Freshwater fish functional and taxonomic diversity above and below Niagara Falls

Karl A. Lamothe · Justin A. G. Hubbard ·
D. Andrew R. Drake

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Abstract The Niagara River, which connects two Great Lakes (Erie and Ontario) and forms a border between Canada and the United States, has experienced decades of abiotic and biotic disturbance as well as long-term restoration efforts. Given the iconic riverscape and importance as a binational fisheries resource, a biodiversity assessment of the mainstem Niagara River fish assemblage is overdue. Here, fish assemblage and habitat data from a standardized boat electrofishing program of the Niagara River were combined with species trait data related to substrate associations, diet preferences, reproductive strategies, and body size to quantify biodiversity patterns among river sections (sites above and below Niagara Falls), seasons (spring, summer, fall), and years (2015–2017). Sixty-five species were captured representing a variety of trait combinations. Significant differences in functional dispersion and divergence (i.e., functional diversity) were observed between river sections, seasons, and (or) years. The fish community captured in the lower river in spring 2015 had both the

highest average functional dispersion (2.08 ± 0.32 SD) and divergence (0.88 ± 0.04 SD) compared to the other seasonal sampling efforts, but relatively few fishes were captured ($n = 686$). Although non-native fishes represented a small portion of the catch over the 3 years (8.6% of catch), the seasonal presence (spring and fall) of mostly introduced large-bodied salmonids expanded functional trait space in the lower river during these periods. The importance of rare species on functional diversity metrics suggests further insight on local species detection probabilities is needed to understand if differences in functional diversity reflect ecological patterns or are driven by sampling design.

Keywords Biodiversity · Great Lakes · Large rivers · Non-native species · Multivariate

Introduction

Biodiversity assessments are often used to inform species conservation and habitat management, but have traditionally focused on taxonomic metrics of diversity dependent on evolutionary history (e.g., species richness). Although maintaining species richness increases the likelihood that ecosystem function will be preserved when disturbance occurs (i.e., insurance hypothesis of biodiversity; Yachi and Loreau 1999), traditional taxonomic metrics do not always correlate with the suite of ecological functions present in a community (Cadotte et al. 2011). As such, functional diversity metrics were developed to help characterize what species do in the

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K. A. Lamothe (✉) · J. A. G. Hubbard · D. A. R. Drake
Great Lakes Laboratory for Fisheries and Aquatic Sciences,
Fisheries and Oceans Canada, Burlington, Ontario, Canada
e-mail: karl.lamothe@dfo-mpo.gc.ca

Present Address:

J. A. G. Hubbard
Department of Physical & Environmental Sciences, University of
Toronto Scarborough, Scarborough, Ontario, Canada

environment and how species traits contribute to ecosystem functioning (Tilman 1999; Mason et al. 2005; Petchey and Gaston 2006; Laliberté et al. 2010).

Quantifying changes in functional diversity over space and time, and the traits that support these metrics, can reveal the mechanisms underlying changing community and ecosystem dynamics. For example, functional diversity metrics have been used to understand the mechanisms leading to species extinctions (Cardinale et al. 2012), to evaluate the success of management actions and inform environmental protection efforts (Ikin et al. 2019), and to estimate the vulnerability of ecosystems to the effects of future disturbance (Mouillot et al. 2013a). Furthermore, functional diversity metrics can be used to identify species that are functionally redundant in an ecosystem due to similar feeding, reproductive, and (or) behavioural attributes (Lamothe et al. 2018), or alternatively, species that have disproportionately large roles in maintaining ecosystem function due to unique functional attributes (Mouillot et al. 2014). However, local increases in functional diversity or redundancy can also be caused by the introduction of non-native species (Campbell and Mandrak 2017; Toussaint et al. 2018) that may or may not be detrimental to the persistence of local biota. Combining traditional taxonomic metrics with functional diversity metrics can therefore provide a more robust understanding of local and regional biodiversity patterns (Cadotte 2011).

