 2009). The index is rescaled to a maximum value of 100 with the final multiplication factor. Since nodes in our stream networks had a uniform unit length, we estimated fragment size using the number of isolated nodes based on barrier locations in the transition matrix (i.e., fragmented nodes corresponded with those for which dispersal was altered in the transition matrix). For this process we used the same randomly drawn barrier locations used for simulated fragmentation in the context of functional connectivity, so that responses to altered structural connectivity were related to the same barrier locations as functional connectivity. We began by calculating the DCI for riverscapes containing only one barrier to assess how barrier location influenced DCI measurements, and then extended calculations to scenarios for addition of two through five barriers. To assess relationships between structural and functional connectivity, we used regression and plotted DCI as the independent variable and riverscape occupancy as the dependent variable and calculated the coefficient of determination. Data were \log_{10} transformed before analysis to address skewness in distributions.

2.4. Effect of barrier location

We evaluated the effect of barrier location on patterns in riverscape occupancy and DCI estimates by comparing estimates to known locations of a single barrier. This approach linked barrier locations with declines in habitat availability and declines in occupancy. We first combined all simulations during which a barrier was placed at one of 14 possible locations (labeled A–N in Fig. 2) for each riverscape, dispersal level, and barrier permeability scenario. Effect of barrier location on node occupancy was evaluated by plotting the mean (\pm standard deviation) percent of nodes occupied across the 1000 replications computed for each scenario. Effect of barrier location on DCI calculations was evaluated by computing the index for each barrier location in the riverscape. This approach allowed for assessing the effect of barrier placement on the relationship between structural connectivity (habitat availability) and functional connectivity (node occupancy).

The structure of riverscapes developed during this study resulted in specific numbers of nodes being isolated when a single barrier was in place (i.e., 1, 3, 4, 5, 10, 11, 13, and 14 nodes). This pattern was driven by barriers being placed on headwaters (first-order nodes; one node isolated), mid-order reaches (second-order nodes; three, four or five nodes isolated) and “mainstems” (third-order nodes; one, 10, 11, 13, or 14 nodes isolated) for each riverscape. We compared the number of nodes in which fish became extirpated to the number of isolated nodes caused by a single barrier to evaluate the occurrence of thresholds in fish response to fragmentation. We interpreted a threshold as a disproportionately large change in extirpation over a relatively small change in the number of isolated nodes. Thresholds were evaluated for each riverscape assuming all dispersal and barrier permeability scenarios.

2.5. Change in fragment size distributions

We investigated changes in fragment size distributions as a function of the number of barriers present in the riverscape. Although riverscapes consisted of 15 linked nodes in the absence of

fragmentation, the number and placement of barriers added contributed to an increased number of smaller fragments. Because of this pattern, we characterized how the frequency distribution of fragment sizes varied with the number of barriers present. Barrier locations were randomized and replicated 1000 times for 1–5 barriers in each riverscape. To illustrate patterns in changing size distributions caused by an increasing numbers of barriers, we plotted mean (\pm standard deviation) frequencies of fragment size classes among the three riverscapes for one through five barriers. Finally, initial results suggested fish of both dispersal levels exhibited threshold responses in occupancy when three or fewer nodes were isolated by a single barrier (see Section 3.3). Consequently, we assessed the relationship between numbers of small habitat fragments (i.e., ≤ 3 nodes) present in a riverscape and the percent of nodes occupied. This approach allowed for assessing fish response to the number of small fragments in a riverscape regardless of the number of barriers present.

3. Results

3.1. Fish response to barriers

Upstream bias in transition probabilities resulted in a greater percent of the population being located at the upstream extent of riverscapes and complete riverscape occupancy in the absence of fragmentation. At a barrier permeability value of 0.5, neither high nor low dispersing fish indicated a change in riverscape occupancy regardless of the number of barriers present in the riverscape (Table 1). When barrier permeability was reduced to 0.05, distribution of low dispersing fish declined as barriers were introduced and reached approximately 77% occupancy (averaged across 1000 simulations) when five barriers were present, whereas high dispersing fish declined to 56% occupancy. When barrier permeability was reduced to 0.00, low dispersing fish declined to approximately 59% occupancy averaged across riverscapes when five barriers were present; whereas, high dispersing fish declined to approximately 38%. Addition of barriers characterized by permeability 0.05 and 0.00 resulted in an increase in extirpations among nodes, and nodes nearer the upstream extent of riverscapes tended to exhibit a greater extent of extirpation as the population was restricted to the lower portions of riverscapes (Fig. 4). There was a general pattern of greater decline in occupancy as riverscapes became more elongated, so that riverscape C generally exhibited the greatest decline in occupancy because of fragmentation.

3.2. Network-scale measurement of habitat connectivity

The DCI explained 37–69% of variation in occupancy among riverscapes, dispersal levels, and barrier number and permeability values (Fig. 5). Percent riverscape occupancy and DCI, averaged by numbers of barriers, were strongly positively related (overlay in Fig. 5). Variation among DCI estimates was least in the presence of a greater number of barriers; however, variation among occupancy estimates was least when few barriers were in place. The DCI captured more variation in occupancy for the high dispersal level relative to the low level, as well as for barrier permeability 0.00 relative to 0.05. There was little variability among the three riverscapes in terms of the amount of variation in occupancy explained by the DCI.

