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Diversity and Distributions

BIODIVERSITY RESEARCH

Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities

Thomas K. Pool[1]*, Gaël Grenouillet[1] and Sébastien Villéger[2]

[1]*Laboratoire Évolution et Diversité Biologique (EDB), UPS, CNRS, UMR5174, Université de Toulouse, 31062 Toulouse, France,* [2]*Laboratoire Écologie des Systèmes Marins Côtiers (ECOSYM), CNRS, IRD, IFREMER, Université Montpellier 2, Place Eugène Bataillon, 34095 Montpellier, France*

ABSTRACT

Aim We examined the current biogeographical patterns of native fish communities throughout France, using a multifaceted taxonomic, functional and phylogenetic diversity approach. We then identified the contribution of individual species to each facet of watershed's native fish diversity.

Location Continental France.

Methods The taxonomic, functional and phylogenetic diversity of the fish communities were quantified at the watershed-scale (i.e. alpha diversity approach), and congruencies between diversity facets were assessed. Variation between watersheds was then quantified (i.e. beta diversity approach) using Jaccard's dissimilarity index for all three facets of diversity, and congruencies were assessed. We subsequently determined the relationship between alpha and beta diversity for each diversity facet. Lastly, the mean relative contribution of each species to watershed's alpha taxonomic, functional and phylogenetic diversity was quantified. The conservation status of each species was considered to determine if threatened and endangered species contributed more significantly to watershed alpha diversity than common species.

Results Across all watersheds, taxonomic, functional and phylogenetic diversity facets were found to be highly congruent using both the alpha and beta diversity approaches. In contrast, the relationship between the watersheds' alpha and beta diversity was primarily negative; watersheds with decreased beta diversity tended to have increased alpha diversity for all three facets. Individual species also rarely contributed prominently to more than one diversity facet, with conservation status insignificantly influencing species relative contributions.

Main conclusions We found that native fish diversity 'hotspots' exist in France; exhibited in our results by areas of high, overlapping taxonomic, functional and phylogenetic diversity. Consequently, conservation planning approaches supported by species-based metrics may concurrently target areas of increased ecological and evolutionary importance at the watershed-scale. Interestingly, a diverse mosaic of species accounted for the different facets of diversity, suggesting that future reductions in species richness could have differential effects on each watershed's diversity facets.

Correspondence: Thomas K. Pool, Laboratoire Évolution et Diversité Biologique (EDB), UPS, CNRS, UMR5174, Université de Toulouse, 31062 Toulouse, France. E-mail: thomas.pool@univ-tlse3.fr

INTRODUCTION

Since the pioneering research of Alfred Russel Wallace in the late 19th century, species-based metrics (i.e. taxonomic) have primarily been used to study the diversity and distributions of flora and fauna. However, in recent decades there has been a growing consensus amongst ecologists that studying patterns of species occurrence and abundance will not

sufficiently explain many ecological phenomena, including multispecies interactions, determinants of species' distributions or the development of community structure (Wellborn *et al.*, 1996). Ecosystem managers and conservationists have similarly begun to broaden their conservation objectives to include multiple facets of diversity and the preservation of ecosystem services (Naeem *et al.*, 2012), requiring a more comprehensive management approach. Towards this aim, multi-dimensional approaches to characterizing diversity within landscapes have begun to be used with increasing frequency and effectiveness (Cadotte, 2011).

In addition to examining spatiotemporal patterns of taxonomic diversity (TD), biodiversity studies are more commonly quantifying the trait and genetic variation occurring within populations, communities and ecosystems (Shackell *et al.*, 2005; Priest *et al.*, 2012). Characterizing functional diversity (FD) (i.e. the range of unique morphological, physiological or ecological traits in a community) can identify how communities are able to respond to human disturbances at both local and large scales, consequently impacting the ecosystem services those communities provide (Díaz & Cabido, 2001; Petchey & Gaston, 2002; Mouillot *et al.*, 2013). Alternatively, characterizing phylogenetic diversity (PD) (i.e. the evolutionary relationships among species) can identify a community's ability to generate new evolutionary solutions as environmental conditions change in the future (Faith, 1992) and can account for unmeasured FD (Cadotte, 2011). By adopting a multifaceted approach to studying biodiversity patterns, a unique perspective on the mechanisms influencing communities' composition, structure and dynamics can thus be gained (Díaz *et al.*, 2007; Graham & Fine, 2008; Cadotte *et al.*, 2009; Reiss *et al.*, 2009). Unfortunately, our understanding of how various facets of diversity are associated with each other and how individual species contribute to those diversity facets in complex multi-use landscapes is currently limited (but see Devictor *et al.*, 2010; Mouillot *et al.*, 2011). This knowledge-gap poses a significant restriction to ecologists' and managers' ability to map, and simultaneously protect, multiple facets of biodiversity in an increasingly impacted world (Pimm *et al.*, 1995; Vitousek *et al.*, 1997).

