RESEARCH PAPER

Increased taxonomic and functional similarity does not increase the trophic similarity of communities

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ABSTRACT

Aim Despite a long-standing research interest in the association between the bio-diversity (i.e. taxonomic and functional composition) and trophic structure of communities, 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 the trophic niche of those communities. The aim of our study is to test this prediction.

Location North America.

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, using linear mixed models (i.e. an alpha-diversity approach), we tested whether the taxonomic diversity of communities was positively associated with their functional diversity and if their functional diversity was positively associated with their trophic diversity. Second, we assessed the taxonomic, functional and trophic similarity of communities using multiple regression on distance matrices (MRM) and their respective 'turnover' and 'nestedness-resultant' components to test if the taxonomic similarity of communities was positively correlated with their functional similarity and if their functional similarity was positively associated with their trophic similarity (i.e. a beta-diversity approach).

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

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 for a better understanding of how future species loss and species introductions will affect food web structure and ecosystem functioning.

Keywords

Alpha diversity, beta diversity, compositional similarity, functional diversity, trophic diversity.

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INTRODUCTION

A time-integrated assessment of species relationships and energy flow within ecosystems can be quantified using stable isotopes to identify the ecological scaffolding that forms the trophic structure of communities (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 the structure of food webs is linked to the functioning and stability of ecosystems (Thompson *et al.*, 2012). Despite these advances, substantial gaps remain in our knowledge of community assembly with regard to how a community's taxonomic and functional composition is linked to its trophic architecture. For example, the extent to which 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 now occurring at a global scale it is therefore critical to improve our theoretical and empirical understanding of the relationships between the taxonomic, functional and trophic diversity of communities.

Recent studies have hypothesized that the trophic structure of communities may be more closely linked to their functional diversity than their taxonomic diversity (Petchey & Gaston, 2006). This is because the functional traits of communities are reflections of the biological, ecological and physiological constraints resulting from 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 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 the functional composition of a community and its trophic structure remains largely untested.

Studies of trophic ecology typically investigate the trophic diversity of individual communities (i.e. an 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. a beta-diversity approach), as is commonly done in studies of taxonomic and functional diversity (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 whether there are reoccurring trophic interactions leading to a similar trophic structure associated with communities that contain 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. an alpha-diversity approach). We predicted that the taxonomic and functional diversity of individual communities would be positively correlated with their functional and trophic diversity. Second, we investigated the pairwise similarity of communities (i.e. a beta-diversity approach) and predicted that the taxonomic similarity of communities would be positively correlated with their functional similarity along with their functional and trophic similarity. These predictions are based on niche partitioning theory (McKane *et al.*, 2002). This theory predicts 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 a continental scale.

METHODS

Community selection

Candidate fish communities were identified by 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 stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) for species 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. different areas were sampled along a drainage) or temporally (i.e. areas were sampled during different years). Second, data for 12 biological and ecological traits (i.e. behavioural, life-history, morphological and dietary traits) 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 functional diversity studies in fish (Winemiller & Rose, 1992; Olden *et al.*, 2008). If more 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 that targeted specific species), a minimum richness threshold criterion of five species was set for inclusion in the database. To validate this multitiered approach, the corresponding authors for each study were contacted to determine if all the fish species collected during their field sampling were analysed 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 analysed for stable isotopes, demonstrating that our data can be considered an accurate estimation of the taxonomic, functional and trophic diversity of fish communities. 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) that differed 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 $n = 34$, 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). 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 one or two 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 the trait matrix (i.e. 29.0, 26.1 and 20.4%, respectively) based on the randomized broken-stick method and $\alpha = 0.05$ (Jackson, 1993). Those trait-based principal coordinate scores, along with the species-by-community matrix, were then used to measure the functional diversity of each community 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 used 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 one most analogous to our functional diversity approach. The convex hull quantified the minimum area encompassing the stable isotope values for species 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 & 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-

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. The model degrees of freedom (d.f.), model estimates with standard errors (SE) and P-values are given.