3.3. Effect of barrier location

Barrier location affected estimates of occupancy and the DCI differently. Declines in occupancy were consistently observed among scenarios with barriers between first-order nodes; however, barriers between second and third-order nodes generally caused little

Table 1
Mean and standard deviation for percent of riverscape occupied by simulated fish with low and high dispersal ability in the presence of zero through five barriers among riverscapes.

Barrier number	Riverscape A				Riverscape B				Riverscape C			
	Low dispersal		High dispersal		Low dispersal		High dispersal		Low dispersal		High dispersal	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Permeability = 0.5												
0	100	0	100	0	100	0	100	0	100	0	100	0
1	100	0	100	0	100	0	100	0	100	0	100	0
2	100	0	100	0	100	0	100	0	100	0	100	0
3	100	0	100	0	100	0	100	0	100	0	100	0
4	100	0	100	0	100	0	100	0	100	0	100	0
5	100	0	100	0	100	0	100	0	100	0	100	0
Permeability = 0.05												
0	100	0	100	0	100	0	100	0	100	0	100	0
1	96	4	93	6	96	3	93	7	97	3	94	7
2	92	5	85	9	93	5	86	9	94	5	86	10
3	88	6	77	11	89	6	77	12	90	6	76	13
4	83	8	69	14	83	8	67	13	84	8	62	16
5	77	9	61	14	76	10	57	16	73	12	50	17
Permeability = 0.00												
0	100	0	100	0	100	0	100	0	100	0	100	0
1	96	4	91	8	96	4	91	8	96	4	92	8
2	91	6	81	11	91	6	81	13	92	6	81	13
3	84	8	69	15	85	8	67	19	85	9	64	21
4	74	12	57	19	75	13	51	22	73	13	46	22
5	64	13	44	19	60	17	36	21	54	20	33	20

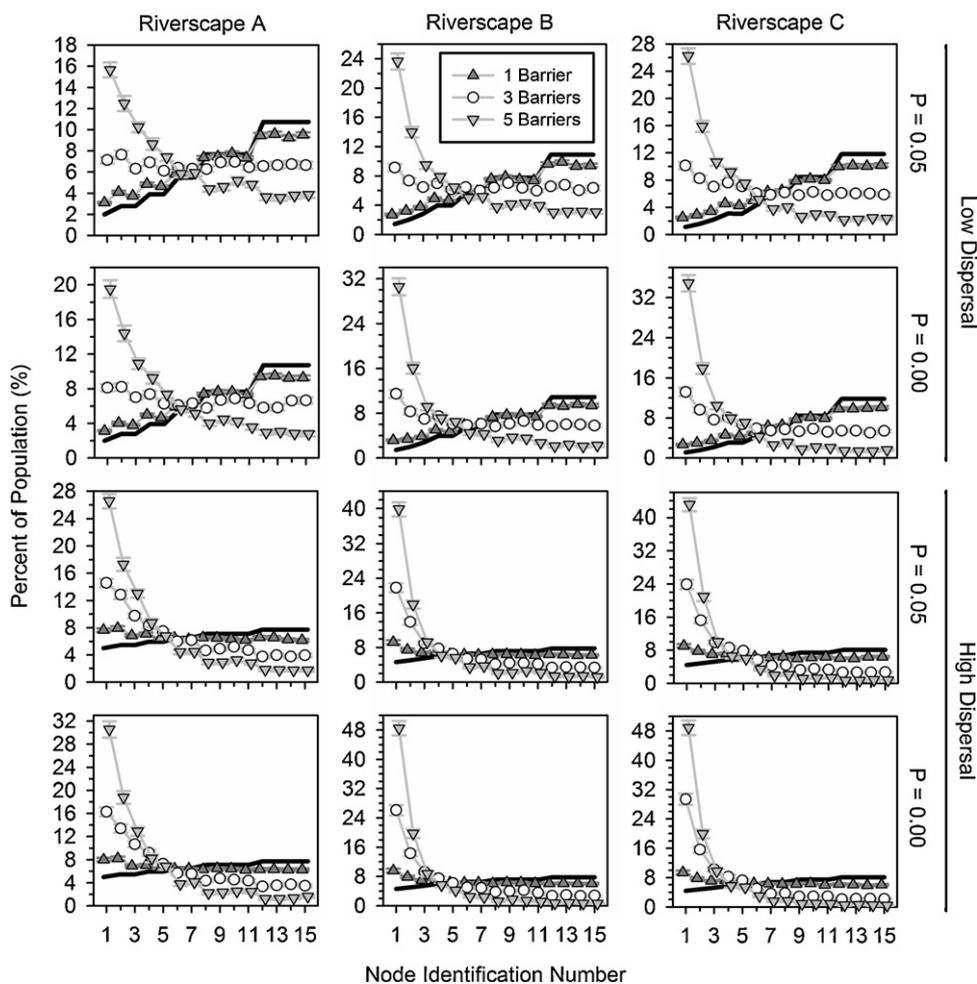


Fig. 4. Percent of fish distributed among nodes (solid black lines) during the neutral condition (i.e., no barriers) and change in population distribution after the addition of one (dark gray triangle up), three (open circle), or five (light gray triangle down) barriers for three riverscapes assuming low (upper six panels) and high (lower six panels) dispersal and two barrier permeability values ($P=0.05$ and $P=0.00$). Node locations are numbered 1–15 for each riverscape (see Fig. 2 for reference). For clarity, values for two and four barrier scenarios are excluded, points are slightly jittered among node identifications, and mean (95% confidence intervals) are illustrated. Note y-axis scale varies among panels.

