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Title: Assessing the Biological Relevance of Aquatic Connectivity to Stream Fish Communities

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23 Abstract:

24       Recent advances in the ability to quantify longitudinal connectivity of riverine systems is  
25 enabling a better understanding of how connectivity affect fish assemblages. However, the role  
26 of connectivity relative to other factors such as land use in structuring biological assemblages is  
27 just emerging. We assessed the relevance of a structural connectivity index to stream fish  
28 communities in five watersheds and examined whether species' sensitivities to connectivity are  
29 in accordance with expectations of life history. While controlling for the confounding effect of  
30 land use, elevation, and stream topology, we demonstrate that structural connectivity explains  
31 significant amounts of variation in community structure (1 to 5.4% as measured by Bray-Curtis  
32 similarity) and single species metrics (3 of 7 species abundances). The lower explanatory power  
33 of our models compared to studies done at smaller scales suggests that the relevance of  
34 connectivity to fish communities is scale dependent and diminishes relative to other  
35 environmental factors at larger spatial extents.

36 Keywords: Fragmentation, Structural Connectivity, Functional Connectivity

37

38 Introduction:

39       The increased awareness of the effects of anthropogenic structures that may act as  
40 barriers on aquatic ecosystems has prompted new research to understand, quantify, and mitigate  
41 fragmentation impacts (Fullerton et al. 2010). Previous work has focused on individual barriers  
42 and how they influence aquatic communities (Coffman 2005, Mahlum et al. 2014, Warren and  
43 Pardew 1998). However, recent efforts have extended the spatial scope to consider the effects of  
44 multiple potential barriers (Cote et al. 2009, O’Hanley 2011, Padgham and Webb 2010); which  
45 theoretically can act in a cumulative fashion at the scales fish operate.

46       Terrestrial landscape-scale metrics of connectivity have been well studied over the last 30  
47 years, with aquatic environments simply being regarded as a habitat feature embedded within the  
48 terrestrial landscape (Wiens 2002). Increasingly, basic principles from landscape ecology have  
49 been tailored for river ecosystems (Fausch et al. 2002, Ward 1998, Ward et al. 2002). Following  
50 this foundational work, several research efforts have developed ways to measure structural  
51 connectivity that are appropriate for the dendritic nature of aquatic systems. These include score  
52 and ranking methods (Pess et al. 1998, Poplar-Jeffers et al. 2009, Taylor and Love 2003),  
53 optimization techniques (Kemp and O’Hanley 2010, O’Hanley 2011), patch-based graphs (Erős  
54 et al. 2012, Erős et al. 2011, Schick and Lindley 2007), and connectivity indices (Cote et al.  
55 2009, Padgham and Webb 2010). These methods are particularly accommodating and valuable in  
56 prioritizing restoration efforts, as reconnecting aquatic habitats can be costly (Bernhardt et al.  
57 2005, Januchowski-Hartley et al. 2013). However, the use of structural indices are predicated on  
58 being able to efficiently improve ecological integrity by maximizing *assumed* biological gains by  
59 increasing structural connectivity (Cote et al. 2009, O’Hanley 2011, Schick and Lindley 2007),  
60 from the removal or restoration of particular barriers. Although these indices provide

conceptually simple methods to systematically improve structural connectivity, it is poorly understood whether the recommendations yield biologically meaningful results (see Perkin and Gido 2012 for an exception). It is therefore necessary to understand the limitations (both statistical and ecological) of structural indices at predicting ecological responses in aquatic communities (Kupfer 2012).

One method to assess the ecological relevance of structural indices is to test for relationships between a given structural index and biological community patterns across stream systems with variable degrees of fragmentation. For instance, Perkin and Gido (2012) found a strong relationship between fish community structure, within second and third order stream units, and a structural connectivity index. Understanding the response of structural indices at small spatial extents is an important development, yet it remains unknown whether these relationships will continue to be present at broader spatial extents where confounding variables may have an increased influence on aquatic communities. For example, Branco et al. (2011) found that environmental and human pressures, but not the presence of barriers, were the dominant driver of the distribution of several potamodromous and resident fish species in a 3600 km<sup>2</sup> watershed. However, Branco et al. (2011) acknowledged that they used a relatively simple index of connectivity and called for a more thorough assessment of connectivity at broader spatial extents.

We analyzed the relationship between structural connectivity and patterns in the fish community using data from five 5<sup>th</sup> and 6<sup>th</sup> order watersheds in southern Ontario, Canada, (ranging in extent from 98 km<sup>2</sup> - 283 km<sup>2</sup>) which have a high degree of biodiversity (regional species richness of 38). The focus of this study was to determine if a relatively simple structural index, the Dendritic Connectivity Index (DCI), has biological relevance. Although we expect multiple confounding variables (e.g., elevation, watershed land use, stream network topology) to

contribute to the explanation of patterns in community structure; we expected changes in fish community data in response to variation in the DCI. Specifically, once other habitat factors are accounted for, elevated connectivity will reflect habitat attributes of increased patch size and accessible habitat and should support a broader range of stream biota (Bain and Wine 2009, Peterson et al. 2013). Therefore, it is expected that we would see relative increases in species richness and fish abundance with increases of the DCI. We also tested the importance of the DCI for individual fish species for both presence and abundance data. At an individual species level, we expect to see an increase in species presence and abundance as connectivity increases across sites. Primarily, it is anticipated that individual species that have life histories that require broad scale movements (e.g., salmonids) will be more affected by losses in connectivity than species that may not require the same broad scale movements (e.g., cottids).

#### Methods:

##### *Study Area:*

Southern Ontario exhibits a high degree of freshwater fish biodiversity (Chu et al. 2003). The diversity is attributed to a combination of postglacial dispersal and the anthropogenic introduction of non-native species (Dextrase and Mandrak 2006). The study was conducted in the watersheds of Wilmot, Oshawa, Ganaraska, Cobourg, and Duffins in southern Ontario, just east of the metropolitan area of Toronto (Figure 1). The five watersheds studied are dominated by developed urban areas at their confluence with Lake Ontario, agricultural landscape in the mid reaches, and a mixture of forest and low intensity agriculture in the headwaters. They range in watershed size of 98 km<sup>2</sup> for Wilmot to 283 km<sup>2</sup> for Ganaraska.

