ORIGINAL ARTICLE

Freshwater Biology WILEY

Cross-taxon congruence of multiple diversity facets of freshwater assemblages is determined by large-scale processes across China

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Abstract

1. An intensively debated issue in ecology is whether variability in the patterns of diversity of different groups of organisms is congruent in space, a phenomenon referred to as cross-taxon congruence. Whereas this has been previously mainly tested in terms of taxonomic dissimilarity, the role of ecological processes in determining the congruence of multiple diversity facets (i.e. α- and β-diversity, taxonomic, and functional) remains poorly understood.

2. We used a data set of observation records for 469 macrophyte and 543 fish taxa at the catchment-scale from the existing literature and data bases to test the existence of multi-faceted congruence patterns and investigate the variables driving them across 214 catchments covering the whole Chinese mainland.

3. We found cross-taxon congruence of multiple diversity aspects between fish and macrophyte communities. The *energy* (i.e. diversity is limited by energy availability), *area/environmental heterogeneity* (i.e. diversity is higher in larger and more heterogeneous areas), and *dispersal* (i.e. diversity is driven by dispersal) hypotheses were all significantly attributed to the cross-taxon congruence, suggesting the existence of key repeated mechanisms underlying assemblage organisation.

4. Our study provides new evidence that can further our understanding of the factors and underlying processes explaining cross-taxon congruence patterns at broad spatial scales in the freshwater realm, the studies of which significantly lag those in the marine and terrestrial realms. The present findings also provide important baseline information for freshwater conservation initiatives.

KEYWORDS
cross-taxon congruence, dissimilarity, fishes, functional diversity, macrophytes

1 | INTRODUCTION

Assessing the degree to which different groups of organisms show similar patterns of species diversity across space, i.e. cross-taxon congruence, is one of the most significant challenges facing ecologists, biogeographers, and conservation biologists (Özkan et al., 2014; Rooney & Azeria, 2015; Su, Debinski, Jakubauskas, & Kindscher, 2004; Tisseuil et al., 2013). Cross-taxon congruence is not only central to understanding the scale-dependent mechanisms driving spatial patterns of biodiversity (Wolters, Bengtsson, & Zaitsev, 2006), thus contributing to the improvement of general models for predicting assemblage patterns at multiple spatial scales (Qian & Kissling, 2010; Westgate, Barton, Lane, & Lindenmayer, 2014), but it is also of considerable conservation interest. The existence of spatial congruence in diversity patterns allows the possibility for using surrogate taxa when monitoring and managing less well-known taxonomic groups (Lewandowski, Noss, & Parsons, 2010). The existence of common patterns in the spatial arrangement of biodiversity is a recurrent feature in nature (Gaston, 2000; Tittensor et al., 2010), yet consensus regarding the generality of the underlying processes driving spatial variation in biodiversity remains elusive.

Three main mechanisms have been proposed to explain the existence of congruent diversity patterns among different groups of organisms. First, cross-taxon congruence may be generated by similar yet independent responses of taxa to environmental factors (Hawkins et al., 2003; Mittelbach et al., 2007; Willig, Kaufman, & Stevens, 2003), thus making spatial changes in assemblages of different taxa predictable from those in the environment (Gioria, Bacaro, & Feehan, 2011; Heino, 2010; Oertli, Müller, Steiner, Breitenstein, & Dorn, 2005). Second, congruence may be determined by a shared biogeographic history, whereby different organismal groups have exhibited similar evolutionary histories or dispersal routes (Gouveia, Hortal, Cassemiro, Rangel, & Diniz-Filho, 2013; Gove et al., 2013; Ricklefs & Schluter, 1993). Third, the diversity of one group of species may partly determine that of another group of species, as in the case of hosts and their parasites or prey and their specialist predators (Burkle & Alarcón, 2011; Qian & Kissling, 2010; Sandom et al., 2013).

Here, we focus on the environmental factors and dispersal history underlying cross-taxon congruence. This mechanism has gained previous support as an explanation for the diversity gradients observed in many groups of organisms at broad spatial scales (Field et al., 2009; Ricklefs, 2004; Whittaker, Willis, & Field, 2001). Specifically, the expectation of common, independent cross-taxa responses to environmental variation has been formulated via three non-exclusive hypotheses: the *energy*, *area/environmental heterogeneity*, and *dispersal* hypotheses. The energy hypothesis, a climatically based hypothesis, claims that species richness within an area is limited by energy availability (Clarke & Gaston, 2006). In general, species richness tends to be higher in areas where the energy supply is higher. In contrast, the heterogeneity hypothesis states that species richness is higher in larger and more heterogeneous areas through increasing habitat availability and diversity (Whittaker et al., 2001). Finally, the dispersal hypothesis, which includes many variants, proposes that diversity patterns are related to differential speciation or extinction rates, coupled with dispersal limitation related to historical contingency (Ricklefs, 2004, 2007). These three hypotheses have received increasing support in explaining cross-taxon congruence in multiple terrestrial and marine taxa, including mammals, birds, insects, and vascular plants (Cabra-García, Bermúdez-Rivas, Osorio, & Chacón, 2012; Miranda & Parrini, 2015; Oertli et al., 2005). Evidence on freshwater taxa is, however, comparatively much more scarce, and it is unclear to what extent the same mechanisms affect cross-taxon congruence in the freshwater realm, because knowledge from other systems is not directly transferable to freshwaters, especially at broad spatial scales (Heino, 2010, 2011).