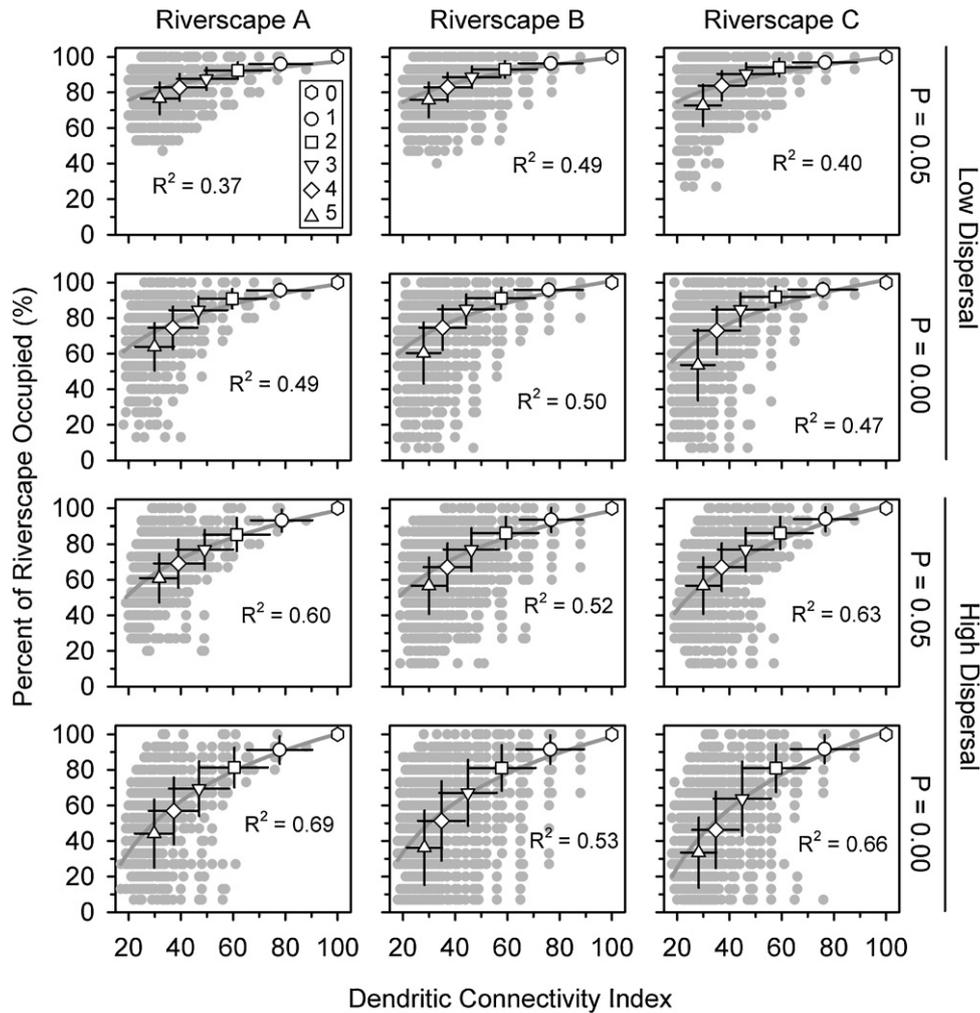


Fig. 5. Relationship between the dendritic connectivity index (DCI) and percent of riverscape occupied for fish species with low (upper six panels) and high (lower six panels) dispersal ability in three riverscapes assuming two barrier permeability values (0.05 and 0.00). Gray points represent scatter plots ($N = 6000$) for replicated ($n = 1000$) addition of 0–5 barriers. Central tendencies are illustrated with the dark gray regression line (coefficient of determination for logarithmic data are given). White points are means (standard deviation) for DCI versus occupancy relationships for each number of barriers.