##### *Data Layers:*

107 Fish community data and habitat variables (including the structural index) were  
108 incorporated into the analysis (Table 1). Fish sampling was conducted from 1997 to 2009 by  
109 various agencies as part of a collaborative monitoring program (TRCA, 2010) using the Ontario  
110 Stream Assessment Protocol (Stanfield 2010). Sample site locations are based on random  
111 stratified designs to characterize conditions within stream segments. A handful of long-term  
112 monitoring sample sites were initially selected based on their representative conditions which  
113 were averaged across sampling periods to eliminate pseudo-replication. Sites were a minimum  
114 length of 40 m and were bounded by “crossovers” (where the thalweg crossed to the opposite  
115 side of the stream) to ensure adequate sampling of all habitat types (Stanfield 2010).  
116 Furthermore, sample site lengths reflect from 5 to 10 bankfull widths and have been shown to  
117 provide reliable measures of fish assemblages across time and space for this study area (Stanfield  
118 et al., 2012). Single-pass electrofishing was used to capture fish at a targeted effort of 7 to 15  
119 s/m<sup>2</sup>. All fish were measured, weighed, and identified to species with the exception of lampreys  
120 (*Petromyzontidae*), which were identified to family due to inconsistencies in identification to the  
121 species level. Finally, we also excluded 16 sites from the analysis that appeared to exhibit  
122 difficulties with identification of one or more individuals to the species level.

123 *Connectivity index:*

124 To measure the structural connectivity across the 5 watersheds, we employed the  
125 Dendritic Connectivity Index (Cote et al. 2009). The DCI is calculated based on the probability  
126 that an individual can move freely among random points in a dendritic network. This takes into  
127 consideration the amount of potential habitat between barriers along with a measure of  
128 passability for each barrier. Furthermore, the DCI is flexible in that it can be modified to address  
129 the natural connectivity of a stream based on both potamodromous (DCI<sub>p</sub>) and diadromous

(DCI<sub>d</sub>) life histories. The DCI<sub>p</sub> applies to life histories of species that typically live in riverine systems and do not require diadromous migration. DCI<sub>p</sub> is defined as:

$$D_p = \frac{\sum_{i=1}^n \sum_{j=1}^n c_{ij} \frac{l_i l_j}{L^2}}{1}$$

where  $l$  is the length of the segment  $i$  and  $j$ ,  $c_{ij}$  is the connectivity between segments  $i$  and  $j$ , and  $L$  is the total stream length of all stream segments. The DCI<sub>d</sub> applies to all life histories that migrate between a fixed point (e.g., estuary) and all upstream areas within a riverine system. DCI<sub>d</sub> is calculated as:

$$D_d = \frac{\sum_{i=1}^n c_i l_i}{L}$$

where  $L$  is the total length of the stream sections,  $l_i$  is the length of section  $i$ ,  $c_{ij}$  is the connectivity between segments  $i$  and  $j$ . While the DCI<sub>p</sub> and DCI<sub>d</sub> measure the overall connectedness of a system, it could be beneficial to apply a structural connectivity metric at finer spatial scales (e.g., stream reach) to control for local pressures of connectivity on the biotic community. As noted in Cote et al. (2009), the DCI<sub>d</sub> can be applied to measure the connectivity from any stream segment to the rest of the watershed. We denote this value as DCI<sub>s</sub>, and used this in models for data collected at the scale of the stream segment. We used the Fish Passage Extension (FIPEX v2.2.1) for ArcGIS (v9.3.1) using a hydrological stream network provided by OMNR to calculate connectivity scores ( $c_{ij}$ ) described above.

#### *Determining barrier passability:*

Identifying all potential barriers in a system is imperative in order to accurately assess connectivity (Cote et al. 2009, Januchowski-Hartley et al. 2013, O’Hanley 2011). A list of barrier locations was provided by OMNR which consisted of 298 locations of dams, perched culverts, and natural barriers across the 5 watersheds used in this study. We also used the

152 National Hydro Network obtained via GeoBase (<http://www.geobase.ca/>) to identify dams not in  
153 the OMNR dataset. Furthermore, road culverts are thought to outnumber dams by up to 38 times,  
154 with as much as 2/3 being designated as complete or partial barriers to fish movement  
155 (Januchowski-Hartley et al. 2013). Therefore, to help identify potential barriers not in the OMNR  
156 database, we used ArcGIS and files from GeoBase to identify intersections between streams  
157 (National Hydro Network) and roads (National Road Network) that would indicate a potential  
158 barrier and help create an inclusive barrier database to calculate the DCI. All sources of barrier  
159 locations were cross checked to prevent multiple occurrences of the same barrier in the dataset.  
160 We calculated and analyzed the DCI with regards to community structure and species richness  
161 with only known barriers and then again with the inclusion of potential barriers identified  
162 through GIS (stream/road intersections). The intent of this analysis was to provide insight into  
163 GIS-derived barrier locations and the potential benefits of modeling all potential barrier  
164 locations.

165 Determining passability values for potential barriers in these watersheds was challenging  
166 due to their vast number and the limited information available for them. This limitation is not  
167 unique to this study and underscores some of the common obstacles to riverscape-scale analyses  
168 in larger watersheds (for an example see Meixler et al. 2009). For the DCI, passabilities are  
169 defined as a value between 0 (impassable) and 1 (fully passable). Passability scores of zero were  
170 first assigned to all dams and perched culverts. Culverts were considered perched when the outlet  
171 bottom elevation was greater than the height of the outlet pool (Stanfield 2010). The remaining  
172 75% of potential barriers lacked a passability score. Previous studies have found a relationship  
173 between culvert passabilities and channel slope (McCleary and Hassan 2008, Poplar-Jeffers et al.  
174 2009), and we followed this approach to infer values for barriers with unknown passability. We



