

11-2015

Increased Taxonomic and Functional Similarity Does Not Increase the Trophic Similarity of Communities

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Citation Details

Pool, T. K., Cucherousset, J., Boulêtreau, S., Villéger, S., Strecker, A. L., & Grenouillet, G. (2015). Increased Taxonomic and Functional Similarity Does Not Increase the Trophic Similarity of Communities. *Global Ecology and Biogeography*, 25(1), 46–54.

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1 **Title: Increased taxonomic and functional similarity does not increase communities'**
2 **trophic similarity**

3

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26 **Running title:** Functional vs. trophic diversity similarity

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30 **Word count:** 3,635 main text

31 **Reference count:** 45 general references

32 **ABSTRACT**

33 **1. Aim** Despite a long-standing research interest in the association between communities'
34 biodiversity (i.e. taxonomic and functional composition) and trophic structure, our
35 understanding of the relationship remains limited. Community assembly theory predicts
36 that niche partitioning will result in communities with a diverse array of functional traits,
37 which in turn, may facilitate a correspondingly diverse array of trophic interactions that
38 define those communities' trophic niche. The aim of our study is to test this prediction.

39 **2. Location** North America

40 **3. Methods** We built a database composed of functional traits and stable isotope values
41 ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for 63 freshwater fish communities containing 109 species in 34 lentic and
42 29 lotic ecosystems. First, we tested whether communities' taxonomic diversity was
43 positively associated with their functional diversity and if communities' functional
44 diversity was positively associated with their trophic diversity using linear mixed models
45 (i.e. alpha diversity approach). Second, we assessed communities' taxonomic, functional
46 and trophic similarity using multiple regression on distance matrices (MRM) and their
47 respective 'turnover' and 'nestedness-resultant' components to test if communities'
48 taxonomic similarity was positively correlated with their functional similarity and if
49 communities' functional similarity was positively associated with their trophic similarity
50 (i.e. beta diversity approach).

51 **4. Results** We found that communities' functional diversity increased as taxonomic
52 diversity increased. Similarly, communities' trophic diversity increased as functional
53 diversity increased. The pairwise taxonomic and functional similarity of communities were

54 also positively associated but there was a weak relationship between communities'
55 functional and trophic similarities.

56 **5. Main conclusions** Our study demonstrates that communities with similar functional
57 characteristics can have disparate food web structures suggesting that additional site
58 specific factors influence community variation in trophic niche geometry. Determining the
59 relative importance of functional characteristics and site-specific factors in shaping trophic
60 interactions is crucial to better understand how future species loss and species
61 introductions will affect food web structure and ecosystem functioning.

62 **6. Keywords** Functional and trophic diversity, alpha and beta diversity, compositional
63 similarity.

64 INTRODUCTION

65 A time-integrated assessment of species relationships and energy flow within ecosystems
66 can be quantified using stable isotopes, identifying the ecological scaffolding that forms
67 communities' trophic structure (Fry, 2006; Layman *et al.*, 2012). Employing a stable
68 isotopic approach has provided valuable insight into trophic processes such as omnivory
69 (Thompson *et al.*, 2007), ontogenetic dietary shifts (Freedman *et al.*, 2011), and resource
70 partitioning (Esteves & Lobón-Cerviá, 2001) while also demonstrating that food web
71 structure is linked to the functioning and stability of ecosystems (Thompson *et al.*, 2012).
72 Despite these advances, substantial gaps in our knowledge of community assembly remain
73 regarding how a community's taxonomic and functional composition is linked to its trophic
74 architecture. For example, the extent that species will consistently fill similar 'roles' (i.e.
75 occupy a similar trophic niche) within different communities that are constrained by
76 unique biotic (e.g. competition, predation) and abiotic (e.g. ecosystem size, geographical
77 location) environmental factors is poorly understood. Conversely, it is unknown whether
78 and how often communities with dissimilar taxonomic or functional compositions may
79 possess similar trophic structures. With unprecedented changes in the composition of
80 communities occurring at a global scale, it is therefore critical to improve our theoretical
81 and empirical understanding of the relationships between communities' taxonomic,
82 functional, and trophic diversity.

83 Recent studies have hypothesized that communities' trophic structures may be
84 more closely linked to communities' functional diversity than their taxonomic diversity
85 (Petchey & Gaston, 2006). This is because communities' functional traits are reflections of
86 the biological, ecological and physiological constraints made in response to the temporal

87 and spatial variations in environmental conditions, competition for resources, and
88 predation (i.e. the functional niche; Winemiller, 2005). While previous studies examining
89 various aspects of communities' functional diversity have assisted with providing
90 mechanistic links between species compositions and the critical factors that influence
91 specific systems (e.g. Poff, 1997; Pool *et al.*, 2010; Suding *et al.*, 2008), our ability to predict
92 the relationship between a community's functional composition and its trophic structure
93 remains largely untested.