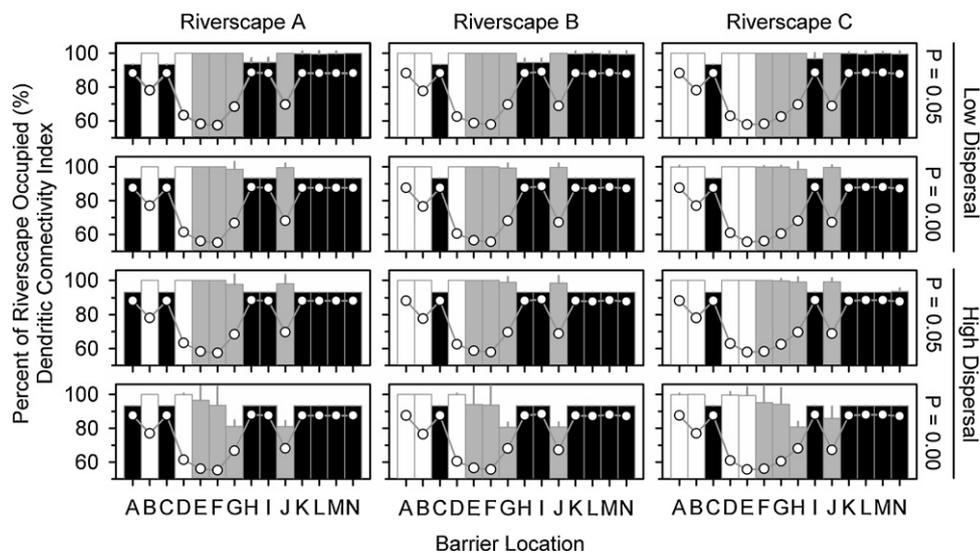


Fig. 6. Relationships between barrier locations (see Fig. 2 for reference) and percent of riverscape occupied (bars) as well as dendritic connectivity index (DCI; points) for fish with low (upper six panels) and high (lower six panels) dispersal ability in three riverscapes assuming two barrier permeability values ($P = 0.05$ and $P = 0.00$). Bars represent mean (standard deviation) of occupancy estimates for 1000 replications during which barriers were randomly placed at one of 14 locations (A–N) and are color-coded by first- (black), second- (gray), and third-order (white) stream segments. Points represent DCI values related to placing a barrier at each of the 14 locations; only one DCI value is produced when a single barrier is in place (i.e., no error bars are presented).

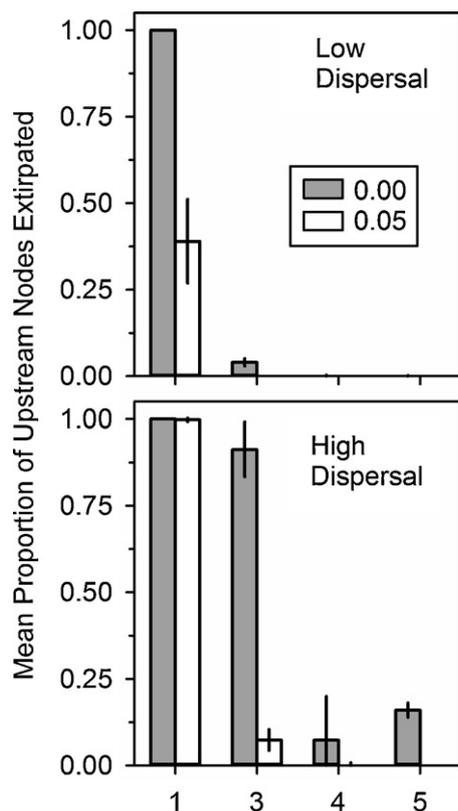


Fig. 7. Relationship between isolated fragment size and the proportion of upstream nodes from which fish become extirpated for low (upper panel) and high (lower panel) dispersal ability and barrier permeability 0.00 (gray) and 0.05 (white) when a single barrier was placed in riverscapes among riverscapes A, B, and C. Bars represent means (standard deviations)

change in occupancy (Fig. 6). Occupancy declined with increased dispersal affinity or lower permeability values and was most notable for high dispersing fish when barrier permeability was 0.00. Contrary to patterns observed for occupancy, the greatest declines in DCI caused by a single barrier were associated with locations on second- and third-order nodes. In particular, large magnitude declines in DCI were caused by barriers between nodes near the center of riverscapes (i.e., upstream third-order or downstream second-order nodes). Among all riverscapes, barrier locations, and barrier permeability values, there was a general mismatch between DCI values and occupancy when a single barrier was in place.

Relationships between fragment size and the proportion of upstream nodes from which fish became extirpated in the presence of only a single barrier were indicative of threshold responses. When fragment sizes were small (i.e., ≤ 3 nodes), the proportion of extirpated upstream nodes was high; however, as fragment size increased beyond three, extirpations declined rapidly or were absent (Fig. 7). For the low dispersal scenario when barrier permeability was 0.05, fish were extirpated from single, isolated upstream nodes approximately a third of the time across riverscapes. This case resulted from few extirpations when a single upstream node was fragmented near the upstream extent of riverscapes, but relatively greater extirpations from single upstream nodes nearer the base of riverscapes. Among all other scenarios, when a single upstream node was isolated fish became extirpated. Similarly, when three upstream nodes were isolated, fish were extirpated from some fraction of the riverscape (except for the case of low dispersal and barrier permeability 0.05). The greatest extent of extirpation from three fragmented upstream nodes was for the high

