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Abstract: Habitat connectivity is a central factor in shaping aquatic biological communities, but few tools exist to describe and quantify this attribute at a network scale in riverine systems. Here, we develop a new index to quantify longitudinal connectivity of river networks based on the expected probability of an organism being able to move freely between two random points of the network. We apply this index to two fish life histories and evaluate the effects of the number, passability, and placement of barriers on river network connectivity through the use of simulated dendritic ecological networks. We then extend the index to a real world dendritic river system in Newfoundland, Canada. Our results indicate that connectivity in river systems, as represented by our index, is most impacted by the first few barriers added to the system. This is in contrast to terrestrial systems, which are more resilient to low levels of connectivity. The results show a curvilinear relationship

between barrier passability and structural connectivity. This suggests that an incremental improvement in passability would result in a greater improvement to river network connectivity for more permeable barriers than for less permeable barriers. Our analysis of the index in simulated and real river networks also showed that barrier placement played an important role in connectivity. Not surprisingly, barriers located near the river mouth have the greatest impact on fish with diadromous life histories while those located near the center of the river network have the most impact on fish with potadromous life histories. The proposed index is conceptually simple and sufficiently flexible to deal with variations in river structure and biological communities. The index will enable researchers to account for connectivity in habitat studies and will also allow resource managers to characterize watersheds, assess cumulative impacts of multiple barriers and determine priorities for restoration.

Response to Reviewers: July 21, 2008

To the Editor of Landscape Ecology,

Thank you for your thorough review of our manuscript “A riverscape connectivity index” (LAND-08-1528R1). We have addressed each criticism and comment (see indented comments added to the LE decision letter below). In particular we have significantly shortened the introduction, replaced the simulated single channel system with that of a dendritic, added a conceptual cartoon and have changed the title of the index to: “Dendritic Connectivity Index”. Please contact me if you have any questions or concerns.

On behalf of my co-authors,
David Coté

LE Decision Letter received by D. Coté 24-6-2008

COMMENTS FOR THE AUTHOR:

Dear Dr. Cote;

Thank you for your submission to Landscape Ecology. Your paper has been recommended for publication with revisions. The reviews were all positive- each indicating that the connnectivity index is a valuable contribution to the aquatic landscape ecology literature. All of the reviewers suggest, and I concur that the manuscript is far too long, and thus, your major task in the revision will be to reduce the length substantially. The second issue, again raised by Reviewer # 1 is to address the issue of travel distance versus stream length. That reviewer presents a logical arguement that these two measures are not equivalent in dendritic systems. I also agree with Reviewer # 3 that a cartoon depicting how your index works would be a useful addition to the paper. I also strongly agree with Reviewer # 1 that you should change the acronym for your index, given the previously published RCI of Brown (2002) and the fact that the term riverscape is not appropriate in the context
being used. The term riverscape has come to include the channel, floodplain, and riparian zone that influence stream channels and ecosystems (c.f., Ward, 1998; Ward 2002; Alan 2004). Your focus is on the "wet" component of the riverscape, thus it is more appropriate to confine your focus to the channel within the watershed (or more appropriately the catchment). Perhaps Channel connectivity is a more appropriate term. Further, I note that you use the terms watershed and riverscape almost interchangeably, which is not accurate.

When you submit your revision, I would appreciate seeing the response to reviewer's comments along with a copy with "track changes" noting the changes that have been made in response to the comments.

Regards,

Lucinda B. Johnson
Coordinating Editor

*Manuscript length: See below for description of where the manuscript has been shortened.

*Travel distance issue: Specifically the DCI measures the average probability that fish can move between two randomly chosen points in a watershed. The DCI relies on patch size, an adjacency matrix of segments and the passability of watershed barriers as data inputs. It does not incorporate travel distance explicitly in its calculation, but this is by design, and as such, does not represent a logical flaw as suggested by Reviewer 1. The reviewer is rightly concerned about the index needing to capture the dendritic structure of the ecological system, and it does this by keeping track of the barriers between any two sections along the dendritic path. This is reflected in the difference between the potadromous and diadromous connectivity values. An eventual refinement to the index could incorporate travel distance as an additional constraint to segment connectivity. This could make the DCI more biologically relevant in applications that deal with movements of individuals, however it eliminates the possibility of utilizing this approach for other ecological phenomena (e.g. transmission of disease, genetic information, invasions etc.) that can operate at temporal periods that extend beyond the life of an individual.

*Cartoon: As requested, we have added a cartoon illustrating the concepts brought forward by the DCI.

*Renaming of the Index: We agree that a name change is necessary and have renamed the index the Dendritic Connectivity Index. We feel that this addresses the ambiguity about what our approach measures and also is general enough that it could be applied to non-river situations such as hedgerows or caves (see Grant et al. 2007).

*Riverscape vs. watershed: We have changed relevant references of riverscapes to “river networks” as suggested.

*Comments from the reviewers are addressed below.

Reviewer #1: Overall this is a very nice and needed treatment of disruption of longitudinal connectivity in stream drainage networks. The conceptual basis is strong and the examples of application are fairly novel and very compelling.

With the exception of only one (potentially large) concern, the method, results, and discussion seem to be in good shape, tho minor adjustments are needed throughout (see comments inserted into the original .pdf).

*Comments in the original PDF have been addressed.

In thinking thorough the approach, however, I am concern about one potential fault in the application of the RCI to a real dendritic river drainage network. It seems to me that the authors make the assumption that the variables l and L are always equal to the total length of stream. Unless I misunderstand the analysis (which is possible), is seems to me the variables l and L should in fact refer to travel distances (within network section or the entire network, respectively), not total stream length. In the special case of a linear system, travel distance is proportional to total length. However, in a dendritic network, the relationship between travel distance and total length is complex and determined entirely by network topology. Consider this: given a fixed length of stream, the mean travel distance between any to points in a dendritic network will decline as bifurcation ratio increases. So, when the RCI was applied to assess connectivity effect of migration (travel) a real stream drainage networks, it seems to me there should have been some sort of adjustment to l and L to reflect travel distances given the topology of the dendritic network. Such an adjustment has the potential to alter the results of the paper with respect to the application of the RCI to the real network. Note also... given the same dendritic network, I would think that travel distance distributions for potadromous and diadromous life histories would be different because the distance to any point within the network is different from the distance from a point to either the closest downstream barrier or the network mouth.

I freely admit that I may be incorrect regarding my interpretation of l and L and their use within the equations for a read dendritic network. I lack the time to do the analysis that would convince myself one way or another. I am forced to leave this as a question to the authors, but my hunch is that travel distances, not stream length, should be used to calculate RCI in dendritic networks.

*Please see notes on this topic above.

I would encourage the authors to consider the following comments to improve their manuscript.

1) Shorten the introduction by 50%. This is a very nice review, but much of the intro is not really needed for the basic task of laying out a simple mathematical analysis of the effects of barrier location and number on longitudinal connectivity in stream networks.

*The introduction has been shortened by 50% and focuses on laying out the rationale for a mathematical analysis, as requested.

2) The phrases "riverscape" and "fluvial landscape" are applicable at many spatial scales are are not synonyms for "river drainage network." Similarly, "connectivity" occurs in lotic ecosystems in three dimensions. Your analysis assesses influences of barriers on longitudinal connectivity

within stream drainage networks. You are correct in the discussion when you state that it is not applicable to other types of fluvial landscapes. Consider revising the title, abstract, and body of paper to more precisely represent the applicability of your RCI. For instance, you might consider "A longitudinal connectivity index for stream drainage networks" as a title and make similar adjustments throughout the paper.

*As suggested we have changed the title to, “A new measure of longitudinal connectivity for stream networks” and removed references to riverscapes in the manuscript.

3) Brown published a "River Complexity Index" in 2002 (Brown, A. G. 2002. Learning from the past: Palaeohydrology and palaeoecology. Freshwater Biology 47:817-829.) which he referred to as the RCI. This is a very unfortunate clash of acronyms. I hope you will strongly consider revising your acronym (tho I understand you are invested in RCI.)

*Completed as suggested.

4) Literature cited issues:

4a) Cite the correct original sources of the River Continuum Concept and Serial Discontinuity Concept. Poole's 2002 paper works with these concepts, but you cite Poole 2002 as though the ideas originated there. Yes, Poole's take on the RCC and SDC are relevant to your paper, but Poole argues for a DIScontinuum view of rivers, suggesting that patches along a river course might be arranged to look like a continuum, but are more often discontinuous.

*We have specified that we are embracing the “River Discontinuum” view by Poole.

4b) More work on dendritic networks exists than you paper implies. You are fortunate that Grant et al. have recently summarized much of that work in an ecological context (Grant, E. H. C., W. H. Lowe, and W. F. Fagan. 2007. Living in the branches: Population dynamics and ecological processes in dendritic networks. Ecology Letters 10:165-175.) I don't think you want to go to press without citing Grant's work and integrating your results into the context of prior work on dendritic networks (as reviewed in Grant's paper).

*We have incorporated this reference in the introduction and throughout the paper. Grant's work very much complements our own, indeed sections of Grant's papers call for a need to adapt statistics applied to lattice networks for dendritic ones, which is exactly what our paper is about.

4c) Consider reading and citing:

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: How channel networks structure riverine habitats. BioScience 54:413-427.

Thorp, J. H., M. C. Thoms, and M. D. Delong. 2006. The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. River Research and Applications 22:123-147.

Jones, K. L., G. C. Poole, S. J. O'Daniel, L. A. K. Mertes, and J. A. Stanford. In Press. Surface hydrology of low-relief landscapes: Assessing surface water flow impedance using lidar-derived digital elevation models. Remote Sensing of Environment.

*We have looked over these references and cited Benda et al. (2004) in the introduction and Thorp et al. (2006) and Jones et al. (in press) in the discussion.

4) Why is "natural connectivity" included in the RCI only when natural connectivity is <1? For consistency, why not make the RCI include natural connectivity in its most basic form. After all, when natural connectivity = 1, RCI is unchanged whether natural connectivity is included or excluded. This will allow you to describe one RCI and then present its values (as fraction of natural connectivity) without having to distinguish whether you've included or excluded natural connectivity.

*We agree that natural connectivity values of 100% are of interest and have revised accordingly. Nonetheless, standardizing all watersheds based on their natural connectivity may be inappropriate for some uses (e.g. for studies that are looking for effects of fragmentation that are caused naturally or anthropogenically). From the perspective of ecological restoration, it is good to know what the natural baseline connectivity might be, including the effects of natural barriers. On the other hand, for the purposes of managing populations within a watershed, knowledge of the absolute connectivity (regardless of whether it is affected by natural or anthropogenic barriers) is necessary. Measures of absolute connectivity are also useful when comparing one river network to another. Measures of relative connectivity are useful for reporting ecological integrity of a given river network (i.e., how far it is from a natural baseline). Given the dual use of the index (comparing relative and absolute connectivity) we did not see a strong motivation to follow the reviewer's suggestion.

5) You discuss barriers as allowing downstream transport by not upstream. It may be a rule of thumb for hydrologic barriers (tho not universal, e.g., Columbia River dam turbines chew up outmigrating juvenile salmon). Additionally, other types of barriers (thermal, chemical) block connectivity in both directions equally. Consider writing about barriers more broadly - not just focusing on hydrologic barriers.

*Agreed. We have made our references to barriers in this section more general as suggested. We also specify that individuals need to be able to cross barriers in both directions.

6) Label the line directly on your figure. Do not add a legend, just add labels on top of each line.

*Labels have been added on the lines as requested.

Reviewer #2: General comments

The manuscript is very well written and was a pleasure to read. It is clear that the authors took care in researching and developing a case for studying and understanding connectivity in dendritic systems. The topic is highly relevant to the landscape ecology of rivers and streams and potentially may be of interest to terrestrial ecologists who work with animal distributions that are constrained by linear features. The problem with the paper is that it is perhaps longer than it needs to be, given the perceived purpose, which ostensibly is to introduce a straight-forward, but nevertheless useful, index. This methodological aspect forms the substance of the paper, and one wonders whether the article would be better as a note because there are no biological data to provide additional ecological insights into how the index could be used to address ecological questions. Moreover, the stream network used in the analysis is so simple that the quantitative approach almost seems
unnecessary. One does get the sense from the acknowledgements that this manuscript may have been reviewed once, and one section in particular seemed out of place: "Future refinements: applications to biota." The issues discussed in the section on future refinements and applications are certainly concerns that came to mind about biological relevance (i.e., lack of empirical data)

and assumptions made about upstream and downstream movement, passability, and juxtaposition of barriers. Given the simplicity and, arguably, the novelty of the index, the paper could potentially be condensed into a note, by shortening the introduction and discussion but still providing enough detail in the methods and results to communicate the ideas.

*While we have successfully shortened the manuscript, we do not feel we can provide sufficient detail about the DCI within the space constraints of a note. “The Future Refinements: applications to biota” section, in our opinion, is most appropriately placed at the end of the discussion.

Specific comments

Page 1 - The title needs to be more descriptive about the content of the manuscript. Maybe something about "stream networks" and "barriers" could be included.

*As stated above, the title has been revised.

Page 3, bottom line - Citation is formatted incorrectly.

*Addressed.

Page 4, line 24 - Note throughout that a hyphen is not needed after the adverbial ending "ly". In line 25, "myriad" is not a noun.

*Addressed.

Page 4, line 33 - "Two-dimensional networks" is ambiguous. What exactly is meant by "two-dimensional"? It might be helpful to define the terms because stream networks can occupy three dimensions but are often depicted as a series of connected line segments (i.e., one-dimensional space).