In addition to characterizing different facets of community diversity (i.e. alpha diversity), geographic variation across communities can be quantified, (i.e. beta diversity) identifying another vital aspect of biological complexity (Whittaker, 1960; Loreau, 2000; Crist & Veech, 2006). The beta diversity of communities identifies historical and current discontinuities associated with environmental characteristics, ecological interactions and biogeographic history (Hubbell, 2001; Condit *et al.*, 2002; Graham *et al.*, 2006). Furthermore, systematic conservation planning efforts are now incorporating beta diversity derived components to identify optimal areas for management activity (Bonn & Gaston, 2005). In this way, instead of exclusively focusing conservation efforts in areas with elevated local species richness (Reid, 1998), endemic species (van der Werff & Consiglio, 2004), or threatened species (Ricketts *et al.*, 2005), ecologists and managers are taking into account components such as complementarity (i.e. all the diversity for a given area; Fairbanks *et al.*, 2001). To expand on these types of conservation planning efforts, determining whether variation in communities' TD within landscapes corresponds with variation in their FD or PD is of both ecological and conservation interest.

The aim of our study is to examine current biogeographical patterns of native fishes within the major river basins of France. The region's freshwater fish have experienced significant declines in range and abundance, with 27% listed as threatened or vulnerable and 32% listed as data deficient (IUCN, 2012). To better understand the native fish communities of this region, we first quantified the broad-scale distribution of the alpha and beta TD, FD and PD facets for subbasins, hereafter called watersheds. Second, for each facet of diversity, we determined the association between individual watershed's alpha and beta diversity, thereby identifying the relationship between compositional richness and turnover. Third, we determined individual species contributions to the watershed's alpha TD, FD and PD, allowing us to identify the ecological and evolutionary importance of each species. We also assessed if species of conservation interest (i.e. threatened or endangered species) tended to contribute more significantly to communities' functional or PD than species without elevated conservation status. Such an approach can identify species with high conservation value for facets of biodiversity that are not traditionally prioritized for management.

METHODS

Study region and database

The study region encompasses approximately 550,000 km^2; the entirety of continental France (Fig. 1). The diverse landscapes of the region exhibit significant seasonal variation, including oceanic, continental and Mediterranean climate regimes. Flowing into the Atlantic Ocean and Mediterranean Sea, the region's major river basins include the Garonne, Escaut, Loire, Meuse, Rhin, Rhône and Seine. The region is divided into 187 watersheds, with an average 3069 km^2 per watershed (5th percentile = 1654 km^2 and 95th percentile = 5317 km^2). Watershed boundaries were delineated using a spatial hierarchy established by the French National Service for Water Data and Common Repositories Management, based on physical parameters (Sandre, 2013) creating units useful for local watershed management efforts. While watersheds typically included a range of stream orders and habitat types, the average watershed size is considered an effective scale to represent fish communities with relatively similar physiological tolerances and reproductive strategies (Higgins *et al.*, 2005; Sowa *et al.*, 2005).

Our study utilized a database compiled by the French National Agency for Water and Aquatic Environments, containing fish records collected using a standardized
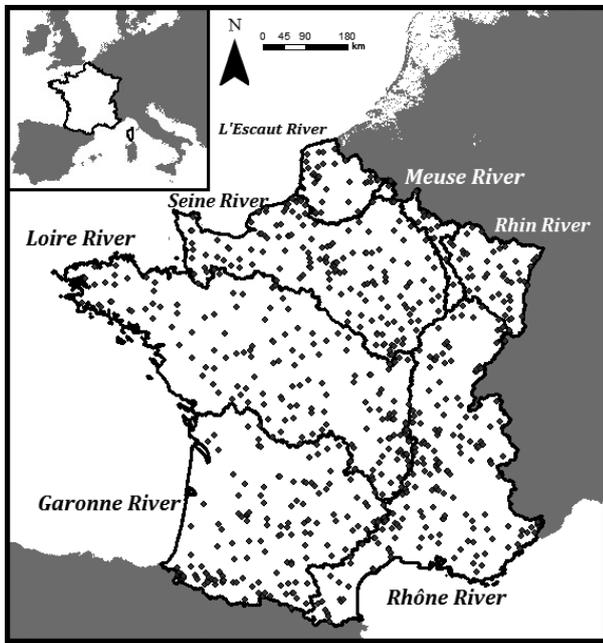
Figure 1 Geographic distribution of the seven major river basins in France. Sampling locations ($n = 765$) are represented as black dots throughout the study region.

