

1 **Title:** Functional diversity and redundancy of freshwater fish communities across biogeographic
2 and environmental gradients

3 **Running title:** Functional redundancy of fishes

4 Karl A. Lamothe^{1,2}, Karen M. Alofs^{1,3}, Donald A. Jackson¹, Keith M. Somers¹

5 ¹Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON
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7 ²Present affiliation: Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and
8 Aquatic Sciences, 867 Lakeshore Rd., Burlington, ON L7T2C8; Orc ID: 0000-0001-9875-8204.
9 Twitter: @KarlLamothe; email: karl.lamothe@alum.utoronto.ca

10 ³Present affiliation: University of Michigan, School for Environment and Sustainability, Ann
11 Arbor, MI 48109

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22 **Biosketch**

23 **Karl A. Lamothe** is a Visiting Fellow with Fisheries and Oceans Canada at the Great Lakes
24 Laboratory for Fisheries and Aquatic Sciences. The presented work was a part of his PhD
25 research in the Department of Ecology and Evolutionary Biology at the University of Toronto.
26 His research focuses on understanding the impacts of anthropogenic disturbances on freshwater
27 ecosystems and biodiversity, including Species at Risk.

28

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30 K.A.L, K.M.A., and D.A.J. conceived the study; K.A.L. and K.M.S. compiled the data; K.A.L.
31 analyzed the data; all authors contributed to the writing of the manuscript.

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DR KARL ANDREW LAMOTHE (Orcid ID : 0000-0001-9875-8204)

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Karl A. Lamothe^{1,2}, Karen M. Alofs^{1,3}, Donald A. Jackson¹, Keith M. Somers¹

¹Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S3B2

²Present affiliation: Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 867 Lakeshore Rd., Burlington, ON L7T2C8; Orc ID: 0000-0001-9875-8204. Twitter: @KarlLamothe; email: karl.lamothe@alum.utoronto.ca

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Abstract

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

36 **Location:** 6,977 lakes in Ontario, Canada.

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

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

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

57 **KEYWORDS:** freshwater fish, functional diversity, functional redundancy, Ontario, resilience

58

59 **1. Introduction**

60 Differences in functional traits among species in a community can influence how that
61 system responds when disturbance occurs (Haddad, Holyoak, Davies, Melbourne, & Preston,
62 2008; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). Like the insurance hypothesis of
63 biodiversity, which states that higher species diversity provides a greater probability that
64 ecosystem conditions will be maintained when disturbances occur (Yachi & Loreau, 1999),
65 functionally diverse communities are thought to be more resilient to disturbances (Peterson,
66 Allen, & Holling, 1998; Standish et al., 2014). Related, functional redundancy describes the
67 situation when more than one species shows overlapping ecological functions (Walker, 1992;
68 Lawton & Brown, 1993; Rosenfeld, 2002) and, similarly, may be an important factor for
69 maintaining ecosystem conditions when faced with environmental disturbances (Angeler, Allen,
70 Barichievy, Eason, & Garmestani, 2016; Angeler & Allen, 2016).

71 Approaches for quantifying functional redundancy continue to be developed (de Bello,
72 Lepš, Lavorel, & Moretti, 2007; van der Linden et al., 2012; Bruno, Gutiérrez-Cánovas, Velasco,
73 & Sánchez-Fernández, 2016; Ricotta et al., 2016), but typically is approached from multiple
74 scales (Allen et al. 2016; Angeler & Allen, 2016; Angeler et al., 2016) and requires community
75 abundance or presence-absence data with a matrix of morphological, behavioral, or life-history
76 traits (i.e. functional traits; Rosenfeld, 2002). Using these trait data, ordinations are commonly
77 performed to develop multivariate functional trait spaces that allow subsequent measures of
78 functional diversity to be calculated (e.g., functional richness; Villéger, Mason, & Mouillot,
79 2008). At the regional scale, functional redundancy can be quantified by regressing measures of
80 functional diversity for individual communities against species richness (Micheli & Halpern,
81 2005; Sasaki et al., 2009; Guillemot, Kulbicki, Chabanet, & Vigliola, 2011; Figure 1).
82 Conceptually, a positive linear relationship between functional diversity and species richness
83 indicates a lack of redundancy at the regional scale and that species equally contribute to
84 function (Figure 1a solid line). Generally, functionally redundant assemblages are expected to
85 show a saturating relationship between functional diversity and species richness (Micheli &
86 Halpern, 2005; Figure 1 dashed line); as species richness increases, the rate of increasing
87 functional diversity declines and then eventually plateaus, indicating that in species rich
88 communities there is greater overlap in species functions. Alternatively, other nonlinear patterns
89 can occur (e.g., Sasaki et al., 2009), where for example, redundancy is observed at high and low

90 levels of species richness, and communities with fewer species show relatively lower levels of
91 functional diversity (Figure 1a dotted line).

92 At the community scale, null models can be used to test whether individual communities
93 are more or less redundant than expected based on weighted or unweighted randomizations
94 (Figure 1b; Gerisch 2014). Communities falling above the null models are considered less
95 redundant than null expectations, whereas communities below the null model would indicate
96 communities that are more redundant than null expectations. At the species level, the extent to
97 which functional traits are distinct or redundant within assemblages can be quantified using
98 functional rarity metrics (Violle et al., 2017) including measures of functional distinctiveness (D;
99 Violle et al., 2017), functional uniqueness (U; Violle et al., 2017), and the distances to provincial
100 (d_P) or regional centroids (d_R) for each species in ordination space. Species that are less ‘distinct’
101 or ‘unique’ are considered more redundant (Buisson, Grenouillet, Villéger, Canal, & Laffaille,
102 2013).

103 Much of what we know about functional redundancy in nature comes from studies of
104 plant (Sasaki et al., 2009; Laliberté et al., 2010; Guerrero, Carmona, Morales, Oñate, & Peco,
105 2014) and marine communities (e.g., Bellwood, Hoey, & Choat, 2003; Micheli & Halpern, 2005;
106 Hoey & Bellwood, 2009); far less research has been directed towards understanding redundancy
107 in freshwater ecosystems, particularly in species depauperate temperate or arctic regions. In this
108 study, we aim to identify patterns of functional redundancy (Figure 1b) among temperate, North
109 American lake fish communities and understand how several factors, specifically, historical
110 biogeography, spatial scale, and environmental variation can contribute to such patterns. We
111 approach this objective using fish community data from Ontario, Canada. Ontario spans an area
112 of over 1,000,000 km² (approximately the combined area of France and Germany) with
113 approximately 250,000 freshwater lakes that are morphologically diverse (Jackson & Mandrak,
114 2002; Lester, Marshall, Armstrong, Dunlop, & Ritchie, 2003) and influenced by different
115 climatic effects occurring across the province. Colonization of most freshwater fish species in
116 Ontario occurred through the Mississippi and Missourian refugia or the southeastern (Atlantic)
117 refugium after the Wisconsinan ice sheet receded (Mandrak & Crossman, 1992), contributing to
118 a larger pool of species at lower latitudes. If redundancy exists among Ontario fishes, we
119 expected it to be among communities in the southeastern region of the province because of the
120 greater number of species in this regional pool, and therefore a greater potential for redundancy

121 to be observed. Conversely, we expected the lowest redundancy in the northeastern region of the
122 province.

123 We also hypothesized that the largest, deepest, warmest, and most productive lakes
124 would harbor the most functionally redundant fish communities. Previous work has
125 demonstrated that lake area, depth, temperature, and productivity are related to local species
126 richness of freshwater fish communities (Matuszek & Beggs, 1988; Minns, 1989; Jackson &
127 Harvey, 1989; Dodson, Arnott, & Cottingham, 2000) and that lake depth and surface area are
128 key factors related to the structure of fish communities (Harvey, 1975; Tonn & Magnuson, 1982;
129 Jackson & Harvey, 1993; Mehner, Holmgren, Lauridsen, Jeppesen, & Diekmann, 2007); larger
130 lakes can provide more structural habitat diversity (Eadie, Hurly, Montgomerie, & Teather,
131 1986; Minns, 1989) while deeper lakes provide a greater diversity of thermal niches (Chu, Jones,
132 Mandrak, Piggott, & Minns, 2008) and reduce the likelihood of winterkill (Casselman & Harvey,
133 1975; Harvey, 1978, 1982). Similarly, species distributions are influenced by temperature and
134 productivity, which play a fundamental role in fish growth, maturity, and survival (Dodson et al.,
135 2000; Venturelli, Lester, Marshall, & Shuter, 2010).

