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1 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

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

66 One method to assess the ecological relevance of structural indices is to test for
67 relationships between a given structural index and biological community patterns across stream
68 systems with variable degrees of fragmentation. For instance, Perkin and Gido (2012) found a
69 strong relationship between fish community structure, within second and third order stream units,
70 and a structural connectivity index. Understanding the response of structural indices at small
71 spatial extents is an important development, yet it remains unknown whether these relationships
72 will continue to be present at broader spatial extents where confounding variables may have an
73 increased influence on aquatic communities. For example, Branco et al. (2011) found that
74 environmental and human pressures, but not the presence of barriers, were the dominant driver of
75 the distribution of several potamodromous and resident fish species in a 3600 km² watershed.
76 However, Branco et al. (2011) acknowledged that they used a relatively simple index of
77 connectivity and called for a more thorough assessment of connectivity at broader spatial extents.

78 We analyzed the relationship between structural connectivity and patterns in the fish
79 community using data from five 5th and 6th order watersheds in southern Ontario, Canada,
80 (ranging in extent from 98 km² - 283 km²) which have a high degree of biodiversity (regional
81 species richness of 38). The focus of this study was to determine if a relatively simple structural
82 index, the Dendritic Connectivity Index (DCI), has biological relevance. Although we expect
83 multiple confounding variables (e.g., elevation, watershed land use, stream network topology) to

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

95

96 **Methods:**

97 *Study Area:*

98 Southern Ontario exhibits a high degree of freshwater fish biodiversity (Chu et al. 2003).
99 The diversity is attributed to a combination of postglacial dispersal and the anthropogenic
100 introduction of non-native species (Dextrase and Mandrak 2006). The study was conducted in
101 the watersheds of Wilmot, Oshawa, Ganaraska, Cobourg, and Duffins in southern Ontario, just
102 east of the metropolitan area of Toronto (Figure 1). The five watersheds studied are dominated
103 by developed urban areas at their confluence with Lake Ontario, agricultural landscape in the
104 mid reaches, and a mixture of forest and low intensity agriculture in the headwaters. They range
105 in watershed size of 98 km² for Wilmot to 283 km² for Ganaraska.

106 *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/m². 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_p) and diadromous

130 (DCI_d) life histories. The DCI_p applies to life histories of species that typically live in riverine
131 systems and do not require diadromous migration. DCI_p is defined as:

$$132 \quad D_p = \frac{\sum_{i=1}^n \sum_{j=1}^n c_{ij} \frac{l_i l_j}{L^2} * 1_j}{L}$$

133 where l is the length of the segment i and j , c_{ij} is the connectivity between segments i and j , and L
134 is the total stream length of all stream segments. The DCI_d applies to all life histories that
135 migrate between a fixed point (e.g., estuary) and all upstream areas within a riverine system.
136 DCI_d is calculated as:

$$137 \quad D_d = \frac{\sum_{i=1}^n c_i * 1_i}{L}$$

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

147 *Determining barrier passability:*

148 Identifying all potential barriers in a system is imperative in order to accurately assess
149 connectivity (Cote et al. 2009, Januchowski-Hartley et al. 2013, O’Hanley 2011). A list of
150 barrier locations was provided by OMNR which consisted of 298 locations of dams, perched
151 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
$$1 \left(\frac{p}{1 + e^{-x}} \right) + \varepsilon_i$$

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 ΔAIC (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_s,
227 DCI_p, and DCI_d, 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?*

243 We used a generalized linear mixed model (GLMM) approach to test the effects of
244 connectivity as determined by the DCI_s on species richness. Treating watershed as a random
245 effect allowed us to account for the potential pseudo-replication within watersheds (Bates et al.
246 2011). Species richness was quantified by calculating the total number of fish species at each
247 site. For sites with repeated sampling, species richness was averaged across sampling periods.
248 Our approach to calculate species richness was chosen to provide a more accurate measure of
249 this indicator than the single “most recent” observation that was used in the analyses by Stanfield
250 and Kilgour (2006). Averaging richness across sampling events captures temporal variability and
251 minimizes effects of sampling bias/error, but potentially undervalues diversity where sampling
252 effort was lower (Kennard et al. 2006, Stanfield et al. 2013). Finally, using the GLMM, we
253 analyzed the relationship between the DCI_s and the species richness of a site while controlling
254 for confounding variables previously identified. All variables but watershed were treated as fixed
255 effects. Significance was determined by the z-statistic at alpha = 0.05.