electrofishing protocol dependent on river width and depth. Small streams were sampled by wading, mostly by two-pass removal and a complete exploration of the stream reach, while large rivers were sampled by boat and by fractional sampling strategies of the different types of mesohabitat (Poulet *et al.*, 2011). We used 10,545 individual fish presence records from 765 sites with each site being sampled at least three times between 2000 and 2010. To determine whether each site's fish community had been adequately sampled, three complementary species richness estimates were used relating species accumulation to the sampling effort at each site. We used Chao 1, first order jackknife and bootstrapping to determine the predicted maximum species richness value for each site (Chao, 1987; Colwell & Coddington, 1994). All the retained sites (Fig. 1) had an observed species richness that was >80% of the predicted maximum species richness by all three estimators (Pineda & Lobo, 2009). To identify fish community composition at the watershed-scale, species lists from the retained sites were aggregated by watershed ($n = 143$), with a mean of five sites per watershed. Simple linear regression was used to test whether the number of sites within each watershed unit was positively correlated with species richness. The results of this test revealed that the number of sites had a minimal influence on the watershed's species richness ($r^2 = 0.0442$; $P < 0.05$).

Taxonomic data

The alpha TD of each watershed was assessed as the native species richness of each fish community (i.e. the aggregated list of species from sites within a watershed). Species with less than five individual records across all sites were excluded from the analysis to minimize the influence of potentially erroneous species identifications. Marine species were excluded while diadromous and exclusively freshwater species were retained. Ultimately, 39 native species were included in all subsequent analyses (see Appendix Table S1 in the Supporting Information).

Functional data

The functional attributes of each species were characterized using ten complementary morphological, behavioural, trophic and life history traits (see Appendix Table S2). These traits were selected to reflect the diversity of fish strategies that exist within the study region. Additionally, these traits are commonly used in the fish functional literature, providing results that are comparable with other studies (Olden, 2006; Villéger *et al.*, 2013). Trait values were assigned using the primary literature, agency reports, and in consultation with regional experts.

A dissimilarity matrix based on all ten traits was constructed using Gower's coefficient, a metric able to accommodate nominal, ordinal, continuous and missing data (Pavoine *et al.*, 2009). Then, a principal coordinate analysis (PCoA; Villéger *et al.*, 2008) was computed to build a synthetic multidimensional functional space. The Euclidean distances between species in functional space obtained using PCoA were highly correlated with the functional distances computed on species traits using Gower's metric (Mantel test, $r^2 = 0.784$, $P < 0.001$) giving confidence that the summarized FD effectively captured the fish communities trait diversity. The alpha FD of each watershed was quantified as the volume of the convex hull filled by the fish species of each community in two-dimensional functional space using the values from the first two functional axes (Villéger *et al.*, 2008).

Phylogenetic data

A phylogeny was built using molecular data from native fish specimens collected throughout France. Phylogenetic relationships were inferred based on three mitochondrial genes (cytochrome *b*, cytochrome oxidase I and ribosomial 16S sub-unit; Grenouillet *et al.*, 2011). The Bayesian method was used under the TVM_I_G substitution model and we implemented the phylogeny estimation with MrBa-yes and paup software. The final evolutionary tree included 26 of the most common native species from the study region; accounting for 86.2% of total species occurrences in our dataset (i.e. a subset of the full 39 native species in the taxonomic and functional analyses because sequence data was not available for all species; Appendix Table S1). The alpha PD was then calculated as the sum of the phylogenetic tree branch lengths for the species in each watershed (Faith, 1992).

