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Assessing upstream fish passage connectivity with network analysis

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Abstract. Hydrologic connectivity is critical to the structure, function, and dynamic process of river ecosystems. Dams, road crossings, and water diversions impact connectivity by altering flow regimes, behavioral cues, local geomorphology, and nutrient cycling. This longitudinal fragmentation of river ecosystems also increases genetic and reproductive isolation of aquatic biota such as migratory fishes. The cumulative effects on fish passage of many structures along a river are often substantial, even when individual barriers have negligible impact. Habitat connectivity can be improved through dam removal or other means of fish passage improvement (e.g., ladders, bypasses, culvert improvement). Environmental managers require techniques for comparing alternative fish passage restoration actions at alternative or multiple locations. Herein, we examined a graph-theoretic algorithm for assessing upstream habitat connectivity to investigate both basic and applied fish passage connectivity problems. First, we used hypothetical watershed configurations to assess general alterations to upstream fish passage connectivity with changes in watershed network topology (e.g., linear vs. highly dendritic) and the quantity, location, and passability of each barrier. Our hypothetical network modeling indicates that locations of dams with limited passage efficiency near the watershed outlet create a strong fragmentation signal but are not individually sufficient to disconnect the system. Furthermore, there exists a threshold in the number of dams beyond which connectivity declines precipitously, regardless of watershed topology and dam configuration. Watersheds with highly branched configurations are shown to be less susceptible to disconnection as measured by this metric. Second, we applied the model to prioritize barrier improvement in the mainstem of the Truckee River, Nevada, USA. The Truckee River application demonstrates the ability of the algorithm to address conditions common in fish passage projects including incomplete data, parameter uncertainty, and rapid application. This study demonstrates the utility of a graph-theoretic approach for assessing fish passage connectivity in dendritic river networks assuming full basin utilization for a given species, guild, or community of concern.

Key words: cumulative effects; dam removal; fish passage; graph theory; habitat connectivity index for upstream passage; Truckee River, Nevada, USA.

INTRODUCTION

Hydrologic connectivity is the "water-mediated transfer of matter, energy, and/or organisms within or between elements of the hydrologic cycle" (Pringle 2001:981). Because rivers are inherently four-dimensional systems (Ward 1989), connectivity can be assessed in longitudinal, lateral, vertical, temporal, or multiple dimensions (Wiens 2002, Kondolf et al. 2006). The ecological benefits of connected ecosystems are well established (e.g., animal movement corridors, nutrient delivery; Pringle 2003, Freeman et al. 2007). However, enhanced connectivity can also have negative consequences, such as invasive species introduction, hybridization of native species, and disease spread (Jackson and Pringle 2010). Thus, hydrologic connectivity must be assessed relative to the objectives and dimensionality of a given problem.

Worldwide, river ecosystems are longitudinally disconnected due to human-induced drivers such as dams (Graf 1999; USACE, database *available online*),[6] road crossings (Forman and Alexander 1998, Jones et al. 2000), water withdrawals or diversions (Smith et al. 2003, Crook et al. 2009), and thermal or water quality barriers (Bednarek 2001). This disconnection is of particular importance to mobile, aquatic obligates such as fish, which serve not only as economically, socially, and culturally important species (Fullerton et al. 2010), but also ecologically important species that alter large-scale ecosystem processes (Freeman et al. 2003). Accordingly, enhancing hydrologic connectivity for fish passage has been a critical focus of river restoration

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efforts (Doyle et al. 2003, Bernhardt et al. 2005). Numerous guidance documents and tools have been developed to direct managers and designers through the fish passage decision-making process (FAO 2002, Clarkin et al. 2005, Hotchkiss and Frei 2007, NRCS 2007, Schilt 2007, Clarkin et al. 2008, NMFS 2008, FPDSS 2012, Hoenke 2012; and the Fish Passage Decision Support System [FPDSS], *available online*).[7] Although fish passage decisions rely on many technical issues, three of the most prominent questions include: (1) What alternatives are available to improve fish passage? (2) How can fish passage rates be assessed at a single barrier? (3) How can the cumulative effect of multiple barriers be considered during the site selection process? This paper focuses primarily on the last question.

The first issue is beyond this paper's scope, except to note that the exceptional variety of alternatives (e.g., fishways, bypasses, dam removal, lifts, operational changes, culvert retrofits, diversion screens, guidance structures, no action) have variable effects on passage rates. Fish passage rates at a single site are often summarized in the form of passage efficiency or barrier passability (Kemp and O'Hanley 2010). O'Hanley and Tomberlin (2005) defined passability at the population scale as the proportion of fish that are able to pass through a barrier while migrating upstream. However, this notion can be assessed alternatively at individual or community scales (i.e., the proportion of successful attempts at passing a barrier or the number of species successfully passing, respectively; Kemp and O'Hanley 2010, Roscoe and Hinch 2010). Furthermore, passage rates vary with species, life history stage, environmental variability, direction of passage, temperature, discharge, and numerous other factors. A variety of techniques can be applied to assess passability, including: empirical observation (e.g., filming, hydroacoustics, telemetry), indirect surveys around a barrier (e.g., abundance and occupancy methods; Norman et al. 2009), genetic surveys, rule-based models coupling fish physiology and hydrodynamics (e.g., Coffman 2005, also FishXing; Furniss et al. 2006), statistical models (e.g., Bayesian Belief Networks; Andersen 2010, Anderson et al. 2012), individual-based models (e.g., Goodwin et al. 2006), and expert opinion (e.g., scoring systems; WDFW 2000, Martin and Apse 2011). Kemp and O'Hanley (2010) provide a thorough review of these methods, as well as their strengths and limitations. In this paper, the terms passage efficiency and barrier passability will be used interchangeably, as the proportion of fish passing a structure scaled from 0 to 1.

Owing to the important role of longitudinal connectivity in watersheds, barriers should not be considered in isolation from the cumulative effects of upstream or downstream structures. Regardless of their efficacy, single-site techniques may be inadequate or inappropriate for barrier prioritization or restoration projects and could result in inefficient solutions (O'Hanley and Tomberlin 2005). Notably, Padgham and Webb (2010) apply cumulative and single-site techniques to demonstrate additive impacts can occur in some watershed topologies.