The Laurentian Great Lakes are among the largest interconnected freshwater ecosystems on Earth and have experienced considerable abiotic and biotic changes over the last century. Paradigmatic of these changes is the freshwater fish assemblage, as over 30 non-native species have established in the Great Lakes, at least five species have gone extinct, and almost two dozen have been extirpated (Mandrak and Cudmore 2010; Roth et al. 2011). As fish species richness (Roth et al. 2011) and functional diversity (Campbell and Mandrak 2017) have increased in the Great Lakes basin over the last century due to non-native species introductions, the abundance and distribution of many native species within individual lakes and their connecting channels (i.e., Niagara River, Detroit River, St. Clair River) have changed. In an effort to improve fish community structure and function in the Great Lakes basin, long-term binational restoration actions in 42 “Areas of Concern (AOC)” were undertaken (Hartig and Thomas 1988; Hartig et al. 2020). Examples of restoration efforts

included remediation of contaminated sediment, habitat enhancement projects, and pollution prevention efforts (Hartig et al. 2020). Given the long-term abiotic and biotic changes, quantifying present-day freshwater fish functional and taxonomic diversity within these AOCs may offer insight into the lasting effects of local ecosystem restoration efforts in combination with the introduction of non-native species.

The Niagara River, which connects lakes Erie and Ontario, is an AOC with a long history of fish community degradation and restoration (Moore 1929; Hartig and Thomas 1988). Despite its importance as a binational fisheries resource, the structural and functional composition of this freshwater fish assemblage have been understudied over the last few decades owing to the challenges of sampling such a large, fast flowing river with prominent waterfalls (but see Yagi and Blott 2012). As such, we sought to characterize the functional and taxonomic diversity of the Niagara River fish assemblage at sites upstream and downstream of Niagara Falls. Specifically, we used data from a standardized, three-year (2015–2017) seasonal fish sampling program to: (i) document present-day species composition and identify abiotic factors influencing compositional patterns; (ii) quantify present-day freshwater fish functional diversity; and, (iii) test whether differences in functional diversity exist seasonally or between river sections. Overall, this study provides an approach for future fish biodiversity assessments and the first description of fish functional diversity in the Niagara River, one of the most iconic riverscapes on Earth.

Methods

Study site

Fish sampling in the Niagara River was performed during the day using a dual-boom, 6.4 m Smith Root electrofishing boat at 10 sites in the spring, summer, and fall of 2015–2017 (Fig. S1; full sampling details are provided in Gáspárdy et al. 2020). All surveys were performed in Canadian waters (i.e., western shore) with four sites downstream of Niagara Falls (i.e., lower river) and six upstream of Niagara Falls (i.e., upper river; Fig. S1). The primary goal of sampling was to characterize the composition of the Niagara River fish assemblage given the challenges of sampling such a fast-flowing system (maximum measured water velocity: 0.66 ms^{-1}).

At each site, two 500 m transects were performed with three passes for each transect. The transects followed a 2 m depth contour with fishing occurring with the direction of flow for approximately 5700 s/site. Power output during sampling was approximately 1800 W with adjustments made to account for differences in temperature and conductivity (Edwards et al. 2006). After each pass, captured fishes were identified, counted, and stored in holding bins until being released following the final pass.

Coarse habitat measurements at each site were taken during and following fish sampling. Habitat variables were selected based on their potential influence on fish community structure or composition. These measurements included: a visual assessment of the proportion of the sampling site covered by submerged aquatic vegetation; surface water quality measures taken with a YSI 7-Port Multi-parameter water quality sonde at the mid-point of the site (conductivity, dissolved oxygen, water temperature, turbidity; Table 1); a visual assessment of the proportion of Wentworth (1922) substrate classes throughout the site, with a Petite Ponar 6 × 6 in. SS scoop grab sampler used to distinguish small substrate classes; and, the average of three depth and water velocity measurements from the upper, middle, and downstream portion of each site (Table 1). Physical river distance (km) between the site and the confluence with Lake Ontario (lower river) and the confluence with Lake Erie (upper river) was measured post-sampling using ArcMap10.2.