256

257 *Is DCI_s related to presence and abundance of individual species?*

258 We also tested to see how connectivity, calculated with known barriers and potential
259 barriers, affected the presence and abundance of individual species. Seven relatively abundant
260 species across three families were selected to represent a wide range of life history characteristics
261 (e.g., diadromous) and that were also relatively abundant across sites (Table 2 and 3). We again
262 used a GLMM approach, with presence modeled as binomial and abundance as a Poisson
263 response variable. Watershed was treated as a random effect to account for potential pseudo-
264 replication of observations within watersheds. The same confounding variables identified in the
265 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

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

321 Species richness was not associated with changes in connectivity based on known
322 barriers (DCI_s ; $z = 1.26$, $n = 273$, $p\text{-value} = 0.204$; Figure 5a). However, when we included
323 potential barriers into the DCI calculation, species richness became weakly correlated with the
324 DCI_s ($z = 1.99$, $n = 273$, $p\text{-value} = 0.047$; Figure 5b) as were ELE and SW ($z = -0.003$, $n = 273$,
325 $p\text{-value} < 0.001$; $z = 0.05$, $n = 273$, $p\text{-value} < 0.001$ respectively). However, the land cover
326 variable used (BUAP) did not show a significant relationship with species richness ($z = 0.068$, n
327 $= 273$, $p\text{-value} = 0.058$).

328 The presence of only two species had a positive relationship with the DCI_s : rainbow trout
329 (*Oncorhynchus mykiss*) and mottled sculpin (*Cottus bairdii*; $z = 0.07$, $n = 273$, $p\text{-value} = <0.001$
330 and $z = 0.017$, $n = 273$, $p\text{-value} = <0.001$ respectively; Table 2). Furthermore, abundance
331 increased for rainbow trout (mean = 0.07, $n = 273$, $p\text{-value} = 0.001$), mottled sculpin (mean =
332 0.09, $n = 273$, $p\text{-value} = 0.001$), and longnose dace (mean = 0.05, $n = 273$, $p\text{-value} = 0.014$;
333 *Rhinichthys cataractae*) with an increase in the DCI_s (Table 3; Figure 6). At least one

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

336

337 Discussion:

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

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

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

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

397 Presenting connectivity at watershed scales is useful to estimate watershed health or to
398 prioritize restoration actions, but can be limiting for analyses aimed at local scales (e.g., studies
399 targeting site-specific relationships between fish communities and habitat variables; Cote 2007).
400 To address the need for locally-focused studies, we modified this watershed scale index into a
401 local habitat variable (DCI_s) and matched it to corresponding biotic information. We consider
402 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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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

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

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

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478

Post-print

Literature Cited:

- 479
480
481 Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle,
482 Second International Symposium on Information Theory, pp. 267-281.
- 483 Allan, D., Erickson, D., and Fay, J. 1997. The influence of catchment land use on stream
484 integrity across multiple spatial scales. *Freshwater Biology* **37**(1): 149-161.
- 485 Allan, J.D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems.
486 *Annual Review of Ecology, Evolution, and Systematics*: 257-284.
- 487 Bain, M.B., and Wine, M.L. 2009. Testing predictions of stream landscape theory for fish
488 assemblages in highly fragmented watersheds. *Folia Zoologica* **59**(3): 231-239.
- 489 Bates, D., Maechler, M., and Bolker, B. 2011. lme4: Linear mixed-effects models using S4
490 classes. In R Package version 0.999375-42. <http://CRAN.R-project.org/package=lme4>.
- 491 Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J.,
492 Clayton, S., Dahm, C., and Follstad-Shah, J. 2005. Synthesizing US river restoration efforts.
493 *Science* **308**: 636-637.
- 494 Betz, R., Hitt, N., Dymond, R.L., and Heatwole, C.W. 2010. A method for quantifying stream
495 network topology over large geographic extents. *Journal of Spatial Hydrology* **10**: 16-29.
- 496 Bourne, C. 2013. How to quantify aquatic connectivity? Verifying the effectiveness of the
497 dendritic connectivity index as a tool for assessing stream fragmentation. M. Sc. thesis,
498 Department of Biology, Memorial University of Newfoundland, St. John's, NL.
- 499 Branco, P., Segurado, P., Santos, J.M., Pinheiro, P., and Ferreira, M.T. 2011. Does longitudinal
500 connectivity loss affect the distribution of freshwater fish? *Ecological Engineering* **48**: 70-78.
- 501 Bray, R.J., and Curtis, J.T. 1957. An ordination of the upland forest communities of southern
502 Wisconsin. *Ecological Monographs* **27**(4): 326-349.
- 503 Burnham, K.P., and Anderson, D.R. 2002. Model selection and multi-model inference: a
504 practical information-theoretic approach. Springer.
- 505 Chu, C., Minns, C.K., and Mandrak, N.E. 2003. Comparative regional assessment of factors
506 impacting freshwater fish biodiversity in Canada. *Canadian Journal of Fisheries and Aquatic
507 Sciences* **60**(5): 624-634.
- 508 Clarke, K.R., and Warwick, R.M. 2001. Change in marine communities: an approach to
509 statistical analysis and interpretation. PRIMER-E, Plymouth.
- 510 Coffman, J.S. 2005. Evaluation of a predictive model for upstream fish passage through culverts.
511 M. Sc. thesis, Department of Biology, James Madison University, Harrisonburg, VA.