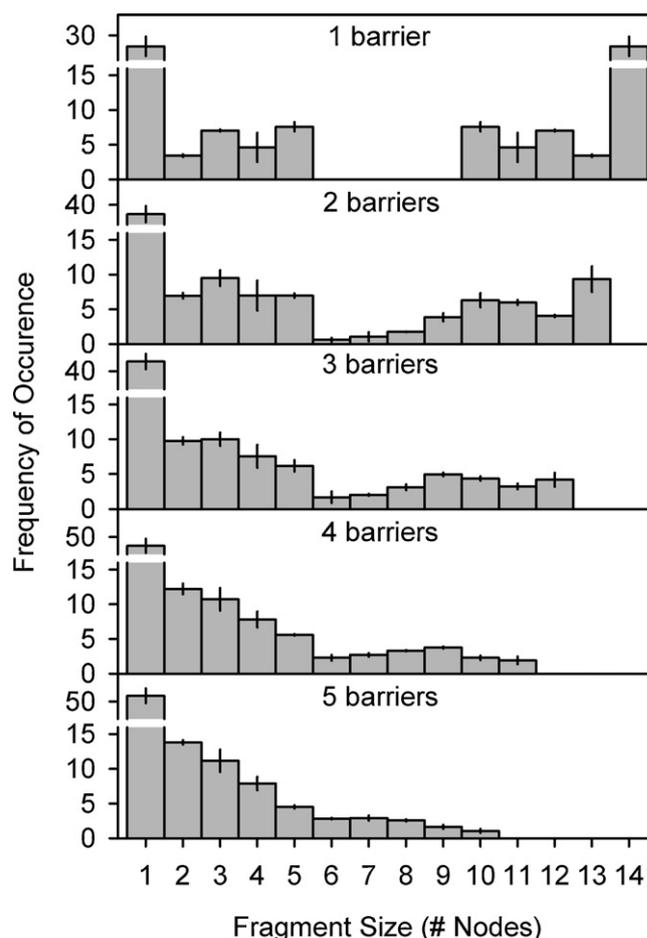


Fig. 8. Change in frequency distribution of fragment sizes when 1–5 barriers are introduced to riverscapes. Bars illustrated means (standard deviations) for riverscapes A, B, and C pooled together.

dispersal scenario when barrier permeability was 0.00, in which fish were extirpated from all three nodes nearly 90% of the time.

3.4. Changes in fragment size distributions

Distributions of fragment sizes became biased toward smaller size classes when a greater number of barriers were in place (Fig. 8). When a single barrier was inserted, the distribution of fragment sizes was symmetrical and characterized by multiple modes (though fragments of 6–9 nodes were not possible because of the architecture of our riverscapes). However, introduction of additional barriers caused distributions to become increasingly skewed toward small fragments with ≤ 3 nodes. This pattern resulted in the proportion of small fragments present in riverscapes increasing as one (38%), two (53%), three (63%), four (70%), and finally five (77%) barriers were inserted among riverscapes.

Increases in the number of small fragments in riverscapes contributed to declines in occupancy (Fig. 9). When zero small fragments were present in riverscapes, either because of the absence of barriers (i.e., neutral condition) or because existing barriers did not isolate small fragments, occupancy was on average greater than 98% for all dispersal levels and barrier permeability values (Table 2). Increases in small fragments caused steady declines in occupancy (R^2 values ranging 0.42–0.56), brought on by either changes in barrier locations or increases in the number of barriers present in the riverscape. The number of small fragments possible in a riverscape was determined in part by the number of barriers, and although sample sizes for simulations involving zero through five

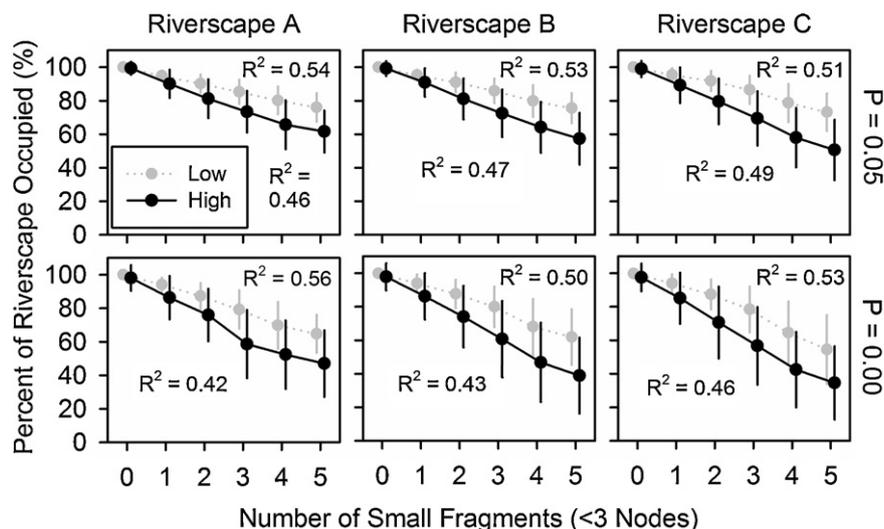


Fig. 9. Relationship between number of small fragments (≤ 3 nodes) and mean (standard deviation) percent of riverscape occupied for fish with low (gray points) and high (black points) dispersal ability for three riverscapes assuming two barrier permeability values (0.05 and 0.00). Coefficient of determination is given for raw data (see Table 2 for sample sizes) for low (upper right R^2 values) and high (lower left R^2 values) dispersing fish.