Although patterns of taxonomic and functional diversities have been characterised for many biological groups (Gioria et al., 2011; Miranda & Parrini, 2015; Rooney & Azeria, 2015), we still lack a general understanding of how cross-taxon relationships vary among the multiple facets of species diversity. At broad spatial scales, much emphasis has been given to patterns of species richness and the ecological and evolutionary processes underlying the origin and maintenance of the associated cross-taxon congruence (Gioria et al., 2011; Hawkins et al., 2003; Qian & Kissling, 2010; Clement Tisseuil et al., 2013). However, biodiversity is a multi-faceted concept, and these facets are complementary and pertain not only to the species comprising local assemblages (α-diversity), but also to the variation in species among assemblages (β-diversity) and not only to their taxonomic but also to their functional traits and phylogenetic relatedness (Baselga, 2010; Dobrovolski, Melo, Cassemiro, & Diniz-Filho, 2012; Heino & Tolonen, 2017; Leprieur et al., 2011). Therefore, it is now widely accepted that taxonomic richness is only a partial descriptor of wholesale biodiversity, and a multi-faceted approach is needed to gain a robust understanding of the mechanisms structuring species assemblages in different ecosystems and geographic regions.

To fill these knowledge gaps, we examined the multi-faceted (i.e. taxonomic and functional α- and β-diversity) cross-taxon congruence of freshwater fishes and macrophytes across the entire catchment network in China. Given the important habitat that macrophytes provide for fish (e.g. refuge, food, breeding), we anticipated the existence of cross-taxon congruence between them (Cook, 1974; Zhang, García Molinos, Zhang, & Xu, 2018). We were particularly interested in testing for: (1) the existence of spatial correlation between cross-taxon patterns of taxonomic and functional richness (Cabra-García et al., 2012; Miranda & Parrini, 2015; Oertli et al., 2005) and of taxonomic and functional dissimilarity (Baselga, 2010; Villéger, Grenouillet, & Brosse, 2014); (2) whether existing cross-taxon congruence patterns for macrophyte and fish assemblages are driven by variations in environmental conditions through any of the described mechanisms (i.e. *energy*, *area/environmental heterogeneity*, and *dispersal* hypotheses; Field et al., 2009); and (3) whether they are consistently congruent for the different diversity facets.

To our knowledge, our study represents the first one testing cross-taxon congruence patterns of multiple facets of taxonomic and functional diversity against variations in environmental conditions at broad scales. This knowledge should contribute to a better understanding of the potential effects of global change, the identification of vulnerable ecosystem structures and functions, and to tests on the degree to which common ecological mechanisms underlie patterns of cross-taxon congruence (Petchey & Gaston, 2002; Qian & Kissling, 2010).

2 | MATERIAL AND METHODS

2.1 | Data acquisition and key definitions

We compiled location records on the native freshwater macrophyte and fish assemblages from within 214 catchments across China (National Remote Sensing Center of China, http://www.nrscc.gov.cn/nrscc/cyyfw/geosjgx2/gxfw/; Figure S1). These catchments have been delimited by the National Council of China as a part of the National Water Resources Strategic Plan, they represent subdivisions of main river basins based on different hydrologic and ecological criteria (e.g. river order, landscape, and climate), and they provide an important basis for the development, utilisation, conservation, and environmental management of hydrological resources in China.

The term *assemblage* refers here to the total number of species and their composition recorded from ponds, lakes, and rivers within a given catchment (i.e. our spatial unit). Pooling data sets into meaningful, large spatial working units such as catchments or ecoregions is a practical, compromise solution frequently used for the analysis of macroscale diversity patterns with spatially sparse data sets such as ours (Veech & Crist, 2007). The multiple factors influencing richness gradients are scale-dependent relative to both the spatial extent of the analysis and the grain size of the sample resolution (Willis & Whittaker, 2002). We focus on catchments defining subdivisions (mean area of 104 km^2) of main river basins across a vast territory (*c.* 3.7×10^6 km^2), encompassing a range of climatic, geographical and hydroecological conditions over which richness may vary, and seek to understand the forces driving macroecological diversity congruence across China. Catchments are also relatively independent entities separated by natural barriers (i.e. mountains), within which there is a high degree of connectivity between habitats and less variation in environmental parameters (Cai, Xu, Zhang, Wang, & Heino, 2019; Cai, Zhang, Xu, & Heino, 2018; Reyjol et al., 2007; Schleuter et al., 2012; Tisseuil et al., 2013). Therefore, they can be effectively used in a comparative analysis to explore the factors driving assemblage patterns amongst them.

Although there are different definitions of *macrophyte* in the literature, we followed that of Cook (1974) and considered a macrophyte as any plant visible to the naked eye "whose photosynthetically active parts are permanently or, at least, for several months each year submerged in freshwater or floating on the water surface". This definition includes all higher aquatic plants, vascular cryptograms and bryophytes, together with groups of algae that can be

seen to be composed predominantly of a single species. Based on this definition, we first made a detailed literature review of aquatic plant species in China. The distribution of different aquatic plant species in China was determined from published (1960–2010) records, most of which are concerned with lakes and rivers and, occasionally, seasonal agricultural ponds. Documented sources included original research papers and monographs relevant to the distribution and ecology of aquatic plants or to their habitats and status, together with the scientific database of China plant species (http://db.kib.ac.cn/eflora/Default.aspx), the database of invasive alien species in China (http://www.chinaias.cn/wjPart/index.aspx), the Chinese species information system (http://monkey.ioz.ac.cn/bwg-cciced/english/cesis/csispage.htm), and grey research reports. This exhaustive literature review provided information on a total of 992 aquatic plant species. We then prepared a data matrix including the taxonomic information and functional traits for the species. To ensure a good quality of the data set, we used five quality-control rules. (1) We used the definition for macrophytes in Water Plants of the World (Cook, 1974) and the records in Flora of China to exclude non-macrophyte species. (2) Scientific names were standardised, and synonyms were removed according to the Chinese Virtual Herbarium (http://www.cvh.org.cn/cms/en/). (3) The varieties were treated as the same species. (4) The habitat traits of the species were corrected following the Flora of China. (5) Non-freshwater species were excluded. The application of these rules resulted in a total of 469 species being kept for analysis, including 93 submerged species, 40 floating-leaved species, 25 free-floating species and 311 emergent species.