94 Trophic ecology studies typically investigate the trophic diversity of individual
95 communities (i.e. alpha diversity approach; Layman *et al.*, 2012) or a small number of
96 communities. Alternatively, variation in trophic diversity between communities can be
97 assessed (i.e. beta diversity approach), as is commonly performed in taxonomic and
98 functional diversity studies (e.g. Ackerly & Cornwell, 2007). Quantifying beta diversity can
99 be informative because it describes a fundamental spatial pattern of compositional change
100 between areas (Whittaker, 1960). Using a beta diversity approach also offers a unique
101 opportunity to determine whether communities with an increased taxonomic or functional
102 similarity also display an increased trophic similarity. Importantly, such an approach can
103 assess if there are reoccurring trophic interactions leading to similar trophic structure
104 associated with communities containing similar species or trait compositions, with limited
105 influence from site-specific factors.

106 In the present study, we aimed to untangle the complex relationships between
107 taxonomic, functional, and trophic diversity using North American freshwater fish
108 communities as model organisms. It is informative to study fish communities and their
109 trophic characteristics because they are documented to influence important ecosystem

110 processes associated with nutrient cycling (e.g. Vanni, 2002) and primary productivity (e.g.
111 Schindler *et al.*, 1997). Furthermore, fishes are suitable for our study because they are an
112 incredibly diverse and multi-trophic group of aquatic species occupying a wide array of
113 trophic roles within food webs ranging from strictly herbivorous grazers to apex predators.
114 First, we assessed the relationship between taxonomic, functional, and trophic diversity
115 (defined here as niche size) within communities (i.e. alpha diversity approach). We
116 predicted that individual community's taxonomic and functional diversity would positively
117 correlate along with their functional and trophic diversity. Second, we investigated the
118 pairwise similarity of communities (i.e. beta diversity approach) and predicted that
119 communities' taxonomic similarity would positively correlate with communities' functional
120 similarity along with their functional and trophic similarity. These predictions are based on
121 niche partitioning theory (McKane *et al.*, 2002) predicting that, as competition for
122 resources between species within a community increases, species tend to have a more
123 diverse array of biological and ecological traits, which in turn, results in a wider spectrum
124 of resource use and a larger trophic niche. Here, lentic and lotic freshwater ecosystems
125 were tested independently to study the association between community composition and
126 trophic structure within and between ecosystems at the continental scale.

127

128 **METHODS**

129 **Community selection**

130 Candidate fish communities were identified using a multi-tiered data collection approach
131 utilizing primary scientific articles, comprehensive texts of regional fish faunas, university
132 reports, and online databases. The search was restricted to North America because a

133 wealth of studies containing functional and trophic (i.e. stable isotopes) data on freshwater
134 fishes are available for this region (Cucherousset *et al.*, 2012; Frimpong & Angermeier,
135 2012). First, we identified 58 studies that provided averaged species stable isotope values
136 ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in 176 fish communities. In some studies, several communities were
137 identified in the same ecosystem but were designated as separate fish communities
138 because sampling events varied spatially (i.e. sampling different areas along a drainage) or
139 temporally (i.e. sampling an area during different years). Second, data for 12 biological and
140 ecological traits (i.e. behavioural, life history, morphological, and diet) were collected to
141 characterize the functional attributes of the species within each community (Frimpong &
142 Angermeier, 2012; Froese & Pauly, 2012; Appendix S1 in Supporting Information). These
143 attributes were selected because they characterize the main dimensions of species
144 ecological niches and are commonly used in fish functional diversity studies (Winemiller &
145 Rose, 1992; Olden *et al.*, 2008). If greater than two trait values were unknown for a species
146 it was excluded and subsequently, every candidate community containing that species was
147 removed from the database. Third, in an attempt to include only communities that had
148 been comprehensively sampled (i.e. avoiding studies targeting specific species), a
149 minimum richness threshold criterion of five species was set for inclusion in the database.
150 To validate this multi-tiered approach, the corresponding authors for each study were
151 contacted to determine if all the fish species collected during their field sampling were
152 analyzed for stable isotopes. The authors (16 of the 18 who responded) indicated that
153 every species collected in sufficient numbers (i.e. enough individuals to estimate a realistic
154 average of stable isotope values; $n \geq 5$) was analyzed for stable isotopes, demonstrating our
155 data can be considered an accurate estimation of the fish communities' taxonomic,

156 functional and trophic diversity. Certainly, rare species may not have been identified in
157 some of our source studies because they are challenging to capture in sufficient numbers to
158 appropriately estimate their stable isotope values. In communities that had rare species
159 with unique trait profiles (i.e. top predators or detritivores) differing from more abundant
160 species, the diversity of those fish communities may have been underrepresented.

161 The final database contained 23 studies and included 63 freshwater fish
162 communities (lentic: n = 34 and lotic: n = 29) composed of 109 species occurring
163 throughout North America (ranging from Florida, USA, to Nunavut Territory, Canada and
164 from Washington State, USA to Maine, USA; Appendix S2 in Supporting Information). This
165 final database utilized in our analyses is a subset of a larger database constructed to study
166 the isotopic structure of fish communities at a global scale (Sagouis *et al.*, 2015).

