

Functional diversity and redundancy of freshwater fish communities across biogeographic and environmental gradients

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Abstract

Aim: Functional redundancy occurs when species share overlapping ecological functions and is considered an important component of ecosystem resilience. However, much of what we know about functional redundancy comes from relatively species-rich terrestrial and marine environments. Here, we examined patterns of functional redundancy among Ontario freshwater fish communities with species richness levels ranging from 4 to 30 species across lakes of differing size, depth, productivities and thermal characteristics.

Location: Six thousand nine hundred and seventy-seven lakes in Ontario, Canada.

Methods: We examined functional redundancy by quantifying the relationship between functional diversity and species richness in lakes across Ontario and within smaller biogeographic regions. We used null models to test whether fish communities had greater redundancy than expected from random assemblages. We then used generalized additive models (GAMs) to predict how patterns of redundancy vary across environmental variables. At last, we compared species-level functional rarity metrics across fish thermal preference groups, body sizes and species occurrence rates.

Results: The functional diversity and species richness relationship were saturating among fish communities at the provincial scale but varied between smaller regions with differing biogeographic histories. Most communities fell within expectations from weighted null models of the functional diversity and species richness relationship. The GAMs indicated that fish communities in the largest, deepest and warmest lakes showed the greatest overall functional redundancy. No differences were observed in functional rarity measures between thermal preference groups, across body sizes or across species occurrence rates.

Main conclusions: Although lakes in this study were relatively depauperate of fish species, Ontario fish communities exhibited functional redundancy at the provincial scale, with variation regionally. North-eastern communities showed the least saturating relationship overall as predicted by historical biogeographic patterns of freshwater fish colonization. Overall, this study provides a broad perspective of freshwater fish diversity patterns and highlights the importance of investigating redundancy from different perspectives and multiple spatial scales.

KEYWORDS

freshwater fish, functional diversity, functional redundancy, Ontario, resilience

1 | INTRODUCTION

Differences in functional traits among species in a community can influence how that system responds when disturbance occurs (Haddad, Holyoak, Davies, Melbourne, & Preston, 2008; Moullot, Graham, Villéger, Mason, & Bellwood, 2013). Like the insurance hypothesis of biodiversity, which states that higher species diversity provides a greater probability that ecosystem conditions will be maintained when disturbances occur (Yachi & Loreau, 1999), functionally diverse communities are thought to be more resilient to disturbances (Peterson, Allen, & Holling, 1998; Standish et al., 2014). Related, functional redundancy describes the situation when more than one species shows overlapping ecological functions (Lawton & Brown, 1993; Rosenfeld, 2002; Walker, 1992) and, similarly, may be an important factor for maintaining ecosystem conditions when faced with environmental disturbances (Angeler & Allen, 2016; Angeler, Allen, Barichiev, Eason, & Garmestani, 2016).

Approaches for quantifying functional redundancy continue to be developed (de Bello, Lepš, Lavorel, & Moretti, 2007; Bruno, Gutiérrez-Cánovas, Velasco, & Sánchez-Fernández, 2016; van der Linden et al., 2012; Ricotta et al., 2016), but typically is approached from multiple scales (Allen et al., 2016; Angeler & Allen, 2016; Angeler et al., 2016) and requires community abundance or presence-absence data with a matrix of morphological, behavioural or life-history traits (i.e., functional traits; Rosenfeld, 2002). Using these trait data, ordinations are commonly performed to develop multivariate functional trait spaces that allow subsequent measures of functional diversity to be calculated (e.g., functional richness; Villéger, Mason, & Moullot, 2008). At the regional scale, functional redundancy can be quantified by regressing measures of functional diversity for individual communities against species richness (Guillemot, Kulbicki, Chabanet, & Vigliola, 2011; Micheli & Halpern, 2005; Sasaki et al., 2009; Figure 1). In a conceptual manner, a positive linear relationship between functional diversity and species richness indicates a lack of redundancy at the regional scale and that species equally contribute to function (Figure 1a solid line). In general, functionally redundant assemblages are expected to show a saturating relationship between functional diversity and species richness (Micheli & Halpern, 2005; Figure 1 dashed line); as species richness increases, the rate of increasing functional diversity declines and then eventually plateaus, indicating that in species-rich communities, there is greater overlap in species functions. In an alternate manner, other nonlinear patterns can occur (e.g., Sasaki et al., 2009), where for example, redundancy is observed at high and low levels of species richness, and communities with fewer species show relatively lower levels of functional diversity (Figure 1a dotted line).

At the community scale, null models can be used to test whether individual communities are more or less redundant than expected based on weighted or unweighted randomizations (Figure 1b;

Gerisch, 2014). Communities falling above the null models are considered less redundant than null expectations, whereas communities below the null model would indicate communities that are more redundant than null expectations. At the species level, the extent to which functional traits are distinct or redundant within assemblages can be quantified using functional rarity metrics (Violle et al., 2017) including measures of functional distinctiveness (D ; Violle et al., 2017), functional uniqueness (U ; Violle et al., 2017) and the distances to provincial (d_p) or regional centroids (d_R) for each species in ordination space. Species that are less “distinct” or “unique” are considered more redundant (Buisson, Grenouillet, Villéger, Canal, & Laffaille, 2013).

Much of what we know about functional redundancy in nature comes from studies of plant (Guerrero, Carmona, Morales, Oñate, & Peco, 2014; Laliberté et al., 2010; Sasaki et al., 2009) and marine communities (e.g., Bellwood, Hoey, & Choat, 2003; Hoey & Bellwood, 2009; Micheli & Halpern, 2005); far less research has been directed towards understanding redundancy in freshwater ecosystems, particularly in species depauperate temperate or arctic regions. In this study, we aim to identify patterns of functional redundancy (Figure 1b) among temperate, North American lake fish communities and understand how several factors, specifically, historical biogeography, spatial scale and environmental variation can contribute to such patterns. We approach this objective using fish community data from Ontario, Canada. Ontario spans an area of over 1,000,000 km² (approximately the combined area of France and Germany) with approximately 250,000 freshwater lakes that are morphologically diverse (Jackson & Mandrak, 2002; Lester, Marshall, Armstrong, Dunlop, & Ritchie, 2003) and influenced by different climatic effects occurring across the province. Colonization of most freshwater fish species in Ontario occurred through the Mississippi and Missourian refugia or the south-eastern (Atlantic) refugium after the Wisconsinan ice sheet receded (Mandrak & Crossman, 1992), contributing to a larger pool of species at lower latitudes. If redundancy exists among Ontario fishes, we expected it to be among communities in the south-eastern region of the province because of the greater number of species in this regional pool and therefore a greater potential for redundancy to be observed. On the contrary, we expected the lowest redundancy in the north-eastern region of the province.