136 Examining the contributions of individual species to functional diversity may allow us to
137 predict the influence of species losses as environmental disturbances tend to impact freshwater
138 ecosystems non-randomly, often causing declines or exclusion of particular niches (Giller et al.,
139 2004). As such, we were interested in how functional rarity differed across species that show
140 differences in species occurrence rates, body size, and thermal preference. For example, Ontario
141 lakes span the northern or southern range boundaries for many fish species (Shuter, MacLean,
142 Fry, & Regier, 1980; Jackson, Peres-Neto, & Olden, 2001) and climate warming is expected to
143 have the most detrimental effect on cold-water species near their species range limits (Chu,
144 Mandrak, & Minns, 2005). Differences in functional rarity metrics across thermal preferences
145 could indicate whether warming temperatures, expected to favor warm-water adapted species
146 and lead to declines in cool and cold-water adapted species (Chu et al., 2005; Poesch, Chavarie,
147 Chu, Pandit, & Tonn, 2016), will increase or decrease functional diversity. Furthermore, fish
148 body size is related to many aspects of fish ecology including reproduction (Blueweiss et al.,
149 1978) and dispersal (Radinger & Wolter, 2014), among others (Woodward et al., 2005; Alofs,
150 2016), and has also been used to predict vulnerability to predation (Alofs & Jackson, 2015) and
151 shifts in species distributions under changing climate (Alofs, Jackson, & Lester, 2014). Finally,

152 functionally distinct species have been demonstrated to play critical roles in maintaining
153 ecosystem functions (Lyons, Brigham, Traut, & Schwartz, 2005; Jian et al., 2014; Violle et al.,
154 2017) but these species are often geographically limited and thus have high extinction
155 probabilities (Harnik, Simpson, & Payne, 2012). Overall, this study should provide insight into
156 factors influencing patterns of functional redundancy at multiple scales, allowing us to better
157 predict how freshwater fish communities may change in the future.

158

159 **2. Methods**

160 **2.1. Data collection**

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

171 The AHI recorded presence or absence of 99 fish species for approximately 10,000 lakes
172 in Ontario. Thirty species were found in fewer than 0.1% of lakes (i.e., less than 10 lakes); lakes
173 where these species occurred were removed from the analyses so that results from multivariate
174 statistical analyses would not be heavily influenced by exceptionally rare species. Subsequently,
175 we eliminated any lakes with fewer than four fish species as this minimum allows calculations of
176 convex hull volumes in 3-dimensions of trait space (see: Functional diversity analysis below),
177 leaving a total of 6,977 fish communities in the analysis (Figure 2). We subsampled the lakes
178 based on watershed distributions and characterized them geographically as either southeastern (n
179 = 1,325), northeastern (n = 1,365), or northwestern (n = 1,541) to investigate regional differences
180 in functional redundancy (Figure 2). From the provincial species pool of 69 species, 18 species
181 were absent in northeastern lakes, five species in southeastern lakes, and nine in northwestern
182 lakes (See Table S1 in the Supplementary Material for list of included species).

183

184 **2.2. Functional traits**

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

197

198 **2.3 Functional diversity analysis**

199 To quantify functional diversity, we first combined functional traits to represent
200 ecological niche dimensions associated with reproduction, diet, habitat, and substrate use with
201 separate principal component analyses (PCAs) of traits from each of the four trait categories for
202 all species in the provincial species pool. By reducing the number of traits into respective trait
203 dimensions, we assume that these niche dimensions have approximately equal weights. Prior to
204 each PCA, Hellinger transformations were performed (Legendre & Gallagher, 2001). Computing
205 a Hellinger transformation on species presence-absence data is mathematically similar to using
206 the Ochiai similarity coefficient (Ochiai, 1957; Hubálek, 1982; Legendre and Cáceres 2013).
207 Based on ease of interpretation of niche axes and overall explanatory power, we retained only the
208 first axis of the PCAs of reproductive mode, species-substrate associations, and dietary
209 components, and the first two axes for species-habitat associations, totaling five dimensions for
210 each species. We then performed a principal coordinates analysis (PCoA) on Euclidean distances
211 of the five trait variables extracted from the PCAs to define the functional trait space (Laliberté
212 et al., 2010; Winemiller et al., 2015).

213 We calculated three measures of functional diversity for each of the 6,977 fish
214 communities to address our hypotheses: functional richness (FRic; Villéger et al., 2008),
215 functional dispersion (FDis; Anderson, 2006; Laliberté & Legendre, 2010), and Rao's quadratic
216 entropy (Rao's Q; Rao, 1982; Botta-Dukát, 2005). FRic describes the volume of multivariate
217 trait space occupied by a set of species (Villéger et al., 2008) calculated as the convex hull
218 volume in ordination space (Cornwell, Schwilk, & Ackerly, 2006). We used the first three PCoA
219 axes to calculate FRic since species richness was set to a minimum of four species (a
220 hypervolume cannot be calculated with more traits than observations). FDis and Rao's Q were
221 calculated from the Euclidean distance trait matrix. FDis describes mean distance in multivariate
222 trait space of each species in a community to the centroid of all species in a community and is
223 unaffected by species richness by construction (Laliberté & Legendre, 2010). Communities
224 showing relatively large FDis values contain a more diverse set of species trait combinations.
225 Rao's Q describes average functional distance between two randomly chosen species in a
226 community (Schleuter, Faufresne, Massol, & Argillier, 2010; Schmera, Heino, Podani, Erős, &
227 Delédec, 2017). As Rao's Q was strongly correlated with FDis ($r > 0.98$; Table S3), we only
228 present results of FDis.

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

244 levels than expected by random assembly from the provincial or regional species pool at a given
245 species richness.

246 In addition to provincial, regional, and lake patterns of redundancy among fish
247 communities, we calculated species-level measures of functional rarity including measures of
248 functional distinctiveness (D; Violle et al., 2017), functional uniqueness (U; Violle et al., 2017),
249 and the distances to the provincial centroid (d_p) for each species. Functional distinctiveness and
250 uniqueness (D and U) were calculated from the Euclidean distance trait matrix. Distinctiveness
251 describes the average functional distance of each species to all other species within a community
252 (Violle et al., 2017), which we averaged across lakes within the provincial pool; low D indicates
253 functionally average species that contribute to redundancy. Uniqueness describes functional
254 distance to the nearest neighbor within the species pool (Buisson et al., 2013; Mouillot et al.,
255 2013; Violle et al., 2017); species that are “less unique,” or are more similar functionally to other
256 species, also contribute to the redundancy of species. Distances to global centroids (d_p) in trait
257 space provide an indication of the influence of individual species on functional diversity
258 measures. Species on the periphery of ordination space generally increase convex hull volumes.

259 We tested for differences in functional rarity metrics across variables related to
260 freshwater niches: thermal tolerance groups (cold-water, cold/cool-water, cool-water,
261 cool/warm-water, warm-water; Coker et al., 2001), body size (average total length [TL]; Holm et
262 al., 2009), and the frequency of occurrence of species (i.e., the proportion of lakes present). We
263 tested for differences in functional rarity among thermal-preference groups with ANOVAs and
264 against body sizes and frequencies of occurrence with least-squares linear regression. We log₁₀-
265 transformed average TL, U, and frequency of occurrence values to fit the distribution assumption
266 of normality for the residuals.

267

268 **2.4. Environmental gradient analysis**

269 We used generalized additive models (GAMs) to investigate the influence of
270 environmental variables on the functional diversity and species richness relationship. At the
271 provincial and regional scales, we examined how maximum depth (Z_{max}), lake surface area (SA),
272 climate (growing degree days; GDD), and productivity (total dissolved solids; TDS) were
273 associated with the functional diversity (FDis and FRic) and species richness relationship. Like
274 Alofs et al. (2014), we estimated the mean number of GDD above 5°C air temperature between

275 1961 and 1990 for each lake using thin-spline smoothing algorithms from the Canadian Forestry
276 Service (<https://cfs.nrcan.gc.ca/projects/3>). Total dissolved solids represents the best available
277 proxy for overall productivity in these lakes during sampling. The environmental variables were
278 centered and scaled prior to the analysis by subtracting the variable means and dividing by
279 standard deviation. Our GAMs were built using functional diversity measures (FDis and FRic) as
280 our response variables and a smooth interaction between species richness and the four scaled and
281 centered environmental covariates, individually, as our predictors (totaling eight models per
282 biogeographic region). Restricted maximum likelihood was used to estimate smoothing
283 parameters. To determine how redundancy patterns varied across environmental variables, we
284 used our models to predict functional diversity at low (1st quartile), medium (median), and high
285 (3rd quartile) values of Z_{\max} , SA, GDD, and TDS.

286 All analyses were performed with R Statistical Software (R Core Team 2017) and ‘ape’
287 (Paradis, Claude, & Strimmer, 2004), ‘vegan’ (Oksanen et al., 2016), ‘FD’ (Laliberté &
288 Legendre, 2010; Laliberté, Legendre, & Shipley, 2014), ‘psych’ (Ravelle, 2016), ‘funrar’
289 (Grenié, Denelle, & Tucker, 2016; Grenié, Denelle, Tucker, Munoz, & Violle, 2017), ‘ggplot2’
290 (Wickham, 2009), and ‘mgcv’ (Wood, 2011) packages.