175 used an available data set from Terra Nova National Park (TNNP), Newfoundland, Canada that  
 176 contained both passability scores and channel slopes. Passabilities in TNNP were calculated  
 177 using FishXing (Furniss et al. 2006) and were based on the percent of time stream flows were  
 178 within a passable range for brook trout (*Salvelinus fontinalis*). We calculated channel slope for  
 179 culverts in Newfoundland and Ontario using a 10-m digital elevation model (DEM) by creating a  
 180 100 m diameter buffer around the barrier and taking the difference in elevation between the  
 181 farthest upstream and downstream points and then dividing by the stream length between those  
 182 points. Finally, we used a nonlinear regression model,

$$183 \quad 1 - \left( \frac{P}{1 + e^{-x}} \right) + \varepsilon_i$$

184 where  $i = 1$  to number of culverts ( $N$ ),  $p$  is passability,  $x$  is channel slope, and  $\varepsilon_i \sim N(0, \delta^2)$ , to  
 185 estimate the relationship between culvert passability and channel slope in TNNP. This model fits  
 186 a sigmoidal curve with a fixed passability of 1, when channel slope is 0. We then applied that  
 187 relationship to the channel slopes associated with potential barriers in southern Ontario.

#### 188 *Accounting for confounding variables:*

189 It is known that stream process and patterns are continually changing along the  
 190 longitudinal gradient of the stream (Vannote et al. 1980) and these changes can significantly  
 191 affect the biotic community (Fausch et al. 2002). Some of these influences can be segregated into  
 192 habitat variables (e.g., elevation and stream width) and landscape use (e.g., urban and farmland).  
 193 Several factors were incorporated into our analysis to control for confounding effects that  
 194 influence community structure (see Table 1). These included elevation (Rahel and Hubert 1991,  
 195 Stanfield and Kilgour 2006), land cover (Allan et al. 1997, Allan 2004, Stanfield and Kilgour  
 196 2006), stream network topology (Betz et al. 2010, Hitt and Angermeier 2008), and stream width  
 197 (Cote 2007). We extracted elevation (ELE) for each sampling site from a 10-m DEM obtained

198 from OMNR. Land cover metrics that were thought to influence stream biota were quantified  
199 using the Southern Ontario Land Resource Information System (SOLRIS; Ontario Ministry of  
200 Natural Resources 2006) by determining the percentage of the watershed in each land cover type  
201 (Table 1). Using a metric analogous to stream order, we quantified the hydrological locations of  
202 sampling sites within the dendritic network using the Upstream Cell Count (UCC) which  
203 consists of the total amount of linear stream habitat above a sampling location (see Betz et al.  
204 2010 for a detailed description). Lastly, stream width (SW) was measured during biological  
205 sampling by taking an average of 10 transects measuring SW throughout the sampling site  
206 (Stanfield 2010).

207 To select co-variables (Table 1) for the inclusion in our analysis, we used Akaike's  
208 Information Criteria (AIC) to select a candidate model that best explains the data and  
209 subsequently can be used for the inclusion of confounding variable in the following analysis of  
210 community structure, species richness, and species abundance (Akaike 1973, Burnham and  
211 Anderson 2002, Oksanen et al. 2012). Before we identified candidate models, we removed  
212 collinear variables (Spearman's rank correlations  $> 0.7$ ). Next using variables identified in Table  
213 1, *a priori* candidate models were created for the distance-based redundancy analysis (db-RDA,  
214 described below) on community similarities ranging from simple (single variable) to more  
215 complex (maximum 9 variables in our global model). To assess how well co-variables  
216 contributed to explaining the community data, we calculated the  $\Delta AIC$  (difference in AIC values  
217 from the model with the smallest AIC value) and AIC weights (the amount of support that a  
218 given model is the best). Only models that were within  $\Delta AIC < 2$  of the top model were  
219 considered for the inclusion in the analysis (Burnham and Anderson 2002). To maintain  
220 consistency between the analyses of community structure, species richness, and species

221 abundances, we incorporated the same variables identified through the model selection procedure  
222 for all levels of analysis.

223 *Analysis:*

224

225 *Is fish community similarity related to the DCI metrics?*

226 A multivariate db-RDA was used to analyze how connectivity, as measured by the DCI<sub>s</sub>,  
227 DCI<sub>p</sub>, and DCI<sub>d</sub>, affects community structure based on species abundances (Legendre and  
228 Anderson 1999). Distance based redundancy analysis is a robust analytical method used to assess  
229 the relationship between meaningful measures of species associations (e.g., Bray-Curtis index)  
230 and fixed effects within a linear model framework. Furthermore, we chose to use a db-RDA to 1)  
231 accommodate for non-Euclidean distance measures used in community similarity metrics; 2)  
232 control for confounding variables; and 3) use nonparametric permutation methods which freed us  
233 from the assumption of normality (Legendre and Anderson 1999). Prior to the multivariate  
234 analysis, a fourth root transformation of the abundance data was employed to emphasize  
235 diversity (Clarke and Warwick 2001). Then, we used the Bray-Curtis Index (Bray and Curtis  
236 1957) as a measure of the similarity of the fish communities between sites because of its  
237 robustness and appropriateness for ecological community data (Clarke and Warwick 2001, Faith  
238 et al. 1987). Finally, a correction factor was not incorporated for the negative-eigenvalues to  
239 correct for Type 1 errors based on McArdle and Anderson (2001). Significance was determined  
240 by a pseudo-F statistic at  $\alpha = 0.05$ .

241

242 *Is DCIs related to fish species richness?*

We used a generalized linear mixed model (GLMM) approach to test the effects of connectivity as determined by the DCI<sub>s</sub> on species richness. Treating watershed as a random effect allowed us to account for the potential pseudo-replication within watersheds (Bates et al. 2011). Species richness was quantified by calculating the total number of fish species at each site. For sites with repeated sampling, species richness was averaged across sampling periods. Our approach to calculate species richness was chosen to provide a more accurate measure of this indicator than the single “most recent” observation that was used in the analyses by Stanfield and Kilgour (2006). Averaging richness across sampling events captures temporal variability and minimizes effects of sampling bias/error, but potentially undervalues diversity where sampling effort was lower (Kennard et al. 2006, Stanfield et al. 2013). Finally, using the GLMM, we analyzed the relationship between the DCI<sub>s</sub> and the species richness of a site while controlling for confounding variables previously identified. All variables but watershed were treated as fixed effects. Significance was determined by the z-statistic at alpha = 0.05.