167

168 **Data analyses**

169 ***Taxonomic diversity***

170 The scientific name of each species was confirmed using Fishbase (Froese & Pauly, 2012),
171 permitting the cross-referencing of community composition lists. '*Taxonomic diversity*' was
172 calculated as the number of species within each community.

173

174 ***Functional diversity***

175 For most species, functional trait values were assigned based on research conducted in
176 North America capturing the natural variation for each species in this region. Whenever
177 possible, continuous trait values were used (e.g. body length, fecundity) but some traits
178 required the use of discrete trait categories (e.g. reproductive guild, primary spawning

179 season). In a few instances, ≤ 2 trait values were unknown (4 of 109 species) and were
180 treated as missing values in the subsequent analyses. The '*functional diversity*' of each
181 community was calculated by standardizing trait values and then creating a dissimilarity
182 matrix using Gower's distance, a metric able to accommodate nominal, ordinal, continuous,
183 and missing data (Pavoine *et al.*, 2009). Then, a principal coordinate analysis (PCoA) on this
184 functional distance matrix was computed to construct a multidimensional functional space
185 (Villéger *et al.*, 2008). The first three principal coordinate axes explained a significant
186 proportion (75.5 %) of the total variation in trait matrix (i.e. 29.0 %, 26.1 %, and 20.4 %,
187 respectively) based on the randomized broken-stick method and $\alpha = 0.05$ (Jackson, 1993).
188 Those trait-based principal coordinate scores, along with the species-by-community
189 matrix, were then used to measure each community's functional diversity calculated as the
190 'minimum convex hull volume' using the Quickhull algorithm (Villéger *et al.*, 2008). More
191 simply, the functional diversity of each community was quantified as the volume created by
192 a group of trait-based points, each representing a fish species.

193 A second trait matrix was also created retaining only behavioural, morphological,
194 and trophic traits to calculate an additional functional diversity value for each community.
195 This reduced trait matrix was created to determine if the results from our full trait matrix
196 analyses were simply an artefact of the particularly wide breadth of selected traits. The
197 functional diversity values generated from the reduced trait matrix were utilized in parallel
198 with our full trait matrix values in subsequent analyses.

199

200 ***Trophic diversity***

201 The '*trophic diversity*' was quantified in each community using the 'convex hull metric'
202 based the averaged $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each species (Layman *et al.*, 2007 & 2012). This
203 conservative metric was selected because it is the most analogous to our functional
204 diversity approach. The convex hull quantified the minimum area encompassing species
205 stable isotope values within each community (Layman *et al.*, 2007).

206

207 **Statistical analyses**

208 ***Community composition***

209 The relationships between the taxonomic, functional, and trophic alpha diversity of fish
210 communities were tested with linear mixed models using article ID as a random variable
211 since, in many cases (19 of 24 studies), more than one community was reported from the
212 same source article (Borenstein *et al.*, 2010). The appropriate transformation parameter
213 for each response variable was identified using the statistical estimation method known as
214 the maximum likelihood approach developed by Box and Cox (1964). First, functional
215 diversity (Box-Cox transformed with $\lambda = 0.22$) was used as a response variable and
216 taxonomic diversity as a fixed predictor. Second, trophic diversity (log-transformed) was
217 used as a response variable and functional diversity as a fixed predictor. All models were
218 run separately for lentic and lotic ecosystems.

219

220 ***Community similarity***

221 The pairwise taxonomic beta diversity of communities was measured using Jaccard's
222 dissimilarity index, i.e. percentage of species not shared by communities compared to the
223 total number of species. To quantify functional beta diversity, convex hulls for each

224 community were used to measure the pairwise functional dissimilarity between
225 communities likewise using the Jaccard's index (Villéger *et al.*, 2008). In an effort to use an
226 approach analogous to our taxonomic and functional analyses, the trophic beta diversity of
227 communities was quantified using a stable isotope 'centroid' approach that aligns the
228 stable isotope convex hull centroids for each community pairing (Schmidt *et al.*, 2011;
229 Appendix S3 in Supporting Information). The centroid of each community was calculated as
230 the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ species value (Schmidt *et al.*, 2011). This approach maximizes the
231 trophic hull overlap between communities as they share the same centroid values,
232 providing a conservative assessment of trophic niche dissimilarity.

233 To evaluate the relationships between taxonomic, functional and trophic beta
234 diversity, we used multiple regression on distance matrices (MRM; Lichstein, 2007). MRM
235 is utilized to study ecological data involving multiple regression of a response matrix on
236 any number of explanatory distance or similarity matrices. For our MRM analyses, spatial
237 dissimilarity was calculated as the Euclidean distance between communities. A
238 randomization was used to test for differences between beta diversity types (n = 4999
239 permutations) and R^2 values were used when there were multiple significant predictor
240 variables (Peres-Neto *et al.*, 2006). While this approach has been criticized for
241 underestimating explained variance (Legendre *et al.*, 2005), we used it primarily as a
242 comparative tool to test for differences between communities' taxonomic and functional
243 beta diversity as well as communities' functional and trophic beta diversity. Using this
244 approach also permitted variance partitioning to be used examining the independent
245 effects of our predictor variables and geographic space.