291

292 **3. Results**

293 **3.1. Observed trends from sampling**

294 Most of the species included in the study had low occurrence rates; 35 species were
295 found in less than 5% of the 6,977 lakes (Figure 3). Similarly, most lakes had few observed
296 species (Figure 3 inset). White Sucker (*Catostomus commersonii*; 83% of lakes), Yellow Perch
297 (*Perca flavescens*; 72% of lakes), and Northern Pike (*Esox lucius*; 54% of lakes) were the most
298 ubiquitous species among lakes that had a species richness greater than 3. In comparison, White
299 Sucker, Yellow Perch, and Northern Pike were present in 49%, 41%, and 34% of lakes,
300 respectively, where species richness was equal to 3.

301

302 **3.2. Functional trait space for provincial and regional pools**

303 Single PCA axes were extracted for the reproduction traits, substrate preferences, and diet
304 preferences, explaining 85.2%, 34.2%, and 39.8% of the total variation, respectively (See
305 Supplementary Figures S1 and S2 for ordination biplots and scree plots). The first axis for

306 reproduction summarized species that guard their brood on the negative end and spawn on open
307 substrate on the positive end (Figure S1a). The size of preferred substrate was summarized
308 across the substrate axis, with larger substrates showing positive scores and smaller substrates
309 with negative scores (Figure S1b). The diet axis showed more piscivorous species on the positive
310 end and more herbivorous species on the negative end (Figure S1c). Two axes were extracted
311 from the habitat variables, explaining 40.2% of the cumulative variation in habitat variables. The
312 ordination summarized lotic vs. lentic traits on the first axis and habitat size on the second axis
313 (Figure S1d). Three axes were extracted from the PCoA of the five functional trait PCA axes
314 with a high reduced space-quality (82.1% of the total variation; Figure S3).

315

316 **3.3. Provincial functional diversity metric analysis**

317 We observed a saturating relationship from weighted null models of FDis against species
318 richness, whereby FDis increased fastest at low species richness and plateaued at higher species
319 richness (Figure 4a). 376 of 6,977 lake communities showed greater redundancy than the 95%
320 confidence intervals of the weighted null model compared to 134 communities with lower
321 redundancy than null expectations (Figure 4a; Table S4). In contrast, the relationship between
322 FRic and species richness was less saturated (i.e., closer to linear; Figure 4b) with 306
323 communities that showed less FRic and 133 communities that showed greater FRic than
324 expected from the null models (Tables S4). Most communities (> 70%) that had less functional
325 diversity than the null expectation (i.e., more redundant) had fewer than 10 species for both FDis
326 and FRic.

327

328 **3.4. Regional functional diversity metric analysis**

329 Null model permutations produced saturating curves relating FDis and species richness
330 across all three regions (Figure 5). However, the southeastern communities and northwestern
331 communities showed the most saturating observed relationship between functional diversity
332 (both FDis and FRic) and species richness (LOWESS lines). Northeastern communities, in
333 contrast, showed a linear trend indicating a lack of redundancy, again by both metrics (Figure 5).
334 Northwestern Ontario had the greatest proportion of communities with less than expected
335 functional diversity at given species richness levels, i.e. lakes falling below 95% confidence
336 intervals generated by null expectations for both FDis and FRic (Tables S5-7).

337

338 **3.5. Environmental and geographic gradients**

339 Generalized additive models of FRic regressed against species richness with
340 environmental variable interactions showed an overall better fit (R^2 range: 0.69-0.82) than FDis
341 models (R^2 range: 0.11-0.32; Table 1; Figures S13, S14). Indicated by the highest R^2 values,
342 models of FDis incorporating smooth interactions of species richness with Z_{\max} had the best fit
343 overall for all biogeographic regions, whereas the best models of FRic included either smooth
344 interactions with Z_{\max} (northwest, northeast) or GDD (provincial, southeast; Table 1).

345 Differences in the shapes of the functional diversity and species richness relationships
346 emerged when incorporating environmental interactions. Our models predicted that FDis and
347 FRic are greatest for lake communities in deeper lakes than shallow lakes, particularly at low
348 levels of species richness (Figure 6a,e). Similarly, lake communities in warmer lakes (higher
349 GDD) had the greatest functional diversity per level of species richness (Figure 6b,f). Predictions
350 of functional diversity at large Z_{\max} or high GDD showed a saturating relationship between FDis
351 and species richness indicating redundancy for deeper and warmer lakes at higher levels of
352 species richness (Figure 6b). When SA was incorporated as an interactive predictor, relationships
353 between FDis and species richness flattened; lake communities in the largest lakes were had the
354 shallowest slope compared to communities in smaller lakes (Figure 6c,g) indicating that each
355 added species in larger lakes contributed less to the over functional diversity. Finally, lake
356 communities in less productive lakes were predicted to have slightly higher FDis per species
357 richness level, but this difference was less pronounced for predictions of FRic (Figure 6d,h).

358

359 **3.6. Species-level functional diversity metric analysis**

360 Uniqueness (U) and distance to a provincial centroid (d_p) were significantly correlated
361 with distinctiveness (D) (U-D: Pearson's $r_p = 0.42$, Spearman's $r_s = 0.39$, $p < 0.001$; d_p -D: $r_p =$
362 0.66 , $r_s = 0.65$, $p < 0.001$), but the correlation was weak between d_p and U ($r_p = 0.17$, $p = 0.16$, r_s
363 $= 0.17$, $p = 0.17$). Blacknose Dace (*Rhinichthys atratulus*) showed the greatest species-level
364 functional rarity compared to other species across species-level metrics (Figure S7). There were
365 no significant differences in U, D or d_p among thermal preference groups (Table S8), across
366 average total lengths (Table S9), or across species occurrence rates (Table S10). Generally, rare
367 species were highly variable in U, D and d_p , whereas prevalent species showed lower U, D and

368 dp. Three of the most ubiquitous species in Ontario (White Sucker, Yellow Perch, and Walleye),
369 all showed relatively low functional rarity values, and were found nearer to the trait-space
370 centroid relative to more ubiquitous species among the sampled lakes (Figure S7).

371

372 **4. Discussion**

373 Our results demonstrate that despite a relatively low species richness, freshwater fish
374 communities across Ontario lakes show redundancy in their ecological traits. There were
375 regional differences in the functional diversity and species richness relationships. Northeastern
376 lakes demonstrated the least functional redundancy in accordance with the region's
377 biogeographical history. As we expected, our models of functional diversity and species richness
378 showed that fish communities in larger, deeper, and warmer lakes contained the most redundant
379 assemblages. Finally, we found no evidence that functional rarity was related body size,
380 occurrence rate, or thermal niche indicating that future changes in functional diversity may be
381 difficult to predict.

382 Biodiversity is a common thread among resilience studies (Chapin et al., 1997; Folke et
383 al., 2004), with many aspects of diversity being cited as important for resilience including
384 species (alpha) diversity (Downing & Leibold, 2010), beta diversity (Thompson, Mackey,
385 McNulty, & Mosseler, 2009; Awiti, 2011), functional diversity (Angeler & Allen, 2016), and
386 response diversity (Folke et al., 2004). The diversity-stability hypothesis states that a greater
387 diversity of traits occurs in species-rich communities, providing a greater likelihood that species
388 and ecosystem functions can be maintained during environmental disturbances (Darwin, 1859;
389 MacArthur, 1955; Peterson et al., 1998; McCann, 2000; Loreau & de Mazancourt, 2013).
390 However, lake fish communities in Ontario are relatively depauperate in species richness
391 compared to marine (Micheli & Halpern, 2005; Mouillot et al., 2014) or terrestrial systems
392 (Laliberté et al., 2010). Instead, redundancy of traits among fishes likely plays a critical role in
393 the maintenance of ecosystem functions in times of disturbance. We attribute the redundancy
394 observed across Ontario, in part, to the large amount of niche overlap among common species.

395 The saturating pattern between functional diversity and species richness observed across
396 Ontario suggests redundancy in the measured ecological traits, and therefore some assurance that
397 functional diversity may be maintained when freshwater lakes are faced with disturbance. The
398 form of the relationship between functional diversity and species richness can vary depending on

399 the chosen metrics of functional and species diversity (Cadotte, Carscadden, & Mirotnick,
400 2011; Schmera et al., 2017), the number of species and traits within the analysis (Guillemot et
401 al., 2011), as well as across environmental (Mason, Irz, Lanoiselée, Mouillot, & Argillier, 2008)
402 and disturbance gradients (Guerrero et al., 2014). Using generalized additive models, we
403 demonstrated how differing functional diversity metrics can provide different patterns of
404 functional diversity and species richness. However, our interpretation of the results between
405 metrics was consistent. Generally, there was a similar number of lakes falling outside the
406 confidence limits of null models indicating more or less redundancy across measures of
407 functional diversity (Tables S4-S7). The lack of saturation when using functional richness, in
408 comparison to dispersion, is likely related to functional richness being correlated with species
409 richness, whereas functional dispersion was designed to be independent of species richness
410 (Laliberté & Legendre, 2010). Given the differences in patterns between the two metrics, we
411 recommend using multiple measures of functional diversity when investigating redundancy
412 through functional diversity and species richness relationships.