Taxonomic diversity analysis

For the analyses described in the following sections, fish capture data were pooled across transects and passes. A redundancy analysis (RDA) was performed on Hellinger-transformed species abundance data with the site-specific habitat covariates to understand how habitat characteristics were associated with the variation observed in fish community structure (Table 1). A Hellinger transformation was used to reduce the influence of abundant species on the analysis (Legendre and Gallagher 2001). An automatic stepwise model-selection approach was used to identify significant site-specific covariates where significance was assessed using 9999 permutations at $\alpha = 0.05$. Prior to the analysis, Pearson correlations were calculated to ensure a lack of correlation between covariates (Fig. S2), and continuous covariates were converted to z-scores. To

Table 1 Mean (minimum - maximum) of aquatic habitat measurements in the upper ($n = 103$ samples) and lower sections ($n = 72$ samples) of the Niagara River

Habitat characteristic	Upper	Lower
Proportion of submerged vegetation cover	0.47 (0.00–0.95)	0.40 (0.00–0.95)
Conductivity ($\mu\text{S cm}^{-1}$)	318.36 (189.30–572.70)	329.11 (201.20–563.80)
Average site depth (m)	1.66 (0.73–3.07)	1.77 (0.67–2.47)
Dissolved oxygen (mg L^{-1})	8.86 (2.08–12.00)	10.06 (8.26–12.32)
Distance from river mouth (km)	17.54 (6.36–25.03)	5.79 (2.25–10.27)
Turbidity (ntu)	4.05 (0.18–141.20)	2.97 (0.84–10.70)
Water temperature ($^{\circ}\text{C}$)	17.83 (7.07–25.45)	18.61 (10.07–25.97)
Average water velocity (m s^{-1})	0.20 (0.02–0.66)	0.15 (0.01–0.60)

supplement the RDA, non-metric multidimensional scaling (NMDS) was performed on the Hellinger-transformed species abundance data, and the significant habitat covariates identified in the RDA were fit to the NMDS ordination, similarly using 9999 permutations. Given the similarity in results between the two analyses (NMDS plot: Fig. S3), only the results of the RDA are presented in the main text.

Fish trait data

Fish trait data were collected from the literature to represent the ecological niche of each fish species. Traits were related to components of species' diet, reproductive guild, substrate associations, and average adult body size (Frimpong and Angermeier 2009; Holm et al. 2009; Lamothe et al. 2018; Table 1). Diet traits initially included seven binary variables representing preferred consumption of: 1) algae or phytoplankton, including filamentous algae; 2) any part of macrophytes and vascular plants; 3) detritus or unidentifiable vegetative matter; 4) aquatic and terrestrial invertebrates including zooplankton, insects, microcrustaceans, annelids, and molluscs. This group also included larval fishes; 5) larger fishes (i.e., fry-adult size fishes), crayfishes, crabs, frogs, etc.; 6) blood; and, 7) eggs of fishes and other aquatic organisms. Reproduction traits were based on elements from Balon

(1975) and included two binary variables based on whether fishes guard their brood and if fishes hide or create nests for their brood. Substrate associations included nine binary variables indicative of preferences for muck, clay or silt substrates, sand substrate, gravel substrate, cobble substrate, boulder substrate, bedrock, vegetation, large woody debris, and organic debris or detritus. Due to a lack of variation, the preference for consuming aquatic and terrestrial invertebrates and blood were not included in the analyses; almost all species in this study feed on invertebrates or larval fishes, whereas only one species (Sea Lamprey *Petromyzon marinus*) feeds on blood. Spearman rank correlations were calculated between each trait variable (Fig. S4). As a result, the preference for feeding on detritus or unidentifiable vegetative matter and algae or phytoplankton, including filamentous algae, was not included in calculating the functional trait space, as well as the preference for muck substrate.