Statistical analysis

Dissimilarity in composition between two communities describes a fundamental pattern of change in diversity across space (Magurran, 2004). In this study, the pairwise beta TD of watersheds' fish communities was measured using Jaccard's dissimilarity index (Anderson *et al.*, 2011).

$$\beta\text{-diversity} = (B + C)/(A + B + C)$$

Part B and part C represent the number of species occurring exclusively in the first and second watersheds, with part A representing the species occurring in both watersheds (Fig. 2a). The total number of species in a pair of watersheds was represented by the sum of parts A, B, and C. The beta FD between watersheds was measured using a Jaccard-like index based on functional convex hull areas (Fig. 2b; Villéger *et al.*, 2011, 2013). Similarly, to measure watersheds beta PD (i.e. dissimilarity of the watersheds' phylogenetic tree branch lengths), we used the UniFrac index which is analogous to the Jaccard's dissimilarity index (Fig. 2c; Leprieur *et al.*, 2012). This index is a broad measure of phylogenetic dissimilarity capable of incorporating differences in evolutionary history between communities. For all the beta diversity analyses, index values ranged from 0 (i.e. two watersheds with identical compositions) to 1 (i.e. two watersheds with no shared elements of diversity).

The spatial congruence of watersheds with high alpha diversity was assessed as the amount of concordance between the top 10% of watersheds (i.e. highest diversity values) for all three facets of diversity. For example, the 14 watersheds with the highest alpha TD values (i.e. the top 10%) were compared to the 14 watersheds with the highest alpha FD values to determine how many watersheds were shared within both

(a) Taxonomic **(b)** Functional **(c)** Phylogenetic
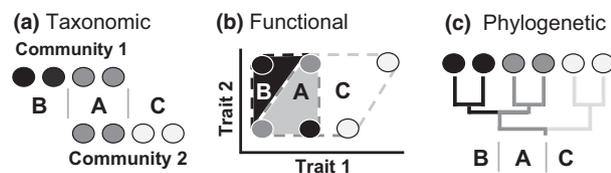
Figure 2 Conceptual framework displaying methods for calculating the taxonomic, functional and phylogenetic beta diversity between two communities. In each model, parts B and C identify unique diversity components within each community (i.e. black circles representing two species exclusively in community 1 and white circles representing two species exclusively in community 2) with part A identifying common diversity components in both communities (i.e. grey circles representing two shared species). (a) The classical representation for assessing taxonomic beta diversity based on the number of species unique or shared by two communities. (b) Two communities' functional convex hulls overlapping in functional space displaying unique (i.e. black and light) and shared (i.e. grey) hull space. (c) The combined phylogenetic tree displaying unique (i.e. black and light grey lines) and shared (i.e. grey lines) tree branch lengths for two communities.

groups. Subsequently, watersheds alpha diversity congruence was assessed at successive 10% intervals. Next, congruence between beta diversity results were assessed by comparing the mean TD, FD, and PD similarity of each watershed with all other watersheds. A randomization procedure was performed ($n = 999$ permutations) for both the alpha and beta diversity analyses to determine whether watershed congruence was greater than what would occur at random.

The relationships between watersheds' alpha and beta diversity were assessed for all three facets of diversity in order to explore the variation between local fish community composition and the remaining regional fish diversity. This provided insight regarding how fish diversity at the watershed-scale related to the mean similarity of all the other watersheds in the study region. Subsequently, we quantified the mean beta diversity 'turnover' component for watershed pairs. This component of diversity identifies the degree of species replacement between communities and provides essential insight because watersheds with high beta diversity values can have either high TD turnover (i.e. many species unique to each community) or low TD turnover (i.e. the species poor community hosts a subset of the diversity present in the species rich community; Baselga *et al.*, 2012). The turnover component was also identified for watersheds in the beta PD and beta FD, following the framework of Leprieur *et al.* (2012) and Villéger *et al.* (2013), respectively.

The contribution of particular species to the alpha diversity of watershed's was quantified by removing individual species from the data set, then recalculating the watersheds' TD, FD and PD and computing the difference in diversity value before and after removing each species. To assess the relative contribution of each species, we then identified the percent change in diversity for those communities exclusively within watersheds containing the species of interest. In this way, we determined the mean relative contribution of each species only when they occurred in a watershed, as opposed to the mean contribution of a species to all watersheds, which would include numerous zero delta values for watersheds where the species were absent. The IUCN conservation status of each species was then identified to determine whether species contribution to watersheds alpha diversity was associated with their conservation status (IUCN, 2012). Nemenyi–Damico–Wolfe–Dunn tests (Nemenyi, 1963) were used for all the pairwise comparisons of species' contributions within each conservation status category. This nonparametric Tukey-type, multiple comparison *post hoc* test is appropriate for group comparisons containing unequal sample sizes. All statistical analyses were conducted in R 2.15.1 (R Development Core Team, 2012).

