The species–area relationship for a highly fragmented temperate river system

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Citation: Carl, L. M., P. C. Esselman, B. L. Sparks-Jackson, and C. C. Wilson. 2021. The species–area relationship for a highly fragmented temperate river system. Ecosphere 12(3):e03411. 10.1002/ecs2.3411

Abstract. Despite the importance of species–area relationships (SARs) to conservation, SARs in human-fragmented rivers have received little attention. Our aim was to test for the presence and strength of SARs for littoral fish assemblages of an extensively dammed river in south-central Ontario, Canada, and to examine long-running hypotheses for the drivers of SARs. Twenty-six navigational dams with locks built between 1837 and 1913 occur along the 160 km length of the Trent River examined in this study. We evaluated the relationship between richness and fragment area, and then used linear models to test whether the area per se, habitat diversity, or other hypotheses were best supported by the data. A power–function relationship with area explained 46% of the variation in fish species richness, and the slope (z = 0.4) was high compared with SARs reported from other ecosystems, indicating that species accumulated rapidly with an increase in fragment area. Multi-predictor models suggested that area was significantly related to richness, but that vegetation cover diversity had a stronger relative effect. The slope of our SAR may indicate that there is a high degree of isolation between populations in different fragments, even though the lock system reportedly allows some passage of organisms. Our findings also suggest that mitigating against local extinction due to small population sizes (i.e., area effects), and enhancing aquatic vegetation cover may be viable strategies for promoting species diversity in the study river. Studies of SARs in fragmented rivers may offer additional benefits to supporting restoration planning where efforts are being made to increase species diversity.

Key words: area per se; fish diversity; fragmentation; habitat; species–area relationships; Trent River.

Received 13 February 2020; revised 31 July 2020; accepted 11 August 2020; final version received 4 January 2021. Corresponding Editor: Hunter S. Lenihan.

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INTRODUCTION

River systems around the world have become fragmented by the construction of dams, contributing to severe reductions in biological diversity and changes to the structure and function of biological communities (Dudgeon et al. 2006, Vörösmarty et al. 2010). The pervasiveness of river fragmentation is staggering, with more than 90,000 large dams greater than 2 m tall (USACE 2020) and as many as 2,000,000 small dams (Graf 1999) in the United States alone. Most of these structures were built prior to 1980 (Doyle et al. 2008). As these dams have aged and become more costly to maintain, dam removal has become more viable, with approximately 1200 dam removals in the past twenty years in the
United States (Bellmore et al. 2017). The prevalence of river fragmentation and the increasing frequency of dam removal indicate a need for new knowledge and tools to support river management and evaluation of trade-offs associated with this river restoration practice.

Riverine fish communities are particularly prone to faunal insularization from habitat fragmentation (Fausch et al. 2002), because the river’s edge places a hard limit on dispersal. This physical constraint makes river species particularly sensitive to the effects of dams, weirs, reservoirs, and locks, which can partially or completely impede upstream and downstream movement. Many river fishes require access to spatially disparate habitats for reproduction, growth, and survival (Schlosser 1995, Fausch et al. 2002), so limiting their ability to disperse can disrupt life cycles and increase vulnerability to local extinction from demographic effects on small populations (Liermann et al. 2012). Additionally, the presence of dams has been shown to alter fish communities by attracting facultative reservoir species to the impoundments above dams (Falke and Gido 2006), to the detriment of cold-water, rheophilic, native, and/or lotic specialists (Kiraly et al. 2015, Miranda and Dembkowski 2016). The net effects of these changes on fish communities are often reflected in aggregate measures of community structure such as species richness through additions and subtractions of species to the community.

Total species richness and richness of functional guilds are frequently used metrics of community change in studies of river fragmentation (Loureis and Pompeu 2019), yet very little work has connected species richness within river fragments to the extensive literature on species–area relationships (SARs). The observation of increasing species richness with increasing area is a foundational pattern in ecology that has been a central theme in biogeography theory (MacArthur and Wilson 1967, Rosenzweig 1995, Hubbell 2001, McGill et al. 2006, Whittaker and Fernández-Palacios 2007). Species–area relationships on islands (as opposed to within nested habitat units) are particularly relevant to the study of habitat fragmentation, because patches of isolated habitat can be conceived as habitat islands isolated from one another by unsuitable matrix habitats. Documentation of habitat island SARs (ISARs) has led to important advances in landscape conservation, protected area design, prediction of extinction from habitat loss, and predicting regional diversity (Brooks et al. 2002, Thomas et al. 2004, Santucci et al. 2005, Gehrner et al. 2014, Chisholm et al. 2018).

The slope ($z$) of a log–log regression of richness vs. area summarizes the rate of species accumulation with area, which can be modified by island isolation, dispersal rates between islands, species trophic ranks, human influence, biotic homogenization, and other factors (reviewed in Fattorini et al. 2017). Numerous studies of SARs have been conducted in freshwater, but we were unable to locate a single study that focused on SARs for river habitats fragmented by human-made barriers. Two extensive meta-analyses of SARs (Drakare et al. 2006, Matthews et al. 2016) also failed to locate studies of ISARs for dammed rivers. Freshwater SARs have been described in lakes as islands (Barbour and Brown 1974, Tonn and Magnuson 1982, Eadie et al. 1986), catchments and rivers with different discharges (Eadie et al. 1986, Hugueny 1989, Watters 1992, Clavero et al. 2004, McGarvey and Hughes 2008, Prachell et al. 2013, Kuglerová et al. 2015), un-fragmented stream reaches (Angermeier and Schlosser 1989), and wetlands (Malchik et al. 2010, Petry et al. 2016). Drakare et al. (2006) concluded from these studies that rates of species accumulation in natural lakes, catchments, and stream pools are significantly lower than ISARs in terrestrial habitat fragments, indicating possible differences in the underlying processes that generate the pattern in freshwater systems. Another general tendency is for the regression slopes of richness vs. area for habitat ISARs to be significantly lower than slopes of true island SARs, potentially because habitat ISARs are less isolated and have increased immigration rates (Whittaker and Fernández-Palacios 2007, Matthews et al. 2016).