We also hypothesized that the largest, deepest, warmest and most productive lakes would harbour the most functionally redundant fish communities. Previous work has demonstrated that lake area, depth, temperature and productivity are related to local species richness of freshwater fish communities (Dodson, Arnott, & Cottingham, 2000; Jackson & Harvey, 1989; Matuszek & Beggs, 1988; Minns, 1989) and that lake depth and surface area are key factors related to the structure of fish communities (Harvey, 1975; Jackson & Harvey, 1993; Mehner, Holmgren, Lauridsen, Jeppesen,

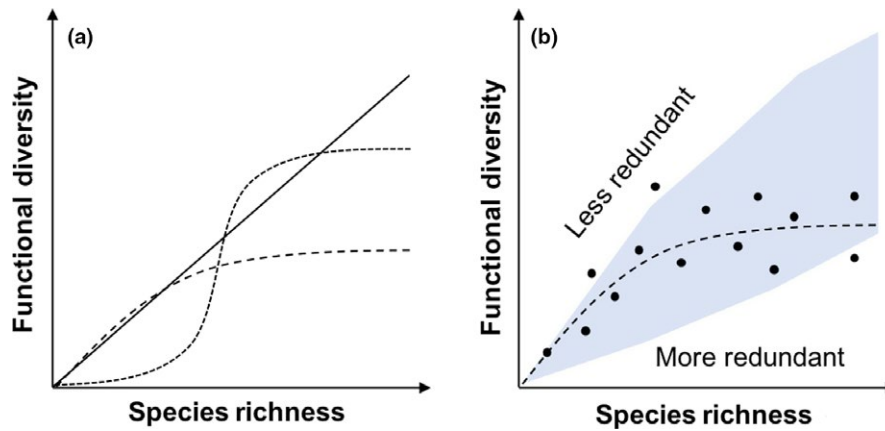


FIGURE 1 (a) Linear, saturating and nonlinear relationships between functional diversity and species richness. Adapted from Micheli and Halpern (2005). (b) Hypothetical example with 14 communities (points) demonstrating a saturating relationship between functional diversity and species richness. The blue area represents the 95% confidence limits of a null model; communities above the null model are less redundant than expected, and communities below the null model are more redundant than expected based on null expectations [Colour figure can be viewed at wileyonlinelibrary.com]

& Diekmann, 2007; Tonn & Magnuson, 1982); larger lakes can provide more structural habitat diversity (Eadie, Hurlly, Montgomerie, & Teather, 1986; Minns, 1989) while deeper lakes provide a greater diversity of thermal niches (Chu, Jones, Mandrak, Piggott, & Minns, 2008) and reduce the likelihood of winterkill (Casselman & Harvey, 1975; Harvey, 1978, 1982). In the same way, species distributions are influenced by temperature and productivity, which play a fundamental role in fish growth, maturity and survival (Dodson et al., 2000; Venturelli, Lester, Marshall, & Shuter, 2010).

Examining the contributions of individual species to functional diversity may allow us to predict the influence of species losses as environmental disturbances tend to impact freshwater ecosystems nonrandomly, often causing declines or exclusion of particular niches (Giller et al., 2004). As such, we were interested in how functional rarity differed across species that show differences in species occurrence rates, body size and thermal preference. For example, Ontario lakes span the northern or southern range boundaries for many fish species (Jackson, Peres-Neto, & Olden, 2001; Shuter, MacLean, Fry, & Regier, 1980), and climate warming is expected to have the most detrimental effect on cold-water species near their species range limits (Chu, Mandrak, & Minns, 2005). Differences in functional rarity metrics across thermal preferences could indicate whether warming temperatures, expected to favour warm-water adapted species and lead to declines in cool and cold-water adapted species (Chu et al., 2005; Poesch, Chavarie, Chu, Pandit, & Tonn, 2016), will increase or decrease functional diversity. Furthermore, fish body size is related to many aspects of fish ecology including reproduction (Blueweiss et al., 1978) and dispersal (Radinger & Wolter, 2014), among others (Alofs, 2016; Woodward et al., 2005), and has also been used to predict vulnerability to predation (Alofs & Jackson, 2015) and shifts in species distributions under changing climate (Alofs, Jackson, & Lester, 2014). At last, functionally distinct species have been demonstrated to play critical roles in maintaining ecosystem functions (Jian et al., 2014; Lyons, Brigham, Traut, & Schwartz, 2005; Violle et al., 2017), but these species are often geographically

limited and thus have high extinction probabilities (Harnik, Simpson, & Payne, 2012). Overall, this study should provide insight into factors influencing patterns of functional redundancy at multiple scales, allowing us to better predict how freshwater fish communities may change in the future.

2 | METHODS

2.1 | Data collection

We used data from the Ontario Ministry of Natural Resources and Forestry Aquatic Habitat Inventory (AHI) survey for this study. Sampling methods are described in Dodge, Tilt, MacRitchie, Goodchild, and Waldriff (1985) and generally consisted of 3- to 5-day surveys of each lake between the late 1960s and early 1980s. Fishes were sampled using different sized mesh gillnets, seine nets and baited minnow traps (Matuszek & Beggs, 1988). In addition, habitat measures recorded included surface area (SA; ha), maximum depth (Z_{max} ; m) and total dissolved solids (TDS; mg/L). Previous studies have demonstrated that the AHI programme undersampled small fishes and lakes in the far northern region of the sampling programme (Bowlby & Green, 1987). Herein, we use the term “community” to refer to the species composition of a single lake.

The AHI recorded the presence or absence of 99 fish species for approximately 10,000 lakes in Ontario. Thirty species were found in fewer than 0.1% of lakes (i.e., less than 10 lakes); lakes where these species occurred were removed from the analyses so that results from multivariate statistical analyses would not be heavily influenced by exceptionally rare species. Next, we eliminated any lakes with fewer than four fish species as this minimum allows calculations of convex hull volumes in 3-dimensions of trait space (see: Functional diversity analysis below), leaving a total of 6,977 fish communities in the analysis (Figure 2). We subsampled the lakes based on watershed distributions and characterized them geographically as either south-eastern ($n = 1,325$), north-eastern ($n = 1,365$) or north-western ($n = 1,541$) to