413 Our hypothesis that the northeastern fish communities would contain the least redundant
414 species pool was confirmed by the lack of a saturating relationship between functional diversity
415 and species richness. In general, northeastern Ontario fish communities are less speciose than
416 northwestern or southeastern communities due to historical biogeographic patterns of dispersal
417 during the recession of the Wisconsinan ice sheet (Mandrak & Crossman, 1992). Coinciding
418 with the smaller species pool, northeastern communities also showed substantially lower
419 functional diversity levels than northwestern or southeastern communities. This finding indicates
420 that perhaps these lakes contain a more generalist species composition that may be less
421 susceptible to future disturbance. For example, White Sucker, Yellow Perch, and Walleye, which
422 all showed relatively low functional rarity values, were observed in most northeastern
423 communities (White Sucker = 83% of sites, Yellow Perch = 65% of sites, Walleye = 42% of
424 sites).

425 Fewer studies have investigated patterns of functional redundancy in freshwater fish
426 communities relative to marine communities. Among freshwater studies, tropical freshwater
427 fishes have garnered the most attention (e.g., Casatti et al., 2015; Leitão et al., 2018), likely due
428 to the greater diversity of fishes in these regions compared to more temperate regions (Toussaint,
429 Charpin, Brosse, & Villéger, 2016). Using uniqueness as a metric for species redundancy,

430 Buisson et al. (2013) found relatively few unique freshwater fish species in French streams and
431 attributed this result to the predominance of cyprinids in the system. Cyprinids are also common
432 among Ontario lakes and streams (e.g., Bendell & McNicol, 1987), however, small fishes were
433 under sampled relative to larger species in some lakes during the AHI (Bowlby & Green, 1985),
434 which may have inflated species-level rarity metrics of cyprinids in this study (e.g., Blacknose
435 Dace, River Darter *Percina shumardi*, Blackchin Shiner *Notropis heterodon*). Erös, Heino,
436 Schmera, & Rask (2009) found low redundancy in fish species in southern Finland boreal lakes,
437 with most species belonging to unique functional groups. Overall, patterns of redundancy tend to
438 vary with location and study system, consistent with what we observed in Ontario, but
439 differences in the species pools and traits used to measure diversity make direct comparisons
440 difficult.

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

457 We must acknowledge several caveats to our study. First, many of the species in Ontario
458 show geographically limited distributions across the province and we removed the rarest, or most
459 geographically limited species (present in <0.1% of sampled lakes). Additionally, the AHI
460 program prioritized important recreational and subsistence fish and under-sampled small fishes

461 in some lakes, which may bias the results that we present here (Bowlby & Green, 1985; Alofs et
462 al., 2014). Further, our study could have been improved if measures of species local abundance
463 were available; if a more abundant species were extirpated in a lake due to some environmental
464 disturbance, a redundant species that contains only a few individuals would likely struggle to
465 maintain the once shared ecosystem function (Rosenfeld, 2002). Abundance-based sampling
466 efforts could improve our understanding of the true redundancy and potential resiliency of lake
467 fish species, however, large scale efforts to accurately measure abundance can be problematic
468 and presence/absence data may more accurately reflect differences among communities in such
469 cases (Jackson & Harvey, 1997).

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

485 With a changing climate, lakes in Ontario are projected to experience increased
486 temperatures (Crossman, Eimers, Kerr, & Yao, 2016) and changes in precipitation (Magnuson et
487 al., 1997), impacting water chemistry (e.g., brownification; Larsen, Anderson, & Hessen, 2011),
488 and ultimately impacting fish species distributions (Jackson & Mandrak, 2002; Chu et al., 2005).
489 These projections have started to come to fruition over the last several decades with local
490 observations of increased lake water temperatures (Schindler et al., 1996; Mason et al., 2016),
491 decreased length of the ice-cover season (Mason et al., 2016), and an associated shift northward

492 in fish species distributions (Alofs et al., 2014). Here, we found patterns of functional
493 redundancy across provincial, regional, and species-based attributes indicative of potential
494 resiliency to some types and degrees of future change. However, most lake communities were
495 relatively depauperate, and among those communities existed high variability in the relationship
496 between functional and species diversity. Overall, understanding patterns of redundancy among
497 relatively depauperate freshwater ecosystems remains an important challenge as a changing
498 climate will alter the geographical distributions of species, creating novel combinations of
499 species and trait within local communities.

500

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795 **Data accessibility statement**

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

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 centered 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
		R * SA	42.76	55.33	453.90	<0.001	0.78
Northwest (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
		R * SA	9.23	12.26	518.50	<0.001	0.81
Southeast (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
		R * TDS	7.18	8.75	331.40	<0.001	0.69
Northeast (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

803

804 **Figure Legends**

805 **Figure 1.** (a) Linear, saturating, and nonlinear relationships between functional diversity and
806 species richness. Adapted from Micheli & Halpern (2005). (b) Hypothetical example with 14
807 communities (points) demonstrating a saturating relationship between functional diversity and
808 species richness. The blue area represents the 95% confidence limits of a null model;
809 communities above the null model are less redundant than expected and communities below the
810 null model are more redundant than expected based on null expectations.

811

812 **Figure 2.** Sampling sites from Ontario, Canada included in this study (n = 6,977; all points).
813 Blue = southeastern (n = 1,325), black = northeastern (n = 1,365); red = northwestern (n =
814 1,541); Yellow = sites included in the full provincial analyses, but not included in the regional
815 analyses (n = 2,746).

816

817 **Figure 3.** The frequency of occurrence of fish species across the 6,977 study lakes. Inset)

818 Frequency distribution of species richness values of lake communities.

819

820 **Figure 4.** (a) Functional dispersion and (b) functional richness versus species richness. Points
821 represent each of the 6,977 lake fish communities. The solid line indicates a LOWESS smoothing

822 algorithm applied to all communities across Ontario. The dashed line represents the mean null
823 community values. The 95% confidence interval for the null models is shaded in gray.

824 Communities above the null model are less redundant than expected and communities below the
825 null model are more redundant than expected based on null expectations.

826

827 **Figure 5.** (a) Functional dispersion and (b) functional richness regressed against species
828 richness. Colors represent measures for the three regions: northwestern (red), northeastern (gray),

829 and southeastern (blue). Ribbons reflect 95% confidence intervals of null models. Solid lines
830 indicate regional LOWESS models. Dashed lines indicate mean values for weighted null models.

831

832 **Figure 6.** Predicted functional dispersion (a-d) and functional richness (e-h) for low (black; first
833 quartile), moderate (blue; median), and high (purple; third quartile) levels of (a,e) depth, (b,g)

834 growing degree days, (c,f) surface area, and (d,h) total dissolved solids at the provincial scale.

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835 **SUPPORTING INFORMATION**

836 **List of Tables**

837

838 **Table S1.** List of species included in the provincial and regional pools.

839

840 **Table S2.** Traits used to build functional trait space.

841

842 **Table S3.** Correlations between functional diversity measures (functional dispersion - FDis,
843 functional richness - FRic, and Rao's quadratic entropy - RaoQ) and species richness (R) across
844 the 6,977 fish communities. Top diagonal = Spearman Rank correlations; bottom diagonal =
845 Pearson correlations. All correlations are significant at $p < 0.001$.

846

847 **Table S4.** Number of communities falling outside the upper and lower 95% confidence intervals
848 of weighted null communities per richness level R for functional dispersion (FDis), functional
849 richness (FRic), and Rao's quadratic entropy (RaoQ) at the provincial scale (n = 6,977 lakes).
850 Number of communities per R provided in parentheses. Proportion of lakes communities outside
851 of the confidence intervals in brackets.

852

853 **Table S5.** Number of northwestern fish communities falling outside the upper and lower 95%
854 confidence intervals of weighted null communities per richness level R for functional dispersion
855 (FDis), functional richness (FRic), and Rao's quadratic entropy (RaoQ; n = 1,541 lakes).
856 Number of communities per R provided in parentheses. Proportion of communities falling
857 outside of the confidence intervals in brackets.

858

859 **Table S6.** Number of southeastern communities falling outside the upper and lower 95%
860 confidence intervals of weighted null communities per richness level R for functional dispersion
861 (FDis), functional richness (FRic), and Rao's quadratic entropy (RaoQ; n = 1,325 lakes).
862 Number of communities per R provided in parentheses. Proportion of communities falling
863 outside of the confidence intervals in brackets.