	Parameter	Source of variation	Ecosystem type	d.f.	Estimate (SE)	P-value
Taxonomic versus functional alpha diversity	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 versus trophic alpha diversity	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.

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 the Jaccard dissimilarity index, i.e. the percentage of species not shared by communities compared with 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 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). 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 used 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); 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 the taxonomic and functional beta diversity of communities as well as their functional and trophic beta diversity. Using this approach also permitted variance partitioning to be used to examine 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, making a positive contribution to the first principal coordinate axis scores with minimal contributions from 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 $P < 0.001$, lotic $P < 0.001$; Table 1, Fig. 1a). The functional and trophic diversity of communities 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

The taxonomic beta diversity of lentic communities was positively correlated with functional beta diversity using MRM
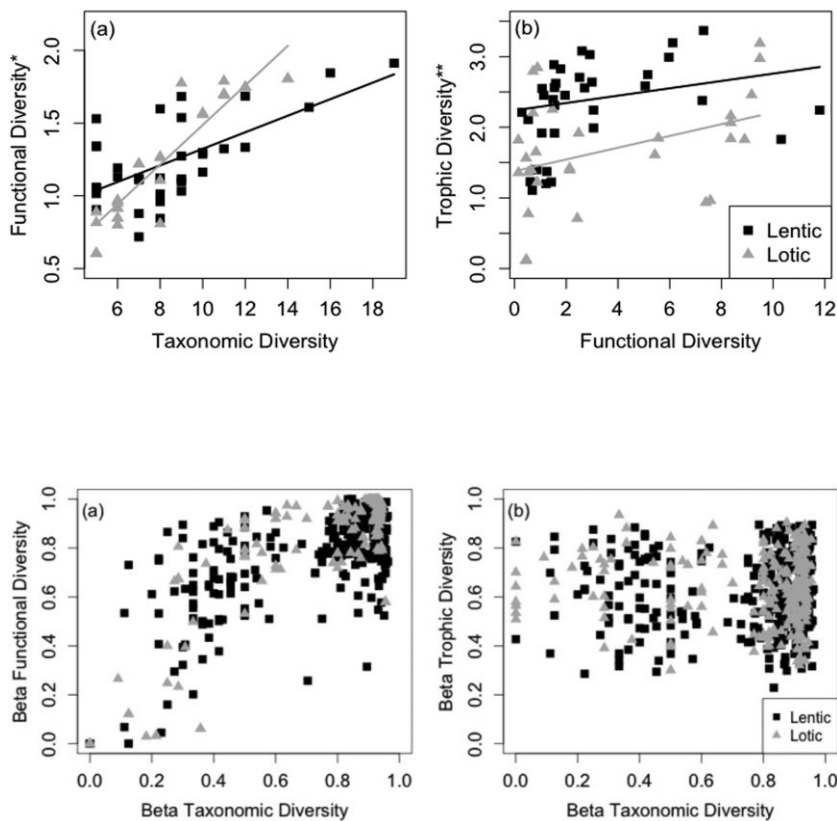
Figure 1 Relationships between (a) the taxonomic and functional diversity and (b) the functional and trophic alpha diversity for communities in lentic (*n* = 34) and lotic (*n* = 29) ecosystems. Solid lines show the best-fitting linear mixed regressions after Box–Cox transformations of dependent variables. 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 $\lambda = 0.22$ (*) and trophic diversity was log-transformed (**).

Figure 2 Relationships between (a) the taxonomic and functional diversity and (b) the functional and trophic beta diversity of fish communities 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.