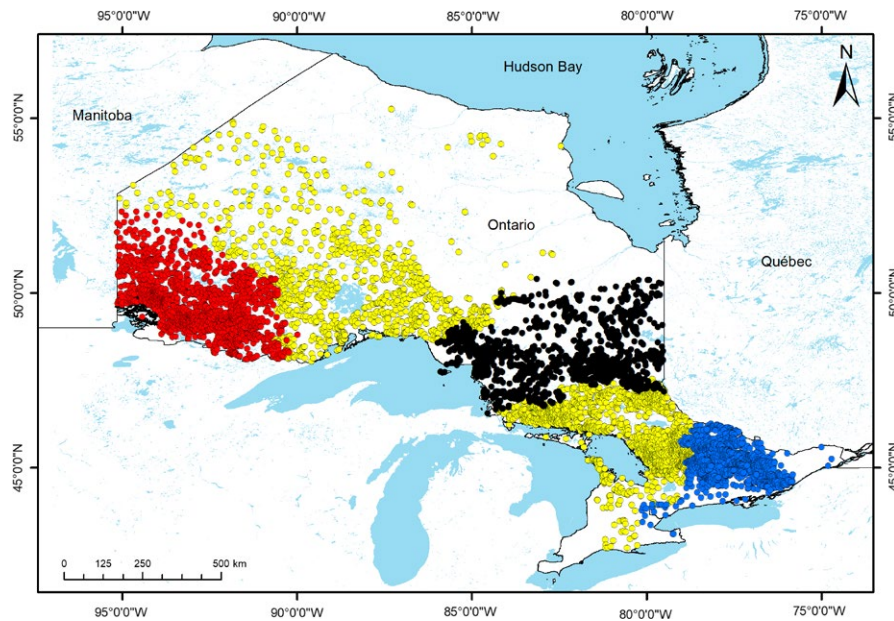


FIGURE 2 Sampling sites from Ontario, Canada, included in this study ($n = 6,977$; all points). Blue = south-eastern ($n = 1,325$), black = north-eastern ($n = 1,365$); red = north-western ($n = 1,541$); yellow = sites included in the full provincial analyses, but not included in the regional analyses ($n = 2,746$) [Colour figure can be viewed at wileyonlinelibrary.com]

investigate regional differences in functional redundancy (Figure 2). From the provincial species pool of 69 species, 18 species were absent in north-eastern lakes, five species in south-eastern lakes and nine in north-western lakes (See Supporting Information Table S1 for list of included species).

2.2 | Functional traits

Fish traits were gathered from multiple sources including FishTraits database (Frimpong & Angermeier, 2009), Freshwater Fishes of Ontario (Holm, Mandrak, & Burrige, 2009), Morphological and Ecological Characteristics of Canadian Freshwater Fishes (Coker, Portt, & Minns, 2001) and Ontario Freshwater Fishes Life History Database (Eakins, 2017). Twenty-six binary traits were chosen to characterize the role of species within communities. The chosen traits represented dimensions of the ecological niche used by adult fishes of each species including modes of reproduction, species–substrate associations, components of the diet and species–habitat associations (Frimpong & Angermeier, 2009; Winemiller, Fitzgerald, Bower, & Pianka, 2015; Supporting Information Table S2). In addition, temperature preferences (cold-water, cold/cool-water, cool-water, cool/warm-water and warm-water species) and average total lengths (TL) were retrieved from Coker et al. (2001) and Holm et al. (2009), respectively, and used to examine relationships between species (see: Functional diversity analysis below; Supporting Information Table S1).

2.3 | Functional diversity analysis

To quantify functional diversity, we first combined functional traits to represent ecological niche dimensions associated with

reproduction, diet, habitat and substrate use with separate principal component analyses (PCAs) of traits from each of the four trait categories for all species in the provincial species pool. By reducing the number of traits into respective trait dimensions, we assume that these niche dimensions have approximately equal weights. Prior to each PCA, Hellinger transformations were performed (Legendre & Gallagher, 2001). Computing a Hellinger transformation on species presence–absence data is mathematically similar to using the Ochiai similarity coefficient (Hubálek, 1982; Legendre & De Cáceres, 2013; Ochiai, 1957). Based on ease of interpretation of niche axes and overall explanatory power, we retained only the first axis of the PCAs of reproductive mode, species–substrate associations and dietary components, and the first two axes for species–habitat associations, totalling five dimensions for each species. We then performed a principal coordinate analysis (PCoA) on Euclidean distances of the five trait variables extracted from the PCAs to define the functional trait space (Laliberté et al., 2010; Winemiller et al., 2015).

We calculated three measures of functional diversity for each of the 6,977 fish communities to address our hypotheses: functional richness (FRic; Villéger et al., 2008), functional dispersion (FDIs; Anderson, 2006; Laliberté & Legendre, 2010) and Rao's quadratic entropy (Botta-Dukát, 2005; Rao's Q; Rao, 1982). FRic describes the volume of multivariate trait space occupied by a set of species (Villéger et al., 2008) calculated as the convex hull volume in ordination space (Cornwell, Schwillk, & Ackerly, 2006). We used the first three PCoA axes to calculate FRic as species richness was set to a minimum of four species (a hypervolume cannot be calculated with more traits than observations). FDIs and Rao's Q were calculated from the Euclidean distance trait matrix. FDIs describes mean distance in multivariate trait space of each species in a community

to the centroid of all species in a community and is unaffected by species richness by construction (Laliberté & Legendre, 2010). Communities showing relatively large FDis values contain a more diverse set of species trait combinations. Rao's Q describes average functional distance between two randomly chosen species in a community (Schleuter, Faufresne, Massol, & Argillier, 2010; Schmera, Heino, Podani, Erős, & Delédec, 2017). As Rao's Q was strongly correlated with FDis ($r > 0.98$; Supporting Information Table S3), we only present results of FDis.

We used null models of the relationship between functional diversity measures (FDis and FRic) and species richness to test whether functional redundancy of fish communities differed from a random assembly of species at both the provincial and regional scales (Gerisch, 2014). For each level of species richness from $n = 4$ to 30, we sampled n species from the provincial or a regional species pool 10,000 times and calculated functional diversity metrics for each randomly assembled community. We weighted the probability of individual species being sampled by their frequency of occurrence within the matrix of provincial or regional lakes to better represent actual combinations of observed species occurrences. We then compared the null models to empirical relationships between functional diversity and species richness provincially and between biogeographic regions. We used locally weighted scatter plot smoothing (LOWESS; Cleveland, Devlin, & Grosse, 1988) to identify the shape of the functional diversity and species richness relationship. A saturating pattern between functional diversity and species richness would indicate functional redundancy at the provincial or regional scale (Figure 1b). Lake communities outside the 95% confidence interval of the null model were considered to have significantly different (higher = less redundant; lower = more redundant) functional diversity levels than expected by random assembly from the provincial or regional species pool at a given species richness.