*We have clarified the description and made reference to linear movement along river channels (sensu Fagan 2002) and contrasted the notion of 2-dimensional movement within a lattice network against 1-dimensional movement up and down the linear elements of a dendritic network. We have made appropriate references to Grant et al. (2007) who elegantly lay out some of the conceptual framework behind our own work (but quite independently of us).

Page 6, line 77 - "Riverscape-scale" is ambiguous just like "landscape scale" (Allen TFH. 1998. The landscape "level" is dead: Persuading the family to take it off the respirator. In Ecological scale: Theory and applications, Peterson D, T Parker (eds). Columbia University Press: New York, USA; 35-54.)

*Due to concerns stated above, we have removed “riverscape” from the manuscript and replaced it with “river network”.

Page 7, lines 97-98 - Are "riverine ecosystems" really synonymous with "riverscapes"? Poole's work focused on the "river discontinuum".

*See comment above.

Page, 8, line 120 - This is confusing. The authors state that barriers are more difficult to pass through (or over) going upstream than downstream, but in spite of this fact, the model assumes that both directions are equal.

*We acknowledge that the inherent directionality of river systems result in direction-specific passability values. Our index uses a passability value that incorporates passability values in both directions but does not assume they are equal. Equation 3, as written, indicates that a barrier’s passability is the product of the upstream and downstream passability.

Page 11, Equation 6 - The "200" and "100" are positioned in a confusing way. Is "200" the exponent of L?

*This error seems to occur upon conversion from Word to the .pdf and has been fixed.

Page 16, line 319 - "This is IN contrast"; missing word.

*Addressed.

Page 18, line 356 - The terminology for "dendritic" and "linear" is confusing. The distinction is between single-channel versus branching systems. From the standpoint of this manuscript, stream networks are also linear because they are made up of line segments.

*As suggested, we have changed references of “linear” to single channel.

Page 32 - An interesting example of biological response (in genetics) to barriers:
Wofford, J., R. Gresswell, and M. A. Banks. 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. Ecological Applications 15:628-637.

*This reference is no longer necessary because the paragraph discussing this topic has been deleted to shorten the introduction.

Reviewer #3: Review of LAND-08-1528

General thoughts: This is a well written clear manuscript that is worthy of publication. As the authors correctly address and point out, spatial ecology has yet to be fully integrated into riverine and aquatic systems. As such, this contribution is merited. I do feel, however, that several elements of the manuscript should be addressed prior to publication.

First, I feel that the presentation of the model could be clarified somewhat. Since, as the authors correctly point out, there hasn't been as much work on connectivity in riverine systems, I feel the "Theoretical Framework" section would benefit from a graphical cartoon of how the connectivity index works. This would tighten the presentation of the index somewhat, and would make the results in the simulation and application sections follow more smoothly.

*Addressed.

Second, the authors spend much of the introduction talking about how connectivity is different in riverine systems from traditional terrestrial systems. While this is true, I felt the strength of the proposed connectivity index was diluted somewhat by using a straight line for the simulated watershed. Where the limitations of the straight line were most apparent were in the results, e.g., Figure 4. This figure seemed almost obvious given the geometry of the simulated system. The results may in fact be qualitatively similar for a fully dendritic system, but my concerns about this were not alleviated in the MS. Fagan (2002) uses a linear system (Fig. 1 a) as the straw-man to illustrate how different even a simple dendritic system is (Fig 1 b). Given that, perhaps a simple dendritic structure would be more informative than a simple linear watershed.

*As suggested, we have replaced the linear network simulation with a simulated dendritic system.

Third, and perhaps most importantly, I worry that the "universality" of the index might not be applicable from watershed to watershed, or from species to species within the same watershed. The authors of course note this in the discussion, but I felt that this should be addressed earlier on. One way around this might be to take the Big Brook system, and extend the real world application by assigning different passability ratings for each barrier, as perceived by different species. Then the applicability and novelty of the index might be more apparent. Burnett's "intrinsic potential" comes to mind, i.e. how a different fish species perceive the same watershed or even the same barrier (Burnett et al. 2007, Ecological Applications, 17:66-80). Burnett et al. were looking at habitat, per se, not general connectivity, but such a framework might be useful to consider.

*We believe the index is applicable across watersheds as long as passability criteria and segment length (or habitat quality) measurements remain consistent. In fact, we address these issues explicitly in the “Future Applications” section of the manuscript. In the interest of shortening the manuscript, we feel that expanding this section further may not be best use of our limited space.

Specific Thoughts:
Abstract is very well written and quite clear.

Lines 13-16: I was confused by the message of this sentence. Do the authors mean this as an issue of scale, i.e. attention has been paid only to species and not communities, or that attention has only been paid to river sections and not whole watersheds? Maybe I'm mis-reading the sentence.

*This sentence was rewritten (now line 34) to clarify our point.

Lines 15-16: I think it might help to clarify what you mean by "aquatic connectivity" here. Having an operational definition early on would help, especially given that you sort of re-visit the idea in the paragraph starting on line 37. Generally in the introduction I wasn't clear how much of Kondolf's ideas about connectivity you were embracing, and perhaps it needs to be clear early on.

*We mean connectivity in a general sense early on, but the index then defines what we mean specifically: the (weighted) average probability of organisms being able to move between two points/sections in a watershed. We have added a general definition for connectivity and revised the second paragraph of the introduction to clarify the differences between terrestrial and aquatic connectivity. The discussion regarding Kondolf's ideas has been deleted to reduce the length of the introduction.

Line 23: Urban and Keitt, 2001, should probably be included as well.

*This has been done.

Lines 25-28: Perhaps elaborate this with an example of each?

*This paragraph has been deleted in the interest of shortening the introduction, so the suggestion is no longer applicable.

Lines 37-43: I wasn't sure what the main point of this paragraph was.

*This paragraph has been deleted.

Lines 41, 42 (and other places throughout): be consistent with use of commas after "e.g."

*We have ensured the consistent application of commas after "e.g." and "i.e." in all cases.

Lines 45-46: This sentence reads a bit funny, but might be made clearer with an example of each. The rest of the paragraph talks about these, but do not explicitly link back to this sentence.

*Examples have been added as suggested (line 25).

Lines 66-67: Seemed a bit out of order to "revisit" Kondolf's ideas here given that you brought them up earlier (lines 37-43). Perhaps bring these ideas closer together in the intro?

*This paragraph has been deleted in the interest of shortening the introduction.

Lines 70-85: wasn't clear to me if the authors were arguing that we should embrace Kondolf's model or not. It seems that the RCI addresses at least one component of it, but if the intention is to "quantify" the qualitative ideas from Kondolf, than that needs to be clearer in this paragraph.

*This paragraph has been deleted in the interest of shortening the introduction.

Lines 76: suggest adding Fortuna et al. (2006) Proceedings of the Royal Society, Schick & Lindley (2007) Journal of Applied Ecology.

*The work of Schick and Lindley is now highlighted in the introduction and discussion. Fortuna et al. (2006) cannot be integrated in the revised introduction but it is now highlighted in the discussion.

*References added as suggested.

Lines 90-93: Additionally if one goal is to quantify Kondolf's model for connectivity, than it should be at least mentioned why only one of the three elements is being addressed.

*This paragraph has been deleted in the interest of shortening the introduction, so the suggestion is no longer applicable.

Lines 102-103: suggest switching slope and culvert length to keep consistent with the order from line 101.

*We have removed these specific references to culverts while addressing previous comments.

Lines 105-107: Earlier (13-16) you note that efforts have looked at fish movement, but haven't focused on larger scale aquatic connectivity. But here you note that you're looking at aquatic connectivity via fish movement. This needs to be made a bit clearer.

*We have clarified this point.

Equations 5 & 6: looks like the line numbers have been ingested into the formulas.

*As stated earlier, this appears to be a problem during conversion from Word to .pdf.

Lines 241: suggest changing "a naturally occurring waterfall" to "one naturally occurring waterfall"

*Changed as suggested.

Lines 275-281: Note my general comments about the geometry of the simulated watershed. Figure 4 seems an intuitive result given the watershed is a straight line.

*As suggested, we have removed this figure and described these results in the text.

Lines 286-288: Does this assume the natural barrier is a full barrier for all species?

*We have specified that, in this example, it was a full barrier. Further, since we are using a general, theoretical passability value for all barriers, we feel it unnecessary to specify that it applies to all species.

Lines 291-292: The sentence isn't clear. What do you mean by "the effect of the full natural barrier.?" Should the sentence starting on 296 be moved up?

*This has been clarified in the text.

Lines 298-301: not sure what is meant by "one strategically selected barrier could be equivalent to the removal of 11 poorly chosen barriers.." Should this be clear from the figure? Ditto for the sentence about the potadromous life history.

*We have clarified this paragraph as suggested. To make this apparent in the figure would be complicated and we feel it would make the figure less readable.

Lines 300-301: suggest moving this sentence before the preceding sentence to stay consistent with the order in Figure 5.

*Our discussion of potadromous and diadromous is not consistent with the order portrayed in the figure. However, we designed the figure based on its first reference in the text. We feel that the order presented in this paragraph flows best and thus we would prefer to leave it as is.

Line 304: Do you mean potadromous instead of diadromous?

*Changed as suggested.

Lines 367-369: But isn't one of Fagan's (2002) main points that even a single event low down in the trunk of a watershed can completely fragment large sections of habitat? Are you assuming for only certain life history types?

*First, spatial arrangements affect both life history types we talk about, but in different ways. The citation of Fagan simply discusses how a barrier splits a watershed, irrespective of life history. However, we do specify life history in each point we make in the text that follows.

Lines 376-378: See Schick and Lindley, 2007.

*We have addressed Schick and Lindley's notable contribution in both the introduction and in the discussion.

Lines 386-390: Suggest citing Cooper and Mangel (1999) Fishery Bulletin, 97:213-226.

*We have added this citation as suggested.

Lines 405-422: See earlier "general" comments about the discussion of passability and different species. The authors do a nice job in this paragraph highlighting how the RCI could be changed or modified, but I think this might be brought up a bit earlier in the presentation of the index.

*We feel it would be premature to discuss future refinements until the behaviour of the index is outlined. As such, we would prefer to leave this paragraph near the end.

Table 1: Not sure what the grey boxes are to signify.

*We have removed the grey boxes. Bold text remains to highlight high priority barriers.

Lines 479 & 481: "panels" should read "panel"

*Changed as suggested.

~~A connectivity index for river~~A new measure of longitudinal connectivity for stream networks~~scapes~~

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7,~~965~~~~436~~299

Abstract

Habitat connectivity is a central factor in shaping aquatic biological communities, but few t~~. However, unlike for terrestrial environments, there are no suitable means available toT~~ools exist to describe and quantify this attribute at a ~~terrestrial network connectivity quantify are difficult to apply to landscape-scale (riverscapewatersheddrainage~~ network scale ~~) connectivity in linear habitats (i.e.i.e.,~~in riverine systems~~)~~. Here, we develop a new index to quantify ~~structural~~ longitudinal connectivity of ~~riverscapewatersheds~~river networks based on the expected probability of an organism being able to move ~~moving~~ freely between two random ~~ly chosen~~ points of the network. We apply this index to two fish life histories and evaluate the effects of the number, passability, and placement of barriers on ~~riverscapewatershed~~river network connectivity through the use of simulated ~~watersheds~~dendritic ecological networks. We then extend the index to a real world dendritic river system in Newfoundland, Canada. Our results indicate that ~~fragmentation~~ connectivity in river systems, as represented by our index, is most impacted by the first few barriers added to the system. This is in contrast to terrestrial systems, which are more resilient to low levels of ~~fragmentation~~connectivity. The r~~Our r~~esults show a curvilinear relationship between barrier passability and structural connectivity. This suggests that an incremental improvement in passability would result in a greater improvement to ~~watershed~~ river network connectivity for more permeable barriers than for less permeable barriers. Our analysis of the index in simulated and real ~~watersheds~~ river networks also showed that barrier placement played an important role in connectivity. Not surprisingly, ~~B~~barriers located near the river mouth have the greatest impact on fish with diadromous life histories while those located near the center of the ~~watershed~~ river network have the most impact on fish with potadromous life histories. The proposed index is conceptually simple and sufficiently flexible to deal with variations in river structure and biological communities. The index will enable researchers to account for connectivity in habitat studies and will also allow resource managers to characterize watersheds, assess cumulative impacts of multiple barriers and determine priorities for restoration.

Keywords: aquatic connectivity, barriers, connectivity indices, dendritic ecological networks, fish passage, fragmentation, river networks, ~~riverscape~~watersheds

Introduction

Decades of research have highlighted the critical importance of habitat connectivity in ecology and conservation within terrestrial ecosystems. However, little of this work has been translated into aquatic systems, despite the fact that landscape and riverine ecology share many attributes and organizing principles (Benda et al. 2004), including the concept of connectivity (Wiens 2002). ~~The degree of connectivity or isolation of a watershed is reflected in the productivity (Dryden and Stein 1975; Baker and Votapka 1990; Stanford et al. 1996), species composition (Sheldon 1987, 1988; Spens et al. 2007), extinction risk (Dunham et al. 1997; Fagan et al. 2002; Morita and Yamamoto 2002), population size (Preston 1962a, b), genetic stability (Morita and Yamamoto 2002; Wofford et al. 2005), morphological characteristics (Reznick 1982; Crossin et al. 2004), life history (Dingle 1996), and ability of the biota to recover from disturbance (Stanford et al. 1996).~~ Alteration to this defining structural element has undoubtedly result~~s~~ed in considerable short-term and long-term shifts in the aquatic community. ~~Although a great deal of attention has been given to analyzing the effects of barriers on fish movements (e.g.e.g.,, Jungwirth et al. 1998; Peter 1998; McLaughlin et al. 2006), surprisingly little attention has been~~

~~given to the effect of barriers aont watershed the scale of river drainage networksaquatic connectivity (i.e., connectivity of the "riverscape") as a whole~~. ~~Here, we take the definition for habitat connectivity used in the terrestrial sense, where it is used to describe and measure the~~

~~In a terrestrial sense, habitat connectivity is defined simply as "spatial continuity of a habitat or cover type across a landscape" (Turner et al. 2001: 3)~~. ~~and fragmentation as "breaking up of a habitat or cover type into smaller, disconnected parcels" (Turner et al. 2001: 3)~~. ~~However, we expand on the concept of terrestrial connectivity and explore how it can be explicitly applied to measure longitudinal river drainage network connectivity, that is, the connectivity within a dendritic river channel~~.