#### *Is DCIs related to presence and abundance of individual species?*

We also tested to see how connectivity, calculated with known barriers and potential barriers, affected the presence and abundance of individual species. Seven relatively abundant species across three families were selected to represent a wide range of life history characteristics (e.g., diadromous) and that were also relatively abundant across sites (Table 2 and 3). We again used a GLMM approach, with presence modeled as binomial and abundance as a Poisson response variable. Watershed was treated as a random effect to account for potential pseudo-replication of observations within watersheds. The same confounding variables identified in the model selection procedures described above were also included as fixed effects. Because the

266 abundance data exhibited considerable overdispersion, we used a resampling approach (Markov  
267 Chain Monte Carlo) to assess significance (Hadfield 2010). All statistical analysis was carried  
268 out with the statistical program R (v. 2.15.2, R Development Core Team 2012).

269

270 Results:

271 A total of 273 stream sites were selected across 5 watersheds (range of 27 to 70 sites per  
272 watershed). We used the selected sites for all levels of analysis within this study. A total of 38  
273 species were sampled across the study sites with a mean of 25.4 species per watershed (range =  
274 21 to 28). In addition to the 298 barriers identified by OMNR, we identified an additional 85  
275 dams and 1,041 potential barriers. The relationship between stream slope and passability  
276 obtained from barriers in Terra Nova National Park was reasonably strong ( $r^2 = 0.68$ ; Figure 2).  
277 When applied to potential barriers in southern Ontario, the predicted passabilities of un-surveyed  
278 barriers ranged from 0.0 to 0.99 with the passabilities strongly skewed towards the right, which  
279 indicates greater passability (Figure 3). Calculated connectivity scores for our study area  
280 watersheds in southern Ontario ranged from 0.0 to 41.1 for  $DCI_s$  at the site scale, 14.9 to 22.6 for  
281 the  $DCI_p$ , and 0.3 to 31.2 for the  $DCI_d$ , the latter two versions calculated at the watershed scale  
282 (Table 4).

283 Twenty-two different models were analyzed with AIC scores (Table 5). Results of the  
284 Spearman's correlation matrix indicated that SW and UCC were highly correlated ( $r = 0.8$ ). As a  
285 result, we did not include SW and UCC in the same model. The top model for the db-RDA of  
286 community similarity ( $\Delta AIC < 2$ ) included ELE, SW, and the land cover metric of built-up area-  
287 pervious (BUAP), which indicates areas of urban development. All other additional confounding  
288 variables did not adequately explain community structure given the dataset and were represented

289 in models that had  $\Delta AIC > 2$ . The top model had a weight of evidence of 80 percent in support of  
290 the top model, and to maintain consistency between the different analyses, we elected to use  
291 ELE, SW, and BUAP to control for confounding effects in subsequent facets of our analysis.  
292 Furthermore, while it is likely that we would identify that the selected variables would relate  
293 differently to each level of analysis (e.g., community structure vs individual species) and within  
294 different univariate analyses (e.g., individual species), we chose to run a single model selection  
295 procedure to simplify the analysis and subsequent interpretation of the results between the  
296 different levels of the analysis. Moreover, we also found that several variables (e.g., elevation  
297 and stream width) remained consistent between this study and other studies within the same  
298 geographic area (see Stanfield et al. 2006), indicating that we would gain relatively little from  
299 additional model selection procedures.

300 We explained 21.1, 21.4, and 24.4 percent of the total variation in species composition  
301 with the db-RDA models used to analyze the relationships between the  $DCI_s$ ,  $DCI_p$ , and  $DCI_d$ ,  
302 calculations based on known barriers, and community structure for abundance data. Furthermore,  
303 we used a type III sum of squares and found all three co-variables significantly related to  
304 community structure in all three models (Models 1-3; Table 6). The  $DCI_s$ ,  $DCI_p$ , and  $DCI_d$  was  
305 significantly related to community structure as well ( $F = 3.67$ ,  $df = 1$ ,  $p < 0.01$ ;  $F = 4.74$ ,  $df = 1$ ,  
306  $p < 0.005$ ;  $F = 15.64$ ,  $df = 1$ ,  $p < 0.005$  respectively). A positive correlation was also seen for the  
307  $DCI_s$  ( $r = 0.65$ ) and  $DCI_d$  ( $r = 0.48$ ) for axis 1 and a negative correlation was seen for the  $DCI_p$   
308 with axis 2 ( $r = -0.67$ ).

309 The db-RDA models used to analyze the relationships between the  $DCI_s$ ,  $DCI_p$ , and  $DCI_d$ ,  
310 calculated with known barriers and potential barriers, and community structure for abundance  
311 data, with the co-variables of ELE, SW, and BUAP, explained 21.9, 22.2, and 24.4 percent of the

total variation in species composition respectively (Models 4-6; Table 6 and Figure 4). Using additional barrier information derived from GIS data modestly improved our models and the amount of variation explained with our connectivity metric by 1.5, 1.3, and 0.0% respectively. Following the trends with the models which used only known barriers (models 1-3), we found that all confounding variables for models 4-6 significantly explained community structure (Table 6). In these models, the  $DCI_s$ ,  $DCI_p$ , and  $DCI_d$  were also significantly related to community structure ( $F = 6.37$ ,  $df = 1$ ,  $p < 0.005$ ;  $F = 7.64$ ,  $df = 1$ ,  $p < 0.005$ ;  $F = 15.52$ ,  $df = 1$ ,  $p < 0.005$  respectively). However, the directions of the relationships were confounded between models for elevation, stream width, BUAP and  $DCI_s$  (Table 6).

