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

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

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Running title: Functional vs. trophic diversity similarity

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ABSTRACT

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

2. Location North America

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

4. Results We found that communities' functional diversity increased as taxonomic diversity increased. Similarly, communities' trophic diversity increased as functional diversity increased. The pairwise taxonomic and functional similarity of communities were also positively associated but there was a weak relationship between communities' functional and trophic similarities.

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

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

INTRODUCTION

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

Recent studies have hypothesized that communities' trophic structures may be more closely linked to communities' functional diversity than their taxonomic diversity (Petchey & Gaston, 2006). This is because communities' functional traits are reflections of the biological, ecological and physiological constraints made in response to the temporal and spatial variations in environmental conditions, competition for resources, and predation (i.e. the functional niche; Winemiller, 2005). While previous studies examining various aspects of communities' functional diversity have assisted with providing mechanistic links between species compositions and the critical factors that influence specific systems (e.g. Poff, 1997; Pool *et al.*, 2010; Suding *et al.*, 2008), our ability to predict the relationship between a community's functional composition and its trophic structure remains largely untested.

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

In the present study, we aimed to untangle the complex relationships between taxonomic, functional, and trophic diversity using North American freshwater fish communities as model organisms. It is informative to study fish communities and their trophic characteristics because they are documented to influence important ecosystem processes associated with nutrient cycling (e.g. Vanni, 2002) and primary productivity (e.g. Schindler *et al.*, 1997). Furthermore, fishes are suitable for our study because they are an incredibly diverse and multi-trophic group of aquatic species occupying a wide array of trophic roles within food webs ranging from strictly herbivorous grazers to apex predators. First, we assessed the relationship between taxonomic, functional, and trophic diversity (defined here as niche size) within communities (i.e. alpha diversity approach). We predicted that individual community's taxonomic and functional diversity would positively correlate along with their functional and trophic diversity. Second, we investigated the pairwise similarity of communities (i.e. beta diversity approach) and predicted that communities' taxonomic similarity would positively correlate with communities' functional similarity along with their functional and trophic similarity. These predictions are based on niche partitioning theory (McKane *et al*., 2002) predicting that, as competition for resources between species within a community increases, species tend to have a more diverse array of biological and ecological traits, which in turn, results in a wider spectrum of resource use and a larger trophic niche. Here, lentic and lotic freshwater ecosystems were tested independently to study the association between community composition and trophic structure within and between ecosystems at the continental scale.

METHODS

Community selection

Candidate fish communities were identified using a multi-tiered data collection approach utilizing primary scientific articles, comprehensive texts of regional fish faunas, university reports, and online databases. The search was restricted to North America because a wealth of studies containing functional and trophic (i.e. stable isotopes) data on freshwater fishes are available for this region (Cucherousset *et al.*, 2012; Frimpong & Angermeier, 2012). First, we identified 58 studies that provided averaged species stable isotope values (δ^{13}C and δ^{15}N) in 176 fish communities. In some studies, several communities were identified in the same ecosystem but were designated as separate fish communities because sampling events varied spatially (i.e. sampling different areas along a drainage) or temporally (i.e. sampling an area during different years). Second, data for 12 biological and ecological traits (i.e. behavioural, life history, morphological, and diet) were collected to characterize the functional attributes of the species within each community (Frimpong & Angermeier, 2012; Froese & Pauly, 2012; Appendix S1 in Supporting Information). These attributes were selected because they characterize the main dimensions of species ecological niches and are commonly used in fish functional diversity studies (Winemiller & Rose, 1992; Olden *et al*., 2008). If greater than two trait values were unknown for a species it was excluded and subsequently, every candidate community containing that species was removed from the database. Third, in an attempt to include only communities that had been comprehensively sampled (i.e. avoiding studies targeting specific species), a minimum richness threshold criterion of five species was set for inclusion in the database. To validate this multi-tiered approach, the corresponding authors for each study were contacted to determine if all the fish species collected during their field sampling were analyzed for stable isotopes. The authors (16 of the 18 who responded) indicated that every species collected in sufficient numbers (i.e. enough individuals to estimate a realistic average of stable isotope values; $n \geq 5$) was analyzed for stable isotopes, demonstrating our data can be considered an accurate estimation of the fish communities' taxonomic, functional and trophic diversity. Certainly, rare species may not have been identified in some of our source studies because they are challenging to capture in sufficient numbers to appropriately estimate their stable isotope values. In communities that had rare species with unique trait profiles (i.e. top predators or detritivores) differing from more abundant species, the diversity of those fish communities may have been underrepresented.