The information on the distribution of fishes follows a similar exhaustive literature review as that of macrophytes, comprising the scientific and grey literature (1960–2010), as well as the Chinese species database and biodiversity information system. Of the total of 1,331 fish species initially documented from the literature, we retained 543 species after the revision using a similar set of quality-control rules. These included the following: (1) all records not determined to the species level or not geo-referenced to county and lower spatial levels were excluded; (2) scientific names were standardised according to the Fishbase (http://www.fishbase.org); (3) infraspecific taxa were merged to the species level; (4) multiple entries referring to the same specimen were removed; (5) records of species native to China but occurring outside their natural range were excluded from the database; and (6) catadromous and brackish water species were excluded from the database.

2.2 | Functional traits considered in this study

We gathered information on five categorical functional traits to calculate the functional distance between macrophyte species according to the Flora of China, including life form (i.e. submerged, floating-leaved, emergent, free-floating), life cycle (i.e. annual, perennial), morphology (i.e. turion, stem, roset, leafy), sexual propagation (monoecism, dioecy), and habitat preference (i.e. lake, agriculture, river, estuary; Zhang, García Molinos, Su, Zhang, & Xu, 2019; Zhang et al., 2018).

Fish species were functionally characterised using seven traits commonly used in studies on fish functional diversity (Matsuzaki, Sasaki, & Akasaka, 2013). Two of these traits were continuous numeric variables (maximum total body length and maturation), and the remainder (mouth position, morphology, dietary traits, diet breadth, and vertical position in the water column) were categorical traits (Table S1). All the functional traits were taken from the ichthyography (Chu & Chen, 1989, 1990) and Fishbase (Froese & Pauly, 2010).

2.3 | Environmental variables

We selected seven variables to quantify the environmental conditions in each catchment. These variables were used as proxies for testing the *energy, area/environmental heterogeneity*, and *dispersal* hypotheses (Clarke & Gaston, 2006; Currie et al., 2004; Ricklefs, 2004, 2007; Whittaker et al., 2001) in relation to the ecological processes responsible for cross-taxon congruence between macrophytes and fishes. These variables are often associated with regional- to global-scale diversity patterns (Clarke & Gaston, 2006; Currie et al., 2004; Ricklefs, 2004, 2007; Whittaker et al., 2001).

To test the energy hypothesis, we used the annual normalised difference vegetation index (NDVI), mean annual temperature (MAT), mean annual precipitation (MAP), solar radiation (SOLAR), and annual run-off within each catchment. NDVI is an index of terrestrial plant photosynthetic activity and is one of the most commonly used terrestrial vegetation indices (Crippen, 1990). Here, we used NDVI as an indicator of the processes of weathering, leaching, and input of terrestrial organic material into waterbodies, which can be a very important energy source of aquatic ecosystems (Correa & Winemiller, 2018; Griffith, Martinko, Whistler, & Price, 2002). These variables are used as surrogates for energy entering each catchment. Indeed, energy can regulate the biodiversity of producers and consumers by means of two very different processes: (1) resource availability (i.e. productive energy) and (2) the physiological limits of the species (i.e. ambient energy; Clarke & Gaston, 2006; Hawkins et al., 2003).

To test for the area/environmental heterogeneity hypothesis, we used the total surface area of each catchment (AREA), altitudinal range (ALTVAR), land cover heterogeneity (LANDVAR), and climate heterogeneity (i.e. spatial climatic ranges of MAT, MAP, and SOLAR), including MATVAR, MAPVAR, and SOLARVAR. LANDVAR is measured as the Shannon diversity index based on the proportions of land cover classes (forest, grass, farm, urban, water, and desert) within each catchment (Tisseuil et al., 2013). ALTVAR is a proxy for topographic heterogeneity, calculated as the range between the maximum and minimum altitude for each catchment (Astorga, Heino, Luoto, & Muotka, 2011). These variables are recognised as important factors shaping biodiversity through increasing habitat heterogeneity and availability, thus favouring speciation while reducing species extinction rates (Tisseuil et al., 2013; Whittaker et al., 2001).

To test for the *dispersal* hypothesis, we used spatial location, including longitude, latitude, and altitude. Biodiversity patterns are often associated with latitudinal (Hof, Brandle, & Brandl, 2008) and altitudinal (Davies et al., 2007; Rahbek, 1995) gradients.

Geographical distance is also important in relation to the dispersal of species among catchments.

All data sets had a nominal horizontal resolution of 0.5 × 0.5° and were obtained from the Data Sharing Infrastructure of the Earth System Science, National Science & Technology Infrastructure Center (http://www.nstic.gov.cn/) and the Data Center of the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences. Environmental variables were calculated for each catchment as the average value of the variable for all 0.5° cells comprising the catchment (i.e. having their cell centroid within the catchment boundary).

2.4 | Measurement of different facets of diversity

Taxonomic and functional richness were calculated, respectively, as the number of species comprising an assemblage and the value of the convex hull volume filled by a community in multidimensional functional space defined by the species traits (Villéger, Mason, & Mouillot, 2008). Functional richness thus equals the total branch length needed to join all species in an assemblage and standardised to range between 0 (assemblages composed of one species) and 1 (Villéger et al., 2008). Functional richness aims to quantify resource use complementary, and it has been suggested that it generally performs better as a predictor of ecosystem functioning than alternative methods (Petchey & Gaston, 2002).