864

865 **Table S7.** Number of northeastern communities falling outside the upper and lower 95%
866 confidence intervals of weighted null communities per richness level R for functional dispersion
867 (FDis), functional richness (FRic), and Rao's quadratic entropy (RaoQ; n = 1,365 lakes).
868 Number of lake communities per R provided in parentheses. Proportion of lakes falling outside
869 of the confidence intervals in brackets.

870
871 **Table S8.** Results of ANOVA for distinctiveness, uniqueness, distance to the provincial centroid,
872 and distance to the regional centroid across thermal preference groupings.

873
874 **Table S9.** Results of linear models for distinctiveness, uniqueness, distance to the provincial
875 centroid, and distance to the regional centroid regressed against log10 transformed average total
876 length.

877
878 **Table S10.** Results of linear models for distinctiveness, uniqueness, distance to provincial
879 centroid, and distance to regional centroid versus log10 transformed species occurrence.

880 **List of Figures**

881
882 **Figure S1.** Principal component analysis biplots of a) reproduction, b) substrate, c) diet, and d)
883 habitat variables at the provincial scale. Species codes are listed in Table S1 and trait variable
884 codes are listed in Table S2.

885
886 **Figure S2.** Scree plots for the provincial a) reproduction, b) substrate, c) diet, and d) habitat
887 principal component analyses.

888
889 **Figure S3.** Principal coordinates analysis of the Euclidean distance based on functional trait
890 matrix for the provincial species pool. a) First and second components and b) second and third
891 components are shown. Species codes are listed in Table S1 and trait variable codes refer to the
892 axes retained from the principal component analyses of reproduction, substrate, diet variables,
893 and habitat variables (Habitat1 = axis 1 and Habitat2 = axis 2).

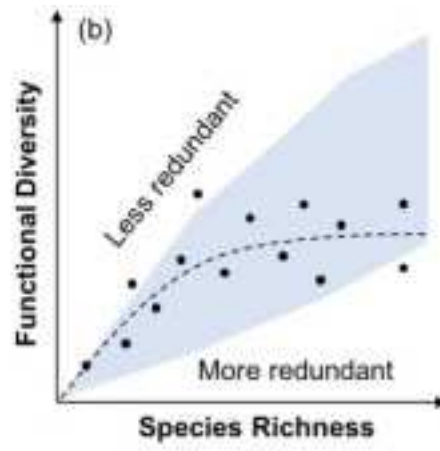
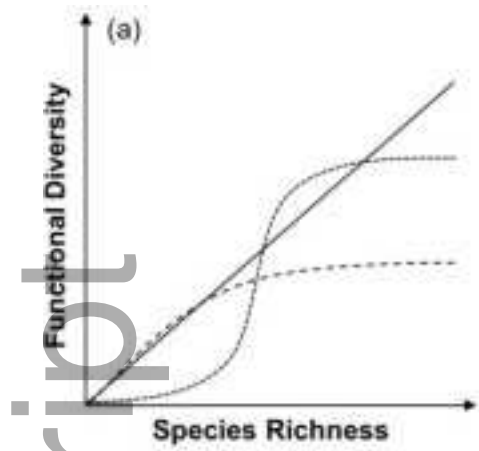
894

895 **Figure S4.** Predicted functional dispersion (a-d) and functional richness (e-h) for low (black;
896 first quartile), moderate (blue; median), and high (purple; third quartile) levels of (a,e) depth,
897 (b,g) growing degree days, (c,f) surface area, and (d,h) total dissolved solids using generalized
898 additive models of northwest Ontario communities.

899
900 **Figure S5.** Predicted functional dispersion (a-d) and functional richness (e-h) for low (black;
901 first quartile), moderate (blue; median), and high (purple; third quartile) levels of (a,e) depth,
902 (b,g) growing degree days, (c,f) surface area, and (d,h) total dissolved solids using generalized
903 additive models of northeast Ontario communities.

904
905 **Figure S6.** Predicted functional dispersion (a-d) and functional richness (e-h) for low (black;
906 first quartile), moderate (blue; median), and high (purple; third quartile) levels of (a,e) depth,
907 (b,g) growing degree days, (c,f) surface area, and (d,h) total dissolved solids using generalized
908 additive models of southeast Ontario communities.

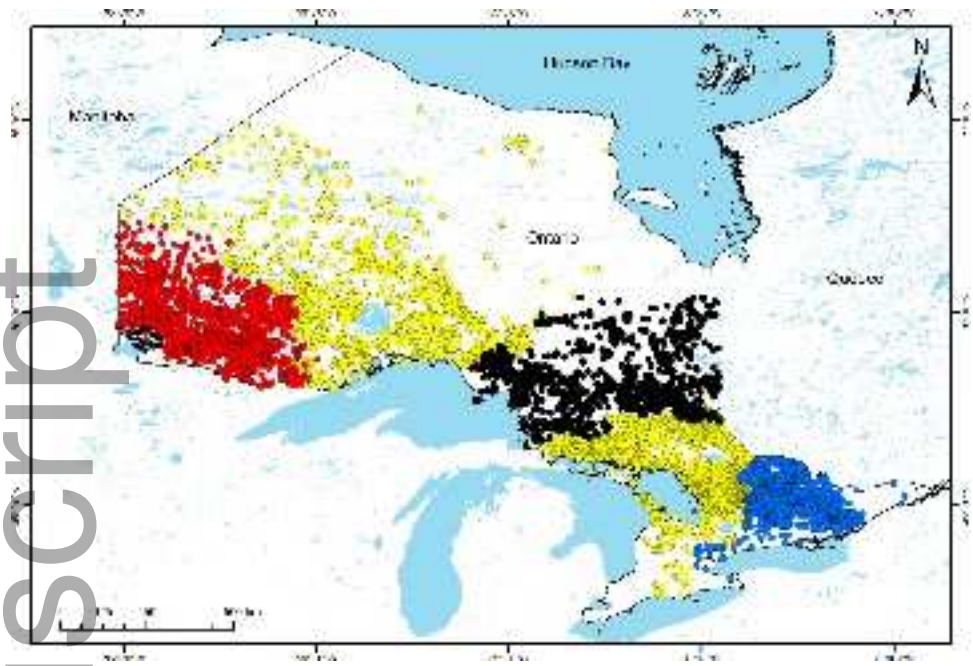
909
910
911 **Figure S7.** Scaled and centered functional rarity metrics for each species including functional
912 uniqueness (red), distinctiveness (black), and distance to provincial centroid (blue).



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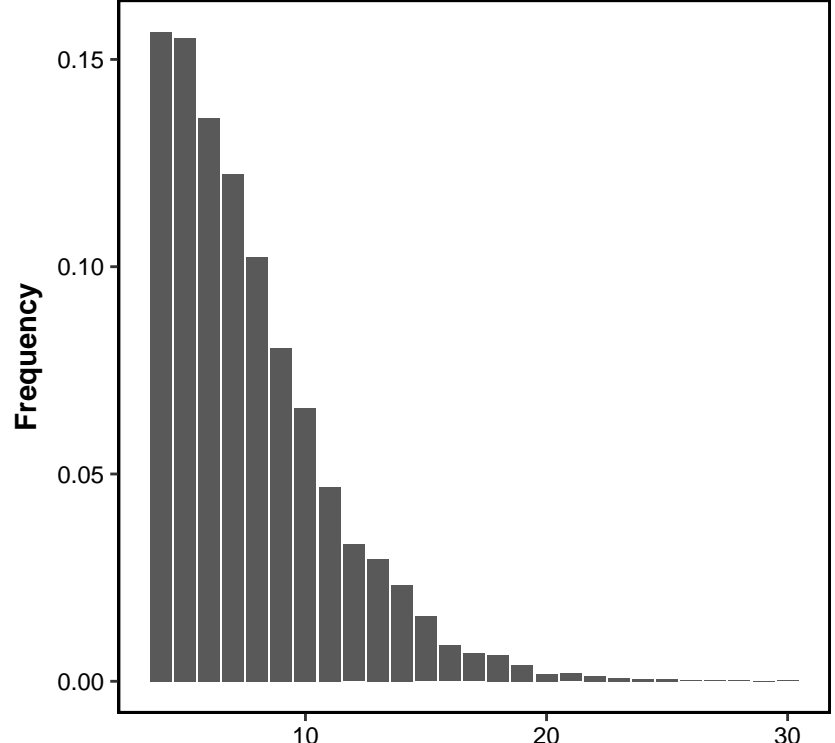
Species