RESULTS

Relationships between TD, FD, and PD

Watersheds' alpha TD, FD and PD represented on average 64.4%, 82.3% and 71.1%, respectively, of the total diversity

for each facet in our study region. Interestingly, watersheds' alpha TD, FD and PD co-varied, with the most diverse watersheds primarily occurring in the Seine, Rhône, and Loire River basins (Fig. 3a). Specifically, alpha TD was associated with watersheds' alpha FD and PD ($F_{1,141} = 292.9$; $P < 0.001$; $R^2 = 0.675$; $n = 143$; and $F_{1,141} = 1902.9$; $P < 0.001$; $R^2 = 0.931$; $n = 143$). Alpha FD was likewise associated with watersheds' alpha PD ($F_{1,141} = 285.4$; $P < 0.001$; $R^2 = 0.669$; $n = 143$). When the top 10% of each type of alpha diversity was identified within the watersheds, the highest congruence occurred between the TD and PD (78.5%; Fig. 3a). The lowest congruence occurred between the alpha FD and PD (57.1%; Fig. 3a). All alpha diversity combinations were found to be significantly more congruent than random expectations ($n = 999$ permutations; $P < 0.001$).

The watersheds' mean beta TD, FD and PD values were 0.48, 0.25 and 0.23 respectively. In contrast to the spatial pattern of the watersheds' alpha diversity, the greatest beta TD, FD and PD values were primarily concentrated in the upper Garonne, lower Rhône and lower Seine River basins (Fig. 3b). However, the patterns of beta TD, FD and PD relationships mirrored the alpha diversity results, with the watersheds' beta FD and beta PD associated with beta TD ($F_{1,141} = 395.3$; $P < 0.001$; $R^2 = 0.737$; $n = 143$; and $F_{1,141} = 1061.9$; $P < 0.001$; $R^2 = 0.882$; $n = 143$). Beta FD was likewise associated with the watersheds' beta PD ($F_{1,141} = 393.5$; $P < 0.001$; $R^2 = 0.736$; $n = 143$). The TD turnover of watersheds was also associated with FD and PD turnover ($F_{1,141} = 217.8$; $P < 0.001$; $R^2 = 0.607$; $n = 143$; and

$F_{1,141} = 465.2$; $P < 0.001$; $R^2 = 0.767$; $n = 143$) along with the watersheds' FD turnover predicting PD turnover ($F_{1,141} = 97.1$; $P < 0.001$; $R^2 = 0.407$; $n = 143$). Of the watersheds' top 10% of beta diversity, the highest congruence occurred between the TD and PD (57.2%; Fig. 3b), while the lowest congruence occurred between the FD and PD (21.4%; Fig. 3b). As with the alpha diversity combinations, all beta diversity combinations were significantly more congruent than random expectations ($n = 999$ permutations; $P < 0.001$).