Taxonomic dissimilarity, defined as the proportion of species present in only one assemblage within a pair of assemblages, was calculated using the Jaccard index (Villéger et al., 2014). Similarly, functional dissimilarity was estimated as the non-overlap in functional space between assemblage pairs defined by the intersection of their convex hulls. Both taxonomic (Baselga, 2012) and functional (Villéger, Grenouillet, & Brosse, 2013) diversity were partitioned into their turnover and nestedness components to assess the relative contribution of the different processes leading to changes in assemblage composition, namely, species replacement (turnover) and changes in species numbers without replacement (nestedness). At both extremes of the gradient, a high dissimilarity between two assemblages can result from them sharing no species, despite having equal numbers (complete turnover without nestedness), or from the assemblages having very different numbers of species despite sharing them, i.e. the species-poor being a subset of, or nested in, the species-rich assemblage.

2.5 | Statistical analyses

Functional richness and dissimilarity were computed on the functional space made by the first three principal axes of the principal coordinates analysis conducted on the species functional distance matrix using Gower's distance (Villéger et al., 2008). The resulting three-dimensional functional space provided an accurate representation of the functional dissimilarity between species, explaining 65% and 71% of the total functional space for macrophytes and fish, respectively, thus achieving the necessary trade-off between information

quality and computation time (Maire, Grenouillet, Brosse, & Villéger, 2015; Villéger et al., 2013, 2008). Indices of taxonomic and functional richness, dissimilarity and contribution of turnover and nestedness to dissimilarity between each pair of fish and macrophyte assemblages were computed according to recently developed methodology (Baselga, 2010, 2012; Villéger et al., 2008, 2014).

We used Spearman's rank correlation to test for significant cross-taxon congruence in the form of taxonomic and functional richness correlations between fish and macrophyte assemblages across catchments. Similarly, cross-taxon correlations for taxonomic and functional total dissimilarity and its constituent nestedness and turnover components were tested using Mantel tests, a permutation technique that estimates the resemblance between two proximity matrices computed for the same objects (Mantel, 1967).

To test for relationships between changes in taxonomic and functional richness along environmental gradients (i.e. related to *energy*, *area/environmental heterogeneity*, and *dispersal* hypotheses), we first applied a principal component analysis (PCA) on the data matrix related to the suite of environmental covariates used as proxies for each of the hypotheses. This was performed to reduce the multidimensionality and to eliminate collinearity between predictors. We retained the first two PCA components as synthetic predictors (Figure S4), which accounted for at least 70% of the total variability in the original variables in all cases (Figure S4). We then used multiple linear regression with Gaussian errors, where the response variables were the taxonomic or functional richness of fish and macrophytes and the PCA components were the predictor variables. Predictor variables were logarithmic or square-root transformed as required to achieve normality, and they were standardised to a common scale between 0 and 1 before PCA.

To test how taxonomic and functional total dissimilarity and its turnover and nestedness components varied along environmental gradients, we used permuted multiple regression on distance matrices (Lichstein, 2007) with changes of environmental gradients (i.e. related to the *energy*, *area/environmental heterogeneity*, and *dispersal* hypotheses) as predictor Euclidean distance matrices. Predictor variables were also normalised and standardised before the analysis.

The *p*-values (0.05 significance level) for Mantel's permutation test and the multiple regression on distance matrices models were obtained by comparing each observed regression coefficient with a distribution of 10,000 permuted values. All statistical analyses (Table 1) and plotting were produced in R 3.1.0 (R Development Core Team, 2014) using the built-in functions and those in the packages reshape2 (Wickham, 2007), FD (Laliberté, Legendre, Shipley, & Laliberté, 2014), betapart (Baselga & Orme, 2012), lme4 (Bates, Maechler, & Bolker, 2012), ecodist (Goslee & Urban, 2007), vegan (Oksanen et al., 2014), sjPlot (Lüdecke, 2015) and ggplot2 (Wickham, 2009).

3 | RESULTS

Across catchments, macrophyte assemblages (200 ± 47 species, mean ± 1 standard deviation) were, on average, richer in species than fish assemblages (30 ± 51). Although the overall species pool was higher for fish (543 recorded species across China) than macrophytes (468), the representation of the regional species pool at the individual catchment level was, on average, much higher for macrophytes (46%) than for fish assemblages (10%; Figure 1a,e), reflecting a higher degree of differentiation among fish assemblages. This trend was also observed for functional richness (Figure 2a,e), with individual catchments containing, on average, 56% and 34% of the regional macrophyte and fish functional diversity, respectively. The higher representation of regional functional richness relative to taxonomic richness within individual catchments suggests some degree of functional redundancy among species in both groups.

TABLE 1 Statistical methods used in this study

Method	Purpose	Response variable	Predictor variable[a]
Spearman's rank correlation	Correlation between taxonomic and functional richness	Taxonomic and functional richness	Taxonomic and functional richness
Mantel's permutation test	Correlation between taxonomic and functional (total, turnover, nestedness) dissimilarity	Taxonomic and functional total dissimilarity and its constituent nestedness and turnover components	Taxonomic and functional total dissimilarity and its constituent nestedness and turnover components
Principal component analysis (PCA)	Reduction of the multidimensionality and elimination of collinearity between environmental predictors	–	–
Multiple linear regression with Gaussian errors	Effects of environment on richness	Taxonomic and functional richness	PCA components related to energy, heterogeneity and dispersal hypotheses
Multiple regression on distance matrices	Effects of environment on dissimilarity	Taxonomic and functional total dissimilarity and its constituent nestedness and turnover components	Euclidean distance matrices of PCA components related to energy, heterogeneity, and dispersal hypotheses