Species richness was not associated with changes in connectivity based on known barriers ( $DCI_s$ ;  $z = 1.26$ ,  $n = 273$ ,  $p\text{-value} = 0.204$ ; Figure 5a). However, when we included potential barriers into the DCI calculation, species richness became weakly correlated with the  $DCI_s$  ( $z = 1.99$ ,  $n = 273$ ,  $p\text{-value} = 0.047$ ; Figure 5b) as were ELE and SW ( $z = -0.003$ ,  $n = 273$ ,  $p\text{-value} < 0.001$ ;  $z = 0.05$ ,  $n = 273$ ,  $p\text{-value} < 0.001$  respectively). However, the land cover variable used (BUAP) did not show a significant relationship with species richness ( $z = 0.068$ ,  $n = 273$ ,  $p\text{-value} = 0.058$ ).

The presence of only two species had a positive relationship with the  $DCI_s$ : rainbow trout (*Oncorhynchus mykiss*) and mottled sculpin (*Cottus bairdii*;  $z = 0.07$ ,  $n = 273$ ,  $p\text{-value} = <0.001$  and  $z = 0.017$ ,  $n = 273$ ,  $p\text{-value} = <0.001$  respectively; Table 2). Furthermore, abundance increased for rainbow trout (mean = 0.07,  $n = 273$ ,  $p\text{-value} = 0.001$ ), mottled sculpin (mean = 0.09,  $n = 273$ ,  $p\text{-value} = 0.001$ ), and longnose dace (mean = 0.05,  $n = 273$ ,  $p\text{-value} = 0.014$ ; *Rhinichthys cataractae*) with an increase in the  $DCI_s$  (Table 3; Figure 6). At least one

confounding variable had a significant relationship in the individual species analysis, where ELE was the dominant predictor variable most commonly seen between the species.

#### Discussion:

The use of connectivity indices as a tool to assess the fragmentation of a system and assist in prioritizing restoration efforts can be a valuable asset in reconnecting aquatic habitat patches. While minimal, we demonstrated that the DCI has biological relevance with regards to understanding fish communities and individual species distribution and abundance, even in the presence of confounding variables such as elevation, stream width, and land cover. Although it is necessary to address alternate pressures simultaneously when improving biological connectivity, selecting barriers to restore based on structural gains in connectivity can contribute to recovery and persistence of the aquatic community.

This conclusion is also consistent with findings by Perkin and Gido (2012) who found a significant relationship between the same connectivity index analyzed here and community structure within relatively fine scale study units consisting of second and third order streams. However, the fine spatial extents examined in that study likely minimized confounding variables and showed a much stronger relationship between connectivity and fish communities ( $r^2 = 0.66$ ). Since the importance of environmental factors to stream biota is often scale-dependent (Fausch et al. 2002, Poff 1997, Wiens 2002), it remains unknown whether links between structural connectivity and communities will persist at spatial extents broader than the present study. However, it has been shown that increases in interpatch distance significantly decrease landscape connectivity (Goodwin and Fahrig 2003) and it could be expected that the same trends would persist in aquatic environments. Structural indices have been increasingly used to determine the



357 degree of connectivity across watersheds but interpretation of these results are hampered by the  
358 lack of demonstrations of biological relevance to aquatic ecosystems (Tischendorf and Fahrig  
359 2000). Understanding these relationships is important to provide context into the appropriateness  
360 and limitations of simple structural indices, such as the DCI, and their use in aquatic ecosystems.

361         The biology of the species in this study likely impacted the sensitivity of the species to  
362 structural connectivity. This study found relationships between the DCI<sub>s</sub> and the abundance of  
363 several species. As expected, we found species that require extensive movements during their  
364 life history (e.g., rainbow trout) were significantly influenced by a lack of longitudinal  
365 connectivity (DCI<sub>s</sub>). In contrast, other species (mottled sculpin and longnose dace), less known  
366 for extensive migration (Johnston 2003), were also influenced by the presence of anthropogenic  
367 barriers. Past studies have found local scale effects of barriers on small stream fishes (Coffman  
368 2005, Norman et al. 2009, Warren and Pardew 1998). However, as documented by Meixler et al.  
369 (2009), it appears that local scale effects of barriers can translate into population wide impacts on  
370 the persistence of at least some small stream fishes. Furthermore, some of our species-specific  
371 expectations with regards to connectivity did not bear out. For example, we expected brook trout,  
372 a native species to the study area, would be more affected by losses in connectivity than other  
373 species because they require a variety of habitats throughout their life cycle, which could result  
374 in long migrations (Gowan and Fausch 1996). However, the presence of anthropogenic barriers  
375 did not seem to have a significant relationship with brook trout abundance. This may be  
376 attributed to low abundance or confounding variables not modeled in this study. For instance,  
377 brown trout (*Salmo trutta*) impact brook trout through competition of important habitat (e.g.,  
378 spawning habitat and refugia) and predation (Fausch and White 1981). Similarly, others (e.g.,  
379 Stanfield et al. 2006) have found that brook trout distribution and abundance in this area are

affected by the cumulative effects of competition from multiple salmonids and land use. Supporting Fausch and White (1981) and Stanfield et al (2006), we found a strong elevation influence between these two species implying that brook trout are being pushed into the headwaters where competition is lessened. Although fragmentation may be a factor in the eventual recovery of brook trout and other salmonids, it appears that other confounding variables currently have a greater impact on the persistence of this species. Continuing to improve our understanding of the role of fragmentation in species distributions will assist managers in the recovery of imperiled species and how to mitigate the effects of anthropogenic disturbances.

In the absence of anthropogenic barriers, alternate pressures can influence ecological processes and patterns (Fagan 2002, Hargis et al. 1999). In addition to the modest effects of the DCI, elevation, stream width, and land cover had a strong relationship with community structure as well as with individual species (as observed by Stanfield et al. 2006). This supports previous connectivity studies that found environmental factors affected metapopulations (e.g., land cover and water quality; Branco et al. 2011, Meixler et al. 2009). Confounding variables such as the ones modeled here are an important aspect associated with stream communities and controlling for these environmental variables will help assist in determining how structural indices influence stream biota.