A number of alternative techniques address the cumulative effect of multiple barriers and prioritize barrier improvement. By treating passability as a binary outcome (i.e., pass/no pass), Kuby et al. (2005), Zheng et al. (2009), and O'Hanley (2011) applied optimization algorithms to prioritize dam removals at large scales for varying budget levels. O'Hanley and Tomberlin (2005) provide a similar, yet more nuanced, optimization method, whereby dams are assigned upstream passage probability rates (rather than pass vs. no-pass). Likewise, Conyngham et al. (2011) developed a multi-species model of habitat-weighted passage efficiency for comparing separate upstream and downstream fish passage improvement alternatives along a linear river network. Improving on these unidirectional models, Cote et al. (2009) and Diebel et al. (2010) develop habitat-weighted connectivity indices incorporating both upstream and downstream passability for potadromous and diadromous life histories with subsequent applications in river networks (O'Hanley et al. 2010, Bourne et al. 2011). In this paper, we adopted an approach to assessing upstream longitudinal connectivity that considers dendritic network morphology, partial passage improvement, stochastic passage rates, and dependency and nestedness associated with multi-barrier fish passage improvement plans.

The common dendritic (i.e., tree) structure of watersheds is increasingly recognized as a strong governing force in lotic ecosystem structure and function (Benda et al. 2004, Grant et al. 2007, Flitcroft et al. 2012). Eros et al. (2012) highlight the utility of considering this dendritic structure as a spatial graph network problem. Indeed, network analysis tools and graph-theoretic algorithms have proven useful for a variety of terrestrial ecosystem management, restoration, and conservation problems (Urban and Keitt 2001, Estrada and Bodin 2008, Urban et al. 2009, Dale and Fortin 2010, Rudnick et al. 2012). However, these tools are rarely transferred and utilized in watershed applications (Fullerton et al. 2010, Padgham and Webb 2010, Eros et al. 2012).

Dams, roads, and other barriers fragment streams and rivers throughout the world, and the dendritic topology of watersheds creates unique challenges for quantifying and enhancing connectivity of these ecosystems (Pringle 2003, Benda et al. 2004, Grant et al. 2007). We applied a graph-theoretic algorithm to assess upstream fish passage problems and to prioritize watershed-scale restoration efforts. Specifically, our objectives were to develop a generic graph-theoretic algorithm for assessing upstream fish passage connectivity and identify watershed topologies and corresponding dam configu-

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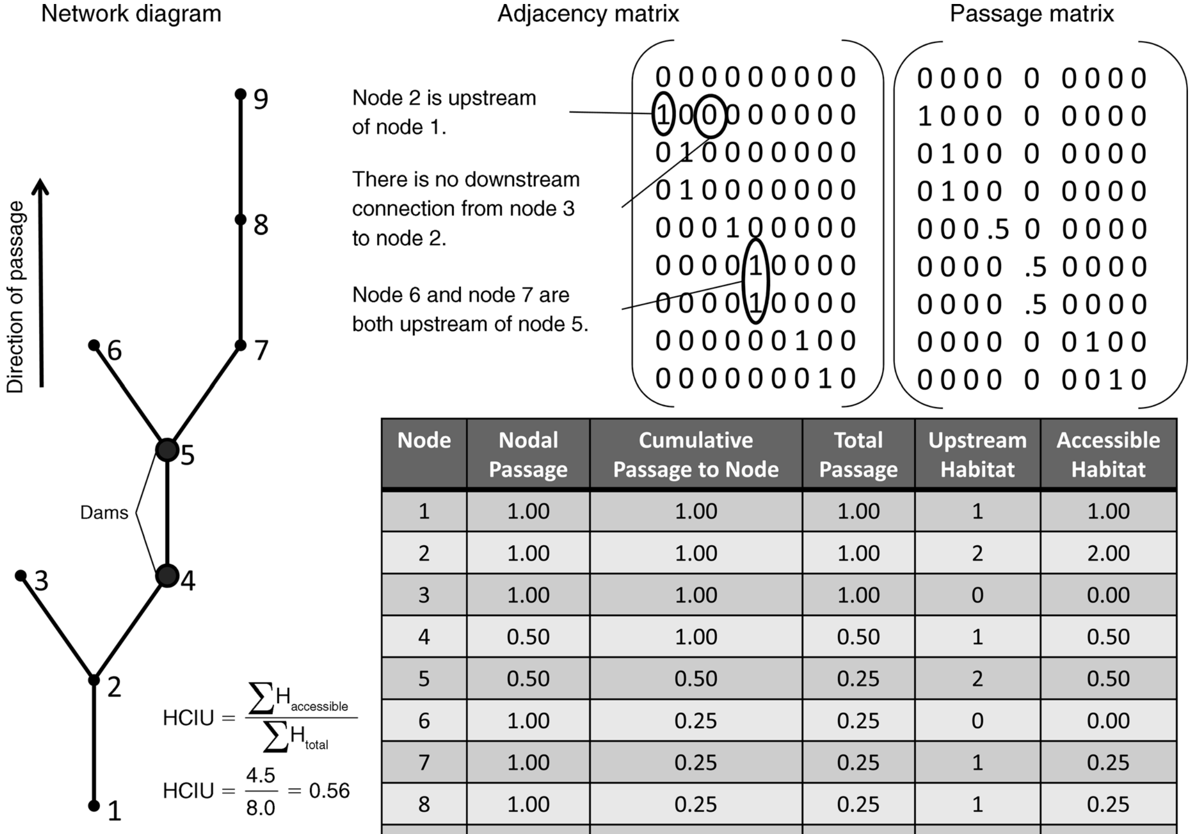
[7] http://fpdss.fws.gov



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$$\mathrm{HCIU} = \frac{\sum H_{\mathrm{accessible}}}{\sum H_{\mathrm{total}}}$$

$$\mathrm{HCIU} = \frac{4.5}{8.0} = 0.56$$

Node	Nodal Passage	Cumulative Passage to Node	Total Passage	Upstream Habitat	Accessible Habitat
1	1.00	1.00	1.00	1	1.00
2	1.00	1.00	1.00	2	2.00
3	1.00	1.00	1.00	0	0.00
4	0.50	1.00	0.50	1	0.50
5	0.50	0.50	0.25	2	0.50
6	1.00	0.25	0.25	0	0.00
7	1.00	0.25	0.25	1	0.25
8	1.00	0.25	0.25	1	0.25
9	1.00	0.25	0.25	0	0.00
Total				8	4.50

FIG. 1. Simplified network to demonstrate computation of the habitat connectivity index for upstream passage (HCIU). Refer to the *Methods* section for additional description of the HCIU computational algorithm; *H* is habitat.

rations most vulnerable to fish passage concerns (application 1), and demonstrate model application to prioritize fish passage improvement in the Truckee River, Nevada, USA (application 2).

METHODS

We assessed upstream fish passage connectivity as a habitat-weighted, cumulative passage rate. In order to track these rates and compute connectivity indices, we developed a generalized network model of river topology. This section details the graph-theoretic model construct, develops the habitat connectivity index for upstream passage (HCIU), and describes two case studies applying the HCIU in hypothetical and real river networks.