246 Finally, to identify underlying patterns in community structure, taxonomic beta
247 dissimilarity was deconstructed into 'turnover' (i.e. species replacement between
248 communities) and 'nestedness-resultant' (i.e. difference in the number of species between
249 communities) components (Baselga *et al.*, 2012). This provided insight because high
250 taxonomic dissimilarity (i.e. high beta diversity) can be driven by taxonomic turnover (no
251 species in common) or nestedness (one community is a subset of the other). For the
252 functional and trophic beta diversity analyses, we also identified the turnover and
253 nestedness-resultant components (Villéger *et al.*, 2013). In-step with our community
254 composition analyses, all community similarity analyses were run separately for lentic and
255 lotic ecosystems. Statistical analyses were conducted in R 2.15.1 using the ape, betapart,
256 cluster, ecodist, FD, geometry, and vegan libraries (R Development Core Team, 2012).

257

258 **RESULTS**

259 **Community composition**

260 The taxonomic diversity of fish communities ranged from 5 to 19 species in lentic
261 ecosystems and from 5 to 14 species in lotic ecosystems. The functional diversity of fish
262 communities was strongly influenced by species behavioural, life history, and
263 morphological traits, positively contributing to the first principal coordinate axes scores
264 with minimal contributions of traits linked to diet (Appendix S1). As predicted, the
265 functional diversity of fish communities significantly increased as taxonomic diversity
266 increased irrespective of the ecosystem type (lentic: $p < 0.001$ and lotic: $p < 0.001$; Table 1;
267 Fig. 1a). Communities' functional and trophic diversity were significantly and positively

268 correlated in lentic ecosystems ($p = 0.039$; Table 1; Fig. 1b) and were marginally and
269 positively correlated in lotic ecosystems ($p = 0.064$; Table 1; Fig. 1b).

270

271 **Community similarity**

272 Lentic communities' taxonomic beta diversity was positively correlated with functional
273 beta diversity using MRM ($R^2 = 0.421$, $p < 0.01$) and variance partitioning with greater
274 variation uniquely explained by the taxonomic predictor ($R^2 = 0.257$) than geographic
275 space ($R^2 = 0.053$). Similarly, lotic communities' taxonomic beta diversity positively
276 correlated with functional beta diversity ($R^2 = 0.207$, $p < 0.01$) with greater variation
277 uniquely explained by the taxonomic predictor ($R^2 = 0.142$) than geographic space ($R^2 =$
278 0.050). Thus, within lentic and lotic ecosystems, pairs of communities that tended to be
279 similar taxonomically also tended to be similar functionally (Fig. 2a).

280 In contrast, lentic communities' functional beta diversity had a weak correlation
281 with trophic beta diversity using MRM ($R^2 = 0.093$, $p < 0.01$) and variance partitioning with
282 greater variation uniquely explained by the functional predictor ($R^2 = 0.092$) than
283 geographic space ($R^2 = 0.001$). Lotic communities' functional beta diversity similarly had a
284 weak correlation with trophic beta diversity ($R^2 = 0.026$, $p < 0.01$) with low variation
285 uniquely explained by both the functional predictor ($R^2 = 0.010$) and geographic space (R^2
286 $= 0.011$). A weak correlation also existed between communities' functional and trophic beta
287 diversity in lentic and lotic systems when the reduced trait dataset was used albeit with
288 slightly stronger correlations between beta diversity types (Appendix S4). Ultimately,
289 within lentic and lotic ecosystems, pairs of communities that tended to be similar
290 functionally did not tend to be similar trophically (Fig. 2b).

291 Finally, the mean compositional dissimilarity of communities' taxonomic and
292 functional diversity was higher than occurred for communities' trophic diversity (Table 2).
293 The variation within communities' taxonomic and functional diversity was primarily driven
294 by compositional turnover (Table 2). In contrast, variation within the trophic beta diversity
295 for community pairings was driven by relatively equal contributions from the turnover and
296 nestedness-resultant components (Table 2). These results were consistent in both lentic
297 and lotic ecosystems.

298

299 **DISCUSSION**

300 In this study, we found a positive relationship between individual fish community's
301 taxonomic and functional diversity along with their functional and trophic diversity within
302 both lentic and lotic ecosystems. In contrast, while communities' pairwise taxonomic
303 similarity was positively associated with their functional similarity, we demonstrated that
304 increased functional similarity of communities did not consistently increase their trophic
305 similarity. This suggests that increased likeness of communities' trait composition does not
306 necessarily result in more similar trophic structures. Taken together these results
307 demonstrate that the relationship between taxonomic, functional, and trophic diversity is
308 complex with a communities' trophic diversity driven, to some extent, by the
309 characteristics of species within that community but also by system-specific factors
310 influencing the architecture of trophic interactions.