- Catostomus commersonii*
- Perca flavescens*
- Esox lucius*
- Sander vitreus*
- Coregonus artedii*
- Coregonus clupeaformis*
- Notropis heterolepis*
- Lepomis gibbosus*
- Etheostoma exile*
- Notropis hudsonius*
- Salvelinus namaycush*
- Micropterus dolomieu*
- Lota lota*
- Chrosomus eos*
- Ambloplites rupestris*
- Salvelinus fontinalis*
- Etheostoma nigrum*
- Pimephales promelas*
- Notemigonus crysoleucas*
- Ameiurus nebulosus*
- Pimephales notatus*
- Luxilus cornutus*
- Margariscus nachtriebi*
- Culaea inconstans*
- Semotilus atromaculatus*
- Notropis volucellus*
- Chrosomus neogaeus*
- Micropterus salmoides*
- Percina caprodes*
- Couesius plumbeus*
- Cottus bairdii*
- Percopsis omiscomaycus*
- Catostomus catostomus*
- Pungitius pungitius*
- Rhinichthys cataractae*
- Moxostoma macrolepidotum*
- Notropis atherinoides*
- Lepomis macrochirus*
- Cottus cognatus*
- Oncorhynchus mykiss*
- Esox masquinongy*
- Notropis heterodon*
- Umbra limi*
- Sander canadensis*
- Osmerus mordax*
- Fundulus diaphanus*
- Pomoxis nigromaculatus*
- Rhinichthys atratulus*
- Semotilus corporalis*
- Lepomis megalotis*
- Hybognathus hankinsoni*
- Prosopium cylindraceum*
- Cyprinus carpio*
- Moxostoma anisurum*
- Noturus gyrinus*
- Acipenser fulvescens*
- Anguilla rostrata*
- Ameiurus natalis*
- Lepomis cyanellus*
- Hiodon tergisus*
- Ictalurus punctatus*
- Amia calva*
- Percina shumardi*
- Alosa pseudoharengus*
- Cottus ricei*
- Labidesthes sicculus*
- Lepisosteus osseus*
- Salmo trutta*
- Gasterosteus aculeatus*