Terrestrial landscape connectivity is manifested in two dimensions, as animals in one patch can often cross a gap to another patch, usually following one of several alternate paths. Landscape ecologists are familiar with conceptualizing such patches and connections as a lattice network (Watts and Strogatz 1998), and have made use of graph theory to describe and analyze such networks (Urban and Keitt 2001). In contrast, movement between habitat patches in aquatic systems is longitudinal ~~(at least for obligate aquatic species such as fish)~~ along the river channel (at least for obligate aquatic species such as fish) (Fagan 2002). In addition, the geometry of river and stream networks presents challenges to applying terrestrial landscape indices. Grant et al. (2007) characterize rivers and streams as dendritic ecological networks (DENs) and suggest that these are a unique subset of spatially structured networks ~~which~~that merit special attention. While graph theory has been usefully applied to DEN's (Schick and Lindley 2007), Grant et al. (2007) maintain that ~~point out,~~statistical indices ~~to~~ describ~~e~~ing connectivity of lattice networks~~,~~ obscure unique ecological processes ~~within~~associated with DENs. These differences ~~Due to such differences between terrestrial and aquatic~~result in ~~systems, the~~a state of knowledge of aquatic~~habitat~~ network connectivity ~~within aquatic networks~~that lags far behind that in terrestrial landscapes (Wiens 2002).

What is well-known is that humans are a significant source of alteration to aquatic habitat connectivity – one to which aquatic communities have had less time to adjust (Stanford et al. 1996). ~~. Landscape ecologists have been investigating terrestrial habitat connectivity/fragmentation for many years, and have moved beyond structural descriptions (e.g., McGarigal and Marks 1995; Schumaker 1996), through to neutral landscape models (e.g., With and King 1997), graph-theory approaches (Bunn et al. 2000; Urban and Keitt 2001); and process-based, spatially-explicit models such as least-cost path analysis (e.g., Meegan and Maehr 2002); individual-based models (e.g., Bélisle and Desrochers 2002); and percolation models (e.g., Williams and Snyder 2005). There are a myriadnumerous of connectivity indices available (Calabrese and Fagan 2004), ranging from those that measure pattern (structural connectivity indices) to those that incorporate measures of species processes (process-based indices). Terrestrial connectivity indices also vary in terms of whether they use a habitat patch-level perspective, or a landscape-scale perspective (Calabrese and Fagan 2004). Unfortunately, intrinsic differences in patch structure make the application of the terrestrial models outlined above inappropriate, or at best, difficult, for riverscapewatersheds (probably a good spot to bring in Grant et al. 2007). In particular, animals inhabiting two-dimensional networks of habitat patches have many potential dispersal routes through a landscape. In contrast, entirely aquatic organisms within river systems are constrained to limited options when moving between patches (Fagan 2002). Due to such differences, the state of knowledge of riverscapewatershed habitat connectivity lags far behind that in terrestrial landscapes (Wiens 2002).~~

~~Aquatic connectivity is manifested in longitudinal, lateral, and vertical planes (Kondolf et~~

~~al. 2006) and varies naturally over space and time (Ward 1989). Watersheds differ in the extent, quality and spatial orientation of habitat and in the permeability of barriers (physical, chemical and biological) within them. Temporal variation is also significant in riverscape~~watersheds~~ as connectivity can change at intervals from hours (e.g. changes to flow volume in small streams from precipitation events) to millennia (e.g. isostatic rebound of landmasses). Such natural variation results in diverse ecological conditions to which aquatic communities adapt.~~

~~What is well-known is that H~~h~~umans are a significant source of alteration to habitat connectivity – one to which aquatic communities have had less time to adjust (Stanford et al. 1996).~~ Human impacts typically decrease aquatic connectivity by creating barriers in river networks (~~e.g.~~e.g., dams)~~,~~ but may also increase aquatic connectivity by providing routes around natural barriers (~~e.g.~~e.g., navigation canals). Barriers, such as dams and culverts, alter current velocity, water depth and create vertical drops at outflows that change the hydrology and thermal regimes of aquatic systems (Berkamp et al. 2000) and -impede the movement of aquatic species (Warren and Pardew 1998; Wheeler et al. 2005). ~~Some of these changes have come about through directed efforts to enhance commercially valuable aquatic species (blasting of natural barriers to improve salmonid access to habitat upstream), while many are unfortunate by-products of economic development (transportation, agriculture, power generation etc.).~~ These alterations are widespread and have had repercussions ranging from drastic alterations to the ecology of the Great Lakes of North America (Mills et al. 1993), to species declines and extirpations in major rivers of Europe (Porcher and Travade 1992), Australia (Barry 1990; Mallen-Cooper and Harris 1990), Asia (Zhong and Power 1996; Morita and Yamamoto 2002), and North America (Quiros 1989; Baum 1994; Meyers 1994; Stolte 1994).

Although a great deal of attention has been given to analyzing the effects of ~~individual~~ barriers, especially on fish, (e.g., Jungwirth et al. 1998; Peter 1998; McLaughlin et al. 2006), surprisingly little attention has been given to the cumulative effect of barriers at the scale of ~~river drainage network~~river networks. -Methods to measure effects of multiple barriers at the extent of the entire landscape are in their infancy~~ considered ~~; ~~(Beechie et al. 1994; Wheeler et al. 2005).~~ ~~H~~hence~~,~~

~~Regrettably,~~ management and land use decisions are often made in the absence of adequate information on hydrological connectivity (Pringle 2003). ~~Barriers, such Structures such as dams and culverts impact connectivity of habitats. DAN TO COVER, but also change hydrology and thermal regimes and can result in drastic habitat change (Berkamp et al. 2000). Other structures, such as road culverts, impede the movement of aquatic species due to high current velocities, shallow depths, and vertical drops at outflows (Warren and Pardew 1998; Wheeler et al. 2005). Though impacts of the latter typically occur at smaller extents, they cannot be marginalized given their pervasive nature (Beechie et al. 1994). Furthermore, cumulative effects of multiple barriers are rarely considered (Beechie et al. 1994; Wheeler et al. 2005) and are poorly understood because methods are not available to measure their effects at the extent of the entire landscape are in their infancy.~~

Recent work by Schick and Lindley (2007) provide an elegant ~~nice~~ example of an empirical method to characterize population connectivity at a larger scale for an aquatic dendritic system. -There is a need, however, for a simple, general framework that can be easily applied in multiple contexts with limited biological information.

In this paper we propose a new method, the ~~Longitudinal Connectivity Index~~Dendritic Connectivity Index (~~LCI~~DCI), to quantify the ~~structural~~ longitudinal connectivity within river

~~drainage~~ networks. We take the definition for habitat connectivity used in the terrestrial sense, where it is used to describe and measure the "spatial continuity of a habitat or cover type across a landscape" (Turner et al. 2001: 3) and explore how it can be explicitly applied to measure longitudinal river network connectivity. Here, longitudinal connectivity refers to connections between upstream and downstream sections of a river network, as opposed to vertical (benthic to pelagic) or lateral (bank to bank) connections (see Kondolf et al. 2006). -Our intent is that this metric will provide an analogous means of quantifying aquatic habitat connectivity ~~as~~to the myriad of terrestrial landscape metrics, and will provide a useful indicator of aquatic ecosystem integrity. We explore this method to assess longitudinal connectivity from the perspective of diadromous (migrations between marine and freshwater) and potadromous (migrations within freshwater) fish life histories and to evaluate the effects of the number, passability and placement of barriers on simulated river networks. We then apply this approach to a real world dendritic system in Newfoundland, Canada.

~~Here, we take the definition for habitat connectivity used in the terrestrial sense, where it is used to describe and measure the "spatial continuity of a habitat or cover type across a landscape" (Turner et al. 2001). However, we expand on the concept of terrestrial connectivity and explore how it can be explicitly applied to measure longitudinal river network connectivity.~~

~~More recently, a conceptual model of aquatic connectivity has been proposed for the purpose of assessing aquatic ecosystem integrity and evaluating restoration efforts (Kondolf et al. 2006). The process involves assessing how the three spatial elements of connectivity (longitudinal, lateral and vertical) are modified by human activities. The result allows managers to qualitatively evaluate if restoration goals have been achieved. However, Kondolf et al. (2006)~~

~~cite the inability to move beyond qualitative assessments of change as a limitation of their conceptual model. Quantification is clearly important for understanding the implications of future development, prioritizing restoration efforts, or for identifying sites where biological communities may be threatened. Quantification of aquatic connectivity may also be useful to enable comparisons of spatially and temporally disjunct ecosystems and the effects of various types of barriers on their biological communities. There have been some attempts to quantify aquatic connectivity in the literature (e.g. Tockner et al. 1999, Fagan 2002, Fortuna et al. 2006; Urban et al. 2006; Schick and Lindley 2007), however, these do not appear to be appropriate for riverscapewatershed-scale analyses, nor for inter-watershed comparisons of structural connectivity. For example, Tockner et al. (1999) describe longitudinal connectivity in terms of surface water connection between upstream and downstream areas. Because this is measured in terms of mean water levels and floodplain discharge, it does not account for whether organisms are able to move from one region of the river to the other, even when there is physical connection. In another example, Urban et al. (2006) adopt a patch-dynamics approach to investigate the impact of urbanization and stream fragmentation on aquatic invertebrate communities. However, their methods do not yield a connectivity measuren index of landscape-levelsufficient scale connectivity that can be compared among watersheds.~~

Methods

Development of the ~~riverscape connectivity index~~Dendritic Connectivity Index (~~RCI~~DCI)

Riverine ecosystems ~~(i.e., riverscapes)~~ can be examined at a variety of spatial scales and here we adopt Poole's (2002) "river discontinuum concept", which recognizes stream connectivity ~~structure~~ as a hierarchical system within ~~process at~~ the scale of the network as a whole and views stream sections (patches) as elements of a river ~~continuum~~ from headwaters to mouth. Here, we define ~~S~~stream sections ~~are~~ as the sections of river channel created by the presence of a barrier (natural or anthropogenic). Barriers ~~carry with them a~~ have an associated passability value, *p*, which depends on ~~a combination of the~~ the physical ~~attributes of the barrier~~ (~~e.g.~~e.g.,~~,~~ dam height~~culvert length, slope~~), chemical and/or the hydrologic ~~conditions~~ (flow rates, which vary temporally)~~,~~ attributes of the barrier ~~and~~ as well as the biology~~movement ability~~ of ~~an~~ the organism in question (which can vary by species, age, etc.)~~.~~ Barriers are assumed to take no real space, and hence do not reduce the total ~~watershed~~ river network length. We developed an index that measures the effect of ~~stream~~ barriers (~~e.g.~~e.g.,~~,~~ culverts) on ~~-~~connectivity~~, as defined through would it not be more accurate to say, “as contiguity ofaccessibility of aquatic within a watershed to organisms such as fish”.?”*effects on fish movement, within a dendritic river drainage at the riverscape scale~~. ~~-~~We focused on fish movement in conceptualizing connectivity since fish play an important ecological role, are commercially important, and a great deal is known about the effects of waterway barriers on fish movement.

Theoretical framework

We assess connectivity in terms of coincidence probability (sensu Pascual-Hortal and Saura 2006), that is, the probability that fish can move between two randomly chosen points in a ~~riverscapewatershed.~~river network. Hence, connectivity depends ~~is constrained by the distance between points, and~~ on how many barriers are between the two points, and the passability of these barriers. Here, passability refers to the probability of fish being able to cross a barrier in ~~either~~both the upstream or downstream direction. An obvious distinction between riverine and terrestrial systems is the effect of the unidirectional water flow on movement. Concretely, this translates into barriers that are ~~much ~~potentially more likely to impede upstream than downstream movement. This conceptual view of connectivity can be simplified by considering that ~~for any ~~pairs of sections in a ~~riverscape~~river network~~,~~ ~~all pairs of points from these two sections have the same connectivity to and from any part of these sections is the same~~share a connectivity value (Fig. 1). We can then think of connectivity having only as many potential values as there are pairs of stream sections. Since our interest is making a single integrated assessment for the river network ~~as a whole~~~~a riverscape~~, we use the ~~average or ~~expected (i.e., weighted average) connectivity value of stream section pairs. More formally, let C be a discrete random variable that denotes connectivity, and let c_{ij} be a realization of C for stream sections ~~1~~ i and j, where {~~1~~i,j} = 1,…,n, where n is the number of stream sections, and is equal to the number of barriers plus one. The ~~riverscape connectivity index~~Dendritic Connectivity Index (~~RCI~~DCI) can be expressed as:

$$DCI = E[C] = \sum_{i=1}^{n}\sum_{j=1}^{n} c_{ij} P(C = c_{ij}). \tag{1}$$

~~Conceptually, the RCI is the average connectivity of two randomly selected points within a watershed~~~~river network.~~ The ~~RCI~~DCI can be calculated for any size stream network, or portion of a stream network. For example, the ~~RCI~~DCI could be calculated for the entire Mississippi river watershed, by choosing the estuary as the furthest downstream point, or for any tributary of the watershed (~~e.g.~~e.g.,~~,~~ the Missouri River), by choosing the intersection of the tributary with the main stem as the furthest downstream point.