In addition to provincial, regional and lake patterns of redundancy among fish communities, we calculated species-level measures of functional rarity including measures of functional distinctiveness (D; Violle et al., 2017), functional uniqueness (U; Violle et al., 2017) and the distances to the provincial centroid (d_p) for each species. Functional distinctiveness and uniqueness (D and U) were calculated from the Euclidean distance trait matrix. Distinctiveness describes the average functional distance of each species to all other species within a community (Violle et al., 2017), which we averaged across lakes within the provincial pool; low D indicates functionally average species that contribute to redundancy. Uniqueness describes functional distance to the nearest neighbour within the species pool (Buisson et al., 2013; Mouillot et al., 2013; Violle et al., 2017); species that are "less unique," or are more similar functionally to other species, also contribute to the redundancy of species. Distances to global centroids (d_g) in trait space provide an indication of the influence of individual species on functional diversity measures. Species on the periphery of ordination space generally increase convex hull volumes.

We tested for differences in functional rarity metrics across variables related to freshwater niches: thermal tolerance groups

(cold-water, cold/cool-water, cool-water, cool/warm-water and warm-water; Coker et al., 2001), body size (average total length [TL]; Holm et al., 2009) and the frequency of occurrence of species (i.e., the proportion of lakes present). We tested for differences in functional rarity among thermal preference groups with ANOVAs and against body sizes and frequencies of occurrence with least-squares linear regression. We \log_{10} -transformed average TL, U and frequency of occurrence values to fit the distribution assumption of normality for the residuals.

2.4 | Environmental gradient analysis

We used generalized additive models (GAMs) to investigate the influence of environmental variables on the functional diversity and species richness relationship. At the provincial and regional scales, we examined how maximum depth (Z_{\max}), lake surface area (SA), climate (growing degree days; GDD) and productivity (total dissolved solids; TDS) were associated with the functional diversity (FDis and FRic) and species richness relationship. Like Alofs et al. (2014), we estimated the mean number of GDD above 5°C air temperature between 1961 and 1990 for each lake using thin-spline smoothing algorithms from the Canadian Forestry Service (<https://cfs.nrcan.gc.ca/projects/3>). Total dissolved solids represent the best available proxy for overall productivity in these lakes during sampling. The environmental variables were centred and scaled prior to the analysis by subtracting the variable means and dividing by standard deviation. Our GAMs were built using functional diversity measures (FDis and FRic) as our response variables and a smooth interaction between species richness and the four scaled and centred environmental covariates, individually, as our predictors (totalling eight models per biogeographic region). Restricted maximum likelihood was used to estimate smoothing parameters. To determine how redundancy patterns varied across environmental variables, we used our models to predict functional diversity at low (1st quartile), medium (median) and high (3rd quartile) values of Z_{\max} , SA, GDD and TDS.

All analyses were performed with R Statistical Software (R Core Team 2017) and "APE" (Paradis, Claude, & Strimmer, 2004), "VEGAN" (Oksanen et al., 2016), "FD" (Laliberté & Legendre, 2010; Laliberté, Legendre, & Shipley, 2014), "PSYCH" (Ravelle, 2016), "FUNRAR" (Grenié, Denelle, & Tucker, 2016; Grenié, Denelle, Tucker, Munoz, & Violle, 2017), "GGPLOT2" (Wickham, 2009) and "MGCV" (Wood, 2011) packages.

3 | RESULTS

3.1 | Observed trends from sampling

Most of the species included in the study had low occurrence rates; 35 species were found in <5% of the 6,977 lakes (Figure 3). In the same way, most lakes had few observed species (Figure 3 inset). White Sucker (*Catostomus commersonii*; 83% of lakes), Yellow Perch (*Perca flavescens*; 72% of lakes) and Northern Pike (*Esox lucius*; 54% of lakes) were the most ubiquitous species among lakes that had a species richness >3. In comparison, White Sucker, Yellow Perch and

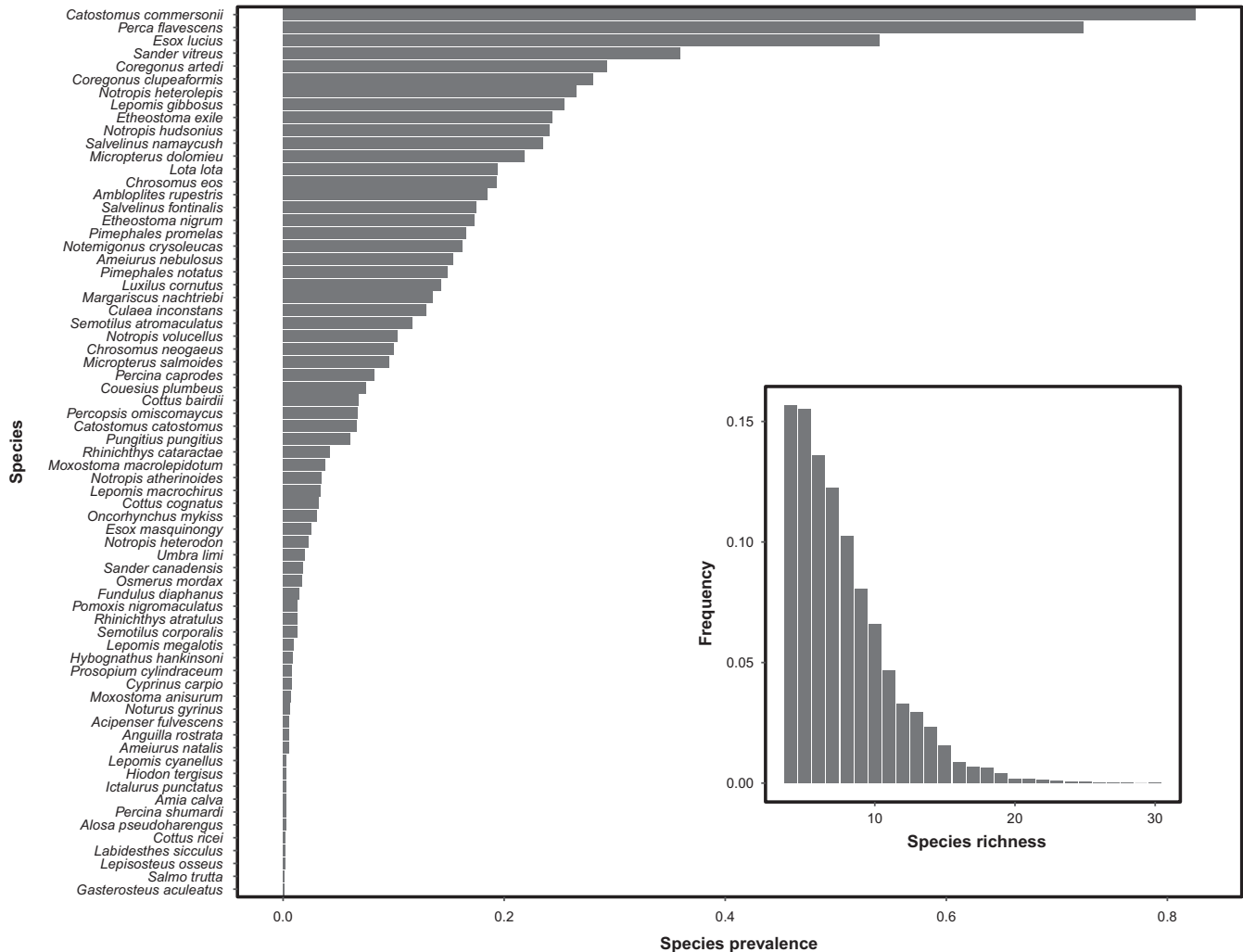


FIGURE 3 The frequency of occurrence of fish species across the 6,977 study lakes. Inset) Frequency distribution of species richness values of lake communities

Northern Pike were present in 49%, 41% and 34% of lakes, respectively, where species richness was equal to 3.