small fragments were high (>600 replications), the number of times six small fragments occurred in a riverscape was generally low (0–9 replications). This was driven by the fact that in order to achieve six small fragments, five barriers must be placed so that three or fewer nodes are isolated by each barrier, and the probability of this happening was low using random barrier insertions. Consequently, we focus on the maximum case of five small fragments occurring in riverscapes. When barrier permeability was 0.05, low dispersing fish declined to approximately 75% occupancy across riverscapes when five small fragments were present; whereas, high dispersing fish declined to approximately 57% occupancy. When barrier permeability was 0.00, low dispersing fish declined to approximately 61% occupancy across riverscapes when five small fragments were present; whereas, high dispersing fish declined to approximately 40% occupancy.

4. Discussion

Modeling habitat connectivity and fish dispersal in three hypothetical riverscapes identified specific properties of fragmented

riverscapes that could lead to altered fish distributions and potentially population declines. These properties include: (i) extirpations occurred most among “smaller” fragments; (ii) barriers with lower permeability caused greater extirpations; and (iii) specific barrier locations were associated with greater levels of extirpation. Though context-dependencies exist for each property, results suggested that habitat connectivity measured at the network scale predicted fish response to multiple barriers in a riverscape. Moreover, the dispersal level of fish interacted with barrier permeability and location to determine the threshold size for “small” fragments within which fish did not persist. We believe these properties have implications for the ecology of stream fish in real-world riverscapes and hold relevance for management of biodiversity in fragmented riverscapes.

4.1. Models reveal properties of fragmented riverscapes

Our modeling approach required several key assumptions that contributed directly to the observed patterns in fish declines. Key model assumptions included: biased upstream movement for both dispersal levels; fish were not lost from the network; downstream

Table 2

Sample size, mean, and standard deviation for percent of riverscape occupied by simulated fish with low and high dispersal ability in the presence of zero through six small fragments (i.e., ≤ 3 nodes) among riverscapes.

Fragment number	Riverscape A						Riverscape B						Riverscape C					
	Low dispersal			High dispersal			Low dispersal			High dispersal			Low dispersal			High dispersal		
	N	\bar{x}	SD	N	\bar{x}	SD	N	\bar{x}	SD	N	\bar{x}	SD	N	\bar{x}	SD	N	\bar{x}	SD
Permeability = 0.05																		
0	1259	100	0	1249	99	4	1228	100	0	1254	99	4	1354	100	1	1330	99	5
1	1134	95	3	1157	90	8	1160	95	3	1123	91	9	1147	95	4	1185	89	11
2	1035	90	5	1050	81	12	1057	91	6	1081	81	12	1053	92	6	1028	80	14
3	1011	85	7	993	73	12	988	86	7	988	72	14	946	86	8	957	69	16
4	929	80	8	901	66	15	949	80	9	862	64	15	891	79	11	885	58	18
5	631	76	9	647	62	12	614	76	9	692	57	15	604	73	11	606	51	18
6	1	67	0	3	47	0	4	65	18	0	-	-	5	71	14	9	38	7
Permeability = 0.00																		
0	1243	100	1	1232	98	8	1254	100	1	1253	98	8	1341	100	1	1335	98	8
1	1185	94	4	1169	86	13	1156	94	5	1167	86	14	1173	94	5	1167	85	15
2	1036	87	8	1027	76	16	1059	88	9	1042	74	18	1026	87	9	1048	71	21
3	993	79	12	992	59	20	1006	80	12	946	61	23	966	78	14	958	57	23
4	917	70	14	963	52	20	892	68	17	971	47	24	887	64	19	881	42	23
5	624	65	11	615	47	20	629	62	17	617	39	23	600	55	21	608	35	22
6	2	40	28	2	20	9	4	68	19	4	22	17	7	43	19	3	36	15

dispersal was not interrupted by the presence of a barrier; all barriers within a simulation had equal permeability; and nodes had uniform quality. The most apparent pattern was the virtual exclusion of fish from small fragments in our riverscapes, which was related to movement out of the fragment in a downstream direction and limited reentry in an upstream direction. This result occurred because of our assumption that movement was biased in an upstream direction (the case for many organism in stream networks; Grant, 2011) but became biased in a downstream direction when a barrier was present and local upstream transition probability was reduced by at least half (i.e., barrier permeability <0.5). Thus, extirpations from small fragments were not related to fish being lost from the network (e.g., because of node-specific demographic rates or extinction probabilities; Labonne et al., 2008; Grant, 2011), but instead were related to accumulations in larger fragments nearer the center or downstream portions of riverscapes. Second, accumulation in larger, centrally located fragments was most evident when barrier permeability was lower. Based on our model assumptions, barriers with permeability values greater than 0.50 posed little threat to network-scale occupancy, though declines did occur at permeability 0.10 (results not shown) and lower even when only a single barrier was in place. This pattern was driven by the manner in which barriers “reflected” fish and caused them to transition downstream rather than upstream (Rodríguez, 2010), and barriers with lower permeability reflected a greater proportion of fish. Finally, declines in occupancy were driven by extirpations among upstream nodes that corresponded with greater fish abundances in the absence of fragmentation (i.e., the neutral condition). Consequently, node-specific responses to fragmentation were greatest among upstream nodes and followed the hierarchical structuring of habitats in riverscapes. By this account, although we assumed equal quality among nodes prior to their arrangement, an intrinsic quality based on their location within the riverscape emerged with respect to patterns in occupancy prior to and following fragmentation.