In the following sections, we illustrate how to apply this general framework to accommodate two different life history constraints (~~e.g.~~e.g., diadromy and potadromy). For simplicity, we first tested the index on a simulated dendritic network~~ (Figure x.) with 50 barriers~~

~~spaced evenly (though no barriers were placed on stream intersections). We calculated index values for both life histories under two scenarios: a) varying the barrier passability (i.e., barrier permeabilities). from 0 to 1 and b) varying the number of barriers from 0 to 50. The latter was done by randomly omitting a specified number of barriers from the network 500 times and calculating the mean index value. For simplicity, we first tested the index in a simulated watershed consisting of a single linear stream(Fig. 2) while varying the number of barriers and their associated passabilities (i.e. barrier permeabilities). We then investigated a number of refinements to the index, namely, the effect of treating barriers independently, and the effect of barrier placement on overall riverscape connectivity.~~ . We ~~also~~ then compared the performance of the index on the simulated dendritic network ~~oin a linearsimulated river drainage network stream system~~ to ~~performance in~~that o~~n~~f a real-world dendritic stream system in Newfoundland, Canada. We illustrate how this index ~~approach~~ could be used to prioritize barrier restoration or replacement in this ~~dendritic~~real stream system. All simulations and tests of the indices were carried out using the R statistical software package (v. 2.7.0, R Development Core Team 2007; code to calculate the index is available on request from the authors).

#FIGURE 1 APPROXIMATELY HERE#

~~#FIGURE 2 APPROXIMATELY HERE#~~

1) ~~Riverscape Connectivity Index~~Dendritic Connectivity Index: Potadromous application (~~RCI~~DCI$_P$*)*

Potadromous fish make adult migrations within freshwater, and we are principally concerned with the ability of fish to make regular migratory movements between patches (Harden Jones 1984; Dodson 1997). Thus patches are only connected if an individual can navigate between patches in both upstream and downstream directions. We assume that potadromous fish are equally likely to move upstream as downstream (Warren and Pardew 1998). For the potadromous context, the probability of observing a particular c_{ij} depends on the lengths of the sections ~~I~~ i and j, identified by l_i and l_j, as a fraction of the total length of the ~~riverscape~~drainage network, L.

$$\mathrm{DCI_P} = \sum_{i=1}^{n}\sum_{j=1}^{n} c_{ij}\frac{l_i}{L}\frac{l_j}{L} * 100. \qquad (2)$$

Note that we multiply the index by 100 simply to rescale the index between 0 and 100. The value of c_{ij} will depend on the number and passability of barriers between sections ~~I~~ i and j. We begin by assuming that the passability of multiple barriers is independent, ~~i.e.~~ i.e., that a fish passing one barrier does not in any way affect the probability of the same fish passing another barrier. If there are M barriers between sections ~~I~~ i and j, then c_{ij} is defined as:

$$c_{ij} = \prod_{m=1}^{M} p^{u}_{m} p^{d}_{m}, \qquad (3)$$

where p^{u}_{m} and p^{d}_{m} are the upstream and downstream passabilities of the m^{th} barrier, respectively. If passability is assessed as a binary outcome ~~i.e.~~ i.e., a potential barrier meets designated fish passability criteria (p^{d}_{m} and $p^{u}_{m} = 1$) or it does not (p^{d}_{m} and $p^{u}_{m} = 0$) (~~e.g.~~ e.g., Clarkin et al. 2005), then the index simplifies to:

$$\mathrm{DCI_P} = \sum_{i=1}^{n}\frac{l_i^{2}}{L^{2}} * 100, \qquad (4)$$

since neighbouring sections separated by fully passable barriers are merged, and hence only impassable barriers remain. Thus the binary case only sums connectivity contributions from ~~pairs of point~~movements within the same stream section.

2) ~~Riverscape Connectivity Index~~Dendritic Connectivity Index: Diadromous application (~~RCI~~DCI$_D$)

Diadromous fish make adult migrations between marine and freshwater environments, and hence we are principally concerned with their ability to reach stream sections from a single section: the river mouth, and return. Therefore, we calculate connectivity in terms of the probability that a fish can move in both directions between the mouth of the river and another section of the ~~riverscape~~ river network (note that ~~RCI~~DCI$_D$ can be applied from any section in the ~~watershed~~network). Assuming that the probabilities of crossing successive barriers are independent, the expected connectivity is the ~~riverscape~~ ~~longitudinal~~Dendritic ~~c~~Connectivity ~~i~~Index for diadromous species:

$$\mathrm{DCI_D} = \sum_{i=1}^{n} \frac{l_i}{L}\left(\prod_{m=1}^{M} p_m^u p_m^d\right) * 100, \quad \mathrm{DCI_D} = \sum_{i=1}^{n} \frac{l_i}{L}\left(\prod_{m=1}^{M} p_m^u p_m^d\right) * 100,$$

(5)

where L is the length of all stream sections in the drainage ~~watershed~~network, l_i the length of section ~~I~~i, (I = 1,…, n), $p^u{}_m$ and $p^d{}_m$ are the upstream and downstream passabilities of the m^{th} barrier (m = 1,…,M) between the river mouth and section ~~I~~i, respectively. If passability is measured as a binary outcome, ~~i.e.~~i.e., a potential barrier meets designated fish passability criteria or it does not (~~e.g.~~e.g., Clarkin et al. 2005), the index simplifies to:

$$\mathrm{DCI_D} = \frac{l_1}{L} * 100, \tag{6}$$

where l_1 is the length of the section closest to the mouth of the system and L is the summed length of all stream sections in the ~~watershed~~drainage network.

Applying the index ~~on~~to a~~o~~ ~~the~~simulated dendritic systems ~~linear system~~

To test our connectivity metric, we developed a simple third order dendritic river network- (Fig. 2) with 50 barriers spaced evenly (though no barriers were placed on stream intersections). We calculated index values for both life histories under two scenarios: a) varying the barrier passability from 0 to 1 and b) varying the number of barriers from 0 to 50. The latter was done by randomly omitting a specified number of barriers from the network 500 times and calculating the mean index value. We then investigated ~~a number of refinements to~~variations of the index, namely, the effect of treating barriers independently~~, and the effect of barrier placement~~ on overall river network connectivity.

#FIGURE 2 APPROXIMATELY HERE#~~began with the simplest scenario: a straight line. By definition, this straight line is a continuous habitat, and discrete patches are created by the insertion of barriers to fish movement. To illustrate the relationship between barriers and the connectivity index, we simulated the addition of a range of different numbers of barriers (from 1 to 100). For each scenario, the barrier locations were chosen from a uniform distribution 1000 times, and the average connectivity index score calculated. We set the passability of all barriers~~

~~in the system to be constant, and varied that constant between 0 and 1. We also examined the spatial effects of barrier placement by simulating one barrier (with p = 0.5) at different points along the stream length, and measuring RCI~~DCI ~~for both diadromous and potadromous life histories.~~

Independent vs. d~~D~~ependent barriers

The proposed index assumes that the probability of passing one barrier is independent of the probability of passing another barrier in the same ~~riverscape~~river network. Such an assumption may not be biologically realistic in a system where connectivity is a function of water flow, and multiple barriers will experience the same water flow conditions simultaneously. To evaluate the impact of this assumption, we also calculated connectivity values when passability values of multiple barriers are completely dependent. In biological terms, this scenario models the case where, if an individual can navigate the worst barrier, all remaining barriers with equal or higher passability values between two given patches are considered fully passable.

Discriminating between Anthropogenic and Natural Fragmentation

In some situations (for example, when considering targets for ecological restoration) it will be desirable to consider existing levels of ~~watershed~~ river network connectivity relative to a natural baseline. Such a natural baseline could include natural barriers (e.g., waterfalls) that restrict ~~fish~~ movement and hence affect connectivity. If we consider the natural barriers to represent an absolute state of “natural connectivity” (NC) ~~of less than 100%,~~ we can evaluate the effect of adding anthropogenic barriers relative to this natural state, by expressing the connectivity index (~~RCI~~DCI$_{P}$ or ~~RCI~~DCI$_{D}$) as a percentage of the absolute “natural connectivity” value.

To illustrate this, we discriminate the effects of anthropogenic barriers from a natural ~~one~~ barrier on a real world dendritic ~~riverscape~~river network.

~~# FIGURE 1 APPROXIMATELY HERE#~~

Extending the ~~RCI~~DCI to a real world dendritic system

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We apply the ~~RCI~~DCI to evaluate the connectivity of the Big Brook stream system (48°30´N, 54°01´W) in Terra Nova National Park, Newfoundland, Canada (Fig. 3~~1~~), to assess how the index performs in a real world stream system. Stream and road networks from the Big Brook watershed, as well as the locations of barriers were ~~examined~~ analyzed using ArcGIS (ESRI v.8.2). Barriers consisted of culverts (n=15) and one~~a~~ naturally occurring waterfall. Length of stream sections (extent defined by adjacent barriers) was measured; their combined length (L) totalled 55.9 km. Since barrier passability is currently unknown for this watershed, we applied a uniform passability of 0.5 to all anthropogenic barriers and a passability of 0 to the natural barrier. We calculated ~~RCI~~DCI for both potadromous and diadromous applications. We also examined how the number of barriers, together with their spatial arrangement, affected the ~~RCI~~$\mathrm{DCI}_{\mathrm{P}}$ and ~~RCI~~$\mathrm{DCI}_{\mathrm{D}}$. To do this for each set of potential barriers i, $i = 1,\ldots,15$, we calculated the ~~RCI~~$\mathrm{DCI}_{\mathrm{P}}$ and ~~RCI~~$\mathrm{DCI}_{\mathrm{D}}$ for all $\binom{15}{i}$ possible permutations of culvert locations, using only the existing culvert locations. This gives the range of possible ~~RCI~~$\mathrm{DCI}_{\mathrm{P}}$ and ~~RCI~~$\mathrm{DCI}_{\mathrm{D}}$ values for a given number of barriers and barrier locations on this ~~riverscape~~drainage network.

FIGURE ~~2~~ 23 APPROXIMATELY HERE#

Results

As expected, connectivity of the simulated ~~linear~~~~river drainage network~~river network ~~stream systems~~ with independent barriers declined as the number of barriers increased. However, the relationship was curvilinear, with the biggest losses to connectivity occurring with the addition of the first few barriers (Fig. 4, ~~2, right-hand panels~~b and d). Subsequent barrier additions had increasingly smaller impacts, with an eventual asymptote as the number of barriers → ∞. These relationships were maintained across all passability standards and are qualitatively similar for both diadromous and potadromous life histories, though the impact of barriers is more severe for diadromous than for the potadromous scenario. One less intuitive property of the index proposed is that, particularly for systems composed of many independent barriers, a greater increase in connectivity is achieved by small improvements to barriers with moderate to good passability than with the same improvement to barriers with poor to moderate passability (Fig. 4~~2~~, ~~left-hand panels~~a and c).

FIGURE 4~~2~~ APPROXIMATELY HERE

FIGURE 5~~3~~ APPROXIMATELY HERE

For scenarios with dependence among barriers, DCI$_P$ ~~connectivity~~ and passability showed a positive linear relationship (Fig. 5~~3~~). However, adding additional barriers beyond a certain point (~5-20, depending on the passability) had very little effect on the connectivity of the system (Fig. 5~~3~~, right-hand panel).

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~~*Spatial effects of barriers*~~

~~Potadromous and diadromous applications of the RCIDCI exhibited different responses to the location of barriers (Fig. 64). For potadromous fish, the relationship between barrier location and the RCIDCI was U-shaped, where barriers located in the middle of the watershed had the biggest negative impact on the RCIDCI, while those at the upstream and downstream extremities had the least impact. In contrast, there was a linear relationship between barrier location and the RCIDCI for the diadromous application. In this case, barriers at the downstream extremities had the greatest impact and barriers at the upstream extremities had the least impact.~~

~~#FIGURE 64 APPROXIMATELY HERE#~~

Extending the ~~RCI~~DCI to a real world dendritic system

The ~~RCI~~DCI for the Big Brook ~~watershed~~ r~~R~~iver network was 29.7~~%~~ and 22.5~~%~~ for potadromous and diadromous life histories respectively. However, when scaled relative to the natural condition (~~RCI~~DCI calculated with only the natural (and assumed to be complete) barrier present) the ~~watershed~~ drainage network scored 57.1% and 56.4% of the ~~potential maximum~~absolute (natural) ~~RCI~~DCI for the respective potadromous and diadromous life histories. -Random removal of existing barriers in the Big Brook watershed produced a slight curvilinear response between average %-of-natural ~~RCI~~DCI and number of barriers for the potadromous life history, but a linear relationship for the diadromous life history (Fig.~~-7~~6~~5~~). -The lack of a strong curvilinear response (as observed in Fig. 4) is an expected by-product of accounting for the effect of the natural barrier (~~i.e.~~i.e., scaling the DCI relative to the natural condition). -Since the natural barrier alone is responsible for a considerable portion of the

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fragmentation in the system, subsequent barriers have weaker effects than they would in the absence of the natural barrier.