Given the prevalence of habitat fragments in many riverine landscapes, there appears to be an untapped potential to use SARs to improve our general understanding of community assembly, and to examine fragmented river habitats through the lens of decades of theory and research. Community ecologists have long sought to understand the drivers of SARs, because it is one of the oldest and most widely observed ecological patterns. Numerous hypotheses have been posed. For instance, the area per se hypothesis predicts that smaller areas...
will support lower richness due to more frequent local extinctions resulting from demographic effects on small populations (Simberloff 1976). The habitat diversity hypothesis (Lomolino 2001) predicts that area serves as a proxy for habitat diversity, because larger fragments contain a greater diversity of habitats, and thus can support a greater diversity of species occupying more niches. Other potential descriptors of species richness in rivers include longitudinal position in the river continuum (summarized by Matthews 1998), land cover effects (Allan 2004), and/or water temperature (Wehrly et al. 2003). Understanding which of these hypotheses is most well supported can be useful to managers of regulated rivers trying to develop strategies to conserve species diversity. For instance, strong support for the habitat diversity hypothesis would suggest that managers evaluate options for using habitat manipulations to promote species diversity.

A lack of knowledge about fragmented river SARs also precludes freshwater scientists and managers from using SARs as a tool to support freshwater conservation planning and scenario exploration. Terrestrial biologists have successfully leveraged SARs to explore how manipulations of fragment size, fragment quality, and matrix quality may affect biodiversity (Huth and Possingham 2011, Freeman et al. 2018); whether movement corridors between fragments may slow species loss (Newmark et al. 2017); and optimal configurations of protected areas. Species–area relationships in a fragmented river context could be useful for exploring potential biodiversity outcomes associated with dam additions or removals (O’Hanley et al. 2020).

Here, we investigated correlative relationships between littoral fish species richness and habitat diversity, area, and other predictors in a river that is extensively fragmented by a century-old system of locks and dams. Specific study objectives were to evaluate the relationship between richness and fragment area, and then test whether the area per se, habitat diversity, or other hypotheses were most well supported by the data. In the discussion, we compare our findings with published meta-analyses of SARs and explore possible conservation implications in the context of the study system and fragmented rivers more broadly.

Methods

Study site

The study was carried out on the lower section of the Trent River in south-central Ontario, between the river mouth at the Bay of Quinte (an embayment in Lake Ontario) and Lakefield, 160 river km upstream (Fig. 1). The Trent River drains an area of about 10,500 km², flowing southward off the Canadian Shield and across a limestone plain to the Bay of Quinte. North—south river sections are interspersed with west-to-east trending sections that contain several natural in-network lakes. No large tributaries join the lower river where our study took place, reducing the possibility of network influences (e.g., rescue effect; Brown and Kodric-Brown 1977) on biological assemblages in the studied portion of the river.

The Trent River system has been extensively modified by 26 dams constructed for navigation between 1837 and 1913. Twenty-four of these structures have lock systems associated with them allowing for some limited direct organism exchange between adjacent fragments over a limited period of the year when the locks are opened for recreational boat passage (e.g., May–October). There is also a network of reservoirs upstream of the study area that is used to stabilize flow for the lock system. Given the age of the structures and the extent of impoundment, the extant fauna is only a remnant of the original community, which once also contained Atlantic salmon (Salmo salar), lake sturgeon (Acipenser fulvescens), and other species. However, neither the historic nor the remnant fauna have been thoroughly documented (but see Reid 2006, Reid et al. 2008a, b). The American eel (Anguilla rostrata)—a threatened species in Canada and the United States—was observed on two occasions by our field team, suggesting that an extant population of naturally reproducing American eels was present as recently at the early 2000s. In addition to the dams and locks, the Trent River watershed is modified by extensive agriculture, pasture, and urban land cover (Fig. 1).

Fish, area, and habitat data

River fragments were defined as sections of river bounded between two dams, excluding those containing natural in-network lakes (e.g.,
Rice Lake; Fig. 1). Within fragments, fishes and habitats were sampled at one to three 600-m sites. The number of sites was determined by how many could fit within the length of a fragment. Eight of the fragments accommodated one site (Fig. 1; fragments 2, 4, 7, 15, 17, 25, 26, and 28), while another nine fragments included two sites (Fig. 1; fragments 1, 5, 6, 8, 16, 18, 23, 24, and 27), and one fragment included three sites (fragment 3). Note that fragments are not numbered sequentially because they were drawn from a larger sample of river habitats and fishes that included non-fragmented reaches not considered here. To ensure good longitudinal representation of sampled habitats, sampling locations within sites were chosen at random from five upstream-to-downstream zones of 100 m each separated by 25-m no sampling zones. A total of eight 50-m long shoreline transects were sampled within each 100-m zone (Appendix S1).