A graph-theoretic habitat connectivity model

A network, at its most basic level, is "a collection of points joined together by lines" (Newman 2010:1). These points are also called nodes or vertices, and lines are designated as edges. For the purpose of our analysis, we constructed a river network with nodes at locations along the longitudinal dimension where conditions change (i.e., tributary junctions, barriers, other pertinent watershed locations) and edges as habitat between these nodes (e.g., length of river between dams). This parameterization was chosen to suit our problem; however, it is important to note that one could also classify nodes as habitat and edges as connections between habitats, as has been the case in other ecological applications of network analysis (Urban and Keitt 2001, Schick and Lindley 2007, Urban et al. 2009, Dale and Fortin 2010). We also assumed barriers and dams take no real space and do not reduce the total river network length (Cote et al. 2009). Applying these assumptions, the topology of a river network may be represented as a series of nodes and edges summarizing connectivity between two points. Fig. 1 presents a simple river network along with its adjacency matrix, which provides a numerical summary of the structural connectivity of the network.

All nodes in a river network may be assigned barrier passage rates. As previously stated, we refer to barrier passability in the general context as the proportion of fish passing a structure scaled from 0 to 1, an index value that combines passage efficiency, delay factors, predation effects, and other relevant characteristics for comparative purposes. Because the focus of this paper is upstream habitat connectivity, we only applied upstream passage rates, and downstream passage is neglected. In other words, we examined diadromous life history whereby a species is migrating upstream from the mouth of the basin (Cote et al. 2009, Diebel et al. 2010), and we implicitly assumed that if a fish can move upstream that downstream loss is minimal relative to upstream movement (Anderson et al. 2012). We also assumed that habitat is utilized equally per unit area or stream length. Finally, species interactions are not examined.

The habitat connectivity index for upstream passage (HCIU) incorporates both the quantity of habitat accessed and the cumulative passage rate to that point to quantify interdependencies of passage improvement benefits. Fig. 1 presents a simple river network with eight units of habitat (i.e., edges) and nine nodes. Two nodes (4 and 5) are barriers with 50% passability, and all other nodes are 100% passable. Cumulative passage to a node is the passage to a point just downstream of that node and is calculated as the product of all downstream passage rates (e.g., cumulative passage to node 5 is the product of passage rates at nodes 1, 2, and 4 or 1.0 × 1.0 × 0.5, respectively). Total passage rate combines cumulative passage to the node and the nodal passage to assess the cumulative passability beyond the node. Upstream habitat is the total quantity of habitat directly upstream of a given node (e.g., 1 unit for node 1 and 0 units for node 3). Accessible habitat is computed as the quantity of upstream habitat weighted by the total passability to that habitat. For instance, there is one unit of habitat above node 4 and 50% total passage. Thus, 0.5 units of habitat are accessible in the immediately adjacent upstream reach. By summing across all reaches, the HCIU is computed as the ratio (0 to 1) of accessible to total habitat in the river network (Diebel et al. 2010). By normalizing habitat relative to total habitat, the metric is most useful for prioritizing barrier improvement within a single watershed. Total accessible habitat may be more useful if multiple watersheds are being compared. Although length is used here as a measure of habitat quantity, the algorithm could also be applied using alternative habitat metrics (e.g., area, volume, quality-weighted area, length-weighted discharge; Grant et al. 2012).

Whereas the watershed in Fig. 1 has an existing HCIU of 0.56 (i.e., 4.5/8.0), an alternative HCIU can be computed for any barrier restoration plan. For instance, by restoring passability at node 4 from 0.5 to 1.0, the HCIU would increase to 0.75. Restoring passability at node 5 from 0.5 to 1.0 leads to an HCIU of 0.69. Of course, all other circumstances being equal, complete barrier restoration (i.e., removal) at the downstream node (i.e., node 4) would be more effective than at the upstream node (i.e., node 5). Also, restoring passability at node 4 from 0.5 to 0.83 is functionally equivalent to complete restoration of node 5 (i.e., HCIU is 0.69 for both conditions).

The HCIU can be computed manually for small networks with simple geometries. However, as network topology becomes more complex and networks increase in size, these calculations become logistically and computationally challenging. By framing the problem as a network, we take advantage of well-defined algebraic relationships. Nodal passage rates substituted into a common graph theory derived adjacency matrix (Śiljak 1991) generates a nondimensional passage matrix **P** that expresses passage probabilities between adjacent nodes (Fig. 1). Established graph theory shows that this matrix, raised to any exponent (matrix multiplication $[\mathbf{P}]^m$ not scalar powers, $p_{i,j}^m$), provides the upstream passage rate between two nodes over the path length specified by the exponent m. For instance, the [9, 1] interstitial element of the passage matrix raised to the sixth power, $\mathbf{P}^6$ (computed to be 0.25), numerically represents the passage rate between nodes 1 and 9 (i.e., a 0.25 cumulative passage rate exists over the six path lengths between them). Thus, the graph-based, matrix formulation of this problem creates a compact method for tracking cumulative passage in complex network topologies.

A suite of numerical routines was developed to compute the HCIU for a specified network topology and dam configuration (i.e., an adjacency and passage matrix) using the R statistical software package (version 2.12.2; R Development Core Team 2007). In accordance with best practices in ecological modeling (Schmolke et al. 2010), code was error checked by the authorship team and annotated to the extent practicable. Numerical algorithms for calculating HCIU were verified by manual calculations with 8, 10, 20, 50, and 100 edges with 1 and 2 dams placed at 10 random configurations. Generalized code, as well as code for applications 1 and 2, is provided in the Supplement.

Application 1: General trends in upstream fish passage connectivity

Following Cote et al. (2009) and Padgham and Webb (2010), we conducted simulations in hypothetical watersheds to test the HCIU metric and examine broader patterns in connectivity. Specifically, we sought to address three questions associated with the effect of watershed topology, number of barriers, and barrier configuration (i.e., barrier locations within the topology) on upstream fish passage connectivity. First, are barrier locations near the mouth of the basin disproportionately important for upstream connectivity? Second, is there an upper threshold in barrier quantity beyond which location becomes irrelevant, and what watershed topologies are most vulnerable to disconnection? Third, how does the number of barriers inducing a threshold response change as the relative passage rate of each barrier increases? These questions can aid managers tasked with rapidly assessing the effects of proposed