Table 1 provides an illustration of how the index can be used for prioritization of barrier removal. For the potadromous case, it is possible to increase the %-of-natural DCI from 57.1 to 66.2, by choosing the most important barrier to remove, whereas most barrier removals would lead to little improvement (1-3%). In the diadromous case, the results are more intuitive, as removing barriers upstream of the full natural barrier had no effect on the index. Removal of either of the two barriers downstream of the natural barrier would increase the %-of-natural DCI from 56.4 to 69.0. ~~expected, as the effect of the full natural barrier has been removed.~~

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Spatial effects of barriers

Barriers impose differential effects on the DCI based on their location in the river network, and these effects are manifested differently for each life history (Table 1; Fig. 6). This is evident from the range of variability in DCI for various restoration scenarios (Fig. 6) and by comparing the results from single barrier restorations (Table 1) with the barrier locations (Fig. 3). Restoring centrally located barriers had the largest affect on the DCI_P (Table 1), whereas restoring barriers near the ocean had the largest affect on the DCI_D (Table 1). Due to these strong spatial effects, ~~Potadromous and diadromous applications of the DCI exhibited different responses to the location of barriers (Fig. 6).~~ ~~For a given number of barriers, the range of potential %-of-natural RCI values (as a result of different spatial combinations of barriers) was greater for the diadromous application (Fig.~~ 76b5). ~~This is due to the greater impact of the full natural barrier on the diadromous case, since the presence of barriers upstream are irrelevant. The large range~~

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~~of values further emphasizes the importance of spatial context and suggests that, ~~if ~~barrier removal~~restorat~~o~~ion is done wisely on Big Brook, the removal of the barrier with the greatest impact on the DCI~~one strategically selected barrier~~ could achieve the same connectivity gains as ~~be equivalent to ~~the removal of 11 poorly chosen barriers for the diadromous life history. Spatial effects are not as strong for potadromous life histories, where ~~Similarly, ~~the removal of one carefully selected barrier would have equal effects to the removal of only 8 poorly chosen barriers for the potadromous life history. ~~To explicitly assess the effect of barrier placement, we also simulated the placement of a single barrier along a linear stream. Although an elementary example, the results were quite dramatic. For the diadromous life history, connectivity increased linearly as the barrier was moved from the mouth towards the headwaters (results not shown). In contrast, DCI was lowest for the potadromous life history when the barrier was at the midpoint of the stream , and highest when it was located at the extremities (results not shown). These results, though somewhat intuitive for a simple stream geometry, emphasize the importance of considering species life histories when making decisions about barrier removal or restoration. Mitigation of barriers near the mouth of a river network will have the most benefit for diadromous species, while mitigation near the midpoint of a river network will be most beneficial for potadromous species.~~

~~# FIGURE 7 APPROXIMATELY HERE #~~

~~Table 1 provides an illustration of how the index can be used for prioritization of barrier removal, and further highlights the importance of spatial location. For the diadromous case, it is possible to increase the %-of-natural RCI from 57.1 to 66.2, by choosing the most important barrier to remove, whereas most barrier removals would lead to little improvement (1-3%). In~~

~~the diadromous case, the results are more intuitive, as removing barriers upstream of the full natural barrier had no effect on the index. Removal of either of the By coincidence, two barriers downstream of the natural barrier, if removed, would have the equivalent, highest effect:increase the % of natural RCI would increase from 56.4 to 69.0.~~

TABLE 1 APPROXIMATELY HERE

Discussion

Fluvial landscape ecology has yet to develop as an integrat~~ive~~ed field, however, the need for concepts and landscape analysis tools tailored to lotic ecosystem dynamics ~~are~~ is recognized (Poole 2002; Wiens 2002). The dramatic rate of alteration to natural connectivity further underscores the urgency for these tools (Pringle 2003). Our index suggests that longitudinal connectivity in ~~riverscapes~~ river networks suffers the most in the early stages of fragmentation, because there are fewer alternative paths available (Jones et al. 2000). This is in contrast to ~~terrestrial~~ 2-D systems (e.g., most terrestrial environments), where overall landscape connectivity is generally maintained until later periods of fragmentation, since there are usually alternative paths available after the first few patches/nodes are lost (Gardner et al. 1987; Plotnick and Gardner 1993; Fortuna et al. 2006). ~~Unlike in terrestrial systems, our simulations suggest that, on average, the first few barriers have a disproportional negative impact on aquatic connectivity. Dendritic ecological networks are more sensitive to fragmentation than terrestrial lattice networks, because there are fewer alternative paths available (Jones et al. 2000).~~ Particular care should be taken in relatively well-connected areas to maintain a high level of barrier passability. ~~In biological communities, such a pattern would be expected for species with large spatial~~

~~requirements that would be sensitive to small levels of impact.~~ In some cases, such impacts can be mitigated somewhat by prudent barrier placement (~~i.e.~~i.e., near a natural barrier or at the extremities of a stream network). ~~Particular care should be taken in relatively well-connected areas to maintain a high level of barrier passability.~~ In ~~riverscapes~~ river networks with natural barriers, where connectivity is expressed relative to a natural level of fragmentation, the effect of additional anthropogenic barriers is predictably diminished, but still of considerable importance. Results from the Big Brook watershed indicate that the current 15 barriers, assuming a barrier passability of 0.5~~0%~~, reduce the connectivity index to almost one half its natural value for both potadromous and diadromous life histories.

Not unexpectedly, ~~structural~~ connectivity from the perspective of a potadromous species is less impacted from reduced habitat connectivity than for diadromous life histories (~~diadromous life history fragmentation~~ DCI_D ~~was~~ had a median difference of ~~~~~9~~%~~ units ~~more sever~~when compared to DCI_P~~e than potadromous~~ over the range of values in our simulations~~ of linear~~single ~~channel~~river ~~watersheds~~networks). By definition, diadromous species must access freshwater environments from the ocean, thus barriers make all habitat upstream unusable. In contrast, potadromous species can make use of habitats above and below the same barriers (assuming that sufficient habitat exists on each side of the barrier to sustain a separate population). The increased sensitivity of diadromous species is exemplified by widespread declines of diadromous species (Pacific Rivers Council 1993; Beechie et al. 1994; Moyle 1995; Berkamp et al. 2000), for which ~~fragmentation~~ loss of connectivity has been at least in part to blame. Nonetheless, the impacts on potadromous fish (~~e.g.~~e.g., Moyle 1995; Muhar 1996; Dunham et al. 1997; Fagan et al. 2002; Morita and Yamamoto 2002) and aquatic invertebrates (Master 1990) are also widespread.

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Location of barriers within the watersheds was also very important in influencing the ~~RCI~~DCI for both ~~diadromomous and potadromous cases~~life histories. As evidenced in the Big Brook river network, ~~B~~barriers located at the headwaters minimized loss of diadromous connectivity, while barriers placed ~~at the extremities~~at the extremities of ~~watersheds~~ river networks minimized loss of~~had less impact on the~~ potadromous connectivity ~~than those placed in a more central location~~. The diadromous results are intuitive given that a greater proportion of diadromous individuals will need to pass through barriers that are closer to the ocean. In the potadromous case, ~~T~~the ~~curvilinear~~ response ~~of the latter~~ can be attributed to the fact that the contribution~~s~~ to the ~~RCI~~DCI$_P$ of a stream section increases proportionally to the squared section size. For example, in a simple network of two patches~~Thus,~~, the ~~RCI~~DCI$_P$ increases as the barrier moves to the extremity of the network and the disparity in patch size increases~~value is always higher when one large patch is maintained after a barrier is added (i.e.~~i.e.,~~, gains in connectivity from a large patch more than compensate for lost contributions as its "twin" become smaller).~~. Such results are consistent with persistence estimates of populations, which scale exponentially to the number of individuals within a population (Lande 1993).

~~Linear River drainage network~~River network configuration~~vs. dendritic systems~~

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Though the results of our ~~linear stream~~ simulated ~~river drainage network~~river networks ~~ions~~ were qualitatively similar to those of a real world dend~~t~~ritic ~~watersheddrainage~~ river network~~s~~, the unique spatial arrangement of stream networks ~~(linear vs. dendritic)~~ ~~should~~ will have implications for ~~fragmentation~~ connectivity impacts. In ~~linear system~~networks with fewer branches, the random placement of a single barrier results in less variability~~ble~~ in patch size~~s~~ compared to ~~dendritic~~ highly branched arrangements (~~i.e.~~i.e., the disparity between resulting patches in ~~dendritic~~ highly branched ~~systems~~ networks would be greater,~~)~~ (Fagan 2002).~~). In potadromous scenarios, barriers at the extremities of the simulated systems~~ ~~networks~~ ~~caused less impact than centrally located barriers that split the system into sections of similar size.~~ ~~Therefore, we would expect that, on average, dendritic systems with a barrier would have higher connectivity values than a comparable linear system.~~ Furthermore, in ~~systems~~ networks with similar stream length and numbers of barriers, the number of barriers an individual (potadromous or diadromous) would have to pass to reach another randomly selected section would, on average, be ~~greater~~ lower in ~~linear~~highly branched configurations ~~systems~~. Therefore, we would expect that, on average, highly branched networks with a barrier would have higher potadromous DCI values than a comparable network with fewer branches. From an ecological perspective, ~~dendritic~~ highly branched ~~systems~~ networks should be more resilient since at low levels of fragmentation, the resulting fragments could leave at least one functioning component for diadro~~a~~mous species (outflow to headwater).

Applications

The approach presented here has utility in both practical and theoretical applications. From a theoretical perspective, connectivity has been identified as a central biological process for terrestrial fauna (~~e.g.~~e.g.,~~,~~ Bennett et al. 1994; Moilanen and Nieminen 2002; Broquet et al. 2006; With et al. 2006) and more recently in aquatic systems (Stanford et al. 1996; Wiens 2002; Pringle 2003). As far as we are aware, w~~W~~e are the first to propose a general purpose methodology, with minimal biological inputs, ~~This is the first methodology that we are aware of~~ ~~to~~ to quantify network-scale ~~structural~~ habitat connectivity in aquatic systems~~)~~. The ability to quantify structural connectivity will provide researchers with a means to better understand how this process affects evolutionary trajectories, population persistence, and community dynamics. Furthermore, though we applied the ~~RCI~~DCI$_D$ specifically to migrations from the marine environment, such a methodology can be applied to any particular point within a ~~watershed~~river network. Thus, the ~~RCI~~DCI can be included as an attribute of habitat studies being conducted at much smaller scales (~~e.g.~~e.g., a single reach).

From a practical perspective, the ~~RCI~~DCI ~~will~~ can facilitate consideration of longitudinal connectivity in ~~watershed management~~river networks. Considerable effort in aquatic systems has been focused on improving or restoring patch quality (~~e.g.~~e.g.,~~,~~ in-stream restoration projects), but this has often been done without recognition of connectivity between ~~habitats~~ patches (Pringle 2003; Kondolf et al. 2006). This can be a crucial oversight in aquatic ecosystem management (Muhar 1996; Stanford et al. 1996; Cooper and Mangel 1999), given that aquatic organisms may require several habitat types as they grow and may exhibit life histories and behaviours that are manifested at several spatial scales. The proposed approach will allow resource managers to characterize watersheds, determine priorities for restoration, optimize resource allocation (~~i.e.~~i.e., barrier passability standards) and infrastructure plans (placement of roads, dams, etc.) and report on connectivity as a component of ecosystem integrity. For example, for the watershed shown in Figure ~~1~~3, potadromous connectivity could be improved between 0-9 % of natural connectivity, depending on which single barrier is restored (Table 1). An advantage of the approach presented here is that it allows the evaluation of impacts on individual projects at the~~a~~ ~~riverscape~~ scale of the entire river network that includes cumulative impacts of many small developments (~~e.g.~~e.g.,~~,~~ Beechie et al. 1994; Pringle 2003). As relationships with structural connectivity and biological communities develop through further research in fluvial landscape ecology, a standardized method such as we propose here will allow comparison of multiple watersheds and will aid in identifying extirpation hotspots or areas in need of enhanced protective measures.

Future refinements: applications to biota

For the sake of simplicity, universal passabilility standards were applied to the simulated river ~~watersheds~~drainage networks. In practice, passability will vary for each barrier, which the index can readily accommodate. Estimating passability is more problematic as it needs to be considered from an organism's perspective. The ability of organisms to pass through barriers will be a function of ~~mobility~~physiology, which differs among and within species (~~e.g.~~ e.g., Berry and Pimentel 1985; Myrick and Cech 2000), and physical conditions (~~e.g.~~ e.g., Belford and Gould 1989; Spens et al. 2007; Jones et al. in press) that would vary spatially and temporally within a watershed ~~as well as temporally~~. ~~Including a separate passability value for each barrier in the index calculation is trivial.~~ As an example of a method to estimate passability of hydrological barriers (e.g., culverts), the proposed connectivity index could be merged with hydrological models that estimate variation in stream flow (discharge) over time and relate these parameters to variation in passability as a function of flow for species with different swimming abilit~~y~~ies.

A second challenge is identifying whether the probability of passing a barrier is independent among nearby barriers. ~~This~~ Independence may not be ~~the case~~appropriate in situations where passability is dependent on discharge (which varies at large spatial scales) or the size of the individual (if an individual is enough large to pass one barrier, it can then pass all more permeable barriers). Where on this spectrum true connectivity lies will depend on the organism, its behaviour and spatial arrangement of the barriers.