311 The idiosyncratic association between communities' functional and trophic diversity
312 may be attributable to the high contribution of behavioural and life history traits in the
313 calculation of fish communities' functional diversity. While the incorporation of non-

314 trophic traits to compute the functional diversity of communities unequivocally has value
315 when attempting to assess the complete ecological niche of a community, our results
316 display that not all traits contribute equally to trophic structure. Given that some species
317 traits will be more closely linked than others to food web structure and possibly also
318 ecosystem processes, modification of specific aspects of communities' functional profile
319 (i.e. a reduction in the breadth of trophic guild types) may be of particular conservation
320 concern. For example, communities could display minimal change in their functional
321 diversity (quantified from a diverse array of trait types) and still exhibit substantial shifts
322 in their trophic structure over time. However, even with the removal of life history traits
323 from our analyses believed to poorly contribute to defining communities' trophic structure,
324 the weak association between communities' functional and trophic similarity remained.
325 Ultimately while the trait composition of a community mechanistically links those species
326 to their environment, claims that alteration of a communities' functional composition will
327 redefine its trophic structure may not consistently be substantiated.

328 The weak association between communities' functional and trophic similarity may
329 have also occurred because static trait values were used to quantify functional diversity.
330 This approach, commonly used in ecology, fails to account for species variance in the
331 expression of traits (i.e. intra- and inter- population trait plasticity) associated with biotic
332 or abiotic factors within diverse environments. In contrast, stable isotope analyses
333 represent an integrative approach that accounts for the direct and indirect interactions
334 occurring in a community (Layman *et al.*, 2012, Cucherousset *et al.*, 2012) and is therefore
335 highly sensitive to specific interactions between species. Accounting for traits intraspecific
336 variation along environmental gradients instead of using species mean trait values could

337 more clearly identify the mechanisms by which communities' functional diversity
338 influences trophic interactions (Ackerly & Cornwell, 2007). Furthermore, associations
339 between communities' functional and trophic similarity may have been difficult to assess
340 because functionally specialized species can exhibit behavioural opportunism within some
341 systems to utilize available resources (Bellwood *et al.*, 2006). Functionally generalized
342 species may alternatively exhibit focused or specialized feeding behaviour obscuring a
343 clear association between communities' functional and trophic diversity (Bellwood *et al.*,
344 2006). Such functional plasticity is known to occur within fish species in association with
345 their life-history stage and dynamic factors such as local environmental variation (Simpson
346 *et al.*, 2010; Zhao *et al.*, 2014). A significant forthcoming challenge in ecology will be to
347 properly incorporate this intraspecific and interspecific trait variation into the study of
348 multiple animal groups (i.e. aquatic insects, reptiles, and fish) at the population and
349 community levels.

350 Several abiotic and biotic factors may have also influenced the site-specific trophic
351 structure of fish communities such as nutrient availability (Jeppesen *et al.*, 2000), habitat
352 heterogeneity (Layman *et al.*, 2007), ecosystem size (Post *et al.*, 2000), human disturbance
353 (Freedman *et al.*, 2013), and non-native species introduction (Cucherousset *et al.*, 2012).
354 Additionally, communities' trophic structure may have been influenced by assembly
355 history, i.e. the sequence of species lost or gained over time (Fukami *et al.*, 2010). For
356 instance, Stier *et al.* (2013) demonstrated that the timing of arrival for carnivorous coral
357 reef fish (*Paracirrhites arcatus*) to natural reefs influenced the assembly of the prey fish
358 community. Therefore, historical variation in the composition of communities (i.e. species
359 colonisation, introduction and extirpation) along with other site-specific factors may

360 account for contemporary discontinuities in pairwise comparisons of communities' trophic
361 diversity.

362 As expected working at a large macroecological scale (i.e. continental scale), the
363 mean taxonomic, functional, and trophic dissimilarity of communities was relatively high;
364 principally associated with high turnover indicating minimal overlap in their taxonomic
365 and functional compositions. Interestingly, even when calculating communities' trophic
366 beta diversity by aligning their isotope centroids, turnover remained a substantial
367 contributor to the total compositional dissimilarities between communities suggesting
368 highly variable trophic structures. For example, some communities that contained almost
369 identical species profiles, and in turn similar functional compositions, had very different
370 isotopic values resulting in different "trophic niche" shapes. These results further validate
371 that fish trophic structures are highly variable, potentially providing unique information
372 about the functioning of local communities and ecosystems.