Functional diversity analysis

To construct the multidimensional functional trait space, three principal component analyses (PCAs) were performed to combine species traits from three trait type categories (diet, substrate, and reproduction) into respective trait dimensions (Lamothe et al. 2018). The trait data were Hellinger-transformed prior to performing each PCA (Legendre and Gallagher 2001). The number of axes to retain was chosen through a permutation approach, where each column of the trait matrix was permuted, followed by a PCA 9999 times; nontrivial axes were retained if the proportion of variance explained was greater than 95% of the permuted PCAs for that component (Peres-Neto et al. 2003, 2005). The nontrivial trait dimensions were then used to build the functional trait space by performing a principal coordinates analysis (PCoA) on the three trait dimensions and a scaled and centered (i.e., z -scores) average total length (cm) variable (Laliberté et al. 2010). Fish total length, here represented by the Ontario average adult total length for each species (Holm et al. 2009), is a variable related to many processes relevant to individual niches including reproduction (Blueweiss et al. 1978), dispersal (Radinger and Wolter 2014), and vulnerability to predation (Alofs and Jackson 2015).

We calculated two functional diversity metrics unaffected by species richness, functional dispersion (Anderson 2006; Laliberté and Legendre 2010) and

functional divergence (Villéger et al. 2008). Functional dispersion describes the average distance of individual species in functional trait space to the centroid, weighted by the relative abundance of each species (Anderson 2006; Laliberté and Legendre 2010). Lower values of functional dispersion suggests species with higher relative abundance have more traits in common (i.e., lower functional diversity). Functional divergence describes the position of species relative to the border of the functional trait space and provides a relative measure of uniqueness of species traits in a community (Mason et al. 2005; Villéger et al. 2008); higher divergence suggests that the abundance distribution of fishes in trait space is maximizing the full suite of functional niches within the community (Mason et al. 2005). Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; McArdle and Anderson 2001) was used to test for differences in functional dispersion and divergence between years, seasons, and river sections. Significance was assessed at $\alpha = 0.05$ using 9999 permutations. All statistical analyses were performed using the R statistical software (R Core Team 2020). Code and data are accessible at <https://github.com/KarlLamothe/NiagaraRiver>.

Results

Fish sampling results

Over 41,000 fishes representing 65 species, 44 genera, and 21 families were sampled from the Niagara River between 2015 and 2017 and identified to the species level (Table S1; Gáspárdy et al. 2020). In total, 55 species were observed in the lower Niagara River compared to 57 in the upper river. Substantially more fishes were captured in the upper river ($n = 32,028$ fishes) compared to the lower river ($n = 9321$). A similar number of fishes were captured in 2015 and 2016 (2015 = 15,685 fish; 2016 = 15,694), whereas the sampling in 2017 captured 9970 individual fish. White Sucker (*Catostomus commersonii*) was the most abundant species sampled ($n = 10,949$ individuals; 95.5% of sites), followed by Emerald Shiner (*Notropis atherinoides*; $n = 8715$; 87.5% of sites) and Yellow Perch (*Perca flavescens*; $n = 5136$; 89.8% of sites; Fig. 1). White Sucker and Emerald Shiner showed particularly high relative abundance in the upper river, whereas the CPUE

distribution was more evenly distributed in the lower river (Fig. 1).

Seasonal differences were observed in the number of fishes captured, with 19,042, 12,893, and 9414 fishes captured in the fall, summer, and spring, respectively. The fewest fishes were captured in summer 2015 during sampling of the lower river ($n = 491$ fish), whereas 8562 fishes were captured in the upper section in fall 2015. Overall, more species were captured in the fall ($n = 59$ species) compared to the spring ($n = 53$) or the summer ($n = 52$). Less than 100 individuals were captured for 35 species over the 3 years of sampling. Among all the species captured, 14 are considered introduced, reintroduced (Atlantic Salmon *Salmo salar*), probably introduced, or reportedly introduced in at least one of the Great Lakes (Table S1), comprising a total of 8.6% of the total catch ($n = 3568$ fish).

The number of individuals captured and total species richness were greatest during fall sampling, when several species showed particularly high relative abundance, including Bluntnose Minnow (*Pimephales notatus*), Brook Silverside (*Labidesthes sicculus*), Coho Salmon (*Oncorhynchus kisutch*), Emerald Shiner, Greater Redhorse (*Moxostoma valenciennesi*), Rainbow Smelt (*Osmerus mordax*), Round Goby (*Neogobius melanostomus*), White Perch (*Morone americana*), White Sucker, and Yellow Perch. Compared to the lower river, the upper river appeared to be missing several large species, whereas 10 mostly small-bodied species were observed in the upper river but not detected in the lower river (Table 2). The unique species captured in the upper river made up 0.2% of the catch ($n = 72$ individuals), whereas the unique species captured in the lower river made up 4.5% of the catch ($n = 419$ individuals; Table 2).