~~As landscape ecology applications to aquatic systems are further developed, other theories from terrestrial landscape ecology will no doubt be incorporated into refinement of the RCILCI. A fundamental principle in landscape ecology is the issue of scale. This is a common critique of terrestrial structural connectivity indices (Gustafson 1998). The RCILCI is directed toward measuring longitudinal connectivity, which manifests itself at relatively large scales in a riverscape. Other types of connectivity (lateral and vertical; Kondolf et al. 2006) operate on smaller scales and in two or more dimensions and are not suitable for the RCILCI. Such elements may be better addressed with existing terrestrial metrics.~~

The ~~RCI~~DCI can be further developed to incorporate aspects of lotic ecological theory. As presented in this paper, stream sections are treated with equal weight regardless of where they occur within the ~~watershed~~drainage network. ~~The~~ As discussed by Poole (2002), the physical characteristics and ecology of sections would be expected to vary along longitudinal gradients (V~~e.g., River Continuum Concept, V~~annote et al. 1980, Poole 2002; Thorpe et al. 2006) as well as within sections (~~Serial Discontinuum Concept, Poole 2002~~Ward and Stanford 1983; Stanford and Ward 2001; Thorp et al. 2006). Improved biological inference will also require improved quantification of what constitutes habitat versus movement corridors (Fagan 2002). In the simulations described in this paper, stream length was considered the metric of available habitat. Habitats in ~~riverscapes~~river networks, however, are patchy and differ in quality (Poole 2002). With enhanced knowledge of habitat suitability, stream length can be replaced by any measure of habitat extent.

In cases where more biological insight is available, this additional information could be incorporated to refine the model, analogous to the detail provided by Schick and Lindley (2007) for a model to estimate independence (a measure of connectivity) of riverine populations of salmon.

Conclusions

The proposed index provides a means to quantify ~~structural~~ (longitudinal) connectivity within ~~one-dimensional habitats~~dendritic ecological networks (Grant et al. 2007). It is conceptually simple and sufficiently flexible to deal with variations in river structure (~~linear~~linear through highly branched dendritic networks ~~vs. dendritic~~) and biological communities (~~e.g.~~ e.g., diadromous vs. potadromous life histories). Quantifying and addressing issues of habitat connectivity continue to be an important research focus in terrestrial landscape ecology. The importance of aquatic connectivity and the need to develop fluvial landscape ecology research have begun to be recognized. It is our hope that the metric proposed here will stimulate further discussion and collaboration between landscape and aquatic ecologists and lead to a greater understanding of the landscape-scale effects of human disturbance on riverine patterns and processes.

Acknowledgments

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Table 1. An example of barrier prioritization for restoration efforts in the Big Brook ~~riverscape~~ r~~R~~iver drainage network in Newfoundland, Canada (Fig. 3~~1~~) using the ~~RCI~~DCI. Prioritization is based on the elimination of 1 of the 15 culverts and recalculating the ~~RCI~~DCI values. Culvert letters correspond to culvert identifiers on the map in Figure ~~1~~3. Since the watershed contains a full natural barrier, the results are presented as %-of-natural ~~RCI~~DCI$_P$ and ~~RCI~~DCI$_D$ values. Higher values of the connectivity index indicate higher priorities for culvert restoration. The highest priorities for restoration are indicated in bold. Culverts had an assumed net passability (product of upstream and downstream passability) of 0.5, and all barriers (culverts and the natural barrier) were assumed to be independent.

Culvert restored	***% of natural ~~RCI~~DCI$_P$***	***% of natural ~~RCI~~DCI$_D$***
None	57.1	56.4
a	58.8	61.0
b	60.1	**69.0**
c	60.2	63.1
d	57.1	56.5
e	62.4	**69.0**
f	57.4	56.4
g	**66.2**	56.4
h	58.4	56.4
i	63.4	56.4
j	58.0	56.4
k	64.1	56.4
l	57.1	56.4
m	57.0	56.4

n	57.6	56.4
o	59.9	56.4

Figure 1. Components of the Dendritic Connectivity Index (DCI). In systems with no barriers, the system is fully connected and the DCI has a maximum value of 100 for both life histories considered: potadromous (a) and diadromous (b). The introduction of a single barrier creates two stream sections, and the DCI is based on both the sizes (total channel lengths) of the resulting sections, the permeability of the barrier in both upstream and downstream directions (in this case, the product of the two permeabilities = 0.5) and in the diadromous case, the location relative to the downstream end (represented by the ocean) of the system (b and c). Changing the barrier location to create a greater inequality in stream section sizes results in a more connected system (higher DCI) for the potadromous life history (e), and moving the barrier closer to the ocean -significantly reduces connectivity (lower DCI) for the diadromous life history (f).

~~**Figure 1**. Components of the Dendritic Connectivity Index (DCI). In systems with no barriers, the DCI is based on a) the average connectivity of all possible pairs of randomly selected points for potadromous applications and b) average connectivity from the ocean to all randomly selected points for diadromous applications. In potadromous systems with barriers, the DCI is based on c) the within-segment connectivity and among-segment connectivity. Connectivity among segments in c,e) and between the ocean and non-adjacent segments in d,f) account for intervening barrier passability. DCI values are sensitive to spatial location of barriers and to life history constraints. Movement of the barrier in c,d) to a downstream extremity increased the DCI in potadromous fish (e) but decreased it in diadromous fish (f).~~

Figure 2. A simulated three-order dendritic stream network with 50 systematically placed barriers used to test the Dendritic Connectivity Index.

Figure 3~~1~~. The Big Brook r~~riverscape R~~iver drainage network of Terra Nova National Park, Newfoundland, Canada. ⬢~~● represent b~~Anthropogenic barriers ~~from culverts and~~ are indexed by letters. The waterfall is a ~~full natural barrier.s~~ — ~~;~~ ◆ ~~▲ is a~~ complete natural barrier.

Figure ~~32~~4. The effect of passability (a and c) and number of barriers (b and d) on the potadromous (a and b) and diadromous (c and d) ~~Riverscape Connectivity IndexDendritic Connectivity Index~~DCI when barriers are considered independently in a simulated ~~simple~~ dendritic river system. Lines in the left hand panels (a~~,~~ and c) represent different numbers of barriers (b = 0, 1, 2, 4, and 50). Lines in the right hand panels (b and ~~,~~d) represent different passability values for the barriers (p = 1, 0.9, 0.8, 0.6, and 0).

Figure ~~43~~5. The effect of passability (a) and number of barriers/road density (b) on the potadromous ~~Riverscape Connectivity IndexDendritic Connectivity Index~~DCI when passability of barriers is dependent (~~i.e.~~i.e., an individual that passes though the worst barrier is assumed to be able to pass through all barriers with higher passability values) in a simulated linear simple dendritic river system. Lines in ~~the left hand~~ panel~~s (a,c)~~ a represent different numbers of barriers (b = 0, 1, 2, 4, and 50). Lines in the ~~right hand~~ panel~~s (b,d)~~ b represent different passability values for the barriers (p = 1, 0.9, 0.8, 0.6, and 0).

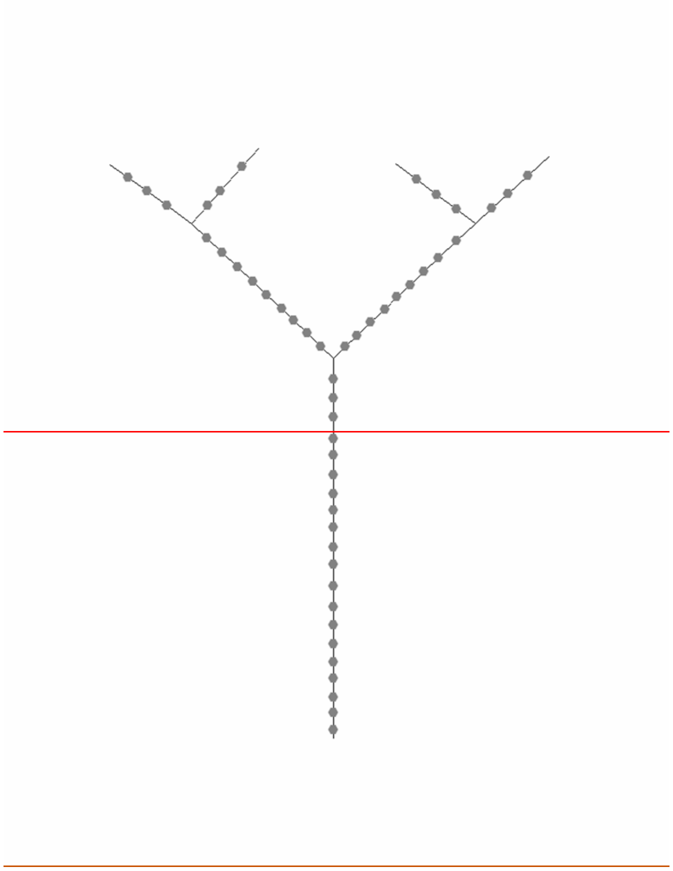
~~**Figure 42.** The effect of passability (a and c) and number of barriers/road density (b and d) on the potadromous (a and b) and diadromous (c and d) Riverscape Connectivity IndexDendritic Connectivity Index when barriers are considered independently in a simulated dendritic river drainage networklinear river system. Lines in the left hand panels (a,c) represent different~~

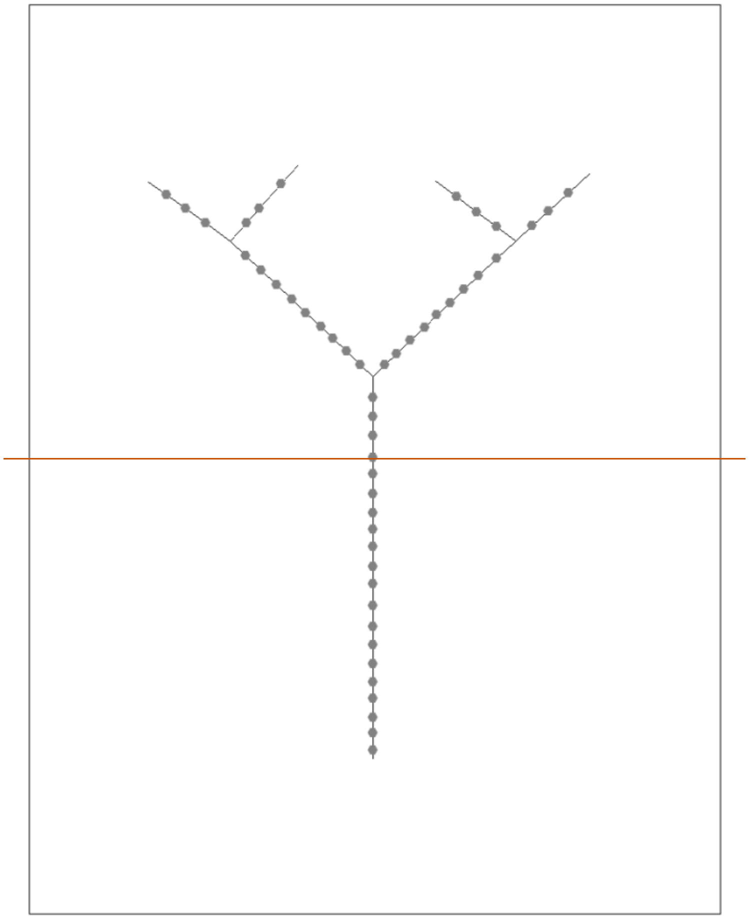
~~numbers of barriers (from top to bottom 1, 2, 4, 8, 16, 30, 60, 100). Lines in the right hand panels (b,d) represent different passability values for the barriers (from top to bottom: 1,0.95,0.9, 0.8,0.7,0.6,0.4,0).~~

~~**Figure 53.** The effect of passability (a) and number of barriers/road density (b) on the potadromous Riverscape Connectivity IndexDendritic Connectivity Index when passability of barriers is dependent (i.e.i.e., an individual that passes though the worst barrier is assumed to be able to pass through all barriers with higher passability values) in a simulated dendritic river drainage networklinear river system. Lines in the left hand panels represent different numbers of barriers (from top to bottom 1, 2, 4, 8, 16, 30, 60, 100). Lines in the right hand panels represent different passability values for the barriers (from top to bottom: 1,0.95,0.9, 0.8,0.7,0.6,0.4,0).~~

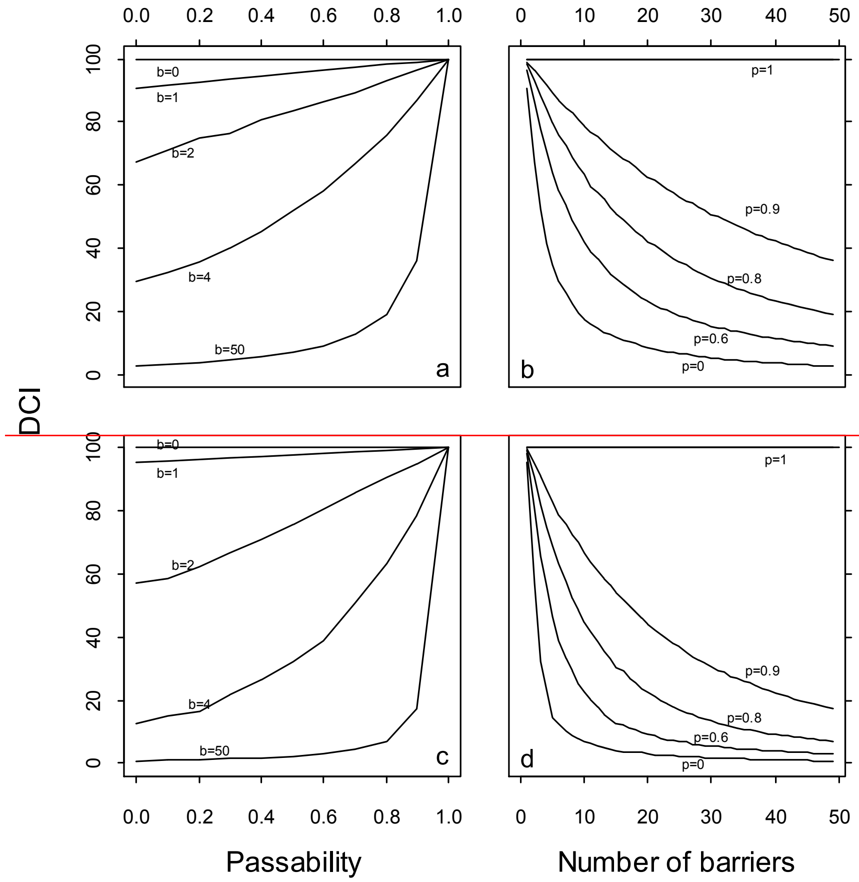
~~**Figure 64.** The effect of barrier location placement on the Riverscape Connectivity IndexDendritic Connectivity Index for potadromous (solid line) and diadromous (dashed line) life histories for the simulated lineardendritic river drainage network system. The results are from a single barrier (with a passability value of 0.5) inserted at different points in the stream section from mouth to headwater.~~