($R^2 = 0.421$, $P < 0.01$) and variance partitioning, with greater variation uniquely explained by the taxonomic predictor ($R^2 = 0.257$) rather than geographic space ($R^2 = 0.053$). Similarly, the taxonomic beta diversity of lotic communities positively correlated with functional beta diversity ($R^2 = 0.207$, $P < 0.01$) with greater variation being uniquely explained by the taxonomic predictor ($R^2 = 0.142$) rather 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, the functional beta diversity of lentic communities had a weak correlation with trophic beta diversity using MRM ($R^2 = 0.093$, $P < 0.01$) and variance partitioning with greater variation being uniquely explained by the functional predictor ($R^2 = 0.092$) rather than geographic space ($R^2 = 0.001$). The functional beta diversity of lotic communities similarly had a weak correlation with trophic beta diversity ($R^2 = 0.026$, $P < 0.01$) with low variation being uniquely explained by both the functional predictor ($R^2 = 0.010$) and geographic space ($R^2 = 0.011$). A weak correlation also existed between the functional and trophic beta diversity of communities 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 trophically similar (Fig. 2b).

Finally, the mean compositional dissimilarity of the taxonomic and functional diversity of communities was higher than that for their trophic diversity (Table 2). Variation within the taxonomic and functional diversity of communities was primarily driven by compositional turnover (Table 2). In contrast, variation within 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 the taxonomic and functional diversity of individual fish communities and their functional and trophic diversity within both lentic and lotic ecosystems. In contrast, while the pairwise taxonomic similarity of communities 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 similarity of community 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 community's trophic diversity being driven, to some extent, by the characteristics of species within that community but also by system-specific factors that influence the architecture of trophic interactions.

The idiosyncratic association between the functional and trophic diversity of communities may be attributable to the

Table 2 Summary table of the taxonomic, functional and trophic beta diversity of pairs of fish communities 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.

large contribution of behavioural and life-history traits to the calculation of the functional diversity of fish communities. While the incorporation of non-trophic traits to compute the functional diversity of communities is of unequivocal value when attempting to assess the complete ecological niche of a community, our results show 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 the functional profile of communities (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 from our analyses of life-history traits believed to make a poor contribution to defining the trophic structure of communities, the weak association between the functional and trophic similarity of communities remained. Ultimately, while the trait composition of a community mechanistically links those species to their environment, claims that alteration of the functional composition of a community will redefine its trophic structure may not consistently be substantiated.

The weak association between the functional and trophic similarity of communities may also have 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 interpopulation 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 (Cucherousset *et al.*, 2012; Layman *et al.*, 2012) and is therefore highly sensitive to specific interactions between species. Accounting for intraspecific variation of traits along environmental gradients instead of using species mean trait values could more clearly identify the mechanisms by which the functional diversity of communities influences trophic interactions (Ackerly & Cornwell, 2007). Furthermore, associations between the functional and trophic similarity of communities 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 the functional and trophic diversity of communities (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 intra- 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 also have 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 the introduction of non-native species (Cucherousset *et al.*, 2012). Additionally, the trophic structure of communities 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 of 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 colonization, introduction and extirpation) along with other site-specific factors may account for present-day discontinuities in pairwise comparisons of community trophic diversity.

As expected when working at a large macroecological scale (i.e. continental scale), the mean taxonomic, functional and trophic dissimilarity of communities was relatively high – principally associated with high turnover indicating minimal overlap in their taxonomic and functional compositions. Interestingly, even when the trophic beta diversity of communities was calculated by aligning their isotope centroids, the contribution of turnover to the total compositional dissimilarity between communities remained substantial, 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 in maintaining the stability and resilience of ecosystems (Hooper *et al.*, 2005), but it has been challenging to identify how variation in the composition of individual communities is linked to the functionality of those ecosystems. Our results indicate that exploring how the trophic structure of communities 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 modelled communities. Additionally, with the preservation of ecosystem processes becoming an increasingly important 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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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

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 analyses using a reduced total of seven traits.

BIOSKETCH

Thomas K. Pool is a post-doctoral research fellow in the laboratory 'Evolution et Diversité Biologique' (University of Toulouse, France). His research interests include studying the patterns and drivers of aquatic species diversity with a focus on how anthropogenic disturbances influence native species distributions. He is particularly interested in studying how non-native species can impact the persistence of threatened native species in lotic systems.

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