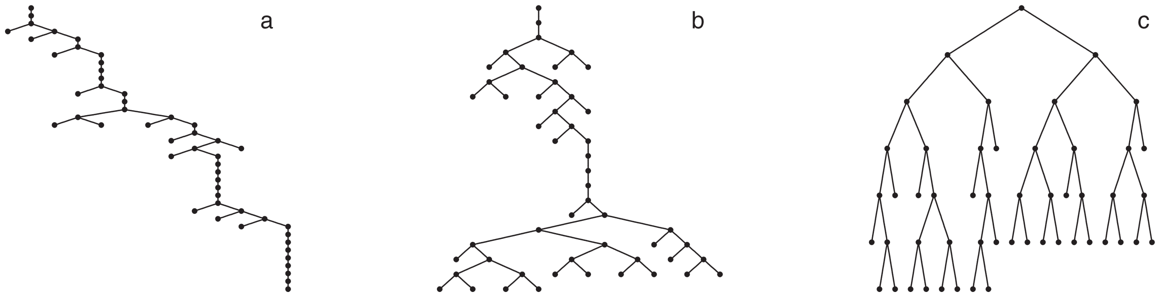

FIG. 2. Three sample networks demonstrating the variation in watershed topology generated by our random network construction algorithm. All networks have 50 edges and 51 nodes. These networks represent the (a) maximum, (b) median, and (c) minimum basin diameters constructed by our algorithm (diameters are 39, 19, and 6, respectively). Network diameter is the longest path between any two nodes in the graph, where the path length between these nodes is itself the shortest possible path, which is a metric of network shape addressing the number of edges between two points in a basin.

structures, weighing needs for and arrays of alternatives for restoration of connectivity in highly fragmented systems, choosing basins for large projects, and other applications.

We conducted a suite of experiments using randomized watershed topologies, each with 50 edges and 51 nodes to address the above questions. For simplicity, each edge was assigned a habitat value of unity representing quantity and quality (i.e., one habitat unit could be either a single mile of river with perfect quality or two miles of river with 50% quality). Therefore, 50 units of habitat are available in each watershed configuration. Watershed topologies were constructed moving from downstream to upstream with each node having a 50% probability of being a junction (i.e., two streams combining at a confluence). Network construction was constrained by prohibiting more than one split at a given node (i.e., only two streams, not three or more, may combine at a confluence) and preventing network crossing (i.e., between subwatersheds). For each simulation, we generated a random watershed topology, specified the quantity of barriers to be distributed throughout the network, and examined multiple configurations of those barriers in the network. Fig. 2 provides three examples of randomly generated basins with alternative watershed topology. Passage rate was assumed equal for all barriers in the watershed. We assumed that barriers exhibit independent passage rates, and an individual's physiological capacity to pass a barrier is not influenced by downstream structures (Cote et al. 2009, Kemp and O'Hanley 2010). HCIU was then computed as the response variable for each topology–configuration–passage rate combination. Table 1 summarizes simulations conducted for each question identified in the previous paragraph. The number of simulations attempted to balance the needs for a diversity of randomized conditions and larger sample sizes with the computational burden of additional iterations.

Application 2: Prioritizing Truckee River fish passage improvement

We applied the HCIU to determine what combination of fish passage improvement actions cost-effectively improves system-wide connectivity of the Truckee River, Nevada. The Truckee River is a closed basin flowing 194.9 km from Lake Tahoe to its terminus at Pyramid Lake (Fig. 3). More than 30 structures impede upstream and/or downstream fish passage on the Truckee River, and several agencies and owners are exploring fish passage improvement options. Conyngham et al. (2011) studied the system by evaluating numerous fish passage improvement alternatives. They assessed upstream and downstream passage for eight fish species using model parameters (passage efficiency, habitat suitability, population condition, mobility, and so on) elicited from a panel of experts. The elicited information included estimates of habitat quality and passage efficiency

TABLE 1. Test matrix for hypothetical basin simulations.

Question	No. watersheds	No. dams per watershed	No. dam configurations per watershed	Passage rate per dam	Total simulations	Figure
1	5000	1	51†	0.5	255 000	4
2	500	0, 1, 2, 3, . . . , 25	20	0.5	250 001‡	5
3	500	0, 1, 2, 3, . . . , 25	20	0.0, 0.1, 0.2, 0.3, . . . , 1.0	2 500 002‡§	6

Notes: Each watershed topology includes 50 units of habitat (i.e., 50 edges and 51 nodes). The questions can be found in the *Methods: Application 1: General trends in upstream fish passage connectivity*. Specified figures present pertinent results associated with these simulations.

† Dams were configured nonrandomly at each of the 51 nodes.

‡ Only one simulation was required for the condition with zero dams.

§ Only one simulation was required for the condition with a passage rate of 1.0.

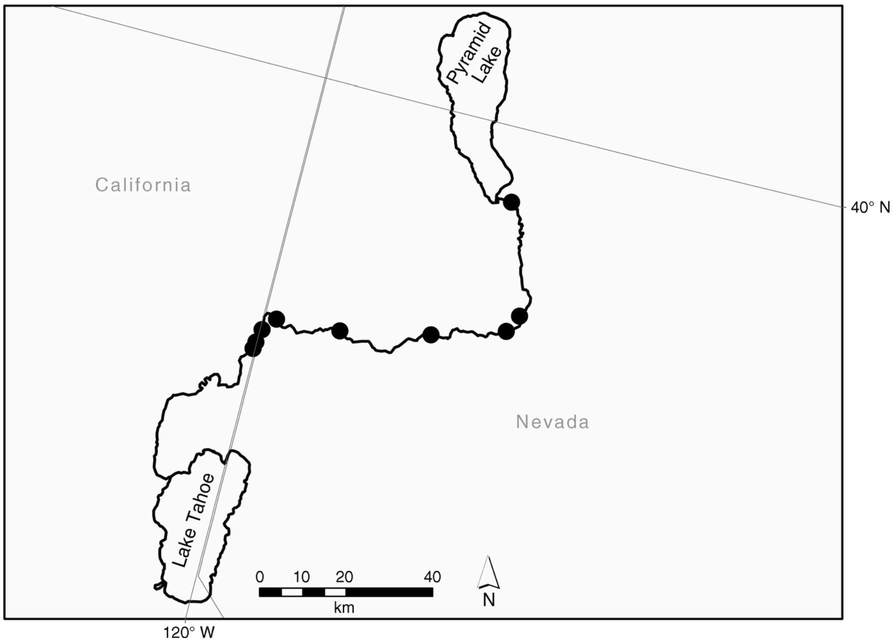

FIG. 3. Truckee River study location (USA). The river flows north from Lake Tahoe to Pyramid Lake. Black circles denote barriers under examination in this study (see Table 2).

(interpreted here as a passage rate), including high, average, and low estimates of the latter for sensitivity analysis.

In the present study, we prioritized upstream fish passage improvement at nine "actionable" structures that range significantly in construction, purpose, size, and impact to upstream fish passage. Two to four fish passage alternatives were assessed at each location using the parameterization of Conyngham et al. (2011); see Table 2. Because all of the existing barriers are not addressed, this analysis provides a heuristic tool to examine the *relative* connectivity of the watershed rather than the absolute value. In effect, this approach assumes 100% passage efficiency in the projects planned or implemented by other agencies. The HCIU is functionally similar to the habitat-weighted, cumulative passage rate of Conyngham et al. (2011) with the exception that the HCIU is more adaptable to dendritic watershed topology. We also simplified the analysis presented by Conyngham et al. (2011) by focusing on upstream passage for a single species, the threatened Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*), whose decline has been associated with fragmentation (Dunham et al. 1997). An average of the panelists' passage efficiency scores was used in the HCIU calculations (Table 2), and the range of values were retained to demonstrate sensitivity.