Emergent properties are common in hierarchically structured landscapes such as streams and highlight the potential for riverscape patterns (e.g., architecture, connectivity) to influence ecological processes such as organism dispersal at broad scales (Grant et al., 2007). Although habitat connectivity and quality have the potential to interact and cause variable responses in fish occupancy throughout a riverscape, previous work suggests such interactions can be minor in a modeling framework such as ours (Padgham and Webb, 2010) and supports our assumption of homogenous node quality in favor of emphasizing responses to changing connectivity. Despite homogenous node quality, we found patterns in extirpation were not equal among all nodes and that headwaters emerged as most susceptible to extirpation when riverscapes were fragmented. This pattern might be expected given our assumption of biased upstream movement, but we found declines were exacerbated by the addition of multiple barriers that fragmented a greater portion of the riverscape (even outside of headwater nodes). In this context, interplay between shifts in node connectivity and fish occupancy occurred at the riverscape scale, which likely explains the success of the DCI in predicting fish response to fragmentation. Habitat connectivity measured using the DCI predicted 30–50% of variation in fish distribution for low dispersal and 50–70% of variation for high dispersal. Because we assumed homogeneity in barrier permeability within simulations, lower DCI values should be interpreted as a greater splitting of the riverscape, either through barrier arrangement (i.e., contributing to variability within the number of barriers) or barrier number (i.e., contributing to variability among the number of barriers). The greatest variation in DCI estimates occurred for the single barrier scenario, when the barrier could produce a greater range of fragment sizes. As additional barriers were inserted, the range of

potential fragment sizes declined and DCI values were restricted accordingly. On the contrary, variability in estimates in riverscape occupancy increased as barrier number increased, likely as an artifact of the distribution of barriers and consequently number of small fragments in the riverscape. Consequently, we hypothesize the mechanism by which the DCI predicted changes in occupancy was the threshold response by fish caused by isolation of small fragments, so that highly predictable declines in occupancy occurred when 1–3 nodes were isolated. This pattern resulted in a near-linear decline in riverscape occupancy as the number of small fragments in the riverscape increased and produced comparable predictions regarding occupancy relative to the DCI.

4.2. Dispersal ability determines response to fragmentation

High dispersing fish species respond to fragmentation of river networks to a greater extent than do relatively sedentary fish. In our study, the high dispersal level indicated greater declines in occupancy relative to the low dispersal level regardless of riverscape architecture, barrier permeability, or barrier number. This is in part because dispersal events incorporating greater distances (i.e., higher transition probabilities) stand a better chance of encountering barriers and either moving to adjacent stream sections or being reflected by a barrier (Rodríguez, 2010). Furthermore, downstream transition probability was greater for the high dispersal level, both in overall magnitude (i.e., 0.11 vs 0.05) and proportion of upstream probability (i.e., 0.11/0.12 vs 0.05/0.07), which contributed to a greater number of fish moving out of fragmented nodes. Thus fish that exhibit dispersal over greater distances tend to respond strongly to fragmentation (Pépin et al., 2012). For example, Hitt and Angermeier (2008) found fish in families Catostomidae and Cyprinidae dispersed over distances of at least 6–8 stream km in the James River drainage, Virginia, USA. The authors concluded that habitat connectivity was therefore important for local persistence of these fish, at least at a spatial scale of up to 10 stream km. It is not surprising then that catostomids and cyprinids indicated strong responses to fragmentation in Kansas, USA stream networks measured at comparable spatial scales (i.e., up to 10 stream km), or that species in these families tended to become locally extirpated when barriers were in place downstream (Perkin and Gido, 2012). Furthermore, fish that exhibited little response to fragmentation of Kansas streams were similar to those with low dispersal rate according to Norman et al. (2009), including stonerollers (genus *Camptostoma*) and darters (genus *Etheostoma*); whereas, fish that experienced local declines or extirpations upstream of perched road crossings were similar to those with high dispersal rates (genera *Cyprinella* and *Notropis*; Perkin and Gido, 2012). These patterns illustrate how appropriate matches in the spatial extent at which (i) fish interact with riverscapes and (ii) structural (i.e., habitat) connectivity is measured can enhance conservation of stream fish (Fausch et al., 2002). However, addressing such context-dependencies and determining appropriate spatial scales for network measures of connectivity can be challenging (Erős et al., 2012; Geheber and Piller, 2012).