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

Data analyses

Taxonomic diversity

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

Functional diversity

For most species, functional trait values were assigned based on research conducted in North America capturing the natural variation for each species in this region. Whenever possible, continuous trait values were used (e.g. body length, fecundity) but some traits required the use of discrete trait categories (e.g. reproductive guild, primary spawning season). In a few instances, ≤ 2 trait values were unknown (4 of 109 species) and were treated as missing values in the subsequent analyses. The '*functional diversity'* of each community was calculated by standardizing trait values and then creating a dissimilarity matrix using Gower's distance, a metric able to accommodate nominal, ordinal, continuous, and missing data (Pavoine *et al*., 2009). Then, a principal coordinate analysis (PCoA) on this functional distance matrix was computed to construct a multidimensional functional space (Villéger *et al*., 2008). The first three principal coordinate axes explained a significant proportion (75.5 %) of the total variation in trait matrix (i.e. 29.0 %, 26.1 %, and 20.4 %, respectively) based on the randomized broken-stick method and α = 0.05 (Jackson, 1993). Those trait-based principal coordinate scores, along with the species-by-community matrix, were then used to measure each community's functional diversity calculated as the 'minimum convex hull volume' using the Quickhull algorithm (Villéger *et al*., 2008). More simply, the functional diversity of each community was quantified as the volume created by a group of trait-based points, each representing a fish species.

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

Trophic diversity

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

Statistical analyses

Community composition

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

Community similarity

The pairwise taxonomic beta diversity of communities was measured using Jaccard's dissimilarity index, i.e. percentage of species not shared by communities compared to the total number of species. To quantify functional beta diversity, convex hulls for each community were used to measure the pairwise functional dissimilarity between communities likewise using the Jaccard's index (Villéger *et al*., 2008). In an effort to use an approach analogous to our taxonomic and functional analyses, the trophic beta diversity of communities was quantified using a stable isotope 'centroid' approach that aligns the stable isotope convex hull centroids for each community pairing (Schmidt *et al*., 2011; Appendix S3 in Supporting Information). The centroid of each community was calculated as the mean $\delta^{13}C$ and $\delta^{15}N$ species value (Schmidt *et al*., 2011). This approach maximizes the trophic hull overlap between communities as they share the same centroid values, providing a conservative assessment of trophic niche dissimilarity.

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

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

RESULTS

Community composition

The taxonomic diversity of fish communities ranged from 5 to 19 species in lentic ecosystems and from 5 to 14 species in lotic ecosystems. The functional diversity of fish communities was strongly influenced by species behavioural, life history, and morphological traits, positively contributing to the first principal coordinate axes scores with minimal contributions of traits linked to diet (Appendix S1). As predicted, the functional diversity of fish communities significantly increased as taxonomic diversity increased irrespective of the ecosystem type (lentic: $p < 0.001$ and lotic: $p < 0.001$; Table 1; Fig. 1a). Communities' functional and trophic diversity were significantly and positively correlated in lentic ecosystems ($p = 0.039$; Table 1; Fig. 1b) and were marginally and positively correlated in lotic ecosystems ($p = 0.064$; Table 1; Fig. 1b).

Community similarity

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

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

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

DISCUSSION

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

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

The weak association between communities' functional and trophic similarity may have also occurred because static trait values were used to quantify functional diversity. This approach, commonly used in ecology, fails to account for species variance in the expression of traits (i.e. intra- and inter- population trait plasticity) associated with biotic or abiotic factors within diverse environments. In contrast, stable isotope analyses represent an integrative approach that accounts for the direct and indirect interactions occurring in a community (Layman *et al*., 2012, Cucherousset *et al*., 2012) and is therefore highly sensitive to specific interactions between species. Accounting for traits intraspecific variation along environmental gradients instead of using species mean trait values could more clearly identify the mechanisms by which communities' functional diversity influences trophic interactions (Ackerly & Cornwell, 2007). Furthermore, associations between communities' functional and trophic similarity may have been difficult to assess because functionally specialized species can exhibit behavioural opportunism within some systems to utilize available resources (Bellwood *et al*., 2006). Functionally generalized species may alternatively exhibit focused or specialized feeding behaviour obscuring a clear association between communities' functional and trophic diversity (Bellwood *et al*., 2006). Such functional plasticity is known to occur within fish species in association with their life-history stage and dynamic factors such as local environmental variation (Simpson *et al*., 2010; Zhao *et al*., 2014). A significant forthcoming challenge in ecology will be to properly incorporate this intraspecific and interspecific trait variation into the study of multiple animal groups (i.e. aquatic insects, reptiles, and fish) at the population and community levels.