Costs associated with each alternative are shown in Table 2, and were calculated in accordance with U.S. Army Corps of Engineers project planning policies (USACE 2000) and annualized over a 50-year horizon (presented in Conyngham et al. 2011). Every site and alternative permutation was calculated, resulting in 1024 potential watershed fish passage improvement plans. The need for sophisticated optimization algorithms (e.g., O'Hanley and Tomberlin 2005) was avoided by considering all potential combinations of locations and alternatives. The most cost-effective alternatives were identified for the full range of costs and HCIU considered (i.e., the alternative offering the lowest cost for that level of HCIU or the alternative offering the highest HCIU for that cost).

Uncertainty analysis was conducted for each of the cost-effective fish passage improvement plans. Passability values were randomly sampled for each location from a uniform distribution bound by the minimum and maximum passage rates. One thousand random sets of passage rates were generated for each cost-effective plan.

RESULTS

Application 1: General trends in upstream fish passage connectivity

In our hypothetical watershed simulations, the HCIU provided a mechanism for assessing general trends in upstream fish passage connectivity. By calculating the index for hypothetical basins, we are able to consider the effects of watershed topology, barrier location, numbers of barriers, and passage rates.

In our first simulation, a single barrier with a passage rate of 0.5 was evaluated over a range of watershed topologies and barrier locations within the watershed. As anticipated, a single dam near the mouth of a watershed is sufficient for reducing connectivity, but the impact to connectivity varies considerably with location

TABLE 2. Summary of Truckee River (Nevada, USA) model parameterization for each site and alternative.

Location and alternative	Node	River km	Upstream habitat quality	Expected passage rates (minimum–maximum)	Annualized cost (US$)
Pyramid Lake	1	0.0	0.58		
No action				1.00 (1.00–1.00)	0
Marble Bluff	2	6.4	0.58		
No action				0.35 (0.15–0.50)	0
Bypass				0.60 (0.35–0.78)	402 821
Fishway				0.55 (0.35–0.78)	805 411
Bypass and fishway				0.75 (0.50–0.88)	1 041 741
Fellnagle	3	43.5	0.58		
No action				0.65 (0.50–0.73)	0
Partial removal				0.78 (0.65–0.85)	52 857
Herman	4	50.7	0.54		
No action				0.50 (0.33–0.63)	0
New structure				0.83 (0.70–0.90)	75 508
Tracy Power Plant	5	70.8	0.70		
No action				0.71 (0.60–0.81)	0
Reduce thermal input				0.85 (0.67–0.90)	76 741
Chalk Bluff	6	112.3	0.85		
No action				0.54 (0.38–0.73)	0
Adaptive management of existing fishway				0.58 (0.40–0.75)	8 058
Washoe-Highlands	7	122.3	0.90		
No action				0.13 (0.10–0.15)	0
Bypass				0.73 (0.60–0.81)	150 198
Verdi	8	129.6	0.92		
No action				0.04 (0.02–0.06)	0
Bypass				0.75 (0.63–0.85)	156 595
Steamboat	9	134.4	0.92		
No action				0.40 (0.27–0.52)	0
Constructed riffle				0.79 (0.63–0.92)	133 599
Fleisch	10	138.4	0.92		
No action				0.04 (0.02–0.06)	0
Bypass				0.77 (0.60–0.90)	124 186
Lake Tahoe	11	194.9			
No action				1.00 (1.00–1.00)	0

within the watershed (Fig. 4a). There is a clear threshold in the minimum observed HCIU for a given distance from the mouth of the basin to the first barrier. The diameter of the network was calculated as a measure of topology for each randomized watershed configuration. Network diameter is "the longest path between any two nodes in the graph, where the path length between these nodes is itself the shortest possible path" (Urban and Keitt 2001:1207), which may be thought of conceptually as the distance from the watershed outlet to the farthest tributary headwater. As diameter increases, the lower 25th percentile of HCIU declines dramatically around diameters of 12–15, while the 50th percentile of HCIU does not show these declines until diameters of 26–30 (Fig. 4b).

In our second simulation, we addressed the potential for thresholds in connectivity associated with the number of barriers and changes in watershed topology. Passage rate was held constant at 0.5, while watershed topology, the number of barriers, and the locations of the barriers were varied. As anticipated, we observed a strong non-linear decline in connectivity associated with the number of barriers. For instance, the median connectivity (HCIU value) over 500 watershed topologies and 20 dam configurations reduces from 1.00 at 0 barriers to 0.52 at 3 barriers, 0.36 at 5 barriers, and 0.17 at 10 barriers. Fig. 5 demonstrates this nonlinearity, stratified by network diameter, where three classes of diameter were identified to contain nearly equal sample size (34.0% of samples have diameters of 6–15, 31.7% of samples have diameters of 16–21, and 34.3% of samples have diameters of 22–39). This figure shows that watersheds with low branching topology and high diameter are more susceptible to disconnection by lower numbers of barriers.

In our third hypothetical simulation, we further assessed the behavior of the nonlinear response described above by varying passage rates. Fig. 6 shows