Thirty sites (stars in Fig. 1) were sampled for fish within 18 fragments in the summer months (June–September) of 2000 and 2001 (Fig. 1), except for one site in fragment 18 that was only sampled in 2001. Along the 50-m length of shoreline for transect samples, fishes were collected in an upstream direction using a 5-kW pulsed DC boat electrofisher with a boom anode and a single netter. Care was taken to maintain power (i.e., the product of voltage and amperage) at 2000 watts for all sampling to ensure equality of effort. Abundance by species of all individuals captured was recorded. These data were pooled for both years and treated as an integrated
a snapshot of summer fish assemblages that captured two years of variability. Pooling was necessary because several of the habitat parameters were only measured in the second year of the study but were taken as representative of habitats present during both years.

Water depth was recorded at upstream, middle, and downstream positions in each 50-m transect in both years. Substrate and velocity conditions were characterized during the second year of sampling and treated as representative of the first sampling year. A submersible fish-eye camera was deployed in 2001 from a boat to classify dominant substrate at each transect as either mud/silt, sand, gravel/cobble/boulders, or macrophytes. Current velocities were measured at all transects using the floating object method; measurements were taken at the upstream end of the transect, 5–7 m from shore. We searched for publicly available discharge data to include as a predictor in models of richness, but only a single gage site was available near the mouth of the Trent River at Trenton (Fig. 1). Discharge at this site showed that most sampling took place during a period of relatively low variability ranging between 30 and 150 cm. Discharge was more variable in 2000 than 2001, with a spate reaching 450 cm during the first month of the study (June 2000; Appendix S2). We acknowledge our inability to control for variable hydrology as a shortcoming of our study but felt that the results were still worth reporting.

One area variable and five habitat diversity variables were calculated to examine potential causal mechanisms for SARs (Table 1). Water surface area (m²) was traced in GIS for each fragment from digital 1:50,000 maps collected close to the time of field data collection (Ontario Geological Survey 2003). Only the main channel was digitized, excluding canals, side channels, and spillways. We characterized four habitat diversity characteristics (diversity of depth, substrate, velocity, and proportional vegetation cover) and one composite habitat diversity measure combining all but vegetation cover. Following Angermeier and Schlosser (1989), we computed habitat diversity indices at the fragment scale using frequency occurrences of discrete classes of depth, substrate, velocity, and proportion vegetation cover within transects using the Shannon diversity index:

$$H' = -\sum p_i \ln p_i$$

where $p_i$ is the proportion of observations belonging to the $i$th habitat class. Depth habitat classes were defined at <0.5 m, 0.5–1.5 m, 1.5–3.0 m, and >3.0 m to represent very shallow, shallow, moderate, and deep habitats, respectively. Three velocity classes were defined at <0.25 m/s, 0.25–0.5 m/s, and >0.5 m/s. Substrate habitat classes comprised the four substrate classes listed in the prior paragraph. Proportion vegetation cover classes were defined as 0–25%, 25–75%, and >75% to represent no, moderate, and abundant vegetation cover, respectively. A composite habitat diversity measure was also calculated using the proportion of observations falling within 48 composite habitat class combinations resulting from crossing categories of depth, substrate, and velocity. Because vegetation was included as a substrate class, diversity in proportion vegetation cover was not included in the overall habitat diversity measure to avoid duplication.

Table 1. Predictor variables evaluated in linear models and associated summary statistics, excluding one outlier (fragment 17, see Data analysis: Species-area relationship).

| Variable     | Description                      | Units      | Min      | 25th pctl. | Median   | Mean     | 75th pctl. | Max     |
|--------------|----------------------------------|------------|----------|------------|----------|----------|------------|---------|
| Area         | Fragment area                    | 1000 m²    | 702      | 1571       | 2384     | 2779     | 3543       | 6097    |
| LnArea       | Ln of fragment area              | m²         | 11.16    | 11.96      | 12.38    | 12.38    | 12.78      | 13.3    |
| Hab_div      | Habitat diversity                | n/a        | 0.95     | 1.37       | 1.76     | 1.73     | 2.02       | 2.32    |
| Dep_div      | Depth diversity                  | n/a        | 1.18     | 1.33       | 1.45     | 1.41     | 1.48       | 1.58    |
| Vel_div      | Velocity diversity               | n/a        | 0.62     | 0.96       | 1.08     | 1.08     | 1.28       | 1.53    |
| Sub_div      | Substrate diversity              | n/a        | 0.00     | 0.18       | 0.45     | 0.40     | 0.59       | 0.94    |
| VegCvr_div   | Vegetation cover diversity       | n/a        | 0.00     | 0.38       | 0.56     | 0.51     | 0.69       | 1.03    |