[a]All predictors were logarithmic or square root transformed as required to achieve normality and standardised to a scale between 0 and 1 before PCA.
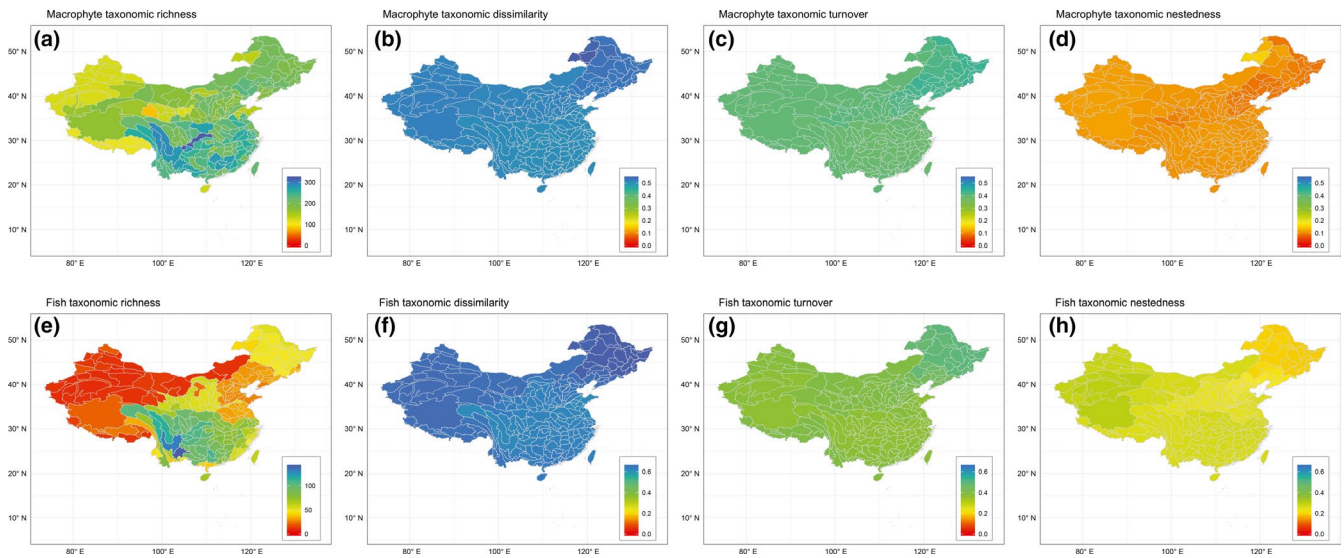
FIGURE 1 Spatial patterns of taxonomic diversity across the 214 catchments. Shown are macrophyte (a–d) taxonomic richness, dissimilarity and its turnover and nestedness components, and fish (e–h) taxonomic richness, dissimilarity and its turnover and nestedness components. Index values for dissimilarity and its turnover and nestedness components correspond to the average of the pairwise comparisons between that assemblage and the other assemblages [Colour figure can be viewed at wileyonlinelibrary.com]
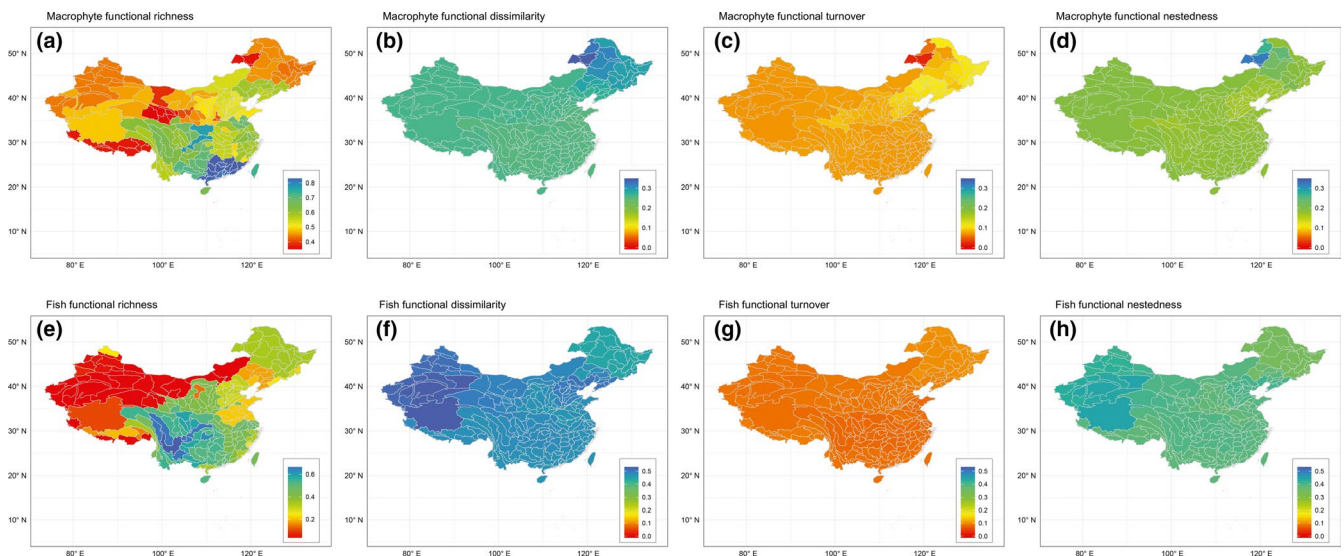
FIGURE 2 Spatial patterns of functional diversity across the 214 catchments. Shown are macrophyte (a–d) functional richness, dissimilarity and its turnover and nestedness components, and fish (e–h) functional richness, dissimilarity and its turnover and nestedness components. Index values for dissimilarity and its turnover and nestedness components correspond to the average of the pairwise comparisons between that assemblage and the other assemblages [Colour figure can be viewed at wileyonlinelibrary.com]