- 512 Cote, D. 2007. Measurements of salmonid population performance in relation to habitat in
513 eastern Newfoundland streams. *Journal of Fish Biology* **70**(4): 1134-1147.
- 514 Cote, D., Kehler, D.G., Bourne, C., and Wiersma, Y.F. 2009. A new measure of longitudinal
515 connectivity for stream networks. *Landscape Ecology* **24**(1): 101-113.
- 516 Dextrase, A.J., and Mandrak, N.E. 2006. Impacts of alien invasive species on freshwater fauna at
517 risk in Canada. *Biological Invasions* **8**(1): 13-24.
- 518 Erős, T., Olden, J.D., Schick, R.S., Schmera, D., and Fortin, M.-J. 2012. Characterizing
519 connectivity relationships in freshwaters using patch-based graphs. *Landscape Ecology* **27**(2):
520 303-317.
- 521 Erős, T., Schmera, D., and Schick, R.S. 2011. Network thinking in riverscape conservation – A
522 graph-based approach. *Biological Conservation* **144**(1): 184-192.
- 523 Fagan, W.F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations.
524 *Ecology* **83**(12): 3243-3249.
- 525 Faith, D.P., Minchin, P.R., and Belbin, L. 1987. Compositional dissimilarity as a robust measure
526 of ecological distance. *Plant Ecology* **69**(1): 57-68.
- 527 Fausch, K.D., Torgersen, C.E., Baxter, C.V., and Hiram, W.L. 2002. Landscapes to riverscapes:
528 bridging the gap between research and conservation of stream fishes. *BioScience* **52**(6): 483-498.
- 529 Fausch, K.D., and White, R.J. 1981. Competition between brook trout (*Salvelinus fontinalis*) and
530 brown trout (*Salmo trutta*) for positions in a Michigan stream. *Canadian Journal of Fisheries and*
531 *Aquatic Sciences* **38**(10): 1220-1227.
- 532 Fullerton, A.H., Burnett, K.M., Steel, E.A., Flitcroft, R.L., Pess, G.R., Feist, B.E., Torgersen,
533 C.E., Miller, D.J., and Sanderson, B.L. 2010. Hydrological connectivity for riverine fish:
534 measurement challenges and research opportunities. *Freshwater Biology* **55**(11): 2215-2237.
- 535 Furniss, M., Love, M., Firor, S., Moynan, K., Llanos, A., Guntle, J., and Gubernick, R. 2006.
536 FishXing Version 3.0. US Forest Service, San Dimas Technology and Development Center, San
537 Dimas, California.
- 538 Goodwin, B.J., and Fahrig, L. 2003. How does landscape structure influence landscape
539 connectivity? *Oikos* **99**(3): 552-570.
- 540 Gowan, C., and Fausch, K.D. 1996. Mobile brook trout in two high-elevation Colorado streams:
541 reevaluating the concept of restricted movement. *Canadian Journal of Fisheries and Aquatic*
542 *Sciences* **53**(6): 1370-1381.
- 543 Hadfield, J.D. 2010. MCMC methods for multi-response generalized linear mixed models: the
544 MCMCglmm R package. *Journal of Statistical Software* **33**(2): 1-22.