Note: Pctl. stands for percentile.
Other potential drivers of richness

In addition to accounting for effects of area and habitat, we investigated the potential influence of variables that could confound the interpretation of area and/or habitat effects. Specifically, we explored whether spatial relatedness (i.e., lack of independence) of variables’ values among fragments could confound interpretation of effect sizes and variable importance as has been shown in previous studies of river fish richness (Grenouillet et al. 2004). We explored whether the position of the fragment within the river continuum influenced fish richness as increases in richness are common with increases in river order and size (reviewed in Matthews 1998). Anthropogenic land cover can have strong influences on riverine ecosystems and species richness (reviewed in Nakano and Murakami 2001, Pusey and Arthington 2003, Naiman et al. 2005). Riparian land cover was summarized from satellite-interpreted land cover data within a 150-m buffer on either side of the wetted channel margin and summarized for each fragment. In each buffer, the percent cover of developed land, forest, agriculture (row crops, orchards, and pasture), and wetlands was quantified from a (25-m resolution) 2000 land cover classification published by Agriculture and Agri-Food Canada (https://geohub.lio.gov.on.ca/data sets/provincial-land-cover). Finally, we explored the relationships between water temperature and fish richness because of temperature’s overriding importance in structuring fish communities in North American Midwest streams (Wehrly et al. 2003). Water temperature was measured in the field at all sites in 2000 and 2001 and averaged across sites and years to calculate a water temperature measure associated with each fragment.

Data analysis

Species–area relationship.—Total richness at a site is almost always under-sampled due to sampling inefficiency and insufficient effort (Gotelli and Colwell 2001). We corrected for under-sampled richness using the Chao1 estimator (Chao 1984, Colwell and Coddington 1994) to predict asymptotic richness for each fragment using transect data as repeated measures of the assemblage in a fragment. We chose the Chao1 estimator because it makes use of abundance in addition to incidence data, it does not make assumptions about the mathematical form of the underlying distribution of species abundance or detection rates, and it has been shown to have relatively high accuracy and precision and low bias when compared to other estimators (Walters et al. 2005, Reese et al. 2014, Chao and Chiu 2016). The Chao1 estimator uses the numbers of singletons and doubletons and the observed richness to calculate the minimum expected asymptotic species richness. We used EstimateS v.9.1.0 (Colwell 2013) to calculate Chao1 from transect catch data pooled across years. As suggested by Chao (1987), we chose the classic or bias-corrected version for each fragment depending on the presence of doubletons.

After calculating asymptotic richness for each fragment, we tested for a relationship between richness and fragment area and asked whether a power function or exponential relationship provided a better fit to the data. The power function SAR equation is as follows:

\[ S = cA^z \]

where \( S \) is species richness, \( A \) is area, and \( c \) and \( z \) are constants for the intercept and slope, respectively (Arrhenius 1921). The power function equation was approximated by a log–log transformation of richness and area, which linearizes the relationship. Alternatively, we tested whether an exponential relationship (Gleason 1922) better represented the SAR, using the following equation:

\[ S = c + z \ln(A). \]

Fragment 17 was excluded from analyses because only four total species were detected in both years of sampling, making it an extreme outlier. We report the slope, \( R^2 \), and \( P \) value for the two regressions, and examined scatter plots of predicted vs. observed richness and regression residuals to assess fit.

Evaluating hypothesized habitat drivers of SARs.—After evaluating the relationship between richness and fragment area, we fit a series of linear regression models to evaluate the relative effects of area, habitat diversity, land cover, water temperature, and vegetation cover predictors alone and in two-predictor models with area. Multiple authors have observed that the area per se and habitat diversity hypotheses may not be mutually exclusive (Ricklefs and Lovette 1999, Triantis et al. 2003, Kallimanis et al. 2008), but rather act...
together. For instance, Kohn and Walsh (1994) observed that area contributes to richness both directly and indirectly through habitat diversity. However, in the present study, area and habitat diversity measures were statistically independent of one another (i.e., not significantly correlated at the $P < 0.05$ level; Appendix S3). Nonetheless, we evaluated the fit of several commonly referenced models that consider multiplicative and other types of joint effects of area and habitat on richness including the Choros model (Triantis et al. 2003),

$$S = c(A \times H)^z$$

where habitat diversity ($H$) and area are modeled as having a multiplicative effect on richness. In our implementation of the Choros model, $H$ was represented by Shannon diversity of habitats (plus one because uniform habitat is valued at 1 in the Choros model and as 0 in our diversity measures). We also modeled the effects of habitat diversity on the slope of the species accumulation curve following Kallimanis et al. (2008),

$$S = c + z_1 \ln A + z_2 H \ln A$$

where $z_1$ and $z_2$ are slope coefficients.

For all models, we report the $F$-ratio, slope(s), $R^2$, adjusted $R^2$, and statistical significances of the models and slope(s) and analyze residuals for normality and lack of fit. The adjusted $R^2$ accounts for replication and model complexity and allows comparison of models of differing complexity. We also report standardized slope coefficients in models with more than one variable, allowing interpretation of the relative effects of each variable on species richness.

Other potential drivers of richness.—Moran’s $I$ statistic was calculated to assess whether spatial autocorrelation was present in species richness, area, and habitat diversity measures using river distance between midpoints of fragments for the inverse distance weights. In general, a Moran’s index value near +1.0 indicates clustering, while an index value near −1.0 indicates dispersion. We also developed linear models that explored whether position (distance to river mouth), riparian land use (percent urban, agriculture, forest, or wetland in the fragment buffer), average proportion of vegetation cover, or water temperature were related to species richness. Linear models included these variables alone and in combination with area. Finally, we conducted nestedness analyses to test whether species found in less species-rich fragments were subsets of those present at species-rich sites. All statistical analyses were performed in R (version 3.3.1; R Core Team, Vienna, Austria).