Average depth, distance to the river mouth, proportion of submerged aquatic vegetation, and water temperature were significant ($p < 0.05$) predictors of fish species abundance in the Niagara River (Fig. 2). Separation was observed between fish communities of different river sections and seasons in the RDA triplot (Fig. 2). Gizzard Shad (*Dorosoma cepedianum*) and Yellow Perch abundance were positively correlated with mean river depth and negatively correlated with the distance from river mouth. Rainbow Smelt and Emerald Shiner showed a positive relationship with fall and spring sampling and a negative relationship with water temperature and the proportion of submerged aquatic vegetation at a site, as both species were captured in greater abundance

during the fall and spring in non-vegetated areas. White Sucker, the most abundant and prevalent species captured across sites (Fig. 1), showed similar compositional patterns to Bluntnose Minnow and Spottail Shiner (*Notropis hudsonius*; Fig. 2).

Functional diversity

The first principal component of the diet and reproduction PCAs were retained as trait dimensions, explaining 53.6% and 81.2% of the variation, respectively (Table S2). Two components were retained from the PCA on substrate associations, explaining 51.5% of the total cumulative variation (Table S2). Using the four trait dimensions and average body size, a PCoA weighted by the relative abundance of species generated a high quality reduced trait-space representation of the fish traits where the first three axes explained 73.0% of the variation (Fig. 3).

Species were broadly partitioned in trait space along Component 1 by body size, diet preference, and substrate associations, with larger piscivores that prefer larger substrates found on the negative end of Component 1 and smaller, more generalist species found on the positive end (Fig. 3). Most of the species abandon their brood ($n = 44$ species) as opposed to guarding ($n = 21$ species), but were equally likely to nest in open substrates ($n = 31$ species) compared to building nests or hiding their brood ($n = 34$ species). In functional trait space, species that guard nests were associated with the positive end of Component 2, which included mostly smaller-bodied species (Fig. 3). Overall, fewer species prefer large substrates (e.g., boulder, bedrock) compared to small substrates (e.g., clay/silt, sand) and most species will feed on larger fishes, crayfishes, and/or frogs ($n = 42$ species). Species associated with vegetation or small substrates (e.g., clay/silt, sand) were found on the negative end of Component 3 and species that prefer larger substrates were positively associated with Component 3 (Fig. 3).

Functional dispersion differed between years and river section, but not between seasons (Table 3). Generally, functional dispersion was highest in 2015 (mean = 1.65 ± 0.34 SD) and in the lower river (1.62 ± 0.34 ; Fig. 4). Functional divergence differed across years, seasons, and river sections (Table 3), with the greatest measured functional divergence observed during spring sampling, in the upper section of the Niagara River, and in 2015 (Fig. 4). Plotting functional dispersion against divergence revealed a positive relationship

Fig. 1 Number of individuals captured and mean catch-per-unit effort (CPUE; catch per electro-fishing second) for species within the lower (black) and upper (grey) section of the Niagara River. Species with less than 100 individuals captured are not shown

in the lower river whereas a negligible relationship was observed in the upper river (Fig. 5). High values of functional dispersion and divergence in the lower river suggests that the assemblage is composed of a diverse set of ecological niches that are maximizing functional trait space. Moderate levels of functional dispersion (~1.6) across moderately high divergence measurements (> 0.7) in the upper river suggests that those sites contain a unique set of ecological niches with abundant

species sharing more traits than fish communities in the lower river.

Summarizing the abundance of unique species captured by river section illustrated why a positive relationship was observed between functional divergence and dispersion in the lower river, but not in the upper river (Fig. 6). In the lower river, functional dispersion and divergence increased with the abundance of the unique species captured, whereas there was no relationship between functional dispersion or divergence with the abundance of unique species captured in the upper river (Fig. 6). Overall, this result suggests that the presence and abundance of the unique, mostly large-bodied species captured in the lower river (e.g., Chinook Salmon, Coho Salmon) increased the observed functional niche space, whereas the unique species captured in the upper river were seemingly redundant in trait composition to other taxa.