373 There is broad consensus that increased taxonomic and functional diversity within
374 communities assists with maintaining ecosystems stability and resilience (Hooper *et al.*,
375 2005) but it has been challenging to identify how variation in individual communities'
376 composition is linked to the functionality of those ecosystems. Our results indicate that
377 exploring how communities' trophic structure is linked to ecosystem functioning may be a
378 particularly informative thread of research to pursue given the variation in trophic
379 structure we observed. Indeed, Poisot *et al.* (2013) found that the structure of trophic
380 interactions within food webs (i.e. trophic complementarity) effectively predicted
381 ecosystem functioning in complex modeled communities. Additionally, with the
382 preservation of ecosystem processes becoming an increasingly emphasized conservation

383 goal, it should be recognized that systems with similar taxonomic or functional profiles
384 might have unique trophic structures potentially driving system specific functionality. As
385 additional work is done to study compositional changes over time beyond characterizing
386 fish communities, analyses should also assess if the trophic structure of communities is
387 becoming more similar given that our results suggest that processes such as taxonomic or
388 functional homogenization might induce ‘trophic homogenization’ in only certain
389 circumstances.

390

391 **ACKNOWLEDGEMENTS**

392 EDB is part of the "Laboratoire d'Excellence" (LABEX) entitled TULIP (ANR-10-LABX-41).
393 Funding support was provided by the French National Agency for Water and Aquatic
394 Environment (Onema) (Convention Onema-EDB 2011-2013) and an “ERG Marie Curie”
395 grant (PERG08-GA-2010- 276969). We graciously acknowledge all the authors of the
396 source data that responded to our inquiry for details associated with their field sampling
397 and data analysis.

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519 **SUPPLIMENTARY MATERIAL TITLES**

520 **Appendix S1** A list of the 12 functional traits used to characterize the functional diversity
521 of each species.

522 **Appendix S2** Map of North America displaying the location of each fish community
523 included in the analyses.

524 **Appendix S3** A conceptual framework displaying the 'centroid' trophic beta diversity
525 approach.

526 **Appendix S4** Results from the multiple regression on distance matrices (MRM) analyses
527 using a reduced total of 7 traits.

528

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600 **TABLES**

601 **Table 1** Results of the linear mixed models used to test for the relationships between
 602 taxonomic, functional and trophic alpha diversity for communities in lentic (n = 34) and
 603 lotic (n = 29) ecosystems in North America. Given are the model degrees of freedom (df),
 604 model estimates with standard errors (SE), and *p*-values (*p*).

Taxonomic vs Functional Alpha Diversity					
<i>Parameter</i>	<i>Source of variation</i>	<i>Ecosystem type</i>	<i>df</i>	<i>Estimate (SE)</i>	<i>p-value</i>
FunD	TaxD	Lentic	19	0.07 (0.01)	<0.001
	Intercept	Lentic	19	0.65 (0.11)	<0.001
FunD	TaxD	Lotic	20	0.11 (0.01)	<0.001
	Intercept	Lotic	20	0.27 (0.11)	0.024
Functional vs Trophic Alpha Diversity					
<i>Parameter</i>	<i>Source of variation</i>	<i>Ecosystem type</i>	<i>df</i>	<i>Estimate (SE)</i>	<i>p-value</i>
TroD	FunD	Lentic	19	0.10 (0.04)	<0.039
	Intercept	Lentic	19	1.80 (0.23)	<0.001
TroD	FunD	Lotic	20	0.08 (0.04)	0.064
	Intercept	Lotic	20	1.40 (0.21)	<0.001

605 TaxD, Taxonomic alpha diversity; FunD, Functional alpha diversity; TroD, Trophic alpha
 606 diversity; SE, Standard error
 607

608 **Table 2** Summary table of the taxonomic, functional, and trophic beta diversity of fish
 609 community pairs with the turnover and nestedness-resultant components of each type of
 610 beta diversity in lentic (n = 560 pairs) and lotic (n = 399 pairs) ecosystems.

	<i>Ecosystem type</i>	<i>Taxonomic</i>	<i>Functional</i>	<i>Trophic</i>
Beta diversity	Lentic	0.85 ± 0.21 (0-1)	0.84 ± 0.16 (0-1)	0.61 ± 0.15 (0.22-0.90)
	Lotic	0.86 ± 0.22 (0-1)	0.85 ± 0.21 (0-1)	0.66 ± 0.14 (0.27-0.95)
Turnover	Lentic	0.81 ± 0.26 (0-1)	0.61 ± 0.32 (0-1)	0.29 ± 0.21 (0-0.89)
	Lotic	0.84 ± 0.25 (0-1)	0.60 ± 0.32 (0-1)	0.26 ± 0.21 (0-0.75)
Nestedness-resultant	Lentic	0.04 ± 0.07 (0-0.42)	0.23 ± 0.22 (0-0.97)	0.32 ± 0.25 (0-0.89)
	Lotic	0.02 ± 0.06 (0-0.38)	0.25 ± 0.27 (0-0.86)	0.39 ± 0.27 (0.01-0.95)

611 The mean ± standard deviation and range (in parentheses) are presented.

612 **FIGURE LEGEND**

613 **Fig. 1** Relationships between communities' (a) taxonomic and functional and (b) functional
614 and trophic alpha diversity in lentic (n=34) and lotic (n=29) ecosystems. Solid lines show
615 the best-fitting linear mixed regressions after Box-Cox transformations of dependent
616 variables. See Table 1 for the linear mixed model results (estimates and p-values)
617 associated with the relationships between alpha diversity types. The functional diversity
618 was transformed with $\lambda=0.22$ (*) and trophic diversity was log transformed (**).