The total taxonomic dissimilarity among macrophyte (Figure 1b) and fish (Figure 1f) assemblages was relatively high (0.51 ± 0.01 and 0.65 ± 0.02, respectively), being mainly driven by the species turnover among assemblages, with a relative contribution towards a total dissimilarity of 0.4 ± 0.03 for both groups (Figure 1c,g), rather than by the isolated effect of species losses or gains (i.e. nestedness; 0.11 ± 0.01 and 0.25 ± 0.03; Figure 1d,h). In contrast, functional dissimilarity was lower for both groups (macrophyte: 0.26 ± 0.02, fish: 0.48 ± 0.02; Figure 2b,f) and had a much larger contribution

from nestedness (0.19 ± 0.02 and 0.39 ± 0.02; Figure 2d,h) than turnover (0.09 ± 0.01 for both groups; Figure 2c,g). These common patterns between the two taxonomic groups are also reflected by the significant correlations found for all taxonomic and functional diversity facets (Figures S2 and S3). Spatially, the variability in taxonomic and functional richness was relatively high and followed the same patterns for both macrophytes and fish assemblages, with higher richness concentrated in catchments from central-southern China (Figures 1a,e and 2a,e). In contrast, taxonomic and functional
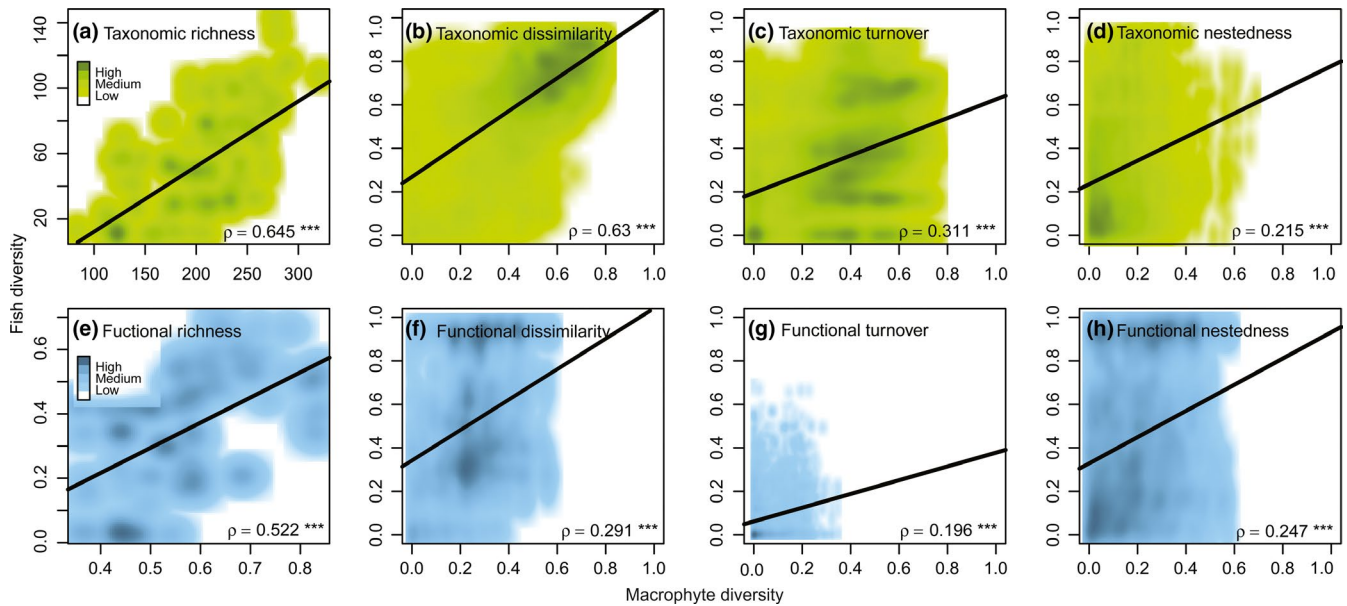
FIGURE 3 Cross-taxon congruence tests for taxonomic and functional diversity facets between macrophyte and fish assemblages across the studied catchments. Panels show smoothed colour density representations of observed paired assemblage values for each facet: (a–d) taxonomic richness, taxonomic dissimilarity, and its turnover and nestedness components; (e–h) functional richness, functional dissimilarity and its turnover and nestedness components. Values displayed in each panel correspond to the (a, e) Spearman rank correlation coefficient and (b–d, f–h) Mantel statistic (***$p < 0.001$). Colour density is obtained through a two-dimensional kernel density estimate, and low, medium, and high density represent 25%, 50%, and 75% of maximum density. Black lines in the panels represent the linear regression trends [Colour figure can be viewed at wileyonlinelibrary.com]

dissimilarity showed very little spatial variation among catchments (Figures 1b–d,f–h and 2b–d, f–h).

Cross-taxon congruence between fish and macrophyte assemblages across catchments was highly significant ($p < 0.001$) for all diversity facets, including taxonomic and functional richness (Spearman's correlation coefficient $\rho = 0.645$ and $\rho = 0.522$, respectively; Figure 3a,e); taxonomic total dissimilarity, turnover and nestedness components ($\rho = 0.63$, 0.311, and 0.215; Figure 3b–d); and functional total dissimilarity, turnover and nestedness components ($\rho = 0.291$, 0.196 and 0.247; Figure 3f–h). Multiple linear regression models based on the full set of predictors explained a significant proportion of the variability of the response variables around its mean (Figure 4). These models provided strong supporting evidence of a combined role of all three hypotheses (i.e. *energy*, *area/environmental heterogeneity*, and *dispersal*) in driving observed taxonomic and functional diversity patterns of fish and macrophyte communities. However, the mean effects of each individual predictor varied across diversity facets and taxonomic groups. Specifically, macrophyte taxonomic richness was higher in more-productive environments associated with higher precipitation and temperature regimes (first PCA$_{ENE}$ axis, Figure 4a,e and Figure S4a), although elevated run-off (second PCA$_{ENE}$ axis, Figure 4e and Figure S4a) appeared to have a significant negative effect on macrophyte functional richness. Similar positive effects of energy availability on taxonomic and functional richness were observed for fish communities, although, in contrast to macrophytes, increased annual run-off had a significantly positive effect on them. Richness patterns for both taxonomic groups also varied significantly along geographical gradients, where lower macrophyte and fish richness was found