3.2 | Functional trait space for provincial and regional pools

Single PCA axes were extracted for the reproduction traits, substrate preferences and diet preferences, explaining 85.2%, 34.2% and 39.8% of the total variation, respectively (See Supporting Information Figures S1 and S2 for ordination biplots and scree plots). The first axis for reproduction summarized species that guard their brood on the negative end and spawn on open substrate on the positive end (Supporting Information Figure S1a). The size of preferred substrate was summarized across the substrate axis, with larger substrates showing positive scores and smaller substrates with negative scores (Supporting Information Figure S1b). The diet axis showed more piscivorous species on the positive end and more herbivorous species on the negative end (Supporting Information Figure S1c). Two axes were extracted from the habitat variables, explaining

40.2% of the cumulative variation in habitat variables. The ordination summarized lotic vs. lentic traits on the first axis and habitat size on the second axis (Supporting Information Figure S1d). Three axes were extracted from the PCoA of the five functional trait PCA axes with a high reduced space-quality (82.1% of the total variation; Supporting Information Figure S3).

3.3 | Provincial functional diversity metric analysis

We observed a saturating relationship from weighted null models of FDis against species richness, whereby FDis increased fastest at low species richness and plateaued at higher species richness (Figure 4a). Three hundred and seventy-six of 6,977 lake communities showed greater redundancy than the 95% confidence intervals of the weighted null model compared to 134 communities with lower redundancy than null expectations (Figure 4a; Supporting Information Table S4). In contrast, the relationship between FRic and species richness was less saturated (i.e., closer to linear; Figure 4b) with 306 communities that showed less FRic and 133 communities that

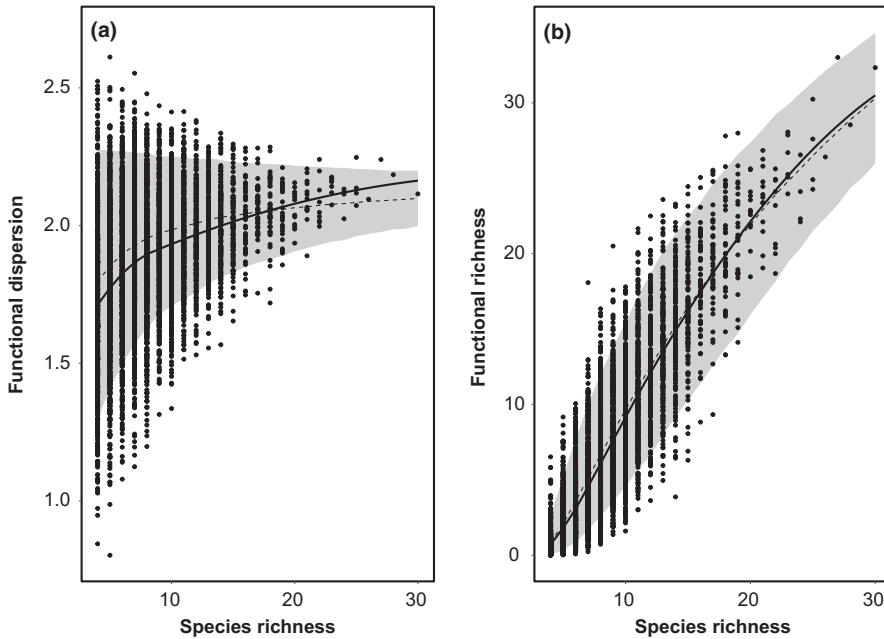


FIGURE 4 (a) Functional dispersion and (b) functional richness versus species richness. Points represent each of the 6,977 lake fish communities. The solid line indicates a LOWESS smoothing algorithm applied to all communities across Ontario. The dashed line represents the mean null community values. The 95% confidence interval for the null models is shaded in grey. Communities above the null model are less redundant than expected, and communities below the null model are more redundant than expected based on null expectations

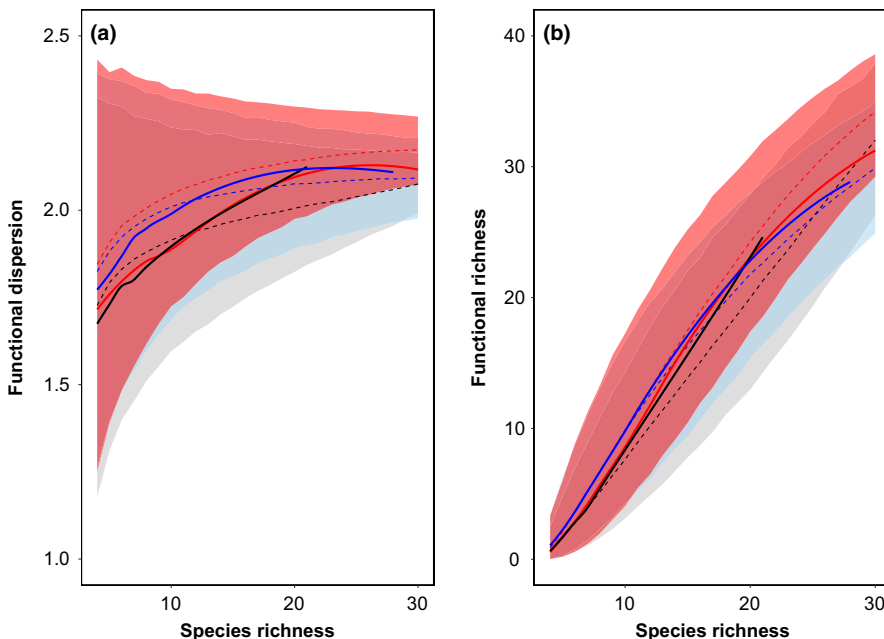


FIGURE 5 (a) Functional dispersion and (b) functional richness regressed against species richness. Colours represent measures for the three regions: north-western (red), north-eastern (grey) and south-eastern (blue). Ribbons reflect 95% confidence intervals of null models. Solid lines indicate regional LOWESS models. Dashed lines indicate mean values for weighted null models [Colour figure can be viewed at wileyonlinelibrary.com]

showed greater FRic than expected from the null models (Supporting Information Tables S4). Most communities (>70%) that had less functional diversity than the null expectation (i.e., more redundant) had fewer than 10 species for both FDis and FRic.