Relationships between alpha and beta diversity

The relationship between the alpha and beta diversity (for TD, FD and PD respectively) of the watersheds was primarily negative, with a trend towards decreased beta diversity with increased alpha diversity (Fig. 4). Interestingly, the turnover component was not a substantial contributor to the beta diversity of most watersheds across all facets of diversity; particularly for watersheds that exhibited high beta diversity values (Fig. 4). The relationships between the alpha TD and both the beta TD and beta TD turnover were negative and significant ($Y = 1.02 - 0.0487x + 0.000956x^2$, d.f. = 2, $r^2 = 0.90$, $P < 0.001$; and $Y = 0.37 + 0.0010x + 0.000380x^2$, d.f. = 2, $r^2 = 0.56$, $P < 0.001$; Fig. 4a). Similar patterns were found in the relationships between the watersheds' alpha FD and both the beta FD and the beta FD turnover ($Y = 1.06 - 0.1704x + 0.007861x^2$, d.f. = 2, $r^2 = 0.94$, $P < 0.001$; and $Y = 0.01 + 0.0336x - 0.000485x^2$, d.f. = 2,
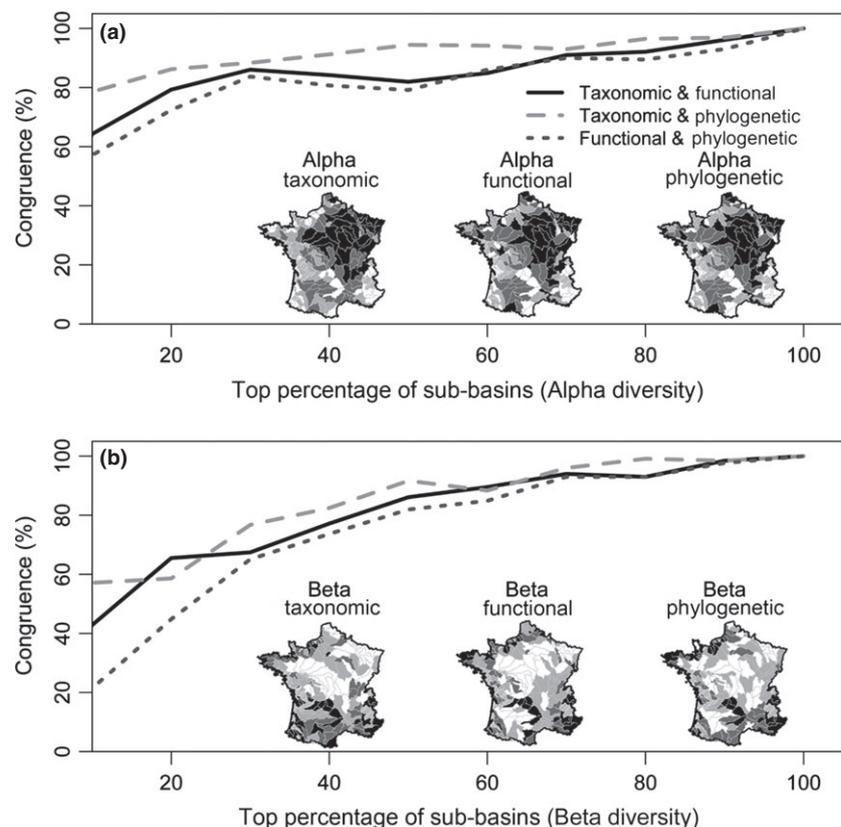
Figure 3 Congruence between watersheds' taxonomic, functional and phylogenetic diversity. (a) Alpha and (b) beta diversity congruence was assessed by comparing the spatial concordance between the top 10% of watersheds and then successively at 10% intervals. For example, watersheds with the highest 10% taxonomic alpha diversity values and watersheds with the highest 10% phylogenetic alpha diversity values had 78.5% congruence. Inset is the spatial distribution for the three different facets of fish diversity within watersheds represented with quartile intervals ranging from low values in white to high values in black. Hatched watersheds were not included in the analysis due to insufficient data for those areas.
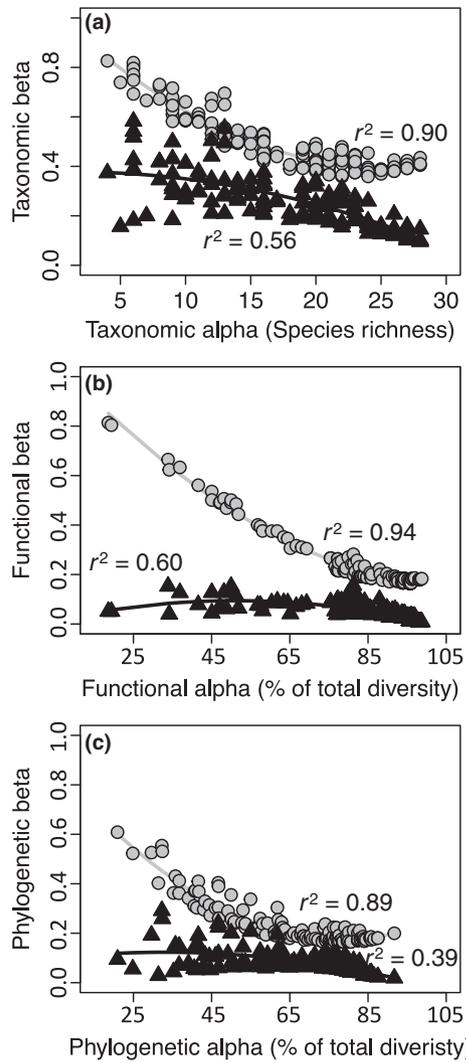
Figure 4 Relationship between watersheds alpha and beta diversity for (a) taxonomic, (b) functional and (c) phylogenetic diversities. Grey circles represent watersheds beta diversity and black triangles represent watersheds beta diversity turnover (i.e. a contributing component of watersheds total beta diversity).