Table 2 Unique species and number caught (aggregate count) in the lower and upper Niagara River

Lower river		Upper river	
Species	Count	Species	Count
American Eel	29	American Brook Lamprey	25
Atlantic Salmon	1	Central Mudminnow	1
Chinook Salmon	227	Channel Catfish	1
Coho Salmon	25	Creek Chub	1
Lake Trout	11	Fantail Darter	3
Longnose Gar	101	Fathead Minnow	1
Sea Lamprey	1	Grass Pickerel	2
Silver Redhorse	24	Rainbow Darter	36
		Trout-perch	1
		White Crappie	1

Introduced species in the Niagara River

Due to the prevalence of captured non-native salmonids, most of the introduced, reintroduced, probably introduced, or reportedly introduced species were partitioned along the left side of Component 1 in functional trait space (Fig. 3), indicating that they are generally larger than other species in the Niagara River assemblage. Rainbow Smelt was the most abundant introduced species captured in the 2015–2017 sampling effort ($n =$

Fig. 2 Redundancy analysis (RDA) triplot of Niagara River fish species abundances across river sections and sampling seasons. Note that only species with high abundances were plotted for visual purposes, but all species were included in the analysis. Abbreviations: BiBu = Black Bullhead; BiMi = Bluntnose Minnow; CoCa = Common Carp; EmSh = Emerald Shiner; GiSh =

Gizzard Shad; LMB = Largemouth Bass; RaSm = Rainbow Smelt; SMB = Smallmouth Bass; SptSh = Spottail Shiner; WhSu = White Sucker; YePe = Yellow Perch; Veg = proportion of submerged aquatic vegetation; dMouth = distance to mouth of river; Temp = water temperature

1365 individuals; Fig. 1). Based on linear distances between species in functional trait space, Rainbow Smelt trait composition was most similar to White Bass (*Morone chrysops* - native) and Rainbow Trout

(*Oncorhynchus mykiss* - introduced; Fig. 3). These three species, although morphologically different, are generally carnivorous, will feed at the surface or throughout the water column, and do not guard their offspring post-

Fig. 3 Functional trait space produced using a principal coordinates analysis. Fish abbreviations are provided in Table S1 and mostly reflect the first two letters of the common names of the species (e.g., NoPi = Northern Pike)

Table 3 Results of the permutational analysis of variance for functional dispersion and divergence across seasons, river sections, and years ($n = 88$ sites)

Functional diversity metric	Factor	df	<i>F</i>	<i>R</i> ²	<i>p</i>
Functional dispersion	Season	2	1.90	0.04	0.15
	Section	1	5.36	0.05	0.02
	Year	2	3.60	0.07	0.03
Functional divergence	Season	2	7.11	0.12	<0.01
	Section	1	18.36	0.15	<0.01
	Year	2	4.31	0.07	0.02

reproduction. Although functionally similar, far fewer Rainbow Trout ($n = 111$ individuals) and White Bass ($n = 41$) were caught than Rainbow Smelt (Fig. 1). Instead, Rainbow Smelt was partitioned closest to Emerald Shiner (native) along the first two components of the RDA (Fig. 2). Although similar in substrate preference

and reproductive traits, Emerald Shiner and Rainbow Smelt show differences in food preferences and body size (i.e., Component 1 in Fig. 3). Rainbow Smelt primarily feeds on aquatic and terrestrial invertebrates, larval fishes, and (or) larger fishes near the surface or within the water column and grow to almost three times the length of Emerald Shiner.