3.4 | Regional functional diversity metric analysis

Null model permutations produced saturating curves relating FDis and species richness across all three regions (Figure 5). However, the south-eastern communities and north-western communities showed the most saturating observed relationship between functional diversity (both FDis and FRic) and species richness (LOWESS lines). North-eastern communities, in contrast, showed a linear trend indicating a

lack of redundancy, again by both metrics (Figure 5). North-western Ontario had the greatest proportion of communities with less than expected functional diversity at given species richness levels, that is lakes falling below 95% confidence intervals generated by null expectations for both FDis and FRic (Supporting Information Tables S5–S7).

3.5 | Environmental and geographic gradients

Generalized additive models of FRic regressed against species richness with environmental variable interactions showed an overall better fit (R^2 range: 0.69–0.82) than FDis models (R^2 range: 0.11–0.32; Table 1; Supporting Information Figures S13 and S14). Indicated by the highest R^2 values, models of FDis incorporating smooth

TABLE 1 Summary of generalized additive models of functional dispersion (FDis) or functional richness (FRic) versus species richness (R) and smooth interactions between maximum depth (Z_{\max}), growing degree days (GDD), total dissolved solids (TDS) or surface area (SA). EDF = effective degrees of freedom for regression spline. Ref.df = reference degrees of freedom used to calculate p -values. Models performed on scaled and centred variables

Region	Response	Predictor	EDF	Ref.df	F	p	Adj. R ²
Provincial (n = 6,973)	FDis	R * Z_{\max}	22.74	31.90	76.44	<0.001	0.26
		R * GDD	31.50	44.35	38.28	<0.001	0.20
		R * SA	18.34	20.67	74.27	<0.001	0.18
		R * TDS	20.85	29.01	39.75	<0.001	0.15
	FRic	R * GDD	50.80	70.25	403.60	<0.001	0.80
		R * Z_{\max}	23.96	33.46	785.70	<0.001	0.79
		R * TDS	26.52	36.78	542.20	<0.001	0.78
North-west (n = 1,533)	FDis	R * Z_{\max}	7.46	9.01	78.27	<0.001	0.32
		R * SA	11.33	14.05	30.16	<0.001	0.22
		R * GDD	9.12	12.68	28.85	<0.001	0.19
		R * TDS	6.81	9.20	33.56	<0.001	0.17
	FRic	R * Z_{\max}	14.86	20.76	327.30	<0.001	0.82
		R * GDD	16.76	23.62	295.70	<0.001	0.82
		R * TDS	9.32	12.43	502.50	<0.001	0.81
South-east (n = 1,325)	FDis	R * Z_{\max}	8.21	10.99	30.60	<0.001	0.20
		R * SA	7.93	8.67	27.70	<0.001	0.15
		R * TDS	6.97	9.21	19.26	<0.001	0.12
		R * GDD	6.86	9.29	19.19	<0.001	0.11
	FRic	R * GDD	26.82	32.92	104.30	<0.001	0.72
		R * Z_{\max}	11.44	15.43	204.60	<0.001	0.70
		R * SA	13.00	15.34	208.10	<0.001	0.70
North-east (n = 1,540)	FDis	R * Z_{\max}	12.67	16.80	34.72	<0.001	0.31
		R * SA	9.93	10.87	49.83	<0.001	0.29
		R * GDD	10.89	14.96	14.04	<0.001	0.14
		R * TDS	9.84	13.38	14.68	<0.001	0.13
	FRic	R * Z_{\max}	13.92	18.67	258.10	<0.001	0.79
		R * SA	12.03	14.00	352.30	<0.001	0.79
		R * GDD	18.50	24.96	167.60	<0.001	0.76
		R * TDS	16.65	22.43	177.60	<0.001	0.76

interactions of species richness with Z_{\max} had the best fit overall for all biogeographic regions, whereas the best models of FRic included either smooth interactions with Z_{\max} (north-west, north-east) or GDD (provincial, south-east; Table 1).

Differences in the shapes of the functional diversity and species richness relationships emerged when incorporating environmental interactions. Our models predicted that FDis and FRic are greatest for lake communities in deeper lakes than shallow lakes, particularly at low levels of species richness (Figure 6a,e). In similar way, lake communities in warmer lakes (higher GDD) had the greatest functional diversity per level of species richness (Figure 6b,f). Predictions of functional diversity at large Z_{\max} or high GDD showed a saturating relationship between FDis and species richness indicating redundancy for deeper and warmer lakes at higher levels of species richness (Figure 6b). When SA was incorporated as an interactive predictor, relationships between

FDis and species richness flattened; lake communities in the largest lakes were had the shallowest slope compared to communities in smaller lakes (Figure 6c,g) indicating that each added species in larger lakes contributed less to the over functional diversity. At last, lake communities in less productive lakes were predicted to have slightly higher FDis per species richness level, but this difference was less pronounced for predictions of FRic (Figure 6d,h).

3.6 | Species-level functional diversity metric analysis

Uniqueness (U) and distance to a provincial centroid (d_p) were significantly correlated with distinctiveness (D) (U-D: Pearson's $r_p = 0.42$, Spearman's $r_s = 0.39$, $p < 0.001$; d_p -D: $r_p = 0.66$, $r_s = 0.65$, $p < 0.001$), but the correlation was weak between d_p and U ($r_p = 0.17$, $p = 0.16$,

