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Continental-scale analysis of taxonomic and functional fish diversity in the Yangtze river

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Effective conservation of ecosystems requires deep knowledge concerning multiple aspects of biodiversity including alpha and beta components of species richness, taxonomic, and functional diversity, as well as their relationships. The taxonomic and functional α-diversity positively correlated to species richness and functional evolution exceeded taxonomic differentiation. We divided the Yangtze whole basin into 56 units, and then the information on fish composition and their distribution in each unit was revised. Results showed that the fish diversity was strongly driven by variation in the species turnover between watersheds with the geological environmental heterogeneity, while the TD and FD variation could be attributed to species nestedness, as taxonomic category or functional trait of species in one unit was a subset of that in other units. The high β-diversity in SR was mostly composed of high turnover, while the high β-diversity of TD and FD resulted from high nestedness. Species functional differentiation was faster than taxonomic differentiation during the process of adoption to environment variation. An integrated index of multifaceted diversity considering the high species richness and important functional role suggested the headwater with abundant endemic species, the middle mainstream necessary to fish migration, and the lakes containing higher diverse species were primarily recommended for conservation.

1. Introduction

Biodiversity is the variation in living forms and can be measured through attributes that include species number and distribution, as well as taxonomic and functional diversity components. In addition, biodiversity is considered a major determinant of ecosystem productivity, stability, and biotic resistance, and an important proxy to conservation status and management decisions (Cleland, 2011; Midgley, 2012; Tilman et al., 2014). Under the pressures of climate change and intensive human activities, biodiversity is now facing unprecedented challenges. Obtaining a real effective resource for conservation especially by determining which are the best trade-offs between economic investment and ecological

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sustainability is extremely challenging and requires comprehensive knowledge concerning various facets of biodiversity (Olden et al., 2010; Mouillot et al., 2013; Arnan et al., 2015).

Species richness (i.e. the number of species per unit area) is the simplest measure of biodiversity. Considering taxonomic relatedness and genetic relationship among different organisms (Harper and Hawksworth, 1994; Devictor et al., 2010), taxonomic diversity was proposed (May 1990; Warwick and Clarke, 1995) to track the whole set of Linnaean classification of species in a sample (Margules and Pressey, 2000). Taxonomic diversity can vary positively or negatively according to SR (Heino, 2005). At large spatial scales (e.g., global) species richness patterns tend to coincide across taxonomic groups (Gaston, 2000); however, this perfect linear tendency is observed to change at smaller spatial scales (Maes et al., 2005). Ecologically, to better understand variation in species function in an ecosystem, functional diversity (FD) was suggested by explaining when, where, and how species can live and interact with each other, using complementarity or redundancy of their morphological, physiological, and ecological attributes (Díaz and Cabido, 2001; McGill et al., 2006; Cadotte et al., 2011). Covariance between FD and species richness helped to discern the dynamic utilization of food and living space and their impacts on ecosystem function. For example, an n-species assemblage could present high (composed of n different species) or low (n similar species) FD. Corresponding to different spatial scale, functional diversity shows a positive linear, nonlinear or asymptotic relationship with SR (Petchey and Gaston, 2002, 2006; Stuart-Smith et al., 2013).

Besides α-diversity (within assemblages) which characterizes different facets of community diversity, in a determined area, the β-diversity (among different assemblages) is generally considered by giving an insight of the changes in species composition by quantifying the geographic variation across communities (Whittaker, 1960). The α-diversity and the β-diversity should be free to vary independently from each other (Jost, 2007), and always showed negative associations between communities driven by different factors (Finn and Poff, 2011). The variation in β-diversity corresponding to α-diversity can clarify if the difference between two subsets is mainly due to SR or endemism. Generally, a subset with both high α- and β-diversity means that this area contains high species richness and most of them are endemic; in contrast, a subset with both low α- and β-diversity only possesses few common species, consequently losing the priority of being a conservative zone (Meynard et al., 2011; Arnan et al., 2015). The β-diversity can be further decomposed into two distinct components as species turnover and nestedness (Baselga et al., 2007). The turnover component reflects the substitution of species by others under environmental constraints (Qian et al., 2005; Baselga, 2009), while the nestedness component implies a non-stochastic process of assemblage decomposition and species loss (Gaston and Blackburn, 2000; Ulrich et al., 2009). Since fish distributional pattern can obviously be affected by species dispersion, habitat homogeneity, fragmentation, and heterogeneity (Gering and Crist, 2002; Olden and Poff, 2004), understanding the relationships among α- and β-diversity, as well as its components, is vital to discover the generating and maintaining mechanisms of diversity (Jost, 2007; Toumisto, 2010).

Using a single component of diversity (i.e. SR, taxonomic or functional) as a surrogate for other components is highly dependent on the diversity measure under consideration, as different indexes can represent differently the aspects on species richness, ecosystem function, genetic diversity, endemic species, and fauna speciality, presenting uncertain relationships. For example, if functional diversity is significantly and positively related to taxonomic diversity with low-to-medium levels of functional diversity, using taxonomic diversity as a surrogate of functional diversity (and vice versa) will be useful only in units with similar levels of functional diversity. Consequently, in units with high levels of functional diversity, the use of one of these two components as a surrogate for the other is not recommended. The inclusion of SR, TD, and FD, as well as their relationships, may provide deep ecological knowledge on how fish diversity in a certain catchment is related to that in another catchment (Higgins, 2010; Stegen and Hurlbert, 2011), thus providing evidence for conservation strategies and planning.

The Yangtze River (Changjiang) is the longest river in China and can be divided into three main geomorphological sections: the upstream area (4504 km long, with steep channel slopes of $1–4 \times 10^{-5}$), the middle area (938 km long, with steeper channel slopes of $2–3 \times 10^{-5}$), and the downstream area (876 km long, with less steep channel slopes of $0.5–1 \times 10^{-5}$) (Changjiang Hydrological Committee of Hydrology Ministry, 1999; Chen et al., 2001), covering multiple types of landforms and climatic zones, and possessing unique biodiversity and important ecosystem functions. Previous studies on the Yangtze fishes shed considerable insight into the fauna composition, diversity and distribution at a rough overall description (Fu et al., 2003; Chen et al., 2009; He et al., 2010; Ye et al., 2014), the knowledge on taxonomic and functional aspects of fauna spatial pattern and interior structure was unknown. We reviewed and updated the freshwater fish species and their distribution, and documented the species richness, the α and β components of SR, TD and FD, as well as the associations among all of the facets of diversity. We hypothesize that (1) Taxonomic and functional diversity are positively related to species richness, on the basis as the more species that occur, the higher the probability of including a wider range of taxonomic units and biologic traits presented. (2) The process of species functional differentiation is faster than that of taxonomy. We supposed that when a species migrated into a new habitat, its biological traits would gradually evolve to adapt to the novel environment during competition, and these changes would accumulate and probably leading to speciation. (3) The high β-diversity of SR is attributed to species turnover, while the high β-diversity of TD and FD is attributed to species nestedness. For instance, from headwater to estuary, though fauna greatly changed by species turnover, the taxonomic category and trait types dramatically increased with little loss as a heavy nestedness. We then pointed out the priority zones for conservation of freshwater fishes in the Yangtze River Basin, according to the combination and trade-offs of different facets of diversity.