0.0

0.2

Species Prevalence



Species Richness

0.15

0.10

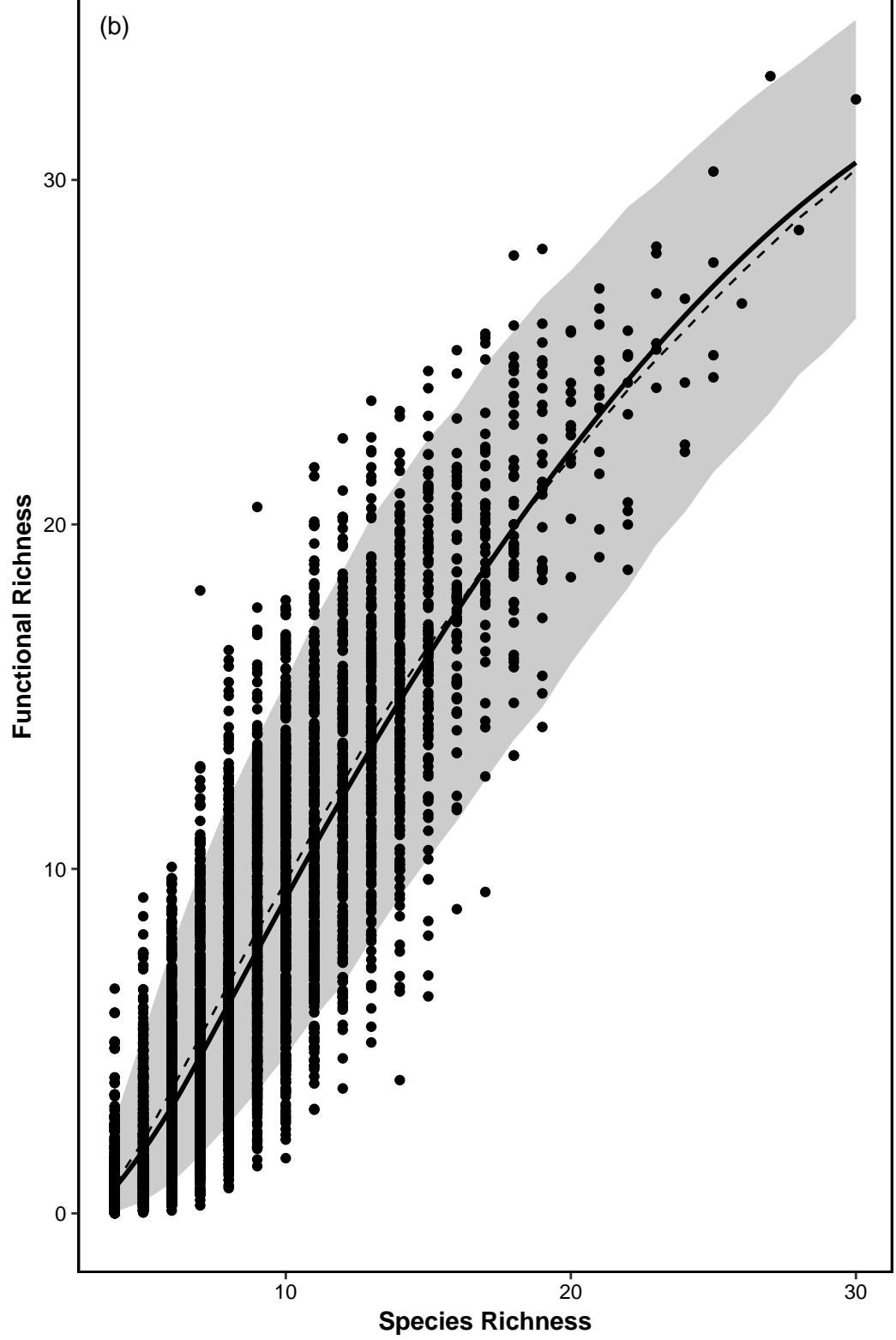
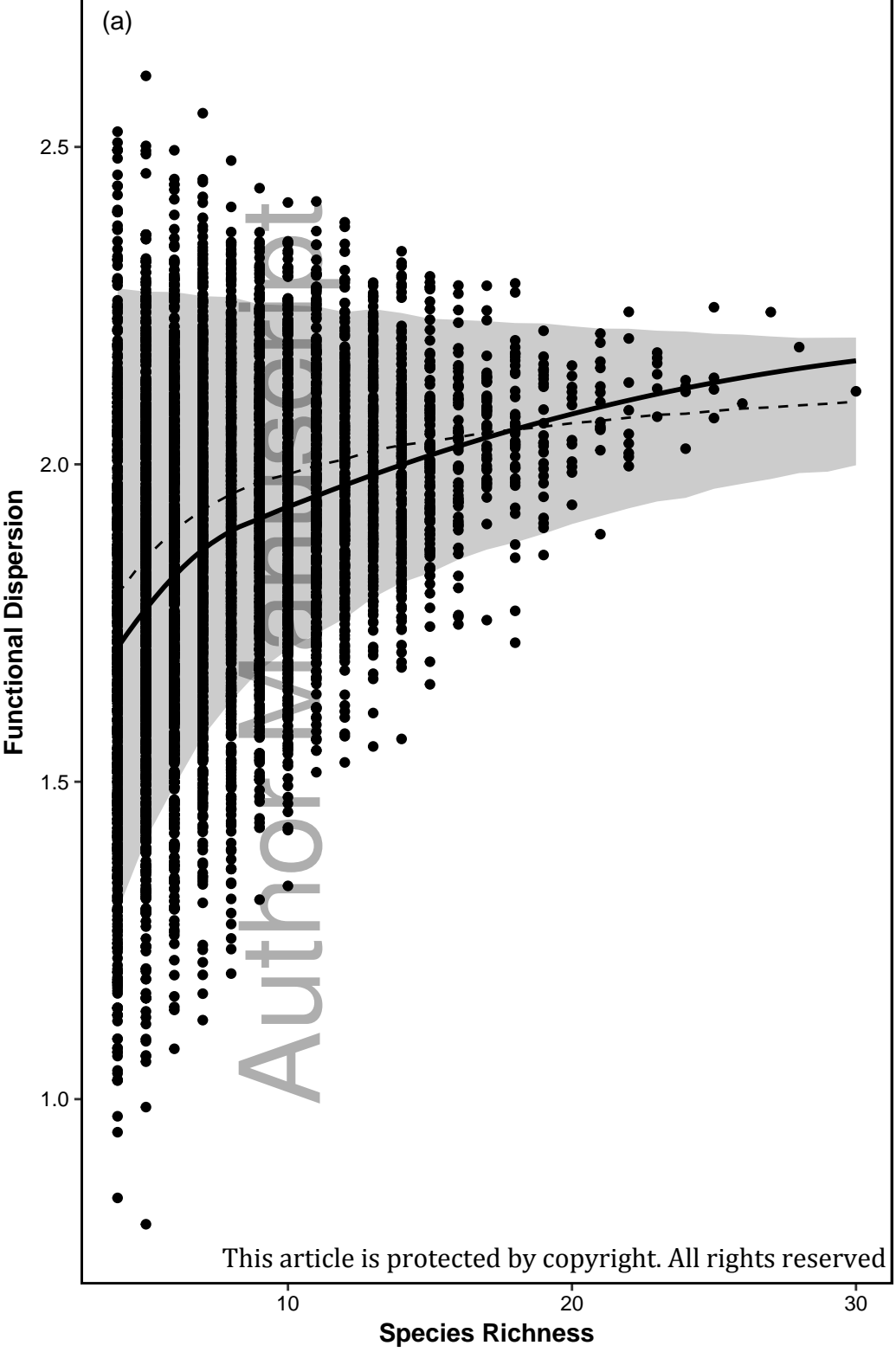
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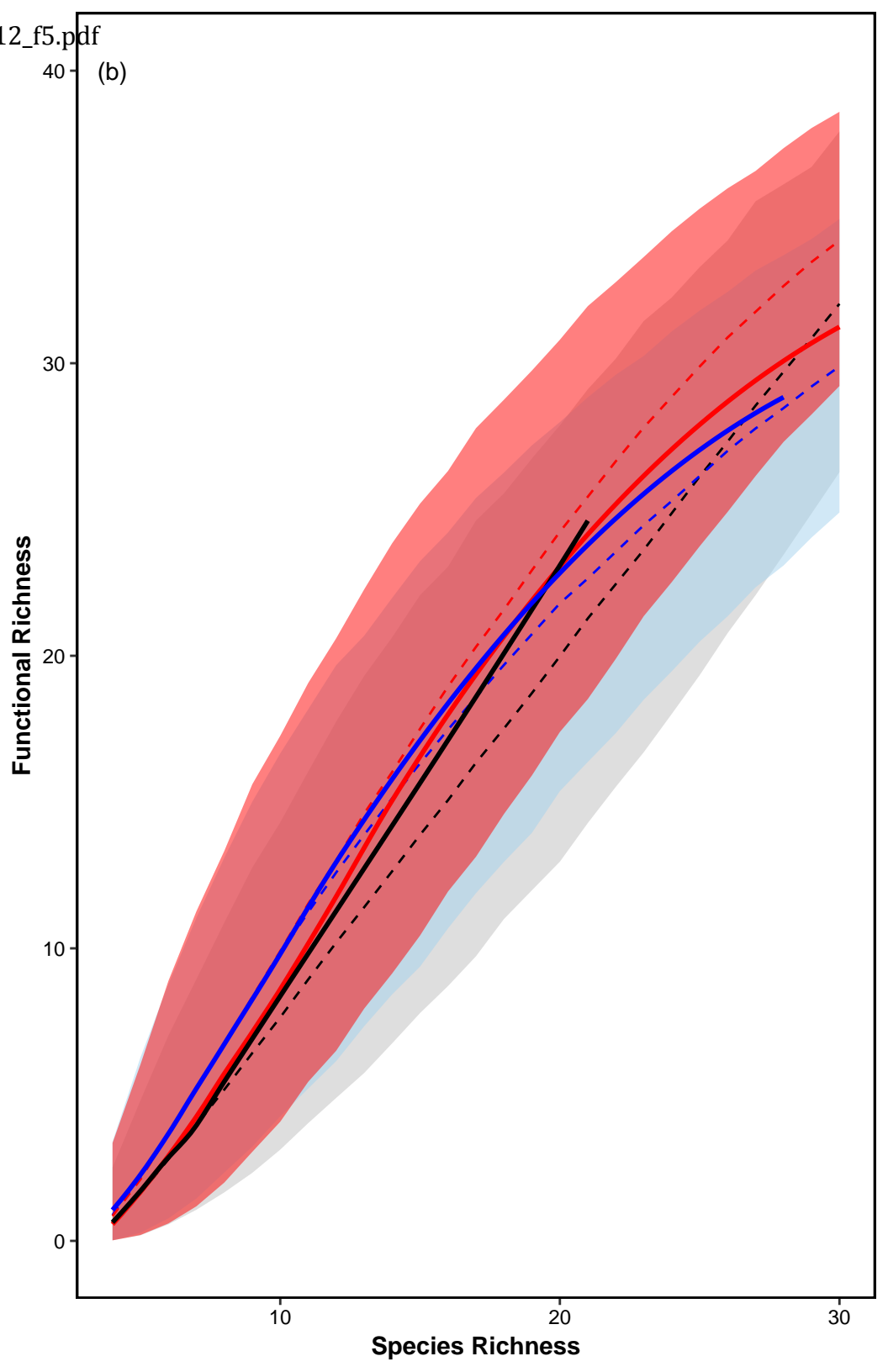
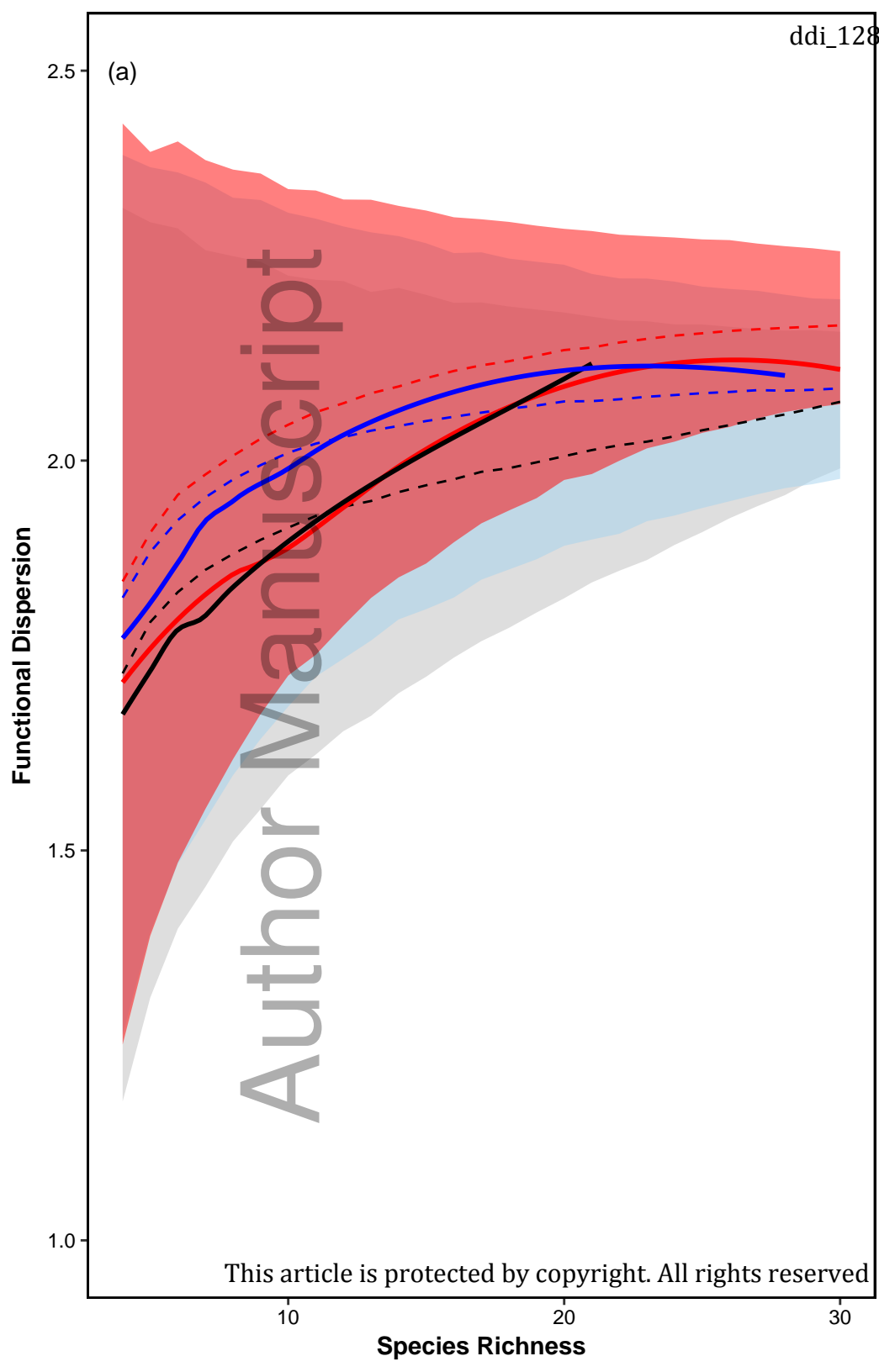
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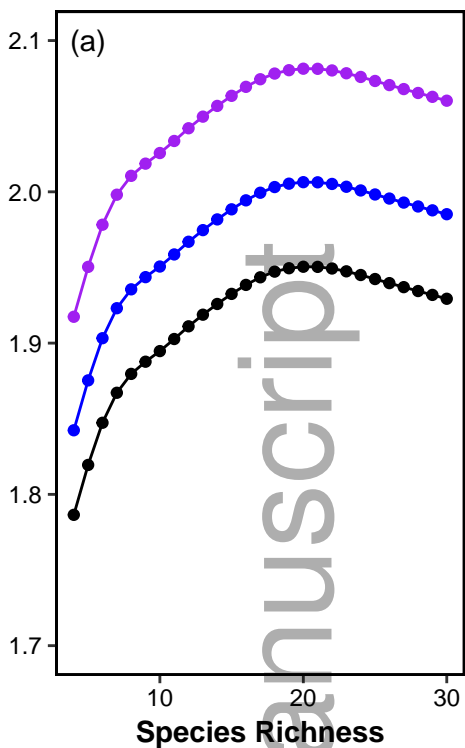
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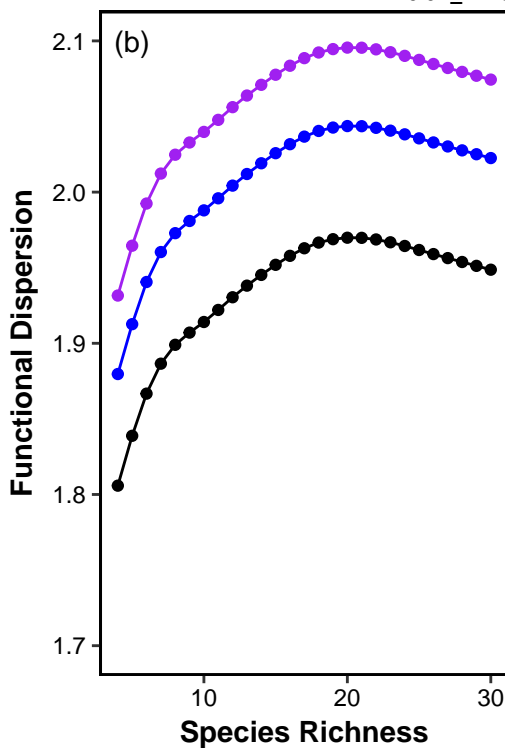