Presenting connectivity at watershed scales is useful to estimate watershed health or to prioritize restoration actions, but can be limiting for analyses aimed at local scales (e.g., studies targeting site-specific relationships between fish communities and habitat variables; Cote 2007). To address the need for locally-focused studies, we modified this watershed scale index into a local habitat variable ( $DCI_s$ ) and matched it to corresponding biotic information. We consider this a useful addition to typical quantification methods of connectivity that either focused

403 primarily on barrier prioritization (Kemp and O'Hanley 2010, O'Hanley 2011, Poplar-Jeffers et  
404 al. 2009) or are overly simplistic (e.g., count of the number of barriers; Branco et al. 2011), and  
405 therefore miss important aspects of fragmentation (for a review see Kindlmann and Burel 2008,  
406 Padgham and Webb 2010). Measuring connectivity at a scale coincident with other aquatic  
407 community variables will expand the understanding of how connectivity processes relate to biota  
408 and will be useful in theoretical and management applications.

409 Identifying barrier locations is an important aspect in the management of aquatic systems.  
410 The failure to account for all barriers may result in costly management actions that produce  
411 negligible ecological benefits if the analysis fails to identify limiting factors (Bernhardt et al.  
412 2005, Januchowski-Hartley et al. 2013). Although minimal barrier information (known barriers)  
413 significantly explained community structure, we saw an improvement with the inclusion of  
414 potential barriers (stream/road intersections) both in explaining community structure and species  
415 richness. This conclusion lends support to Januchowski-Hartley et al. (2013) who advocate for  
416 the incorporation of all potential barriers into current barrier databases.

417 We had relatively low explanatory power to explain community structure and species  
418 richness and we were unable to predict abundance of several species (4 of 7 species) with aquatic  
419 connectivity. One explanation could be in our methodology for calculating passability.  
420 Identifying the passability of barriers was the largest obstacle in assessing connectivity over the  
421 relatively large study area. While direct site evaluations of all known and potential barriers in a  
422 system is recommended and could potentially improve our predictive power, the large number of  
423 barriers within this study required us to identify an alternate method to assess passability. A  
424 priority for future work in these watersheds should be a more comprehensive inventory of dams  
425 on private lands (e.g., ponds). The use of GIS allowed us to identify potential barriers based on

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sampling of barriers

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see what you think.

426 locations where streams and roadways intersected. However, assigning passability values  
427 required estimates based on known relationships with channel slope in another well studied area.  
428 Furthermore, our passabilities were based on brook trout movements. This is not appropriate for  
429 all species and likely overestimates passage for many species (e.g., Cyprinidae; Coffman 2005,  
430 McLaughlin et al. 2006). Thus functional connectivity for these species may actually be lower in  
431 these five watersheds than predicted by our model. Similarly, for species (e.g., *Salmo salar*)  
432 thought to have higher swimming/jumping ability than brook trout, these watersheds may  
433 actually have higher functional connectivity than predicted here. While the relationship between  
434 channel slope and passability allowed us to identify potential barrier passabilities, it is  
435 recommended that managers accurately inventory and assess the passability of all barriers across  
436 study areas to allow them to maximize habitat gains with current connectivity models.

437       Based on organisms' response to fragmentation in terrestrial systems, it is reasonable to  
438 expect that thresholds of aquatic connectivity also exist and are associated with the biology of  
439 the focal organism or community. Within our five watersheds, only the lower end of the  
440 connectivity spectrum were captured and thus critical thresholds may exist outside the range  
441 studied here. Capturing the full spectrum of possible connectivity scores at watershed scales may  
442 be difficult as pristine and highly fragmented stream systems will likely differ from one another  
443 in many other ways. However, identifying ecological thresholds for connectivity will assist with  
444 setting management goals for protection and recovery of focal species..

445       As in terrestrial landscape ecology, where work has been done to link structural  
446 connectivity metrics with ecological response (i.e., functional connectivity, Kindlmann and Burel  
447 2008, Tischendorf and Fahrig 2000), we have shown that aquatic structural connectivity indices  
448 can do the same. The structural indices, derived from relatively straightforward physical

parameters (e.g., stream length, barrier properties), help to explain biologically relevant phenomena such as habitat quality and observed fish movement across barriers. It remains necessary to further incorporate the organisms' perceptions of its landscape into structural indices to achieve meaningful measures of connectivity (Kindlmann and Burel 2008), but doing so comes with tradeoffs such as increased data requirements, computational complexity, and decreased ease of interpretation (Kupfer 2012). Moreover, incorporating more functional metrics without understanding their limitations may not necessarily increase their validity (Kupfer 2012). Recent work by Bourne (2013) found that incorporating a more functional habitat variable into structural indices influenced the magnitude of fragmentation of a system but not necessarily the qualitative conclusions (i.e., prioritization of the restoration action) when compared to physical properties of habitat. This indicates that, at least in some cases, simple physical measurements may be appropriate, and can save considerable time and resources.

Considerable work remains to understand how processes associated with aquatic connectivity relates to faunal communities. The availability of structural connectivity metrics and indices that have been evaluated for their ecological relevance and an understanding of their limitations will prove useful in future research and management efforts in this field.

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641 Tables:

642 Table 1: Categories of variables used in the analysis with the associated symbol used within the  
643 text. Predictions of the db-RDA for abundance is included in the table with (+) indicating a  
644 predicted change in community structure and (-) indicating no predicted change in community  
645 structure.

646

Category	Variable	Symbol	Units
Fish Community	Abundance	A	Count
Structural Index	DCI <sub>d</sub>	DCI <sub>d</sub>	Percentage of natural connectivity
	DCI <sub>p</sub>	DCI <sub>p</sub>	Percentage of natural connectivity
	DCI <sub>s</sub>	DCI <sub>s</sub>	Percentage of natural connectivity
Stream Position	Up-Stream Cell Count	UCC	Count
	Elevation	ELE	Meters
	Stream Width	SW	Meters
Land Cover	Build-up area Pervious	BUAP	Proportion of watershed
	Build-up area Impervious	BUAI	Proportion of watershed
	Cropland	CR	Proportion of watershed
	Pasture and Abandoned Fields	PAF	Proportion of watershed
	Mixed forest	MF	Proportion of watershed
	Deciduous forest	DF	Proportion of watershed

Table 2. The results of the single species presence analysis. Predictions represent the expected relationship between the species and variable. Positive values indicate that species presence is predicted to increase with increases in the corresponding variable while negative values indicate that species presence is predicted to decrease with increases in the corresponding variable.