Figure 5 The mean percentage contribution of individual species to all watersheds' alpha taxonomic, functional and phylogenetic diversity. Point size and colour represent the number of watershed occurrences (small-black are 1–25 watersheds; medium-grey are 25–100 watersheds; large-white are 100–126 watersheds) for each species [39 species in part (a) and 26 species in part (b and c)].

$r^2 = 0.60$, $P < 0.001$; Fig. 4b), as well as between the alpha PD with both the beta PD and beta PD turnover ($Y = 0.86 - 0.1856x + 0.012529x^2$, d.f. = 2, $r^2 = 0.89$, $P < 0.001$; and $Y = 0.09 + 0.0167x - 0.001220x^2$, d.f. = 2, $r^2 = 0.39$ $P < 0.001$; Fig. 4c).

Species contributions

Species varied in their relative contributions to the alpha TD, FD and PD of watersheds (Fig. 5a–c; see Appendix Table S1 for individual species contribution values). With the exception of *Phoxinus phoxinus* (Eurasian minnow) prominently contributing to all three facets of alpha diversity, most species contributed considerably to only one or two facets of diversity. Finally, when species' contributions to each watershed's alpha TD, FD and PD were separated by

conservation status, there were no significant differences (Nemenyi–Damico–Wolfe–Dunn test, $P > 0.05$) in the median contribution between status categories (see Appendix Fig. S1).

DISCUSSION

Our study explored patterns of freshwater fish community composition throughout France finding that watersheds' alpha TD, FD and PD facets were highly congruent. Northern portions of the region's largest river basins (i.e. Loire, Seine and Rhône rivers) tended to have the most diverse fish communities; in-step with the North to South colonization of species from the Danube River Basin refuge following the

last glaciation event (Reyjol *et al.*, 2007). Similarly, Strecker *et al.* (2011) found 75% congruence between the TD, FD and PD of priority areas identified using distribution models for freshwater fishes in the Southwestern United States. In our study region, the high congruency of watersheds' alpha diversity facets occurred because a majority of watersheds contained high TD relative to the total number of fish species in the region, often comprised of a diverse group of species with large distributions. Consequently, at the relatively large watershed spatial scale, we contend that habitat heterogeneity was sufficient to support functionally and phylogenetically diverse pools of species in a majority of fish communities. However, the complex interaction between each watershed's habitat and their species composition also produced some areas of mismatch (i.e. Loire mid-basin and Garonne headwaters). The spatial mismatch of alpha diversity facets may have been driven by fish species divergently responding to environmental and/or disturbance gradients, thus influencing the patterns of FD and PD at the watershed-scale. In future studies, inclusion of additional fish traits associated with human impact and climatic change (i.e. sensitivity to water pollution, oxygenation, water temperature) could assist with defining the spatial influence of anthropogenic disturbance within landscapes, thus enhancing our understanding of differences between multifaceted diversity patterns. Nevertheless, the general congruence of watersheds' alpha diversity provides evidence that a multifaceted effort to conserve native fish communities' functional and evolutionary diversity may be possible by targeting taxonomic 'hotspots' of fish diversity.

Similar to the alpha diversity analysis, the compositional dissimilarity of watersheds was reasonably congruent between diversity facets with high beta diversity values in the Garonne and lower Rhône river basins. However, our results also indicate that all three facets of the watersheds' beta diversity were strongly driven by variation in the species richness between watersheds (i.e. nestedness) and, to a much lesser extent, the proportion of shared diversity (i.e. turnover). This suggests that species in 'low diversity' watersheds were also commonly represented in 'high diversity' watersheds. Leprieur *et al.* (2009) similarly found high compositional nestedness of native fishes at the major river basin scale within Europe. Furthermore, we found that watersheds with high beta diversity values tended to have relatively low species richness (i.e. alpha TD) and were composed primarily of common species and some moderately rare species. García *et al.* (2007) likewise found a negative relationship between the alpha and beta diversity of herpetofauna across latitudinal bands in Mexico's Pacific lowlands and adjacent interior valleys. The pattern of fish community assembly observed within the French rivers of our study may have been strongly influenced by the relatively large size of our watershed units. Our watersheds appear to have included enough habitat variability to simultaneously encompass, for example, both headwater and mid-altitude populations. Consequently, when quantifying variation between communities, the relative importance of

diversity nestedness is of critical importance for interpreting beta diversity outputs.