towards higher latitudes (second PCA$_{DIS}$ axis; Figure 4a,e and Figure S4c) as well as higher altitudes and lower longitudes (first PCA$_{DIS}$ axis). Interestingly, habitat heterogeneity in the form of higher altitudinal, solar and temperature variability (first PCA$_{HET}$ axis; Figure 4a,e and Figure S4b) was associated with significantly taxonomically and functionally richer macrophyte communities, an effect that was not observed for fish communities (Figure 4a,e).

As with richness, energy availability significantly promoted more taxonomically (Figure 4b,c) and functionally (Figure 4f–h) diversified fish and macrophyte communities among catchments. Increasing distance among catchments also tended to result in significantly more-dissimilar communities (i.e. higher β-diversity) for both taxonomic groups. These effects were consistent overall for the turnover and nestedness components of diversity. However, we found opposite significant effects of habitat heterogeneity on β diversity, where more-heterogeneous habitats promoted taxonomic and functional dissimilarity among catchment fish communities but homogenised macrophyte communities. The results for components showed habitat complexity significantly decreased fish and macrophyte turnover (Figure 4c,g) and increased nestedness (Figure 4d,h), although there was a negative effect on functional macrophyte nestedness.

4 | DISCUSSION

Our analysis adds novel insights into previous studies analysing patterns of cross-taxon congruence for three reasons. First, we considered for the first time cross-taxon congruence across six aspects of
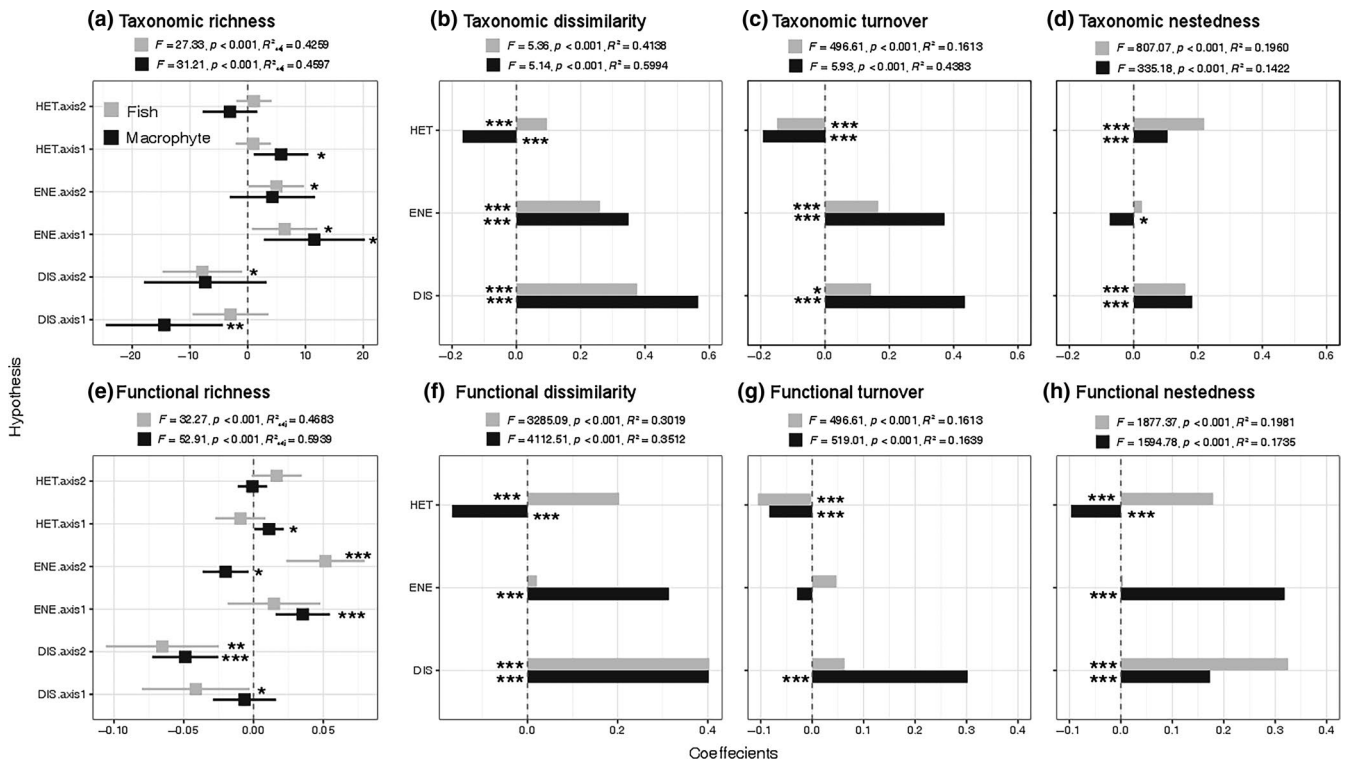
FIGURE 4 Effects of the three alternative hypotheses on fish and macrophyte diversity patterns across catchments. The plots show the mean effects and associated confidence intervals associated with each hypothesis—*energy* (ENE), *area/environmental heterogeneity* (HET), and *dispersal* (DIS) hypotheses—resulting from multiple regression models on (a) taxonomic richness, (e) functional richness, and (b–d) taxonomic and (f–h) functional (b, f) total dissimilarity and its corresponding (c, g) turnover and (d, h) nestedness components (*$p < 0.05$, **$p < 0.01$ & ***$p < 0.001$). Response variables for the richness model (a, e) correspond to the first two axes of a PCA on each group of environmental variables (see Section 2 and Figure S3). Response variables for the dissimilarity model (b–d, f–h) correspond to the average value of all pairwise comparisons between each assemblage with all its peers. See Section 2 for a detailed description of the models