Species	Prediction	Variable	n	Estimate	SE	z-value	p-value
<i>Oncorhynchus mykiss</i>	+	ELE	273	-0.018	0.004	-4.417	< 0.001*
	-	BUAP		-0.518	0.467	-1.111	0.267
	+	SW		0.111	0.057	1.936	0.053
	+	DCI <sub>s</sub>		0.058	0.016	3.757	< 0.001*
<i>Salmo trutta</i>	+	ELE	273	0.003	0.004	0.718	0.473
	-	BUAP		-0.837	0.217	-3.854	< 0.001*
	+	SW		0.349	0.062	5.641	< 0.001*
	+	DCI <sub>s</sub>		0.020	0.016	1.255	0.209
<i>Salvelinus fontinalis</i>	+	ELE	273	0.030	0.005	6.471	< 0.001*
	-	BUAP		-0.674	0.308	-2.191	0.028*
	+	SW		0.109	0.063	1.723	0.085
	+	DCI <sub>s</sub>		0.002	0.016	0.121	0.903
<i>Rhinichthys obtusus</i>	-	ELE	273	-0.018	0.004	-4.485	< 0.001*
	-	BUAP		0.557	0.282	1.977	0.048*
	-	SW		0.014	0.063	0.214	0.830
	+	DCI <sub>s</sub>		-0.019	0.015	-1.253	0.210
<i>Rhinichthys cataractae</i>	-	ELE	273	-0.018	0.005	-3.721	< 0.001*
	-	BUAP		0.375	0.538	0.696	0.486
	-	SW		0.760	0.112	6.758	< 0.001*
	+	DCI <sub>s</sub>		0.019	0.021	0.883	0.377
<i>Semotilus atromaculatus</i>	-	ELE	273	-0.013	0.003	-4.070	< 0.001*
	-	BUAP		0.531	0.210	2.531	0.011*
	-	SW		-0.051	0.051	-0.990	0.322
	+	DCI <sub>s</sub>		0.008	0.013	0.639	0.523
<i>Cottus bairdii</i>	-	ELE	273	-0.005	0.004	-1.310	0.190
	-	BUAP		0.021	0.560	0.037	0.971
	+	SW		0.196	0.059	3.289	0.001*
	+	DCI <sub>s</sub>		0.081	0.017	4.917	< 0.001*

\* indicates significance at  $\alpha = 0.05$

654 Table 3. The results of the single species abundance analysis. Predictions represent the expected  
655 relationship between the species and variable. Positive values indicate that species abundance is  
656 predicted to increase with increases in the corresponding variable while negative values indicate  
657 that species abundance is predicted to decrease with increases in the corresponding variable.

Species	Prediction	Variable	n	Estimate	SE	p-value
<i>Oncorhynchus mykiss</i>	+	ELE	273	-0.02	0.00	0.001*
	-	BUAP		-0.50	0.02	0.310
	+	SW		0.16	0.00	0.001*
	+	DCIs		0.07	0.00	0.001*
<i>Salmo trutta</i>	+	ELE	273	0.02	0.00	0.001*
	-	BUAP		-0.96	0.02	0.082
	+	SW		0.42	0.00	0.001*
	+	DCIs		0.02	0.00	0.126
<i>Salvelinus fontinalis</i>	+	ELE	273	0.03	0.00	0.001*
	-	BUAP		-0.62	0.02	0.084
	+	SW		0.02	0.00	0.792
	+	DCIs		-0.01	0.00	0.722
<i>Rhinichthys obtusus</i>	-	ELE	273	-0.02	0.00	0.001*
	-	BUAP		0.58	0.02	0.154
	-	SW		-0.07	0.00	0.212
	+	DCIs		0.00	0.00	0.756
<i>Rhinichthys cataractae</i>	-	ELE	273	-0.02	0.00	0.001*
	-	BUAP		0.06	0.04	0.920
	-	SW		0.65	0.00	0.001*
	+	DCIs		0.05	0.00	0.014*
<i>Semotilus atromaculatus</i>	-	ELE	273	-0.02	0.00	0.001*
	-	BUAP		0.74	0.03	0.262
	-	SW		-0.18	0.00	0.004*
	+	DCIs		0.00	0.00	0.898
<i>Cottus bairdii</i>	-	ELE	273	-0.01	0.00	0.060
	-	BUAP		0.08	0.06	0.978
	+	SW		0.18	0.00	0.001*
	+	DCIs		0.09	0.00	0.001*

\* indicates significance at  $\alpha = 0.05$

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662 Table 4. Dendritic Connectivity Index scores for each watershed.

Watershed	Known Barriers			Known Barriers with Stream/River Intersects		
	DCI <sub>p</sub>	DCI <sub>d</sub>	DCI <sub>s</sub> Range	DCI <sub>p</sub>	DCI <sub>d</sub>	DCI <sub>s</sub> Range
Duffins	35.4	2.3	0.0 - 58.52	16.1	1.7	0.0 - 35.0
Oshawa	24.2	42.0	0.0 - 46.63	16.8	24.8	0.4 - 33.7
Cobourg	20.4	32.4	0.0 - 32.35	14.9	22.1	0.0 - 26.2
Ganaraska	24.4	0.4	0.0 - 46.63	18.4	0.3	0.5 - 39.1
Wilmot	51.3	67.0	0.0 - 67.02	22.6	31.2	14.9 - 41.1

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665 Table 5. The results of co-variable selection based on the Akaike's Information Criterion for 22  
666 combinations of predictor variables against the db-RDA of community similarity using  
667 abundance data (CS).