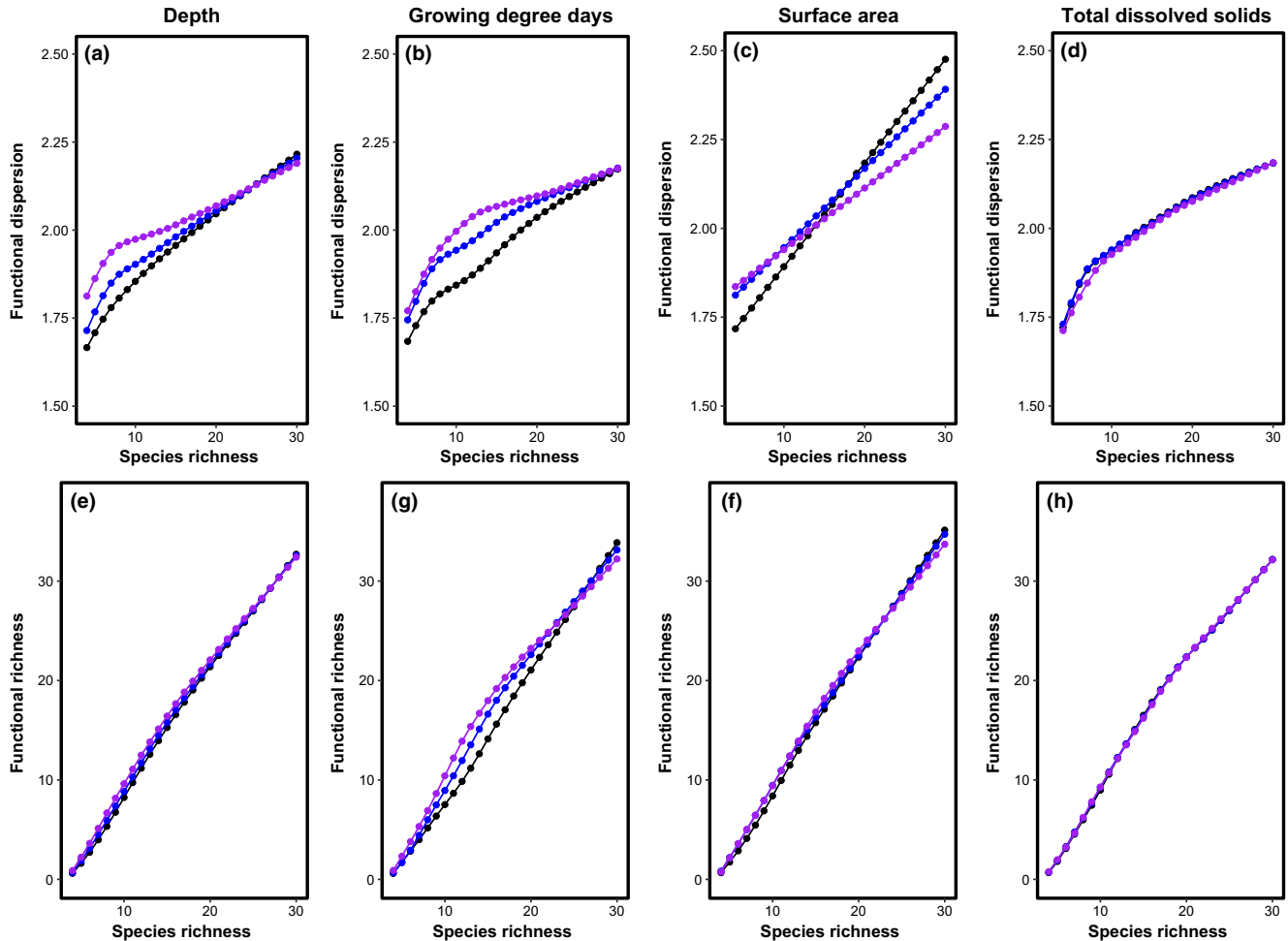


FIGURE 6 Predicted functional dispersion (a–d) and functional richness (e–h) for low (black; first quartile), moderate (blue; median) and high (purple; third quartile) levels of (a, e) depth, (b, g) growing degree days, (c, f) surface area and (d, h) total dissolved solids at the provincial scale [Colour figure can be viewed at wileyonlinelibrary.com]

$r_s = 0.17$, $p = 0.17$). Blacknose Dace (*Rhinichthys atratulus*) showed the greatest species-level functional rarity compared to other species across species-level metrics (Supporting Information Supporting Information Figure S7). There were no significant differences in U , D or d_p among thermal preference groups (Supporting Information Table S8), across average total lengths (Supporting Information Table S9) or across species occurrence rates (Supporting Information Table S10). In general, rare species were highly variable in U , D and d_p , whereas prevalent species showed lower U , D and d_p . Three of the most ubiquitous species in Ontario (White Sucker, Yellow Perch and Walleye), all showed relatively low functional rarity values, and were found nearer to the trait-space centroid relative to more ubiquitous species among the sampled lakes (Supporting Information Figure S7).

4 | DISCUSSION

Our results demonstrate that despite a relatively low species richness, freshwater fish communities across Ontario lakes show

redundancy in their ecological traits. There were regional differences in the functional diversity and species richness relationships. North-eastern lakes demonstrated the least functional redundancy in accordance with the region's biogeographic history. As we expected, our models of functional diversity and species richness showed that fish communities in larger, deeper and warmer lakes contained the most redundant assemblages. At last, we found no evidence that functional rarity was related body size, occurrence rate or thermal niche indicating that future changes in functional diversity may be difficult to predict.

Biodiversity is a common thread among resilience studies (Chapin et al., 1997; Folke et al., 2004), with many aspects of diversity being cited as important for resilience including species (alpha) diversity (Downing & Leibold, 2011), beta diversity (Awiti, 2011; Thompson, Mackey, McNulty, & Mosseler, 2009), functional diversity (Angeler & Allen, 2016) and response diversity (Folke et al., 2004). The diversity–stability hypothesis states that a greater diversity of traits occurs in species-rich communities, providing a greater likelihood that species and ecosystem functions can be maintained

during environmental disturbances (Darwin, 1859; Loreau & de Mazancourt, 2013; MacArthur, 1955; McCann, 2000; Peterson et al., 1998). However, lake fish communities in Ontario are relatively depauperate in species richness compared to marine (Micheli & Halpern, 2005; Mouillot et al., 2014) or terrestrial systems (Laliberté et al., 2010). Instead, redundancy of traits among fishes likely plays a critical role in the maintenance of ecosystem functions in times of disturbance. We attribute the redundancy observed across Ontario, in part, to the large amount of niche overlap among common species.

The saturating pattern between functional diversity and species richness observed across Ontario suggests redundancy in the measured ecological traits, and therefore, some assurance that functional diversity may be maintained when freshwater lakes are faced with disturbance. The form of the relationship between functional diversity and species richness can vary depending on the chosen metrics of functional and species diversity (Cadotte, Carscadden, & Mirotchnick, 2011; Schmera et al., 2017), the number of species and traits within the analysis (Guillemot et al., 2011), as well as across environmental (Mason, Irz, Lanoiselée, Mouillot, & Argillier, 2008) and disturbance gradients (Guerrero et al., 2014). Using generalized additive models, we demonstrated how differing functional diversity metrics can provide different patterns of functional diversity and species richness. However, our interpretation of the results between metrics was consistent. In general, there were a similar number of lakes falling outside the confidence limits of null models indicating more or less redundancy across measures of functional diversity (Supporting Information Tables S4–S7). The lack of saturation when using functional richness, in comparison with dispersion, is likely related to functional richness being correlated with species richness, whereas functional dispersion was designed to be independent of species richness (Laliberté & Legendre, 2010). Given the differences in patterns between the two metrics, we recommend using multiple measures of functional diversity when investigating redundancy through functional diversity and species richness relationships.