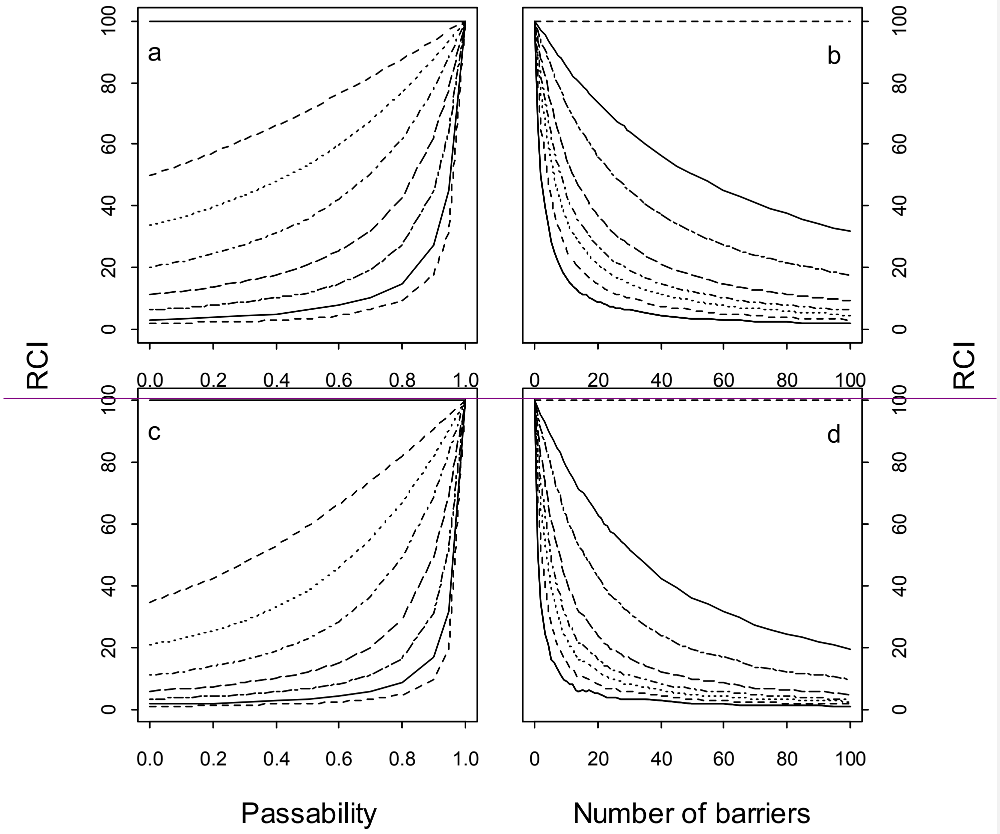
Figure ~~57~~6. The relationship between the number of barriers and the ~~RCI~~DCI for the Big Brook ~~riverscapeRr~~river network, for both the potadromous (a) and diadromous (b) life histories. The relationship is based on removing differing numbers of barriers from the existing set of barriers ~~network~~ on the ~~riverscape~~drainage network, and calculating the ~~RCI~~DCI for all permutations of that number of barriers. Only the 15 barrier locations were used in determining the permutations (see text for additional detail). The dark square represents the mean value from all possible permutations, and bars give the range of potential values from all possible permutations.



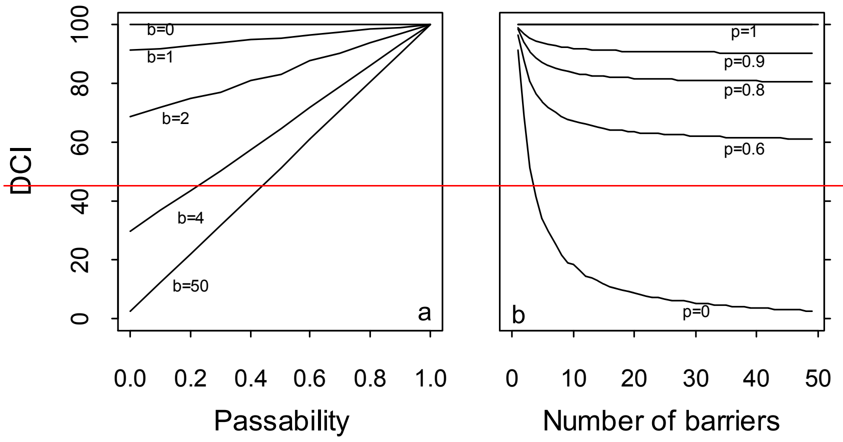


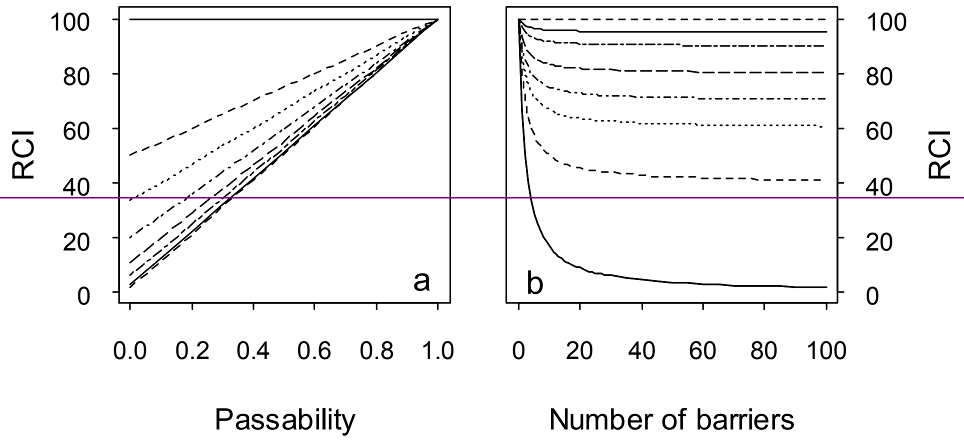
~~**Figure 1.**~~


DCI
Passability
Number of barriers
a
b
c
d
b=0
b=1
b=2
b=4
b=50
p=1
p=0.9
p=0.8
p=0.6
p=0
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
0
20
40
60
80
100

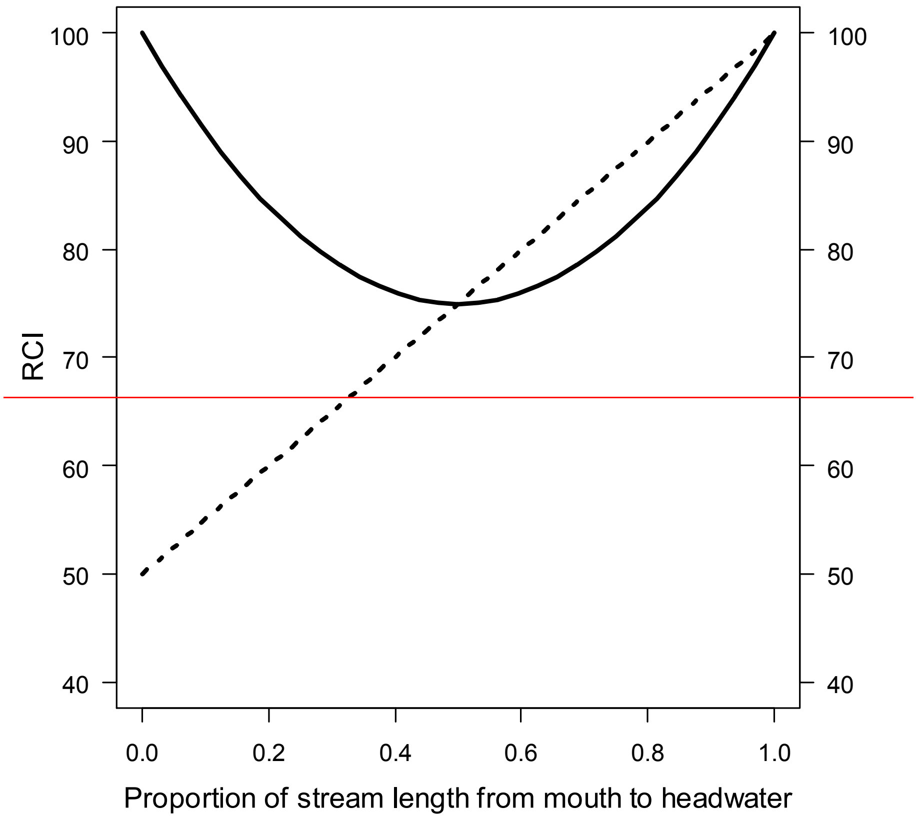


~~**Figure 2.**~~ ~~**replace with dendritic (Dan)**~~

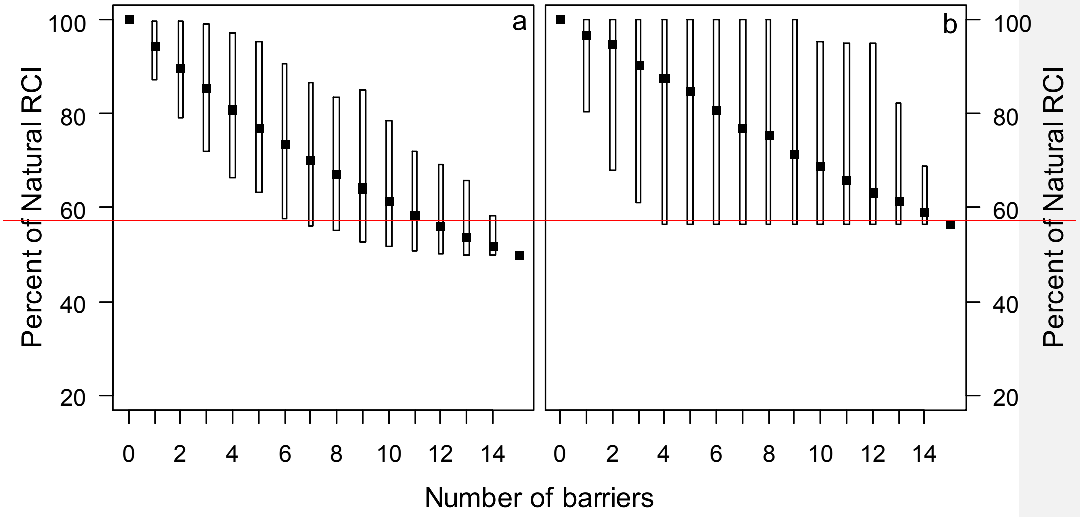




~~**Figure 3.**~~ ~~change to dendritic Dan~~


100
90
80
70
60
50
40
RCI
100
90
80
70
60
50
40
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of stream length from mouth to headwater

~~Figure 64.~~


a
b
Percent of Natural RCI
Percent of Natural RCI
100
80
60
40
20
100
80
60
40
20
0
2
4
6
8
10
12
14
0
2
4
6
8
10
12
14
Number of barriers