4.3. Threshold responses to fragmentation

Non-linear responses by fish to stream fragmentation might be a useful method for determining the appropriate spatial scales at which to measure network connectivity. In realistic river networks, extirpations are generally due less to dispersal out of fragments as in our model and more so to altered demographic rates within fragments (but see Aló and Turner, 2005; Agostinho et al., 2007). Altered demographic rates can result in threshold responses in population persistence and thresholds are therefore a feature in

real-world ecological networks (Dewhurst and Lutscher, 2009). Fish extirpations from cool and warm water stream systems in North America provide examples. Brook trout *Salvelinus fontinalis* is a cool-water species with high dispersal during the reproductive season and reproductively viable populations are now extirpated from small stream fragments in the Fishkill Creek network of New York, USA (Bain and Wine, 2010). The apparent mechanism for extirpation involves inadequate habitat availability for reproduction among stream fragments less than 3.2 km in length (Bain and Wine, 2010), and such threshold responses to fragmentation are reported by other authors (Letcher et al., 2007). Similarly, warm-water, pelagic-broadcast spawning cyprinids in rivers throughout the Plains of North America are now extirpated from many stream fragments <100 stream km in length, though species-specific thresholds can be greater (Dudley and Platania, 2007; Perkin and Gido, 2011). The mechanism for these extirpations is again related to the absence of appropriate reproductive habitat in shorter fragments and loss of source-sink dynamics or rescue effects (Winston et al., 1991; Luttrell et al., 1999). In fact, Dudley and Platania (2007) specifically prioritized stream fragments in the Rio Grande drainage that are currently <100 stream km but would exceed this threshold with the removal of a single barrier. These examples suggest using network-scale measures of fragmentation in which reconnection of fragments less than the estimated threshold required for persistence are prioritized might contribute to increases in targeted species distributions.

Prioritizing specific fragment sizes that have ecological relevance rather than simply removing barriers to obtain maximum fragment sizes represents a paradigm shift in the current approach to barrier prioritization (Fullerton et al., 2010). In the absence of additional information, barriers are prioritized so that the maximum amount of stream length is reconnected by removal of the minimum number of barriers (Cote et al., 2009; Kemp and O'Hanley, 2010), and models specifically targeting reestablishment of a single, large fragment of stream have been developed (O'Hanley, 2011). For such models, when organism interpretation of a riverscape is not taken into account, increases in structural connectivity might not equal increases in functional connectivity. For example, Branco et al. (2011) found fish in four Portugal streams indicated little response to reduced longitudinal habitat connectivity, likely because residual fragment sizes were large enough to allow completion of life history for even potamodromous species that are expected to respond strongly to fragmentation. Similarly, limited dispersal among targeted fish species or high permeability of barriers can contribute to weak relationships between structural and functional connectivity for stream-dwelling fish populations (Pépin et al., 2012). Thus species interpretation of barriers should be taken into account when barriers are prioritized for removal because highly permeable barriers might pose little threat to functional connectivity (Bourne et al., 2011) or because barrier locations do not interrupt fish life cycles (Hudman and Gido, 2012). The latter point will ultimately be the greater challenge for freshwater fish conservation given the paucity of detailed life history and dispersal information for many rare and declining species (Cooke et al., 2012). For species whose life history and dispersal affinities are well documented (e.g., salmonids), riverscape conservation approaches that consider connectivity among critical habitats (i.e., spawning, feeding, refuge; Schlosser, 1991) have helped to enhance conservation-driven management approaches (Fausch et al., 2002; Morita and Yokota, 2002). Consequently, because both measures of connectivity (structural and functional) are scale and target dependent (Crooks and Sanjayan, 2006) an unavoidable context-dependent element must be included in network-scale assessments of organism response to fragmentation (Erős et al., 2012).

5. Conclusions

Fragmentation of riverscapes disrupts the abundance and distribution of numerous stream fish species, but the magnitude of fish response can vary among species and systems (e.g., Alexandre and Almeida, 2010; Branco et al., 2011; Anderson et al., 2012). Our findings suggest that fish response to stream fragmentation is mediated by dispersal affinity as well as the permeability and distribution of barriers throughout a riverscape so that declines are greatest when dispersal is high and barrier permeability is low (Pépin et al., 2012). Because road crossings are common in contemporary landscapes (Gibson et al., 2005), methods for measuring network-scale connectivity and prioritizing barrier removal to enhance habitat connectivity have recently been developed (Kemp and O'Hanley, 2010; Fullerton et al., 2010). However, maximizing structural connectivity with the ultimate goal of enhancing functional connectivity should be directed by specific goals for restoration because there might be little ecological benefit (e.g., Palmer et al., 2010) to maximizing structural connectivity if there is little response in fish abundance and distribution (Fausch et al., 2002). Knowledge of organism-specific threshold responses to fragmentation might therefore provide a greater ecological benefit if barrier prioritization methods are adapted to target specific fragment lengths in riverscapes with the goal of maximizing the number of fragments capable of supporting the organism of interest.

Acknowledgements

This project was funded by the National Science Foundation Experimental Program to Stimulate Competitive Research (award number EPS-0919443). Walter Dodds, Anthony Joern, Charles Rice, and Angus Webb provided helpful feedback on previous drafts.

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