RESULTS

A total of 4232 fishes comprising 34 species were captured (Table 2; Appendix S4). Estimated asymptotic richness (Chao1 metric) within fragments varied from 4 to 22, with an average of 14 (Fig. 2, bars). Cumulative sampled species richness increased almost linearly across the fragments (Fig. 2, line), which ranged from 0.07 to 0.61 km$^2$ in area.

Species–area relationship

Chao1 estimates of asymptotic species richness suggested that sampled richness underestimated total richness in fragments by an average of two species (range of 0–8; Fig. 3). The largest increases in Chao1 as compared to observed richness were in fragments 3, 5, and 23 where observed richness was underestimated because relatively high numbers of species were represented by a single fish (i.e., singletons). The increase in richness with area was most well described by a power function rather than a semi-log relationship. The power function SAR had an adjusted $R^2$ of 0.46 ($F_{1,15} = 12.89$, $P < 0.01$) and a slope of 0.4 (Fig. 4).

Potential drivers of SARs

Analysis of the results of the linear models suggests that both area and habitat had significant effects on species richness independently and in combination (Table 3). Vegetation cover diversity explained more variation by itself than area, accounting for about half of the variation in species richness ($P < 0.001$, $R^2 = 0.51$). The composite habitat diversity measure had a weakly significant effect ($P = 0.09$) on richness, explaining less than 20% of the variation ($R^2 = 0.18$). Individual habitat diversity measures varied in their ability to explain species richness. Depth, velocity, and substrate habitat diversity variables accounted for very little variation in species richness among fragments (Table 3, $R^2 = 0.01–0.10$).
Combining area and habitat diversity resulted in statistically significant multi-predictor models with substantially higher goodness of fit than single-predictor models (Table 3). The Kallimanis model with vegetation cover diversity explained the most variation in species richness (adjusted $R^2 = 0.67$), but the ln(area) term in this model was not significant at $P < 0.05$. An additive model of ln(area) and vegetation cover diversity was highly significant and had a similar goodness of fit as the Kallimanis model (adjusted $R^2 = 0.66$), and both slope coefficients in this

| Common name           | Fragment | Species area (km²) | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|-----------------------|----------|-------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| Longnose gar          | Lepisosteus osseus |              | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Central mudminnow     | Umbra limi |              | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| White sucker          | Catostomus commersoni |         | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Silver redhorse       | Moxostoma anisurus |             | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Common carp           | Cyprinus carpio |          | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Common shiner         | Luxilus cornutus |             | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Blackchin shiner      | Notropis heterodon |           | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Spottail shiner       | Notropis huadonis |            | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Bluntnose minnow      | Pinephales notatus |         | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Fathead minnow        | Pinephales promelas |        | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Fallfish              | Semotilus corporalis |         | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Brown bullhead        | Ameiurus nebulosus |          | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Rock bass             | Ambloplites rapae |           | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Pumpkinseed           | Lepomis gibbosus |           | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Bluegill              | Lepomis macrochirius |         | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Smallmouth bass       | Micropterus dolomieu |        | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Largemouth bass       | Micropterus salmoides |        | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Black crappie         | Pomoxis nigromaculatus |      | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Yellow perch          | Perca flavescens |           | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Walleye               | Sander vitreus |          | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Iowa darter           | Ethostoma exile |           | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Common logperch       | Percina caprodes |         | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Brook silverside      | Labeo slusisculus |         | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Mottled sculpin       | Cottus baideri |          | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |
| Slimy sculpin         | Cottus cognum |           | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  | X  |

Notes: Fragments are arranged from smallest area (left) to largest area (right). See Appendix S4 for full species list including fragment areas, and catch statistics.
model were significant at $P < 0.01$. A comparison of the standardized slope coefficients for the additive model suggested that the relative effect of vegetation cover diversity (0.55) was substantially higher than for $\ln(\text{area})$ (0.29). Comparing this slope with the $\ln(\text{area})$ effect in the single-predictor model with area ($z = 0.40$) suggests that accounting for vegetation cover decreased the apparent rate of species accumulation with area.

The Choros model with area and vegetation cover diversity was also highly significant and had the third highest goodness of fit (adjusted $R^2 = 0.60$) and a slope of 0.39. This model replaced the area term in the Arrhenius model with the product of area and vegetation cover diversity, effectively modeling the total effect of these variables combined. Incorporating the joint effect of composite habitat and area in a Choros model improved model fit slightly over the Arrhenius model with area only (adjusted $R^2 = 0.50$ vs. 0.43), with equal slopes (0.40). Although we identified other statistically significant models, none of them had goodness of fit as high as those described above.

**Other potential drivers of richness**

The effects of spatial relatedness and other variables on species richness were minimal. Richness, area, and habitat variables were not significantly spatially autocorrelated (Appendix S5) suggesting that it was not necessary to account for spatial relatedness in models of species richness in this case. Similarly, assemblages were found to not be significantly nested insofar as species at sites with lower richness were not subsets of those with higher richness (Appendix S6). Water temperature, distance from river mouth, and most riparian land uses did not explain significant variation in species richness, either independently or in conjunction with area (Table 4). However, the additive model including area and the proportion of agriculture cover in the riparian zone was highly significant ($P < 0.001$), with an adjusted $R^2$ of 0.59. The proportion of agriculture in the riparian buffer is moderately correlated with the proportion vegetation cover in the study fragments ($r = 0.43, P = 0.08$), with higher vegetation covers associated with more agriculture.