Discussion

The Niagara River is one of the most unique freshwater ecosystems in North America with a long history of degradation and restoration (Hartig and Thomas 1988; Hartig et al. 2020). Based on several metrics, the Niagara River contains a functionally and taxonomically diverse fish assemblage that varies in site-specific species composition, with species that differ in size,

Fig. 4 Boxplots of functional dispersion and divergence as a function of year, season, and river section. Significant differences in functional metrics across year, season, and (or) section indicated by shaded plots

Fig. 5 Functional divergence versus functional dispersion for freshwater fishes in the lower (square) and upper (circle) Niagara River during the spring (dark grey), summer (light grey), and fall (black), and associated linear regressions (solid lines = lower section, dashed lines = upper section)

reproductive tactics, substrate associations, and diet preferences. Differences in species composition and functional diversity were observed between river sections, seasons, and years. More fish and species were caught in the upper river compared to the lower river, with the greatest number of fish captured during fall sampling. Although appearing to have lower functional

divergence than the upper river community, the relationship between functional dispersion and divergence was positive in the lower river, whereas this relationship was negligible for the upper river fish community. Overall, non-native species consisted of a relatively low proportion of the catch over the 3 years of sampling, but the seasonal presence (spring and fall) of mostly

Fig. 6 Abundance of unique species captured in the lower (grey) and upper (black) sections of the Niagara River against functional dispersion and functional divergence with fitted linear models. Shaded area = 95% confidence intervals

introduced large-bodied salmonids expanded the overall niche space for freshwater fishes in the lower river during these periods.

A difference in the relationship between freshwater fish functional dispersion and divergence was observed between the upper and lower Niagara River, where the lower river showed a positive linear relationship and upper river did not. The positive relationship in the lower river was likely caused by the presence of large-bodied species that seasonally migrate between the lake and river, including introduced salmonids. Large-bodied species corresponded with the negative end of the first component of functional trait space, which led to increased site-specific estimates of functional diversity when these species were present. High estimates of functional diversity in the lower river fish assemblage contrasts expectations based on habitat measures alone, as the upper section of the river is generally perceived to have greater aquatic habitat diversity (e.g., greater vegetated area, depth variation, access to tributaries).

In theory, the introduction of fishes could have positive, negative, or neutral effects on fish functional diversity depending on the competitive ability of native versus introduced species, the configuration of present-day niche space and how the novel traits interact with the native community, and the scale of analysis (Mouillot et al. 2013b; Kuebbing et al. 2018). Globally, non-native freshwater fishes have generally increased riverine functional diversity (Toussaint et al. 2018). This increasing pattern is also present in the Great Lakes proper, which have seen an increase in functional diversity over the last 150 years, ultimately due to the introduction of novel traits of non-native fishes (Campbell and Mandrak 2017). In support of these larger scale studies, our results indicated that the introduction of non-native salmonids into Lake Ontario and the lower Niagara River has led to an influx of novel traits leading to heightened measures of functional diversity.

Our understanding of how the loss of fish species in the Niagara River has affected functional diversity is less certain. Fifty-seven North American freshwater fishes went extinct between 1898 and 2006 (Burkhead 2012), including several species that could have occupied or used the Niagara River at some point during their life-history, such as Blue Pike (a.k.a. Blue Walleye; *Sander vitreus glaucus* - extinct), Harelip Sucker (*Lagochila lacera* - extinct), Sauger (*Sander canadense* - extirpated in Lake Ontario), and (or) Spoonhead Sculpin (*Cottus ricei* - extirpated in lakes Ontario and Erie;

Roth et al. 2011). If these species were extant, functional trait space may have shown few differences given the presence of taxa with similar trait attributes (e.g., Walleye, non-native salmonids, benthic omnivores). If the trait composition of extirpated species was in fact redundant to the present-day fish assemblage, the loss of these species may signify a reduction in resilience to future disturbance. Nevertheless, a unique catch that occurred in October of 2015 at one of the most northern sites in the lower Niagara River was a single Atlantic Salmon. Atlantic Salmon was declared extirpated from Lake Ontario as a result of overharvesting and habitat alteration and destruction in the late 1800s (Parrish et al. 1998; Scott et al. 2005) but has experienced continuous reintroduction efforts since the 1980s (OMNRF 2019). The source of the captured Atlantic Salmon specimen during the Niagara River survey inevitably stems from reintroduction efforts.