Model	K	AIC	$\Delta$ AIC	Exp	Weight
CS ~ ELE + SW + BUAP	4	1181.69	0.00	1.000	0.805
CS ~ ELE + UCC + BUAP	4	1184.79	3.09	0.213	0.171
CS ~ ELE + SW + BUAI	4	1189.69	8.00	0.018	0.015
CS ~ ELE + UCC + BUAI	4	1192.71	11.01	0.004	0.003
CS ~ ELE + SW + PAF	4	1194.27	12.58	0.002	0.001
CS ~ ELE + SW + FAP	4	1194.27	12.58	0.002	0.001
CS ~ ELE + SW + MF	4	1194.54	12.85	0.002	0.001
CS ~ ELE + SW + DF	4	1197.75	16.05	0.000	0.000
CS ~ ELE + UCC + PAF	4	1197.76	16.06	0.000	0.000
CS ~ ELE + UCC + FAP	4	1197.76	16.06	0.000	0.000
CS ~ ELE + SW + CR	4	1197.90	16.21	0.000	0.000
CS ~ ELE + SW + CR	4	1197.90	16.21	0.000	0.000
CS ~ ELE + UCC + MF	4	1198.08	16.39	0.000	0.000
CS ~ ELE + UCC + MF	4	1198.08	16.39	0.000	0.000
CS ~ ELE + SW	3	1201.23	19.54	0.000	0.000
CS ~ ELE + UCC + DF	4	1201.56	19.87	0.000	0.000
CS ~ ELE + UCC + CR	4	1202.14	20.44	0.000	0.000
CS ~ ELE + UCC	3	1205.64	23.95	0.000	0.000
CS ~ ELE	2	1211.63	29.93	0.000	0.000
CS ~ SW	2	1216.68	34.98	0.000	0.000
CS ~ UCC	2	1219.02	37.32	0.000	0.000
<sup>a</sup> CS ~ ELE + UCC + SW + BUAP + BUAI + CR + PAF + MF + DF	8	1226.36	44.66	0.000	0.000

668 <sup>a</sup> Represents the global model (model that includes all variables) used in the model selection.  
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670 Table 6. The output of 6 different models for abundance to determine the relationship between  
671 longitudinal connectivity as measured by the Dendritic Connectivity Index (Cote et al. 2009) and  
672 community structure as measured by the Bray-Curtis similarity. Abundance 1 models used DCI  
673 values calculated with only known barriers whereas Abundance 2 models used DCI values  
674 calculated with known barriers and potential barriers.

Model	df	% Variation Explained	Pseudo-F	p-value	Axis 1	Axis 2
Abundance 1:						
Full Model 1	4	21.1	17.93	0.005		
ELE	1	8	17.83	0.005	0.91	-0.16
BUIP	1	8.7	21.79	0.005	0.11	0.88
SW	1	3.8	12.6	0.005	-0.77	-0.28
DCIs	1	1.2	3.76	0.01	-0.49	-0.14
Residuals	268	78.3				
Full Model 2	4	21.4	18.23	0.005		
ELE	1	9.5	20.06	0.005	-0.92	0.17
BUIP	1	6.5	17.11	0.005	-0.13	-0.87
SW	1	3.9	12.82	0.005	0.79	0.25
DCIp	1	1	4.74	0.005	0.31	0.46
Residuals	268	79				
Full Model 3	4	24.4	21.64	0.005		
ELE	1	9.4	20.6	0.005	-0.77	0.54
BUIP	1	6.5	18.01	0.005	-0.43	-0.68
SW	1	4.3	13.65	0.005	0.74	-0.19
DCId	1	5.4	15.64	0.005	0.54	0.41
Residuals	268	74.4				
Abundance 2:						
Full Model 4	4	21.9	18.74	0.005		
ELE	1	7.1	16.63	0.005	-0.88	-0.28
BUIP	1	8.4	21.33	0.005	-0.2	0.85
SW	1	3.6	12.39	0.005	0.77	-0.16
DCIs	1	2.7	6.37	0.005	0.65	-0.16
Residuals	268	78.1				
Full Model 5	4	22.2	19.14	0.005		
ELE	1	9.8	20.69	0.005	0.93	-0.16
BUIP	1	4.4	12.35	0.005	0.13	0.86
SW	1	4	13.01	0.005	-0.79	-0.23
DCIp	1	2.3	7.64	0.005	-0.22	-0.67
Residuals	268	79.6				

Full Model 6	4	24.4	21.6	0.005		
ELE	1	9.3	20.64	0.005	-0.78	0.52
BUIP	1	7.5	20.24	0.005	-0.41	-0.69
SW	1	4.4	13.66	0.005	0.75	-0.17
DCId	1	5.4	15.52	0.005	0.48	0.37
Residuals	268	73.4				

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678 Figures

679 Figure 1. The study area in southern Ontario with the barrier locations. The insert illustrates an  
680 example area of the Duffins.

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682 Figure 2. Relationship between channel slope and passability in Terra Nova National Park,  
683 Newfoundland and Labrador, Canada. We applied this relationship to barriers in Southern  
684 Ontario to determine the passability of unidentified barriers.

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686 Figure 3. Histogram of barrier passabilities in the study watersheds based on the relationship  
687 between channel slope and culvert passability in Terra Nova National Park, Newfoundland and  
688 Labrador, Canada.

689

690 Figure 4. The distance based redundancy analysis comparing the  $DCI_s$ ,  $DCI_p$  and  $DCI_d$  (panels A,  
691 B, and C respectively) calculated with known barriers and potential barriers; and associated co-  
692 variables (ELE = Elevation, SW = Stream Width, and BUAP = Built-up area-pervious) for  
693 abundance data in southern Ontario.

694

695 Figure 5. Relationship between species richness and the  $DCI_s$  in 5 southern Ontario streams  
696 while controlling for elevation, stream width, and built-up area-pervious. The  $DCI_s$  in panel A is  
697 calculated using only known barriers and the  $DCI_s$  in panel B is calculated using known barriers  
698 and potential barriers.

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700 Figure 6. Relationship of the DCI and species abundances (solid line) and 95% confidence  
701 intervals (dashed line) for rainbow trout, longnose dace, and mottled sculpin.

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