**DISCUSSION**

This paper presents some of the first evidence for the presence of SARs in river habitat fragments and suggests that both area and habitat...
may control fish species richness in the river fragments of the Trent River. A statistically significant power function had the best fit to the data, accounting for nearly half of the variation in species richness and having a slope ($z$) of 0.4. This rate of species accumulation was steep compared with other published SARs from non-fragmented freshwater habitats, and to other non-

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**Fig. 4.** Species–area relationship for estimated richness vs. fragment area. Diamonds show estimated asymptotic richness. The left plot shows untransformed axes, and right plot shows the linearized power function relationship.

**Table 3.** Area and habitat model results.

| Model type, name, or source | Model | $F$-stat. | Intercept | Slope(s) | $R^2$ | Adj$R^2$ |
|-----------------------------|-------|-----------|-----------|----------|-------|----------|
| Area only                   |       |           |           |          |       |          |
| Arrhenius (1921)            | lnS ~ lnArea | 12.89** | -2.41     | 0.40**   | 0.46  | 0.43     |
| Gleason (1922)              | S ~ lnArea  | 12.33*** | -52.01*   | 5.32**   | 0.45  | 0.41     |
| Habitat diversity only      |       |           |           |          |       |          |
| Habitat_div                 | S ~ Hab_div | 3.25†  | 5.85      | 4.65†    | 0.18  | 0.12     |
| Depth_div                   | S ~ Dep_div | 0.08   | 18.31     | -3.14    | 0.01  | -0.06    |
| Velocity_div                | S ~ Vel_div | 0.70   | 10.24*    | 3.39     | 0.04  | -0.02    |
| Substrate_div               | S ~ Sub_div | 1.70   | 11.82***  | 5.18     | 0.10  | 0.04     |
| Veg. cover_div              | S ~ VegCvr_div | 15.42** | 8.83***   | 10.01**  | 0.51  | 0.47     |
| Area and habitat diversity  |       |           |           |          |       |          |
| Area + Habitat_div          | lnS ~ lnArea + Hab_div | 8.17** | -2.00    | 0.32*, 0.23 | 0.54  | 0.47     |
| Choros (Triantis et al. 2003) with Habitat_div | lnS ~ ln(Area x (Hab_div + 1)) | 16.77*** | -2.72†  | 0.40*** | 0.53  | 0.50     |
| Kallimanis et al. (2008) with Habitat_div | lnS ~ lnArea + (Hab_div + 1) x lnArea | 8.17** | -2.00  | 0.32*, 0.02 | 0.54  | 0.47     |
| Area + Veg. cover_div       | Lns ~ lnArea + VegCvr_div | 16.22*** | -1.31  | 0.29**, 0.55* | 0.70  | 0.66     |
| Choros with Veg. cover_div  | lnS ~ ln(Area x (VegCvr_div + 1)) | 25.36*** | -2.40* | 0.39*** | 0.63  | 0.60     |
| Kallimanis with Veg. cover_div | lnS ~ lnArea + (VegCvr_div + 1) x lnArea | 16.26*** | -0.97†  | 0.22*, 0.05* | 0.71  | 0.67     |

**Notes:** Data include model name, and parameters included the following: $F$-statistic ($F$-stat.), slope coefficients, $R^2$, adjusted $R^2$ (Adj$R^2$), and statistical significance. Species richness ($S$) was estimated using the Chao1 metric. Models where all included parameters are significant at $P < 0.05$ are listed in bold.

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. 
Table 4. Linear model results of estimated species richness (S; from the Chao 1 estimator) vs. potential drivers of SAR (alone and in combination with area).

| Model name or source                      | Model                          | F-stat. | Slope(s) | R²  | AdjR² |
|------------------------------------------|--------------------------------|---------|----------|-----|-------|
| Longitudinal pattern                     | \( S \sim DistRivermouth \)   | 0.002   | 0.003    | 0.002 | −0.06 |
| Riparian urban                           | \( S \sim RiparUrban\% \)      | 0.25    | −0.016   | 0.02  | −0.05 |
| Riparian agriculture                      | \( S \sim RiparAg\% \)         | 2.77    | 0.07     | 0.16  | 0.10  |
| Riparian forest                          | \( S \sim RiparFor\% \)        | 1.67    | −0.21    | 0.10  | 0.04  |
| Riparian wetland                         | \( S \sim RiparWet\% \)        | 0.06    | −0.03    | 0.004 | −0.06 |
| Water temperature                        | \( S \sim WaterTemp \)         | 1.29    | −1.12    | 0.08  | 0.02  |
| Area + longitudinal pattern              | \( \ln S \sim \ln Area + DistRivermouth \) | 7.24** | 0.44**, 0.001 | 0.51 | 0.44 |
| Area + riparian urban                    | \( \ln S \sim \ln Area + RiparUrban\% \) | 8.17** | 0.44***, −0.003 | 0.54 | 0.47 |
| Area + riparian agriculture              | \( \ln S \sim \ln Area + RiparAg\% \) | 12.49*** | 0.42***, 0.006* | 0.64 | 0.59 |
| Area + riparian forest                   | \( \ln S \sim \ln Area + RiparFor\% \) | 6.57** | 0.48**, 0.007 | 0.48 | 0.41 |
| Area + riparian wetland                  | \( \ln S \sim \ln Area + RiparWet\% \) | 6.47* | 0.41**, −0.005 | 0.48 | 0.41 |
| Area + water temperature                 | \( \ln S \sim \ln Area + WaterTemp \) | 7.58** | 0.40***, −0.07 | 0.52 | 0.45 |

Notes: SAR, species-area relationships. Model selection results including model name, parameters, F-statistic (F-stat.), slope coefficients, \( R^2 \), adjusted \( R^2 \), and statistical significance. Models where all included parameters are significant at \( P < 0.05 \) are listed in bold.