Our hypothesis that the north-eastern fish communities would contain the least redundant species pool was confirmed by the lack of a saturating relationship between functional diversity and species richness. In general, north-eastern Ontario fish communities are less species rich than north-western or south-eastern communities due to historical biogeographic patterns of dispersal during the recession of the Wisconsin ice sheet (Mandrak & Crossman, 1992). Coinciding with the smaller species pool, north-eastern communities also showed substantially lower functional diversity levels than north-western or south-eastern communities. This finding indicates that perhaps these lakes contain a more generalist species composition that may be less susceptible to future disturbance. For example, White Sucker, Yellow Perch and Walleye, which all showed relatively low functional rarity values, were observed in most north-eastern communities (White Sucker = 83% of sites, Yellow Perch = 65% of sites and Walleye = 42% of sites).

Fewer studies have investigated patterns of functional redundancy in freshwater fish communities relative to marine communities. Among freshwater studies, tropical freshwater fishes have

garnered the most attention (e.g., Casatti et al., 2015; Leitão et al., 2018), likely due to the greater diversity of fishes in these regions compared to more temperate regions (Toussaint, Charpin, Brosse, & Villéger, 2016). Using uniqueness as a metric for species redundancy, Buisson et al. (2013) found relatively few unique freshwater fish species in French streams and attributed this result to the predominance of cyprinids in the system. Cyprinids are also common among Ontario lakes and streams (e.g., Bendell & McNicol, 1987); however, small fishes were undersampled relative to larger species in some lakes during the AHI (Bowlby & Green, 1987), which may have inflated species-level rarity metrics of cyprinids in this study (e.g., Blacknose Dace, River Darter *Percina shumardi*, Blackchin Shiner *Notropis heterodon*). Erös, Heino, Schmera, and Rask (2009) found low redundancy in fish species in southern Finland boreal lakes, with most species belonging to unique functional groups. Overall, patterns of redundancy tend to vary with location and study system, consistent with what we observed in Ontario, but differences in the species pools and traits used to measure diversity make direct comparisons difficult.

Climate change is altering the composition of local fish communities in Ontario (Alofs et al., 2014) and this is expected to continue (Poesch et al., 2016) with geographical range shifts resulting in local introductions and extirpations at range boundaries. In recent times, efforts have been undertaken to predict changes in the functional diversity of freshwater fish communities under climate-change scenarios (Biswas, Vogt, & Sharma, 2017; Buisson & Grenouillet, 2009). Biswas et al. (2017) estimated that with changing climate, species richness will increase in many Ontario lakes, although functional diversity is expected to decline. They predicted an increase in the number of lakes dominated by small-bodied, warm-water species with a decrease in the number of lakes dominated by larger, cold-water species. Although we might expect increases in the frequency of warm-water species across the province, the redundancy of ecological traits across thermal preference groups in our study suggests trait diversity may be maintained. We failed to find significant relationships between species functional rarity, distinctiveness, or uniqueness and occurrence rates, body size, or thermal preference, which limits our ability to predict how lake community functional diversity may change in the near future. However, our models of functional diversity and species richness indicated that communities in warmer regions tended to have greater functional diversity and redundancy at higher levels of species richness.

We must acknowledge several caveats to our study. First, many of the species in Ontario show geographically limited distributions across the province and we removed the rarest or most geographically limited species (present in <0.1% of sampled lakes). In addition, the AHI programme prioritized important recreational and subsistence fish and undersampled small fishes in some lakes, which may bias the results that we present here (Alofs et al., 2014; Bowlby & Green, 1987). Further, our study could have been improved if measures of species local abundance were available; if a more abundant species were extirpated in a lake due to some environmental disturbance, a redundant species that contains only a few individuals

would likely struggle to maintain the once shared ecosystem function (Rosenfeld, 2002). Abundance-based sampling efforts could improve our understanding of the true redundancy and potential resiliency of lake fish species; however, large-scale efforts to accurately measure abundance can be problematic and presence-absence data may more accurately reflect differences among communities in such cases (Jackson & Harvey, 1997).

As is typical of almost all fish community studies, our study was limited to using traits from adult life stages and ignored intraspecific and ontogenetic variation in traits. In nature, organisms will demonstrate a range of preferences and perform differing ecosystem functions with ontogenesis and metaphoetesis (Hutchinson, 1959; Mason, Mouillot, Lee, & Wilson, 2005). Rudolf and Rasmussen (2013) demonstrated that the presence of dragonflies that differ in their developmental stage can lead to differences in local community composition of fishless ponds and differences in ecological processes such as respiration and productivity. In a meta-analysis of 36 terrestrial, vascular plant functional traits from 171 case studies, Siefert et al. (2015) showed that intraspecific variation accounted for 25% of trait variation within communities and 32% of trait variation among communities. In depauperate systems such as the inland lakes of Ontario, ecosystem functions are likely performed by ontogenetically distinct life stages of species that show variability among populations. Incorporating distinct life stages as "pseudo-species" into future analyses could provide a more accurate depiction of functional redundancy patterns in nature; however, ontogenetic variation in various types of traits (e.g., non-dietary) is not well-documented among fishes.

With a changing climate, lakes in Ontario are projected to experience increased temperatures (Crossman, Eimers, Kerr, & Yao, 2016) and changes in precipitation (Magnuson et al., 1997), impacting water chemistry (e.g., brownification; Larsen, Anderson, & Hessen, 2011), and ultimately impacting fish species distributions (Chu et al., 2005; Jackson & Mandrak, 2002). These projections have started to come to fruition over the last several decades with local observations of increased lake water temperatures (Mason et al., 2016; Schindler et al., 1996), decreased length of the ice-cover season (Mason et al., 2016) and an associated shift northward in fish species distributions (Alofs et al., 2014). Here, we found patterns of functional redundancy across provincial, regional and species-based attributes indicative of potential resiliency to some types and degrees of future change. However, most lake communities were relatively depauperate, and among those communities existed high variability in the relationship between functional and species diversity. Overall, understanding patterns of redundancy among relatively depauperate freshwater ecosystems remains an important challenge as a changing climate will alter the geographical distributions of species, creating novel combinations of species and trait within local communities.

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DATA ACCESSIBILITY

All the data for this study are accessible through varying outlets. The Aquatic Habitat Inventory fish community data are accessible through the Ontario Ministry of Natural Resources, and Forestry and the trait data can be obtained from the FishTraits Database (<http://www.fishtraits.info/>; Frimpong & Angermeier, 2009), the Ontario Freshwater Fishes Life History Database (www.ontariofishes.ca; Eakins, 2017), *Freshwater Fishes of Ontario* (Holm et al., 2009) and *Morphological and Ecological Characteristics of Canadian Freshwater Fishes* (Coker et al., 2001).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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