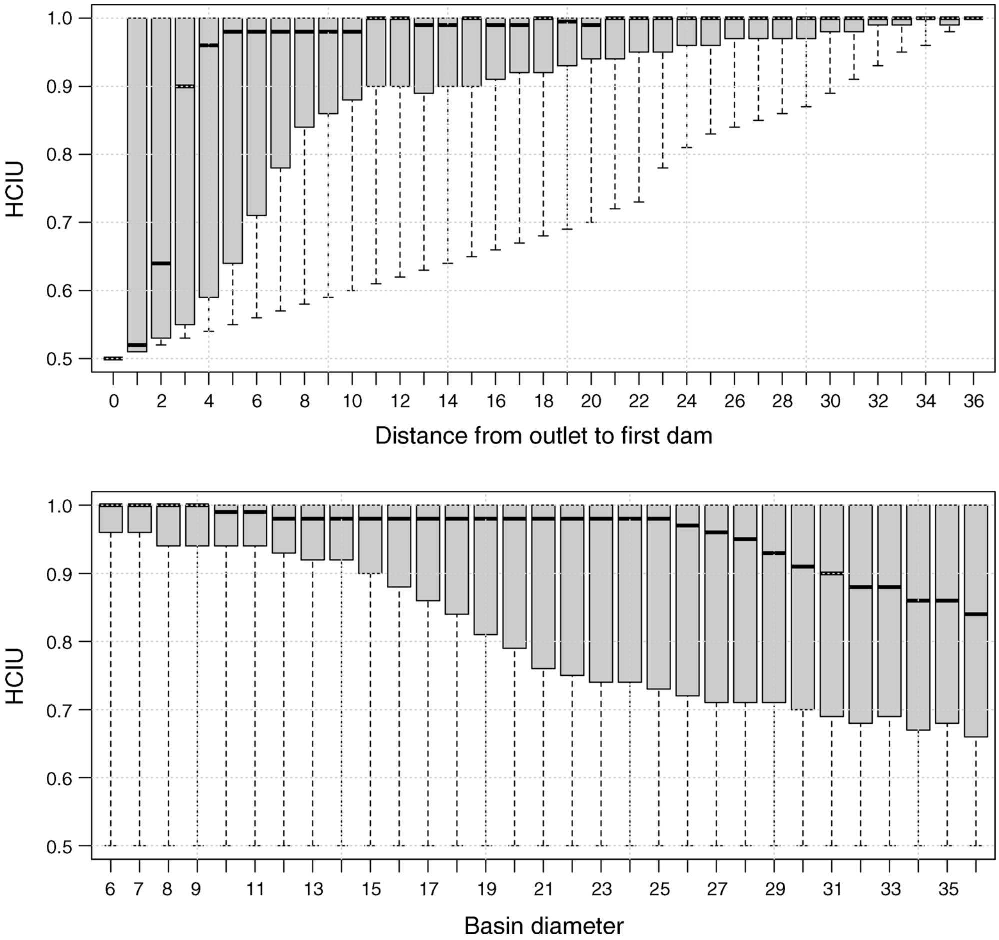

FIG. 4. Hypothetical watershed simulations varying the watershed topology and location of a single dam with a passage rate of 0.5 (habitat connectivity index for upstream passage [HCIU]). Simulation data for both plots are identical with data sorted by (a) distance from the watershed outlet and (b) watershed topology as measured by basin diameter. For this simulation, distance from the watershed outlet is synonymous with the number of nodes between the outlet and the first dam. In each box plot, the thick black line is the median, box extremes are the 25th and 75th percentiles, and whiskers are minimum and maximum observed points.

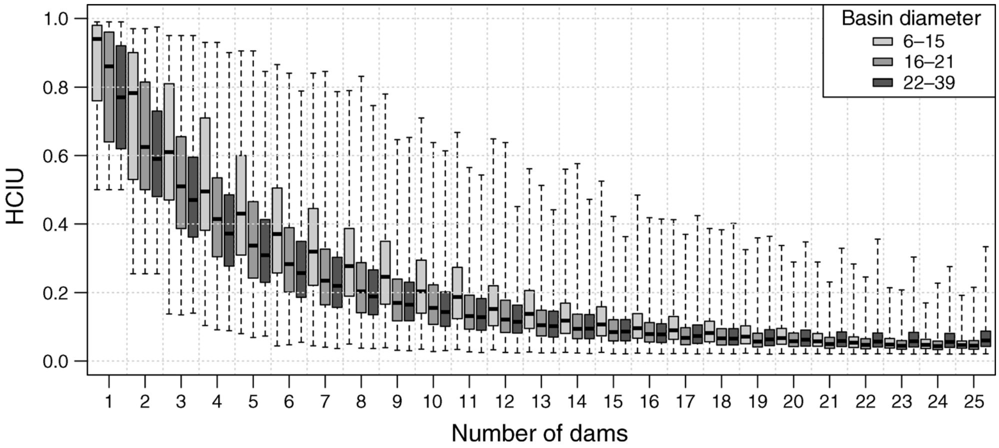

FIG. 5. Hypothetical watershed simulations varying the watershed topology, number of barriers, and location of barriers with passage rate of 0.5. Data are sorted into three groupings by network diameter, which have approximately equal sample sizes (4250, 3961, and 4289, respectively). In each box plot, the thick black line is the median, box extremes are the 25th and 75th percentiles, and whiskers are minimum and maximum observed points.