* \( P < 0.05 \), ** \( P < 0.01 \), *** \( P < 0.001 \).

aquatic fragmented ISARs. Drakare et al. (2006) reported a mean slope of \( z = 0.26 \) from 17 non-nested SARs in non-fragmented freshwater systems. In a more recent review of SARs on true islands vs. habitat islands, Matthews et al. (2016b) reported that habitat islands had significantly lower \( z \) values (median \( z = 0.22 \)) than both continental shelf islands (i.e., those with a relatively close source of colonists, \( z = 0.28 \)) and oceanic islands (\( z = 0.35 \)). Thus, the slope of the habitat island SAR from the Trent River is most similar to true oceanic islands that tend to have distant colonizing source populations.

Whereas Drakare et al. (2006) observed that SARs from freshwater systems may be lower, on average, than other ecosystem types, the SARs used to reach that conclusion were drawn from studies using catchments, lakes, stream pools, and wetlands as replicates. The directionally constrained, low-permeability river environment of the Trent River had much higher slopes. Our finding that species accumulation rates in the Trent River are most similar to highly isolated oceanic islands with limited organism exchange suggests that rates of organism exchange between Trent River fragments may also be quite low. It has been shown that habitat island systems tend to have lower \( z \) values than true island systems due to more permeable matrices surrounding habitat islands, allowing for easier dispersal between them (MacArthur and Wilson 1967, Rosenzweig 1995). However, organisms inhabiting habitat islands in fragmented rivers are exposed to hard limits on virtually all sides (by river banks laterally and barriers longitudinally), making them potentially more similar to true islands than terrestrial habitat islands.

It is impossible to know without further research whether the Trent River is a unique case or whether a more general pattern exists across fragmented river habitats. It can be observed that Trent River mainstem dam density is relatively high, and tributary connections to fragments are very infrequent. Tributary size and position in a drainage network has been shown to influence assemblages in connected river habitats by contributing organisms and lowering extinction rates (Taylor and Warren 2001, Grenouillet et al. 2004, Yan et al. 2011, Li et al. 2016). Such rescue effects would tend to lower the slopes of SARs. Although large tributaries do join the mainstem of the Trent River, they do not join within the study fragments, potentially minimizing rescue effects and resulting in steeper SAR slopes.

Vegetation cover diversity summarizes the proportional representation of low, medium, and high vegetation cover across many transects within a fragment. Fragments with more cover classes present and a greater evenness among these classes had the highest values for this predictor. Taken alone or in combination with area, this predictor accounted for more variation than...
any other single predictor, including area (Table 3). Vegetation cover diversity also had the strongest standardized slope in the additive model with area. This correlative evidence suggests that both the area per se and the habitat diversity may act to influence species richness in the Trent River. Ecological controls on the river macrophytes that provide cover diversity include water velocity, light, substrate, and nutrient availability (Franklin et al. 2008). Conversion of riparian forests to agriculture may improve conditions for macrophytes by increasing light availability, water temperature, fine sediment accumulation, and nutrient availability, but not velocity. The correlation between vegetation cover diversity and riparian agricultural cover (Pearson’s $r = 0.51$, $t = 2.3$, $P < 0.05$) suggests that riparian agriculture may indeed affect the presence (and/or persistence) of aquatic vegetation. The suggestion that riparian agriculture may indirectly lead to an increase in fish diversity contradicts other studies that show negative impacts of riparian forest conversion to agriculture on biodiversity (e.g., Burcher et al. 2008, Effert-Fanta et al. 2019). Interpretation of our species by fragment matrix (Table 2; Appendix S4) suggests that the increase in species richness with vegetation cover diversity and riparian agriculture is due to the presence of five species with strong affiliations to aquatic vegetation and lentic conditions more generally (Lane et al. 1996): common shiner (Luxilus cornutus), blackchin shiner (Notropis heterodon), spottail shiner (Notropis hudsonius), mimic shiner (Notropis volucellus), and banded killifish (Fundulus diaphanus). The absence of these species from small fragments may be a function of either a lack of diverse vegetated habitats, a lack of lentic conditions, or both.

The area per se hypothesis predicts that smaller habitat patches have lower richness because they support smaller populations that are more prone to local extinction from demographic processes (Simberloff 1976). Reid (2007) found that population size was directly correlated with fragment size for two redhorse species in the Trent River. While proneness to local extinction was impossible to ascertain from our data, fitness consequences of small habitat areas may be caused by restricted home range sizes, which can lead to reduced foraging efficiency, lower fertility, and/or increased mortality (Keeley and McPhail 1998). Given that home range size scales allometrically with body size in fishes (Minns 1995) and that more than half of our fragments were <0.2 km² (Table 1), it follows that fitness consequences of restricted home ranges are distinctly possible for larger bodied species (i.e., longnose gar, northern pike, silver redhorse, largemouth bass, walleye). Small areas may also affect fitness through its influences on species behavior. Reid et al. (2008a) observed that redhorses (Moxostoma anisurum, M. macrolepidotum, M. carinatum) only made spawning runs in larger fragments of the Trent River, which may be the result of insufficient densities of reproductive adults to initiate spawning events (Belk and Tuckfield 2011).