Although differences were observed in functional diversity across seasons, years, and river sections, the magnitude of these differences was relatively small, perhaps reflecting the expected level variation given the similarity in species composition between rivers sections and years, and the amount of sampling effort performed. Several rare species in the dataset (Central Mudminnow, Channel Catfish, Fathead Minnow, Grass Pickerel, and Trout-perch) were only captured in 2015 at particular sampling sites, which may have increased functional diversity measures relative to 2016 or 2017. It is unlikely that these rare species are no longer occupying the Niagara River. Instead, the lack of detections was more likely caused by a combination of low detection probabilities, low relative abundance, poor sampling conditions (i.e., high water velocity), and (or) relatively low effort at each site, all of which are causes of zero inflation in ecological datasets (Dénes et al. 2015). In the fast-flowing waters of the Niagara River, many small-bodied fishes rely on structures (e.g., boulders, woody debris) that create areas of reduced flow (Robin Gáspárdy personal communication 2019), which are often more difficult to sample in fast-flowing waters using boat electrofishing techniques. Quantifying the probability of detection for each species in the Niagara River was outside the scope of this study, but is critical to improve future efforts to better understand local species occupancy, abundance, and overall trait distribution in the Niagara River, and the degree of change in these attributes over time.

The use of functional diversity metrics together with the taxonomic analysis confirmed knowledge of regional fish community structure and provided a means for better understanding patterns in fish community composition. For example, White Sucker, Emerald Shiner, and Yellow Perch were among the most abundant fishes captured in the Niagara River, which is consistent with their prevalence in the broader region (Lamothe et al. 2018), and also expected given their life-history (e.g., abandoning brood) and the flow dynamics of the system. Alternatively, Emerald Shiner and Rainbow Smelt showed similar site-specific abundance patterns based on the compositional analysis in the Niagara River, generally occupying cooler sites. Evaluating the trait composition of these two species revealed, however, that the two species demonstrate unique life-history characteristics and behavioural attributes (Holm et al. 2009). Similarly, Greater Redhorse and Muskellunge (*Esox masquinongy*) showed compositional parallels, as nearly every site with Muskellunge contained abundant Greater Redhorse, but these two species differ in body size, feeding characteristics, substrate associations, and thermal preference, and therefore occupy different ecological niches. By omitting the functional diversity analyses and relying on a traditional compositional evaluation, these distinctions could be missed, and therefore suggest a benefit of incorporating trait-based analysis with traditional bioassessments.

Previous studies have demonstrated the value of using functional diversity metrics to assess biodiversity patterns (Villéger et al. 2010; Cardinale et al. 2012), as functional diversity metrics are somewhat less dependent on sampling effort and, therefore, should be more accessible (Gallardo et al. 2011), particularly with the rise of open-access software and packages (e.g., R Core Team 2020). However, gaps remain in functional trait databases for many taxa and there is a degree of methodological complexity when calculating functional diversity metrics, such as choosing the appropriate functional traits and ordination methods (e.g., Poos et al. 2009). These limitations may be slowing the inclusion of functional diversity analyses into management considerations. Nevertheless, the availability of species-specific trait information for freshwater fishes continues to improve (e.g., Fishbase: Froese and Pauly 2019; FishTraits: Frimpong and Angermeier 2009) and opportunities exist to use historical capture data to evaluate

changes in functional diversity over time, particularly as it relates to changes in environmental conditions and species extirpations. Investigating changes in functional diversity over time, however, requires knowledge of historical sampling design, as the lack of detections does not necessarily indicate absence from the system, particularly for freshwater fishes with low detection probabilities. This is critical, as demonstrated in this study, the presence of relatively rare species can strongly influence measures of functional diversity. Future efforts to characterize changes in freshwater fish functional diversity over time would therefore benefit from using multiple gears to ensure a complete representation of the fish community. Overall, our study provides a much needed exploration of the present-day fish assemblage in the Niagara River and provides an example of how combining traditional biodiversity metrics with measures of functional diversity can reveal important nuances in local species composition.

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Compliance with ethical standards

Conflicts of interest/competing interests The authors have no conflicts of interest to declare.

Code availability R code used to perform the analyses for this study is available at: <https://github.com/KarlLamothe/NiagaraRiver>

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