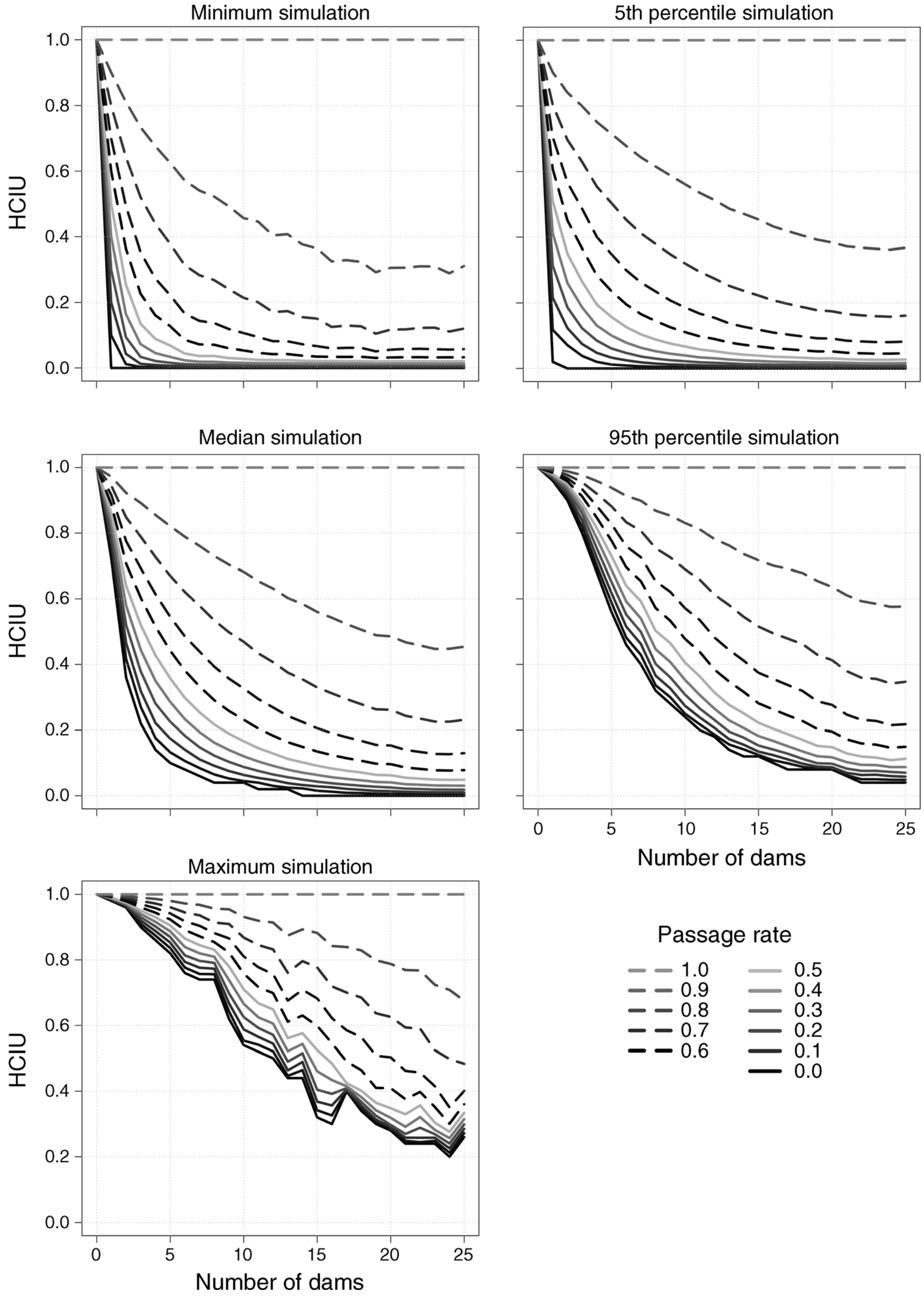

FIG. 6. Hypothetical watershed simulations varying the watershed topology, number of barriers, location of barriers, and passage rates. Barrier locations are captured by alternative simulations. Locations were varied to create the 2.5 million simulations. The simulation percentiles shown represent the range of influence barrier location has on connectivity for a given passage rate and number of dams.

that the nonlinear decline in HCIU is stronger with lower passage rates. The large range of HCIU values between the minimum and maximum simulations is attributable to the variation in watershed topology (e.g., more linear basins vs. more branching basins) and location of the barriers (e.g., mainstem vs. tributary positions). This assessment demonstrates that the topology of a watershed and position of barriers can drastically impact connectivity, as expected. Another important finding is the critical role of passage rates in maintaining connectivity. For instance, the median simulations in Fig. 6c show that five barriers with a

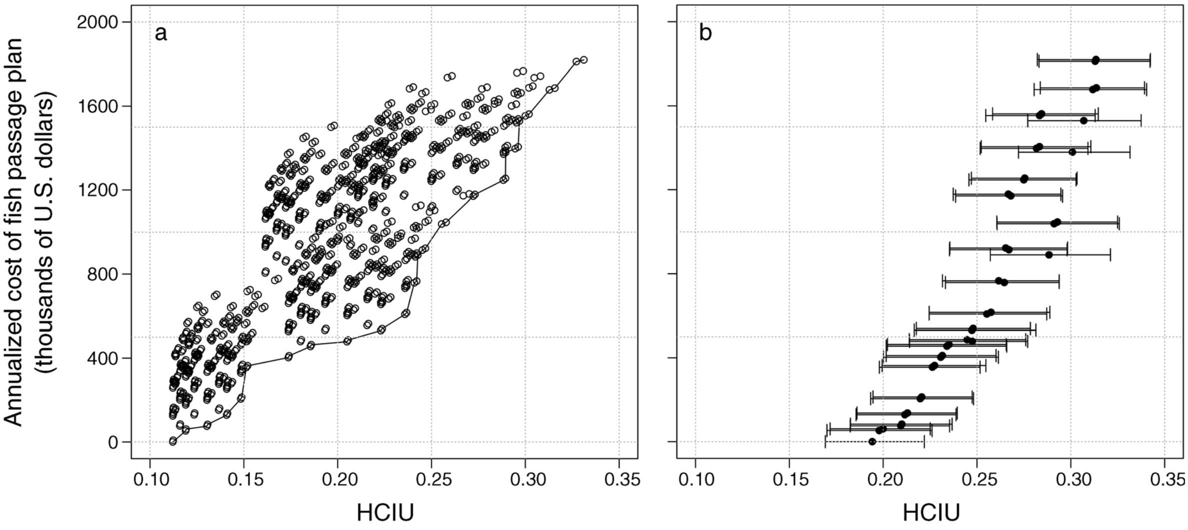

FIG. 7. HCIU values for Truckee River fish passage improvement plans: (a) HCIU values for all fish passage improvement plans with cost-effective alternatives identified by the line; (b) stochastic simulation of cost-effective plans with median (black circles) and 90% confidence intervals (error bars) of HCIU shown.

passage rate of 0.6 (HCIU = 0.44) have nearly equal connectivity to 25 barriers with a passage rate of 0.9 (HCIU = 0.45).

Application 2: Prioritizing Truckee River fish passage improvement

The current HCIU for the Truckee River watershed is 0.11. By implementing fish passage improvements at all proposed locations, the HCIU can be increased to 0.33. All 1024 permutations of proposed fish passage alternatives and locations were examined (Fig. 7a). We identified all cost-effective alternatives, which are shown as the connected set of points forming a frontier to the lower right of the data in Fig. 7a. These alternatives outperform all others in terms of cost for the given level of benefit (i.e., HCIU). This approach for cost effectiveness screens the alternatives into a cost-effective set for further analyses.

We conducted an uncertainty analysis on the cost-effective set of alternatives using the range of model parameter estimates provided by the expert panel for the Truckee River (Conyngham et al. 2011). The analysis reveals the considerable uncertainty associated with professional judgments of passage rates, which are reflected in the HCIU values (Fig. 7b). Mean 90% confidence intervals of HCIU are ±0.03.

DISCUSSION

Methods for quantifying watershed connectivity have recently emerged from landscape ecology and network analysis (e.g., O'Hanley and Tomberlin 2005, Cote et al. 2009, Diebel et al. 2010, Padgham and Webb 2010, Bourne et al. 2011, O'Hanley 2011). We present an index adopted from this family of techniques for assessing habitat connectivity for fish migrating upstream which uses methods from graph theory to conduct connectivity calculations. This algorithm is computationally efficient (<0.2 seconds per topology–configuration–passage combination on a 2.67 GHz processor), which allows for examination of variability in highly uncertain fish passage parameters. Our examination of theoretical and applied problems further demonstrates the algorithm's utility and adaptability.

Because of the computational efficiency of this approach, we were able to survey many random, hypothetical watersheds to observe emerging patterns in connectivity associated with watershed topology, the number and configuration of barriers, and the passage rates around those barriers. These analyses are in agreement with Cote et al. (2009), and indicate a strong nonlinear decline in connectivity with low levels of barrier development. While it is intuitive that the location of the obstruction determines its relative effect on connectivity, the approach described here can demonstrate the magnitude of the effect. Furthermore, these results quantify the vulnerability to disconnection for multiple watershed topologies ranging from high to low degrees of branching. These simulations also demonstrate the importance of partial passage around structures by showing that small improvements in passage rates can lead to large increases in connectivity. Although these results are for watersheds with 50 units of habitat and 51 nodes, the general trends likely persist for smaller or larger watersheds and should be pursued in further work.