~~**Figure 765.**~~

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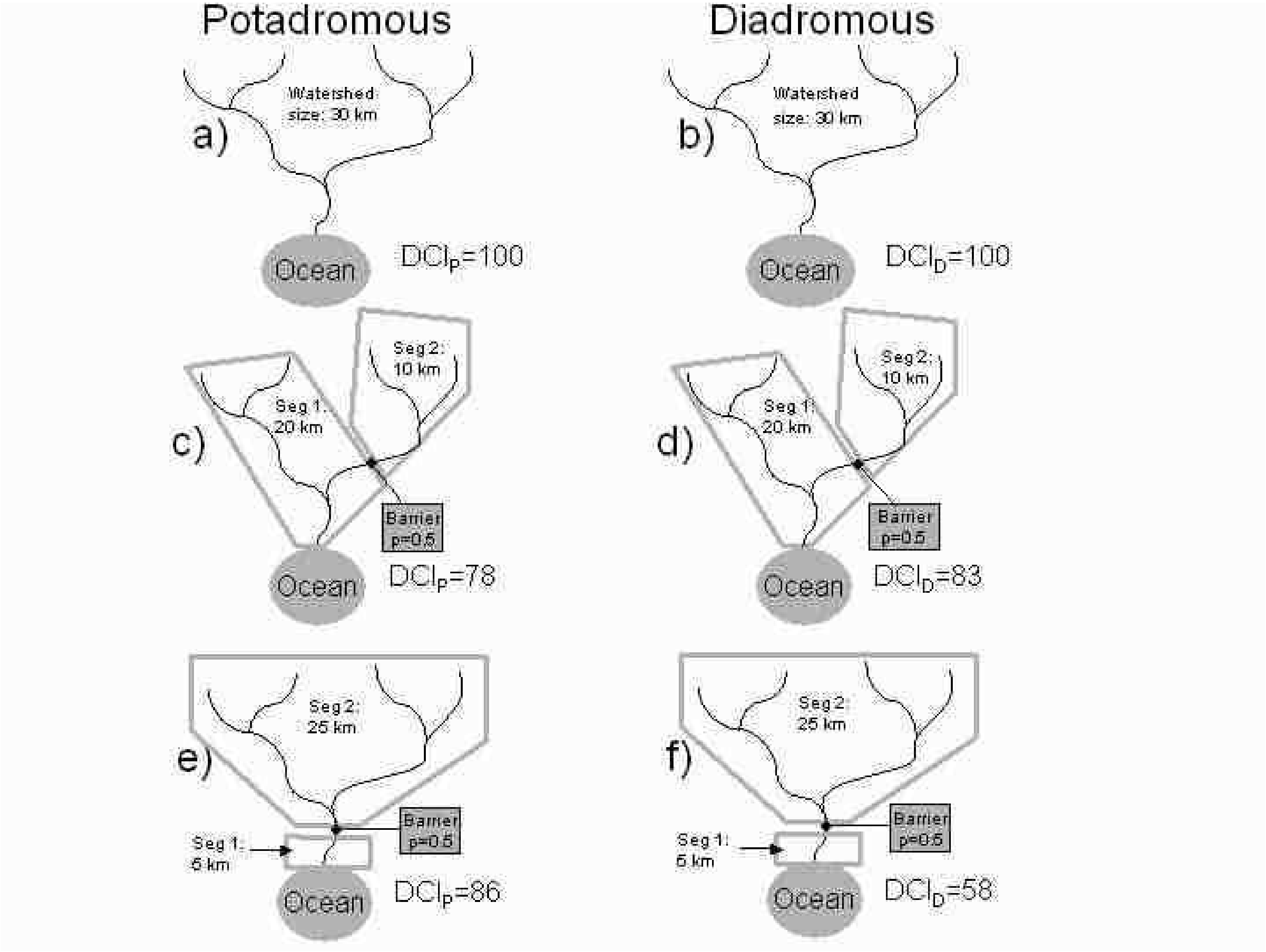

Fig.2

Fig. 3

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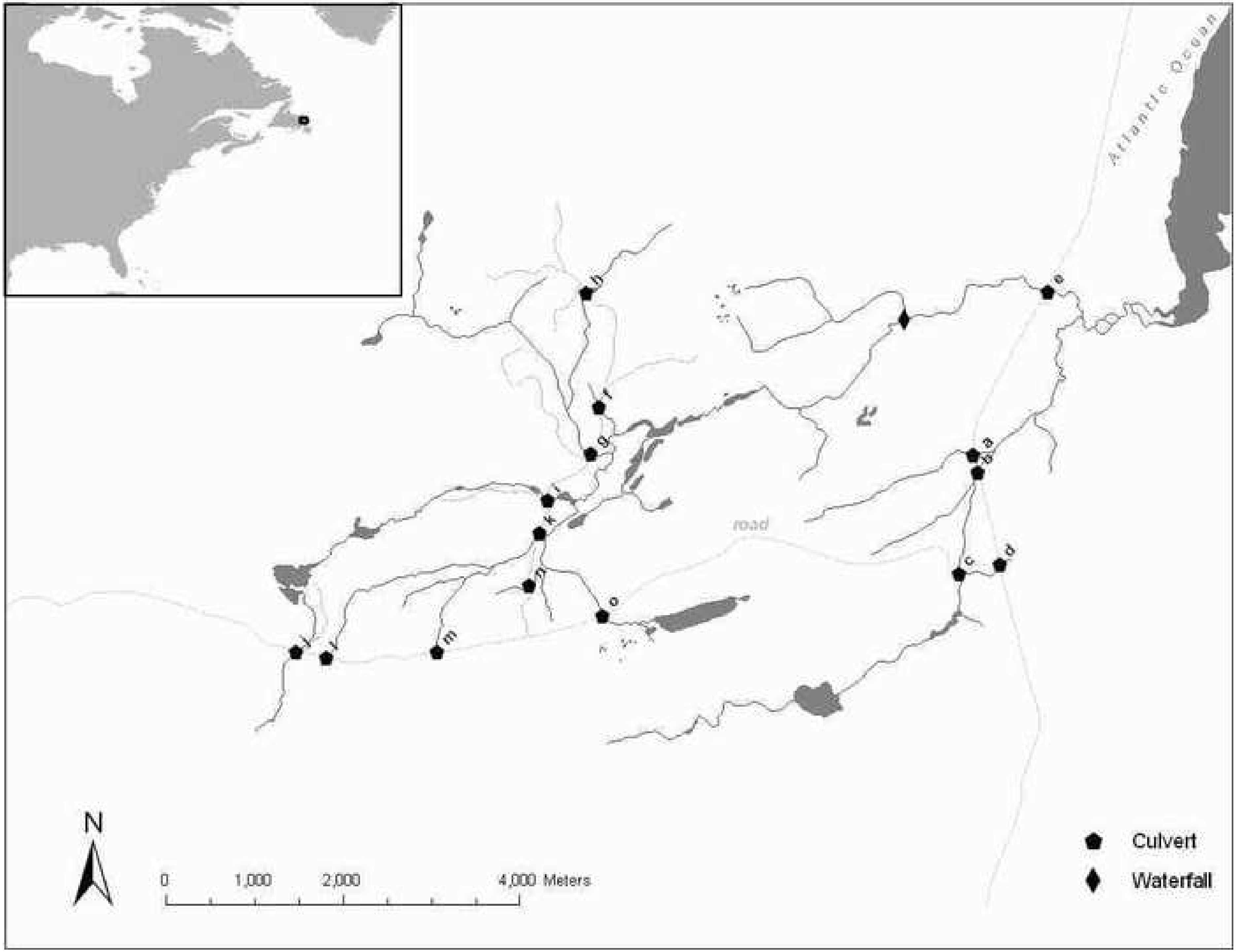

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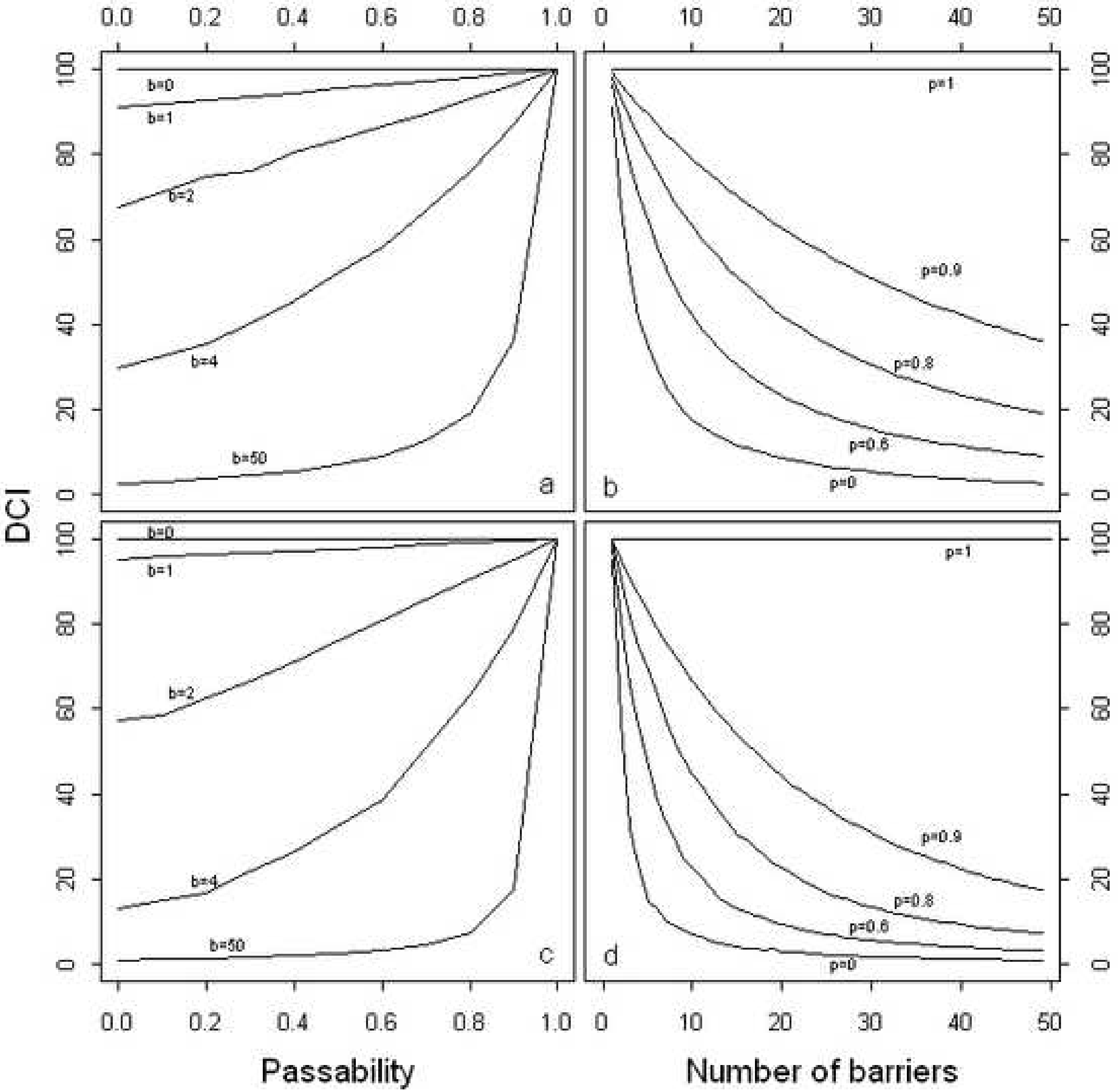

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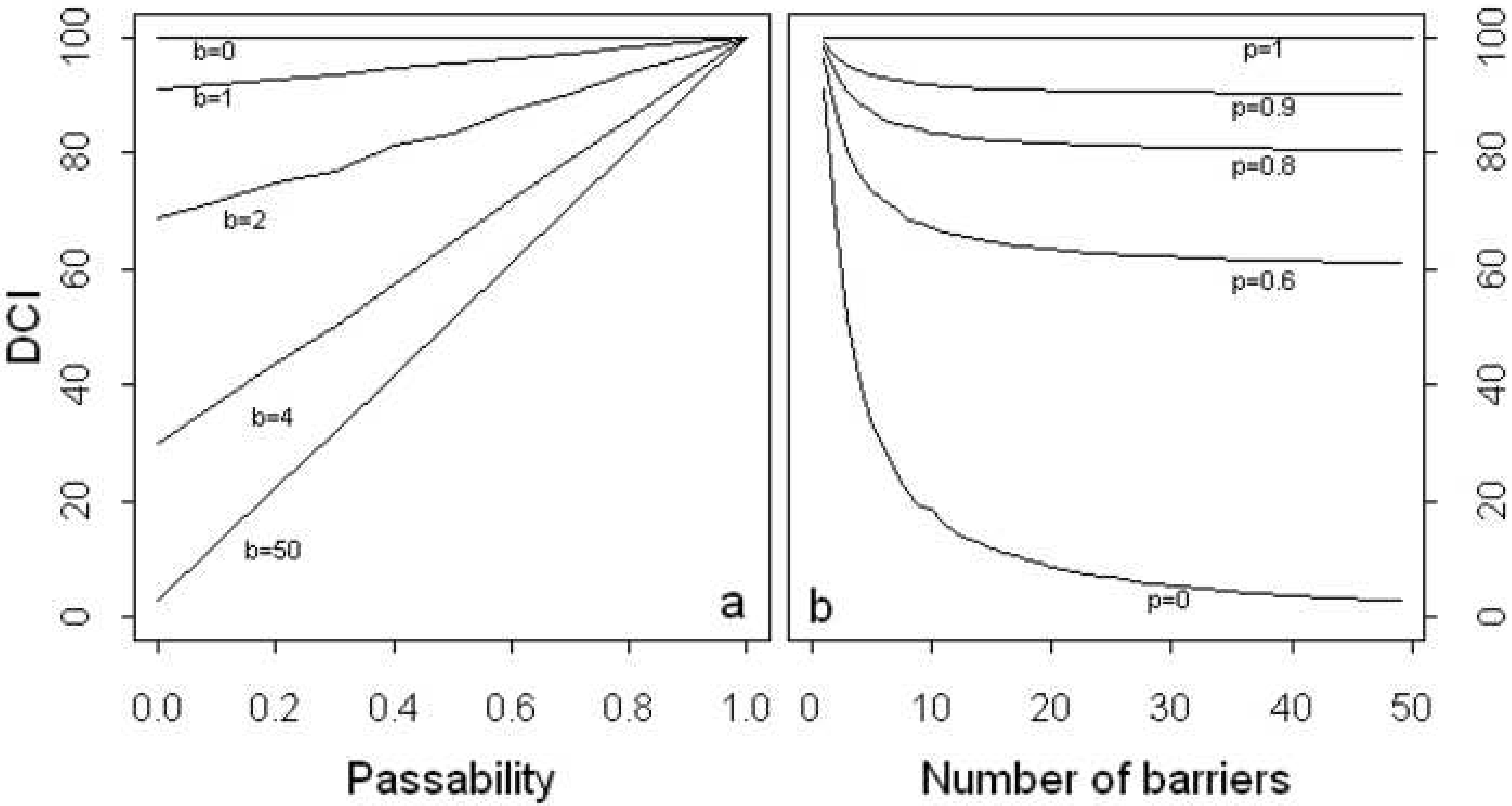

Fig. 6

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