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

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

There is broad consensus that increased taxonomic and functional diversity within communities assists with maintaining ecosystems stability and resilience (Hooper *et al*., 2005) but it has been challenging to identify how variation in individual communities' composition is linked to the functionality of those ecosystems. Our results indicate that exploring how communities' trophic structure is linked to ecosystem functioning may be a particularly informative thread of research to pursue given the variation in trophic structure we observed. Indeed, Poisot *et al*. (2013) found that the structure of trophic interactions within food webs (i.e. trophic complementarity) effectively predicted ecosystem functioning in complex modeled communities. Additionally, with the preservation of ecosystem processes becoming an increasingly emphasized conservation goal, it should be recognized that systems with similar taxonomic or functional profiles might have unique trophic structures potentially driving system specific functionality. As additional work is done to study compositional changes over time beyond characterizing fish communities, analyses should also assess if the trophic structure of communities is becoming more similar given that our results suggest that processes such as taxonomic or functional homogenization might induce ‘trophic homogenization’ in only certain circumstances.

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SUPPLIMENTARY MATERIAL TITLES

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

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

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

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

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TABLES

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

Taxonomic vs Functional Alpha Diversity

Parameter	*Source of variation*	*Ecosystem type*	*df*	*Estimate (SE)*	*p-value*
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

Parameter	*Source of variation*	*Ecosystem type*	*df*	*Estimate (SE)*	*p-value*
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

TaxD, Taxonomic alpha diversity: FunD, Functional alpha diversity; TroD, Trophic alpha diversity; SE, Standard error

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

	Ecosystem type	*Taxonomic*	*Functional*	*Trophic*
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)

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

FIGURE LEGEND

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

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

FIGURES

Fig. 1

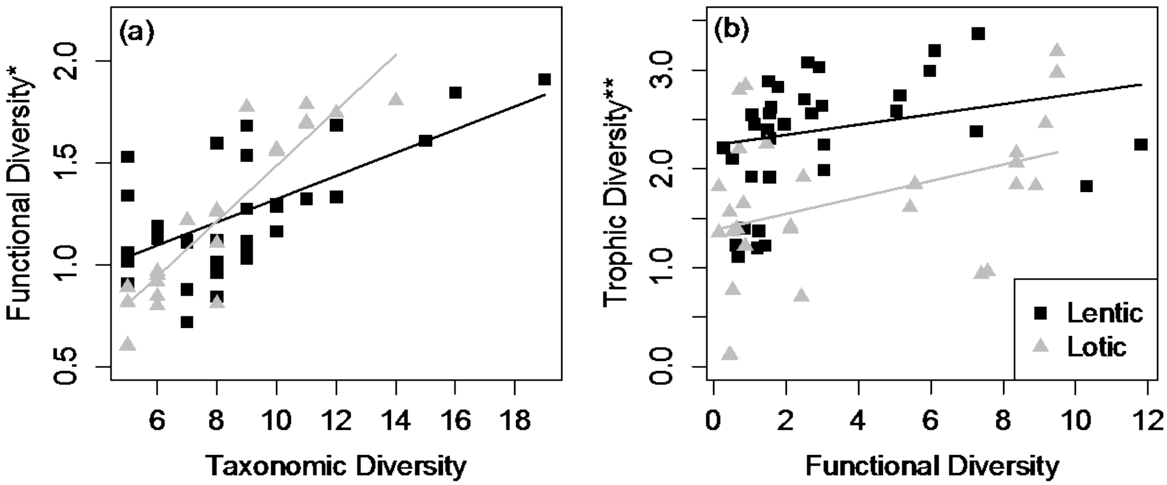
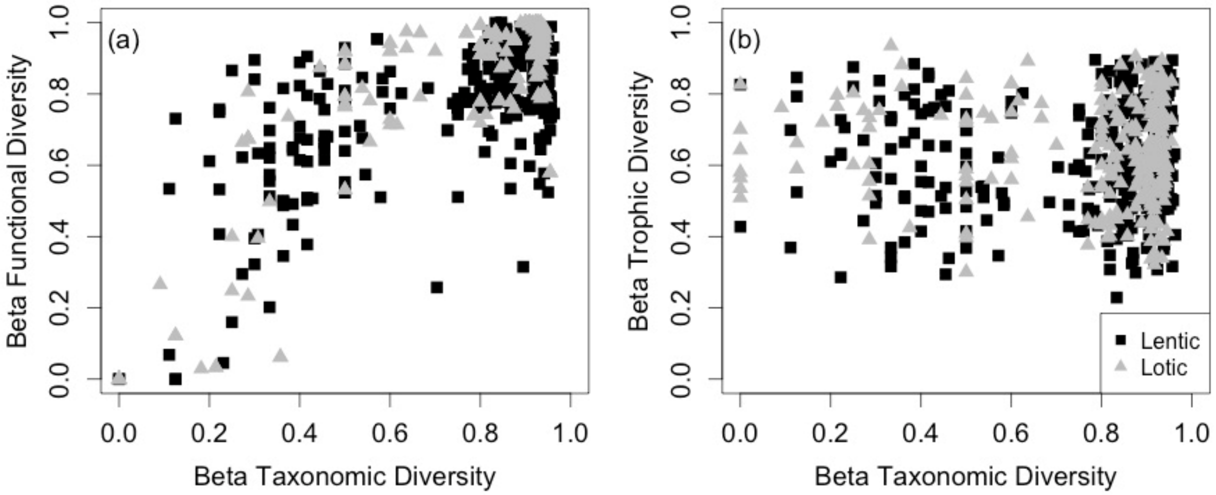