Historically, cumulative effects of multiple restoration projects have been largely ignored in restoration planning (Roni et al. 2002, Pringle 2003, Jansson et al. 2007), with some notable exceptions (Kondolf et al. 2008, Conyngham et al. 2011). This application on the

Truckee River demonstrates quantification of the interdependency of actions within a single watershed to identify the most cost-effective watershed-scale restoration plan, as recommended by O'Hanley and Tomberlin (2005). By examining multiple barriers simultaneously, we can efficiently identify the suites of actions that most cost-effectively restore upstream passage, rather than rely upon a simple barrier-by-barrier prioritization that does not account for interdependencies. In actual restoration practice in highly fragmented systems, the high number of permutations of multiple actions at multiple sites and varying habitat and life history needs necessitate algorithm-based tools such as these to compare logical arrays of actions.

Our analysis of cost-effective alternatives is similar to Kuby et al. (2005), O'Hanley and Tomberlin (2005), O'Hanley (2011), and others with the notable exception that we explored all potential combinations of actions rather optimizing for a particular cost constraint. In doing so, we provide decision makers with the range of potential outcomes associated with different levels of expenditure. Decision makers may use this cost-effective set in conjunction with other decision criteria (e.g., a minimum level of benefit, a maximum available budget, a large incremental benefit for a small incremental cost) to identify an appropriate fish passage improvement plan to pursue. Given the uncertainty in HCIU values, this approach can facilitate comparison of cost-effective plans with those that are nearly cost-effective but preferable for other reasons (e.g., barrier ownership, social preference, and non-passage objectives). Uncertainty in passage rates and accompanying connectivity indices indicates the need for full consideration of all permutations rather than the optimal set when this option is computationally feasible (i.e., when the number of barriers is low).

By recognizing and accounting for uncertainty, we have provided decision makers with additional information not captured by cost-effectiveness alone (Anderson et al. 2012, Rudnick et al. 2012). For instance, given two alternatives with similar levels of HCIU, the alternative with less uncertainty may be preferable. Furthermore, the project team could use this information to identify multiple planning scenarios (e.g., best, expected, and worst case scenarios), and if the same decision is made under all conditions, the project team can be more confident in their selection.

The HCIU provided a suitable network metric for assessing upstream fish passage improvement in both analyses presented. The HCIU is identical to the partial passage improvement metric of O'Hanley and Tomberlin (2005), except the HCIU separates passability with and without barrier repair. The metric is also identical to the Dendritic Connectivity Index for diadromous fishes (DCI_d) without downstream passability included (Cote et al. 2009). We simplified Conyngham et al.'s (2011) general approach by removing non-passage processes and extended their analysis to address nonlinear, dendritic watershed topologies. Based on the theoretical construct of our hypothetical analysis and available data in the Truckee, our study could not justify the distance-weighting of habitat accessibility or segregation of multiple habitat types proposed by Diebel et al. (2010) and O'Hanley et al. (2010). This comparison highlights the rapidly developing science of assessing watershed connectivity, and a logical extension of this work would be to compare these methods and appropriate hybrids to identify the strengths and weaknesses of each approach.

The HCIU was formulated to be highly adaptable to applications beyond those presented here. For instance, by utilizing a generalized definition of passage, population- or community-scale estimates of passage rates could be applied (Roscoe and Hinch 2010). Although we have focused on fish, the HCIU could also be used to assess connectivity for other taxa in stream corridors such as shrimp (Greathouse et al. 2006*a*, Covich et al. 2009, Crook et al. 2009), snails (Greathouse et al. 2006*b*), or amphibians (Lowe and Bolger 2002, Fortuna et al. 2006, Grant et al. 2010). Likewise, we focused on the ecological benefits of connectivity, but there may be negative impacts associated with reconnecting ecosystems related to the spread of invasive species or disease (Rahel 2007, Jackson and Pringle 2010, Neeson et al. 2012). HCIU values could also be calculated for multiple species and a weighted-average computed for an overall guild or taxon passage score (e.g., HCIU multipliers based on species status as invasive, low concern, at risk, or listed; Anderson et al. 2012). The HCIU could also be modified to assess the effects of fragmentation on other important processes. For instance, each structure could be given a 0–1 multiplier associated with movement of large woody debris or sediment. Importantly, if the goal was to compare barrier restoration projects in multiple basins, total accessible habitat or gains in accessible habitat would be appropriate metrics. Thus, our graph-theoretic formulation of the HCIU provides a robust structure to which additional complexity and capability may be added (Urban and Keitt 2001, Eros et al. 2012).

Based on our analyses, six topics emerge as fertile ground for future research. First, few current methods for barrier prioritization address both upstream and downstream connectivity (e.g., Crook et al. 2009, O'Hanley et al. 2010, Padgham and Webb 2010, Agostinho et al. 2011, Conyngham et al. 2011), and to our knowledge, those including bi-directional connectivity treat these processes directionally rather than examining cyclic movement. Existing network analytic methods (Schramski et al. 2011) may provide tools for coupling upstream and downstream passage to more adequately characterize cyclic and bidirectional movement. Second, the HCIU and other cumulative passage models (e.g., O'Hanley and Tomberlin 2005, Cote et al. 2009, Diebel et al. 2010) require estimates of passage rates at individual barriers, and better estimates of passage rates will serve to reduce uncertainty. Third, cumulative passage models should be validated against observed connectivity patterns. Fourth, connectivity models could be applied to develop emergent relationships between network topology, documented life history needs, and ecological endpoints (Hitt and Angermeier 2008, Flitcroft et al. 2012), and geospatial properties could then be calculated for large spatial domains (e.g., barrier prioritization for the Northeastern United States). Fifth, passage rates can fluctuate stochastically or in a nonlinear pattern with hydrologic factors, population composition (e.g., age or sex structure), water chemistry changes, and other variables, and the role of stochasticity in long-term connectivity should be examined beyond the analyses presented here (O'Hanley and Tomberlin 2005). Finally, cumulative passage models should be coupled with population and community models to examine the role of passage restoration in population viability and biodiversity conservation (Fagan 2002, Schick and Lindley 2007, Goldberg et al. 2010, Brown et al. 2011, Lynch et al. 2011, Neeson et al. 2011, Grant et al. 2012, Harvey and Railsback 2012, Neeson et al. 2012, White and Rashleigh 2012), the desired endpoints sought by connectivity restoration projects.

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SUPPLEMENTAL MATERIAL

Supplement

Code to compute the habitat connectivity index for upstream passage (HCIU) for the analyses presented (*Ecological Archives* A023-074-S1).