- 545 Hargis, C.D., Bissonette, J., and Turner, D.L. 1999. The influence of forest fragmentation and
546 landscape pattern on American martens. *Journal of Applied Ecology* **36**(1): 157-172.
- 547 Hitt, N.P., and Angermeier, P.L. 2008. Evidence for fish dispersal from spatial analysis of stream
548 network topology. *Journal of the North American Benthological Society* **27**(2): 304-320.
- 549 Januchowski-Hartley, S.R., McIntyre, P.B., Diebel, M., Doran, P.J., Infante, D.M., Joseph, C.,
550 and Allan, J.D. 2013. Restoring aquatic ecosystem connectivity requires expanding inventories
551 of both dams and road crossings. *Frontiers in Ecology and the Environment* **11**(4): 211-217.
- 552 Johnston, C.E. 2003. Movement patterns of imperiled blue shiners (Pisces: Cyprinidae) among
553 habitat patches. *Ecology of Freshwater Fish* **9**(3): 170-176.
- 554 Kemp, P.S., and O'Hanley, J.R. 2010. Procedures for evaluating and prioritising the removal of
555 fish passage barriers: a synthesis. *Fisheries Management and Ecology* **17**: 297-322.
- 556 Kennard, M.J., Pusey, B.J., Harch, B.D., Dore, E., and Arthington, A.H. 2006. Estimating local
557 stream fish assemblage attributes: sampling effort and efficiency at two spatial scales. *Marine
558 and Freshwater Research* **57**(6): 635-653.
- 559 Kindlmann, P., and Burel, F. 2008. Connectivity measures: a review. *Landscape Ecology* **23**(8):
560 879-890.
- 561 Kupfer, J.A. 2012. Landscape ecology and biogeography rethinking landscape metrics in a post-
562 FRAGSTATS landscape. *Progress in Physical Geography* **36**(3): 400-420.
- 563 Legendre, P., and Anderson, M.J. 1999. Distance-based redundancy analysis: testing
564 multispecies responses in multifactorial ecological experiments. *Ecological Monographs* **69**(1):
565 1-24.
- 566 Mahlum, S.K., Cote, D., Kehler, D.G., Wiersma, Y.F., and Clarke, K.R. 2014. Evaluating the
567 barrier assessment technique FishXing and the upstream movement of fish through road culverts.
568 *Transactions of the American Fisheries Society* **143**: 39 - 48.
- 569 McArdle, B.H., and Anderson, M.J. 2001. Fitting multivariate models to community data: a
570 comment on distance-based redundancy analysis. *Ecology* **82**(1): 290-297.
- 571 McCleary, R.J., and Hassan, M.A. 2008. Predictive modeling and spatial mapping of fish
572 distributions in small streams of the Canadian Rocky Mountain foothills. *Canadian Journal of
573 Fisheries and Aquatic Sciences* **65**(2): 319-333.
- 574 McLaughlin, R.L., Porto, L., Noakes, D.L.G., Baylis, J.R., Carl, L.M., Dodd, H.R., Goldstein,
575 J.D., Hayes, D.B., and Randall, R.G. 2006. Effects of low-head barriers on stream fishes:
576 taxonomic affiliations and morphological correlates of sensitive species. *Canadian Journal of
577 Fisheries and Aquatic Sciences* **63**(4): 766-779.
- 578 Meixler, M.S., Bain, M.B., and Todd Walter, M. 2009. Predicting barrier passage and habitat
579 suitability for migratory fish species. *Ecological Modelling* **220**(20): 2782-2791.

- 580 Monkkonen, M., and Reunanen, P. 1999. On critical thresholds in landscape connectivity: a
581 management perspective. *Oikos* **84**(2): 302-305.
- 582 Norman, J.R., Hagler, M.M., Freeman, M.C., and Freeman, B.J. 2009. Application of a
583 multistate model to estimate culvert effects on movement of small fishes. *Transactions of the*
584 *American Fisheries Society* **138**(4): 826-838.
- 585 O'Hanley, J.R. 2011. Open rivers: barrier removal planning and the restoration of free-flowing
586 rivers. *Journal of Environmental Management* **92**(12): 3112-3120.
- 587 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson,
588 G.L., Henry, H., Wagner, S., and Wagner, H. 2012. *Vegan: community ecology package*. R
589 package version 2.0-3.
- 590 Ontario Ministry of Natural Resources. 2006. Southern Ontario Land Resource Information
591 System (SOLRIS). Science & Information Branch.
- 592 Padgham, M., and Webb, J.A. 2010. Multiple structural modifications to dendritic ecological
593 networks produce simple responses. *Ecological Modelling* **221**(21): 2537-2545.
- 594 Perkin, J.S., and Gido, K.B. 2012. Fragmentation alters stream fish community structure in
595 dendritic ecological networks. *Ecological Applications* **22**(8): 2176-2187.
- 596 Pess, G.R., McHugh, M.E., Fagen, D., Stevenson, P., and Drotts, J. 1998. Stillaguamish
597 salmonid barrier evaluation and elimination project, Phase III. Final report to the Tulalip Tribes,
598 Marysville, Washington.
- 599 Peterson, D.P., Rieman, B.E., Horan, D.L., and Young, M.K. 2013. Patch size but not short-
600 term isolation influences occurrence of westslope cutthroat trout above human- made barriers.
601 *Ecology of Freshwater Fish*.
- 602 Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and
603 prediction in stream ecology. *Journal of the North American Benthological Society* **16**(2): 391-
604 409.
- 605 Poplar-Jeffers, I.O., Petty, J.T., Anderson, J.T., Kite, S.J., Strager, M.P., and Fortney, R.H. 2009.
606 Culvert replacement and stream habitat restoration: implications from brook trout management
607 in an appalachian watershed, U.S.A. *Restoration Ecology* **17**(3): 404-413.
- 608 R Development Core Team. 2012. *R: A Language and Environment for Statistical Computing*. R
609 Foundation for Statistical Computing, Vienna, Austria. Retrieved from [http://www.R-](http://www.R-project.org/)
610 [project.org/](http://www.R-project.org/).
- 611 Rahel, F.J., and Hubert, W.A. 1991. Fish assemblages and habitat gradients in a Rocky
612 Mountain-Great Plains stream: biotic zonation and additive patterns of community change.
613 *Transactions of the American Fisheries Society* **120**(3): 319-332.