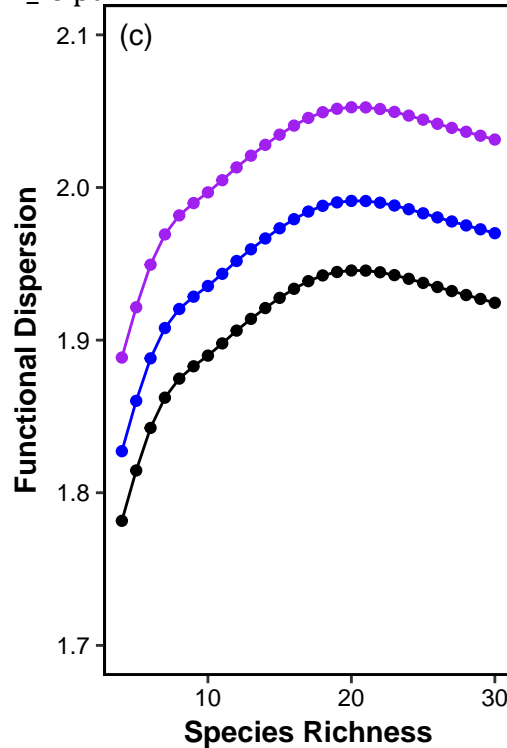
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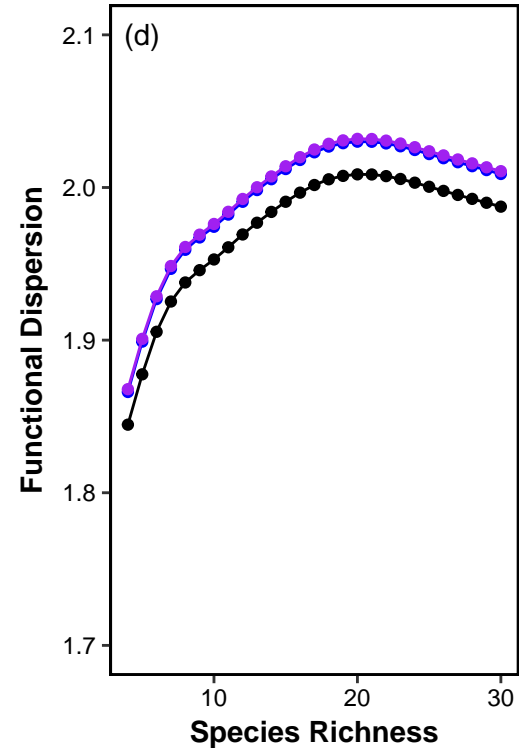
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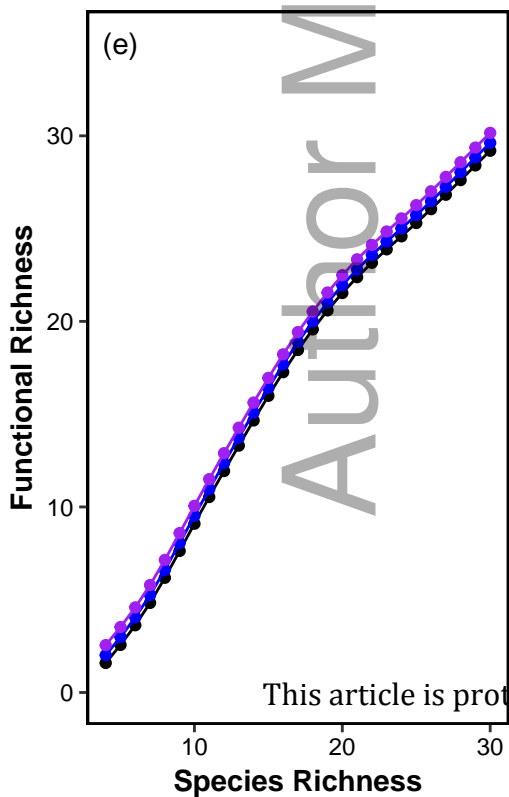
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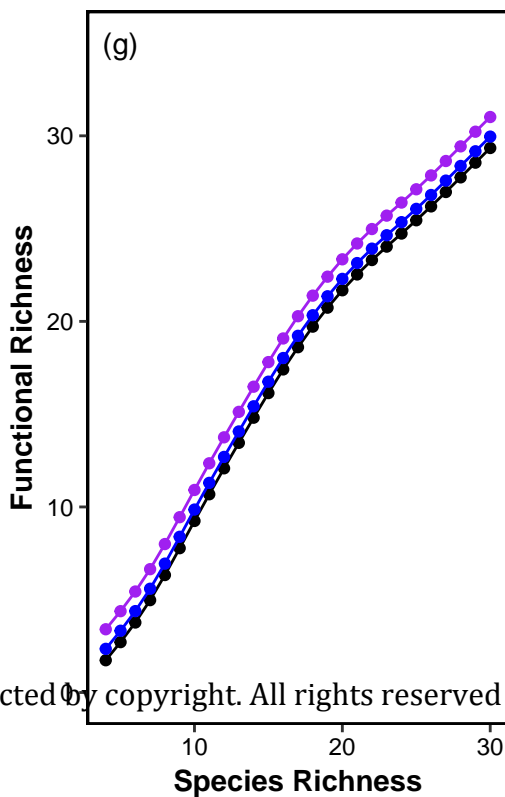
Total Dissolved Solids



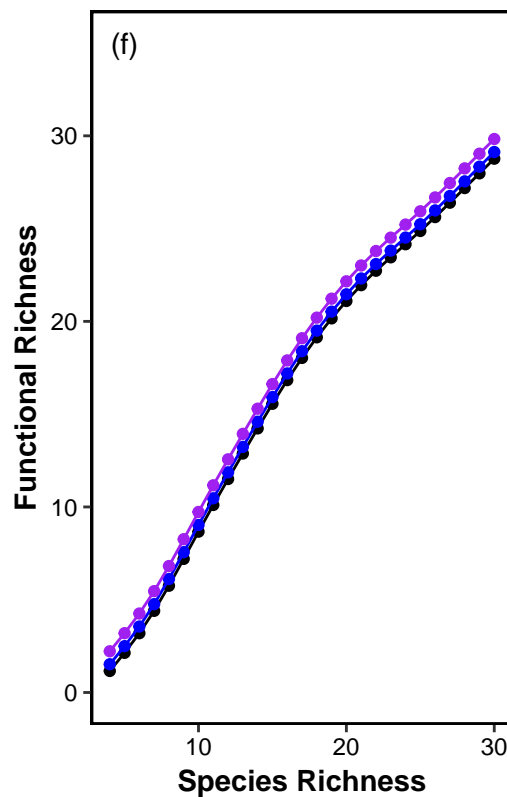
(e)



(g)



(f)



(h)