Fig. 2

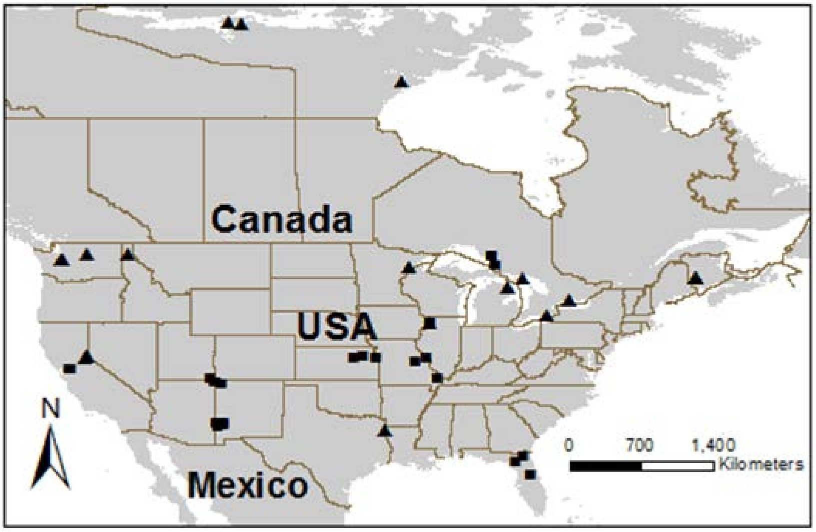

(a)
Beta Functional Diversity
Beta Taxonomic Diversity
0.0
0.2
0.4
0.6
0.8
1.0
(b)
Beta Trophic Diversity
Beta Taxonomic Diversity
■ Lentic
▲ Lotic

SUPPORTING INFORMATION

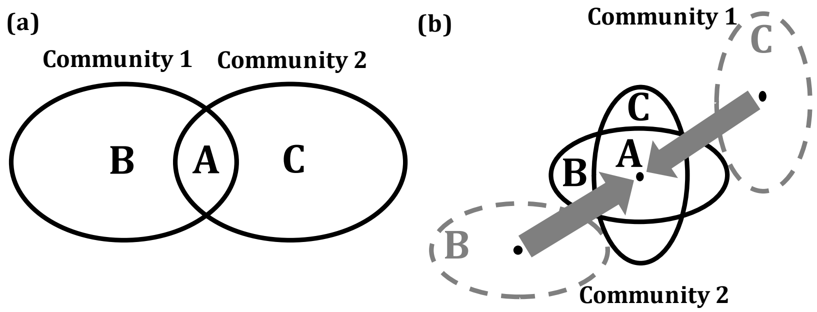
Appendix S1 List of the 12 functional traits used to characterize the functional diversity of each species with the loadings for the first three principal coordinate axes (PCs); the axes utilized to calculate the functional diversity of each fish community.

Category	*Trait*	*Description and (or) units*	*PC1*	*PC2*	*PC3*
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), guarders (substratum choosers), guarders (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, planktavore, invertivore, picivore, 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

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



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



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