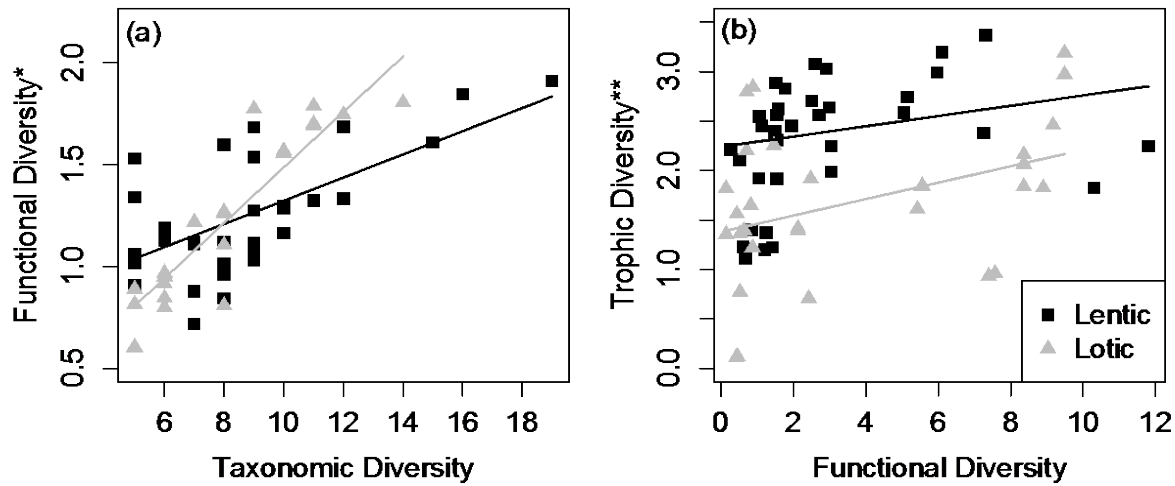
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620 **Fig. 2** Relationships between fish communities' (a) taxonomic and functional and (b)
621 functional and trophic beta diversity within lentic and lotic ecosystems. See the results
622 associated with the multiple regression on distance matrices (MRM) for the statistical
623 significance of the beta diversity relationships represented here.

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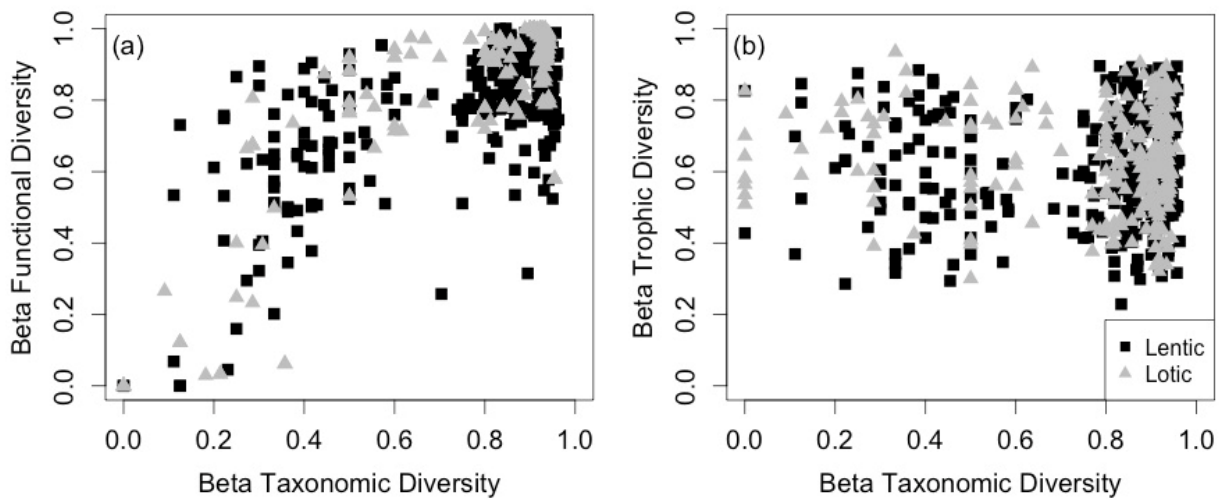
625 FIGURES

626 Fig. 1



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628 **Fig. 2**



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632 **SUPPORTING INFORMATION**