Emigration is another mechanism that may lead to local extinctions in small river fragments. Reid (2007) confirmed that up- and downstream emigration out of small fragments occurs for a limited number of redhorse individuals through locks and over dams. Reid et al. (2008a) found a further lack of genetic differentiation among redhorse populations, reinforcing the notion that Trent River barriers are permeable to them. This finding is at odds with the steep slope of the Trent River SAR, which, previous literature suggests, may result from isolation. It is also possible that movement between fragments is limited to a low number of highly vagile species such as redhorse.

The lack of strong statistical support for alternative drivers of the observed SAR (except for riparian agriculture) serves to reinforce the conclusion that habitat diversity and area may be the most important predictors of richness measured in this study. Although our sampling design led to slightly greater effort in larger fragments, the Chao1 estimator of richness is comparatively unbiased to variable sampling effort (Walther and Martin 2001), which is one reason why it was used here. Spatial autocorrelation among sampled species richness has been shown to affect interpretation of causal factors for richness in other larger rivers (Grenouillet et al. 2004). While there was a high degree of adjacency among our fragments, there was no evidence for spatial relatedness in our richness, area, or habitat measures. Differences in position relative to a major colonizing pool such as Lake Ontario can make assemblages difficult to
compare due to non-equivalence. However, distance to the river mouth failed to explain significant variation in species richness. Finally, the fauna was not composed of nested subsets of fauna (Appendix S6), eliminating these as strong explanatory options.

Our findings suggest several possible applications at the local scale within the Trent River, and potentially at larger scales if our results are found to be consistent across fragmented river settings. If the accelerating rate of dam removals observed in North America and Europe over the last several decades continues (Bellmore et al. 2017, Liuyong et al. 2019), studies will be needed to facilitate efficient decision making about which dams to take out and in what order. Optimization studies of dam placement and removal often emphasize fish species richness as a societally valued attribute of ecosystems. For instance, O’Hanley et al. (2020) developed a spatial optimization model for locating dams to balance trade-offs between hydropower generation and migratory fish species richness. Their study relied on a crude rule-set describing the relationship between richness and undammed river length. Incorporating river fragment SARs would add specificity and rigor to such an analysis. Other studies seeking to optimize barrier removal (O’Hanley et al. 2013, Diebel et al. 2015) relied on maximizing habitat metrics that were assumed to relate to fish populations. Again, incorporating SARs may be useful in these contexts to avoid having to use indirect proxies for species diversity. Several studies have demonstrated the potential to use sample data from smaller areas to predict species richness into larger areas based on existing power law SARs (Kier et al. 2005, Gerstner et al. 2014). Extension of such models to fragmented river SARs may offer benefits for dam removal planning, with the caveat that prediction from habitat ISARs must be undertaken with care (Matthews et al. 2016b).

Dams provide a multitude of benefits to society and will undoubtedly remain an important solution to power demand, water security, navigation, and other factors (Ho et al. 2017). Maximizing the biological diversity remaining in rivers will continue to be an important conservation strategy in many regions of the world (Roper et al. 2018, Rouillard et al. 2018, Stephenson et al. 2019). Our finding of significant effects of both area and vegetation cover diversity suggests that fisheries managers in the Trent River could be justified by guarding against demographic consequences of small population sizes to maximize fish diversity in river fragments. They may also be able to use local-scale vegetation management as an option to promote alpha diversity. Despite a high number of barriers, our finding that species accumulated rapidly across a gradient of small habitat fragment is encouraging.

If this is indeed one of the first studies to document a riverine fragment SAR, more case studies are needed to establish whether the Trent River is a unique case, or whether steeper-than-average slopes are typical of dammed river fragments. While we acknowledge that dam density on many river networks may be lower than observed in the Trent River, settings with dense networks of dams operating together (i.e., cascade dams) are present in many places (Loures and Pompeu 2019, Zhang et al. 2019). In addition to verifying the existence of additional river fragment SARs, explicit tests are warranted of causal drivers of SARs in fragmented rivers, and the role of tributaries for mitigating negative demographic effects on small population sizes within fragments. Additional studies of fragmented river SARs may also serve to make accessible a range of analytical tools that could benefit conservation of riverine biodiversity.

ACKNOWLEDGMENTS

Leon Carl and Chris Wilson designed and carried out the overarching study of the consequences of impoundments in southern Canadian rivers and secured funding for study of the Trent River. Peter Esselman developed the research questions for the paper and wrote the manuscript. Beth Sparks-Jackson and Peter Esselman performed the analyses, and Beth Sparks-Jackson, Peter Esselman, and Leon Carl contributed to editing the manuscript. Primary funding for this project was provided by the Ontario Ministry of Natural Resources and Forestry. The Trent Severn Waterway contributed to the project through the Watershed Science Centre at Trent University, Peterborough, Ontario, Canada, to Leon Carl. The U.S. Geological Survey also provided funding to Leon Carl to complete this analysis. We are grateful to Scott Reid, Sarah Crabbe, Steve Chong, and Zhen Zhang for assisting with data collection, preparation, and
analysis. The inputs of Dr. Paul Seelbach and two anonymous reviewers improved the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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DATA AVAILABILITY

All fish, habitat, and spatial data used in this paper are available at: https://doi.org/10.5066/P9L1AYLW.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3411/full