Negative associations between communities alpha and beta diversity can be driven by different factors at smaller spatial scales. For example, Finn & Poff (2011) found that headwater stream segments with few Chironomidae species and relatively low genetic diversity had high beta diversity values when compared to other stream segments within a 30-km^2 alpine area. In that study, species turnover appeared to account for the high beta diversity values, appropriately identifying areas of conservation and ecological importance. In a study exploring patterns of bird diversity within 2 km plots throughout France, Devictor *et al.* (2010) similarly found that plots with high beta TD, FD and PD were strongly associated with compositional turnover. In contrast, the comparatively large watershed units containing high beta diversity values utilized in our study poorly identified areas of conservation interest, particularly for the watersheds' FD and PD. Clearly, while identifying patterns of beta diversity can be useful to disentangle assembly rules, the utility of such an approach as a conservation metric may depend heavily on the scale of the analyses.

When species' relative contributions to the diversity of watersheds were assessed, individual species rarely contributed considerably to all three facets of watershed's alpha diversity. This suggests that while watersheds had principally congruent facets of diversity, the individual species' contributions to each facet of alpha diversity were more idiosyncratic. Interestingly, a central premise associated with the niche conservatism theory is that niche-related traits will remain similar through speciation events, resulting in closely related species having similar ancestral traits (Holt & Gaines, 1992). In contrast to this expectation, we found the relative contributions of individual species to watersheds' FD and PD were variable; suggesting that in any given watershed a species could have, for example, redundant traits with the existing community while representing a very unique portion of the communities' phylogenetic tree. Additionally, species of conservation interest did not collectively display higher species' contributions to any one facet of watersheds' alpha diversity than species not listed as endangered or threatened. More simply, species identified as having a high conservation status do not collectively represent particularly unique portions of watersheds' trait or genetic diversity within our study region. Nevertheless, the local extirpation of some specific species would result in substantial losses of particular diversity facets within the watersheds where those species occur. For example, the endangered *Misgurnus fossilis* (Weatherfish) is a substantial contributor to watersheds' FD, and the critically threatened *Anguilla anguilla* (European eel) is a substantial contributor to watersheds' PD. Effectively, our results indicate that a diverse array of threatened and common species must be maintained within watersheds to minimize losses to multiple aspects of the fish diversity in France.

Despite the recognized need to simultaneously protect multiple facets of diversity facilitating the maintenance of

both species and ecosystem functioning (Mace *et al.*, 2003; Knapp *et al.*, 2008), studies quantifying the spatial distribution of communities' TD, FD and PD have been equivocal. Limited resources and access to waterways (Nel *et al.*, 2009) also require that conservationists and wildlife managers focus their efforts on areas of high conservation value. Our study displays that, for freshwater fish throughout France, concentrating conservation effort into alpha TD hotspots may be an effective approach to identify watersheds that also contain diverse functional and evolutionary community compositions. However, we caution that complex interactions between diversity facets may occur across different spatial scales, a topic that should be further studied as conservation planning efforts begin to incorporate additional aspects of biodiversity. Furthermore, threats such as non-native species and climate change may impact how diversity facets are associated with each other and must be accounted for in future research.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix Table S1 Freshwater native fish with species % contribution to each diversity facet.

Appendix Table S2 Traits used to characterize the functional diversity of fish in our study.

Appendix Figure S1 Box plot of species contributions to watersheds alpha taxonomic, functional and phylogenetic diversity.

BIOSKETCHES

Thomas K. Pool is a Postdoctoral 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.

Gaël Grenouillet is an associate professor in the laboratory 'Evolution et Diversité Biologique' (University of Toulouse, France). He has experience in species distribution modelling and stream ecology, and his work mainly focuses on the potential impacts of climate change on fish assemblages.

Sébastien Villéger is a CNRS researcher working with the Université of Montpellier. His research activities focus on the functional ecology of communities in temperate and tropical ecosystems. He develops approaches based on morphological traits and multivariate indices and on fish functional roles, especially their contribution to nutrient cycles.

Author contributions: T.P., G.G. and S.V. conceived the manuscript objectives and analysed the data. The writing was led by T.P. and all authors contributed to the final manuscript.

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