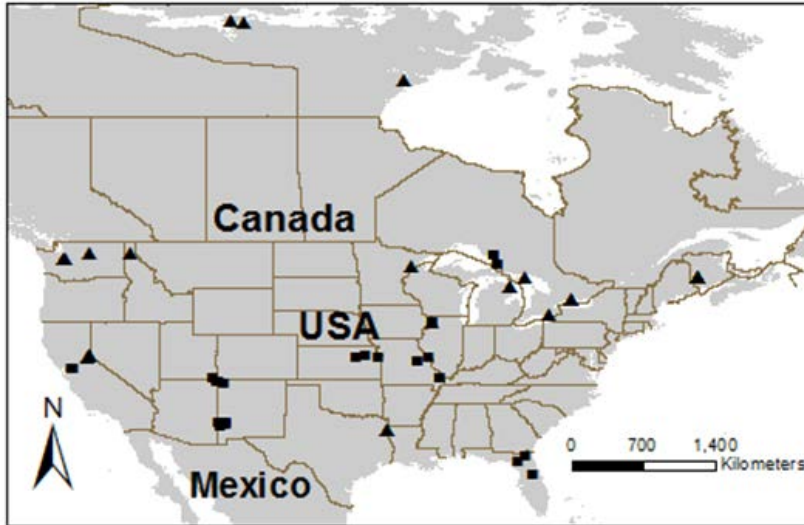
633 **Appendix S1** List of the 12 functional traits used to characterize the functional diversity of
 634 each species with the loadings for the first three principal coordinate axes (PCs); the axes
 635 utilized to calculate the functional diversity of each fish community.

<i>Category</i>	<i>Trait</i>	<i>Description and (or) units</i>	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>
Behavior	Substrate preference	Vegetation, mud-silt-sand, cobble-boulder, or generalist.	-0.187	0.849	0.130
	Fluvial dependence	Slow, moderate, or fast current velocity.	0.411	-0.984	0.030
	Vertical position	Benthic, surface and water column, or generalist.	0.570	1.966	0.055
	Potandromous	Requiring movement through fresh water systems to complete their life cycle (binary).	1.528	-0.018	0.621
Life history	Longevity	Maximum potential life span (years)	1.006	-0.328	-0.092
	Age at maturation	Age at maturation (years)	1.506	-0.415	-0.489
	Fecundity	Total number of eggs or offspring per breeding season	0.536	0.061	-0.420
	Primary spawning season	Fall (Sept-Nov), winter (Dec-Feb), spring (March-May), summer (June-Aug).	1.016	0.324	0.089
	Reproductive guild	Non-guarders (open substratum), non-guarders (brood hiders), guardians (substratum choosers), guardians (nest spawners), substratum indifferent.	-1.260	0.848	0.551
Morphology	Maximum total body length	Maximum total body length (cm)	1.444	0.004	-0.092
Trophic	Trophic breadth	Count of encompassing categories (herbivore, planktivore, invertivore, piscivore, and detritivore).	-0.175	0.407	-1.902
	Trophic guild	Herbivore, plankton-invertivore, invertivore, invertivore-piscivore, piscivore, or generalist.	0.205	0.310	-1.915

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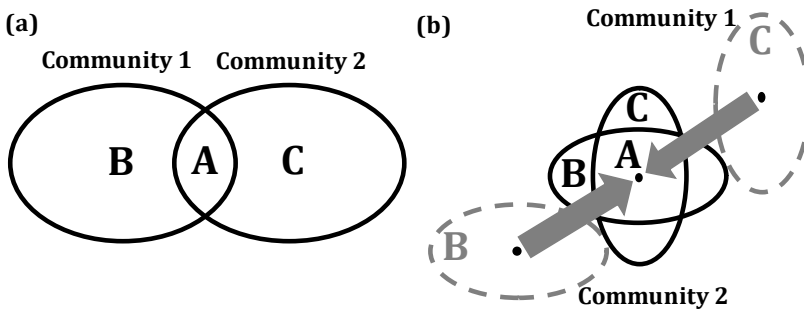
638 **Appendix S2** Map of North America displaying the location of each lentic (n = 34; ■) and
639 lotic (n = 29; ▲) community included in our analysis. Study references for each community
640 are listed below.



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643 **Appendix S3** Conceptual framework displaying a (a) classical Venn diagram illustrating
644 the beta diversity for two communities. Beta diversity identifies, in the case of trophic
645 diversity, the change in ‘trophic space’ occupied by two communities. In each model, part B
646 and part C identifies unique trophic area occupied by each community and part A identifies
647 shared trophic area occupied by both communities. (b) In the ‘centroid’ trophic beta
648 diversity approach, the convex hull centroids of the two communities are aligned (Schmidt
649 *et al.* 2011).

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657 **Appendix S4** After reducing the total number of traits in our analyses down to 7 behavior,
658 morphological, and trophic traits (see Appendix S1), lentic communities' functional beta
659 diversity retained a weak correlation with trophic beta diversity using MRM ($R^2 = 0.143$, p
660 < 0.01) with greater variation exclusively explained by the functional predictor ($R^2 = 0.122$)
661 than geographic space ($R^2 = 0.010$). Similarly, lotic communities' functional beta diversity
662 had a weak correlation with trophic beta diversity ($R^2 = 0.038$, $p < 0.02$) with low variation
663 explained by both geographic space ($R^2 = 0.003$) and the functional predictor ($R^2 = 0.034$).

664

665