- 614 Schick, R.S., and Lindley, S.T. 2007. Directed connectivity among fish populations in a riverine
615 network. *Journal of Applied Ecology* **44**(6): 1116-1126.
- 616 Stanfield, L. 2010. Ontario stream assessment protocol. Version 8.0. Fisheries Policy Section.
617 Ontario Ministry of Natural Resources, Peterborough, Ontario.
- 618 Stanfield, L.W., Gibson, S.F., and Borwick, J.A. 2006. Using a landscape approach to identify
619 the distribution and density patterns of salmonids in Lake Ontario tributaries, 2006, American
620 Fisheries Society, p. 601.
- 621 Stanfield, L.W., and Kilgour, B.W. 2006. Effects of percent impervious cover on fish and
622 benthos assemblages and instream habitats in Lake Ontario tributaries, 2006, pp. 577-599.
- 623 Stanfield, L.W., Lester, N.P., and Petreman, I.C. 2013. Optimal Effort Intensity in Backpack
624 Electrofishing Surveys. *North American Journal of Fisheries Management* **33**(2): 277-286.
- 625 Taylor, R.N., and Love, M. 2003. California salmonid stream habitat restoration manual - Part
626 IX fish passage evaluation at stream crossings. CA: California Department of Fish and Game.
- 627 Tischendorf, L., and Fahrig, L. 2000. On the usage and measurement of landscape connectivity.
628 *Oikos* **90**(1): 7-19.
- 629 Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river
630 continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**(1): 130-137.
- 631 Ward, J.V. 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic
632 conservation. *Biological Conservation* **83**(3): 269-278.
- 633 Ward, J.V., Malard, F., and Tockner, K. 2002. Landscape ecology: a framework for integrating
634 pattern and process in river corridors. *Landscape Ecology* **17**: 35-45.
- 635 Warren, J.M.L., and Pardew, M.G. 1998. Road crossings as barriers to small-stream fish
636 movement. *Transactions of the American Fisheries Society* **127**(4): 637-644.
- 637 Wiens, J.A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater*
638 *Biology* **47**(4): 501-515.
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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 _d | DCI _d | Percentage of natural connectivity |
| | DCI _p | DCI _p | Percentage of natural connectivity |
| | DCI _s | DCI _s | 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 |

647 Table 2. The results of the single species presence analysis. Predictions represent the expected
 648 relationship between the species and variable. Positive values indicate that species presence is
 649 predicted to increase with increases in the corresponding variable while negative values indicate
 650 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 _s | | 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 _s | | 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 _s | | 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 _s | | -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 _s | | 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 _s | | 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 _s | | 0.081 | 0.017 | 4.917 | < 0.001* |

651 * indicates significance at $\alpha = 0.05$

652
 653

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* |

658 * 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 _p | DCI _d | DCI _s Range | DCI _p | DCI _d | DCI _s 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 Akiake'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 | Δ 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 |
| ^a CS ~ ELE + UCC + SW + BUAP + BUAI + CR + PAF + MF + DF | 8 | 1226.36 | 44.66 | 0.000 | 0.000 |

668 ^a Represents the global model (model that includes all variables) used in the model selection.
 669

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.

681

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.

685

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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