diversity, including taxonomic and functional α- and β-diversity, along with their turnover and nestedness components. Second, whereas most of the literature on cross-taxon congruence focusses on local-to-regional scales (Lários et al., 2017), this is the first study examining cross-taxon congruence between fish and macrophyte communities at broad spatial scales encompassing all of China. Cross-taxon congruence can be driven by mechanisms operating at very different spatial scales such as differences in environmental conditions, biotic interactions, dispersal limitations and speciation (Wolters et al., 2006). Such scale-dependent effects have also implications for diversity-related ecosystem functionality (Pasari, Levi, Zavaleta, & Tilman, 2013). Consideration to multiple scales is therefore necessary for disentangling difference in the relative contribution of large and small-scale processes across taxa (Burrascano et al., 2018). Lastly, we used different environmental variables as proxies for testing different plausible driving mechanisms for the observed cross-taxon congruence patterns. Thus, our study helps researchers to understand the factors and underlying processes explaining cross-taxon congruence patterns at broad spatial scales in the freshwater realm, thus bridging the gap in the field with respect to marine and terrestrial studies (Collen et al., 2014; Leprieur et al., 2011; Tisseuil et al., 2013).

In general, the biogeography of the Chinese freshwater fish and macrophytes is determined to some extent by the legacy of the last

glacial maximum. For example, the current distribution of the species richness of freshwater macrophytes and fishes follows a decreasing gradient from the Yunnan-Guizhou region in southwestern China, a former Pleistocene glacial refugia and centre of speciation, to more westerly regions (Li et al., 2011), a pattern identifiable from our data set (Figure 1a,e). Despite the small observed differences, the Yunnan–Guizhou Plateau is the region with the lowest contribution of taxonomic turnover to fish and macrophyte total taxonomic β-diversity (Figure 1c,g). This agrees with recent studies conducted on different animal groups stressing a tendency for macroecological β-diversity patterns to be dominated by nested species losses in areas affected by strong historical environmental disturbance (e.g. Pleistocene glaciations) and by species replacements in areas that experienced less-severe paleoclimatic changes (Baselga, Gómez-Rodríguez, & Lobo, 2012; Hortal et al., 2011; Leprieur et al., 2011). It is nonetheless interesting that the overwhelming contribution of macrophyte and fish species turnover to taxonomic dissimilarity generalised across all Chinese catchments, relative to that of isolated species extirpations or invasions (i.e. nestedness), was reversed for functional dissimilarity, for which nestedness had a much larger relative contribution (Figures 1 and 2). This suggests that the frequent species replacements occurring in both macrophyte and fish assemblages are mostly between species that are functionally

redundant, including species with common trait combinations. The generalised low level of functional turnover in both taxonomic groups and the relatively low functional dissimilarity might result from either functional convergence among these assemblages (Heino & Tolonen, 2017; Logez, Pont, & Ferreira, 2010) or allopatric speciation resulting from dispersal limitation (Baselga et al., 2012). The consistent significant cross-taxon congruence across all facets of diversity found between fishes and macrophytes (Figure 3) and their consistent overall patterns of response to variation in environmental conditions (Figure 4) strongly support the concept that under comparable environmental conditions, the structure of phylogenetically unrelated communities should vary similarly (Oertli et al., 2005; Qian & Kissling, 2010; Rooney & Azeria, 2015; Westgate et al., 2014). This hypothesis holds the deterministic view that assemblage structure can be predicted at least partly from the environment, to which organisms respond in a predictable way both in ecological and evolutionary terms. In our case, the observed significance of multifaceted cross-taxon congruence between fishes and macrophytes confirms the generality of assemblage patterns and the processes causing those patterns at broad spatial scales (Heino, 2010; Qian & Kissling, 2010; Su et al., 2004).

With some exceptions, the strong and consistent overall positive effects of energy availability and environmental heterogeneity on both fishes and macrophytes could be expected. Whereas higher energy levels should lead to higher biomass or abundance and, thereby, higher species richness (Currie, 1991; Currie et al., 2004), heterogeneous habitats and refuges should facilitate the occurrence of larger populations, higher speciation rates and lower extinction rates (Ricklefs, 2007; Ricklefs & Schluter, 1993; Tisseuil et al., 2013).

These effects were not without exceptions. For example, the fact that elevated run-off (ENE axis2) had a significant negative effect on macrophyte functional richness might be related to some types of macrophytes being absent from rivers and lakes that are prone to flooding or that are perhaps under irregular hydrological regimes (i.e. high variability in water levels; Friedman & Auble, 2000; Paillex, Doledec, Castella, & Merigoux, 2009). Similarly, highly heterogeneous landscapes tended to facilitate stronger selective extinction, the main mechanism influencing fish assemblages. This result in assemblages within catchments that is a subset of the regional pool and, hence, show increased nestedness but less turnover (Cutler, 1991; Wright & Reeves, 1992). In contrast, macrophytes showed a significant negative association of overall dissimilarity with more-heterogeneous environments across catchments. The opposite response of fishes and macrophytes to environmental heterogeneity may be explained by a more variable environment allowing more macrophyte species to persist (Figure 4a), increasing catchment species richness and causing lower compositional turnover through time. However, as much as 65% of the macrophytes comprising the regional species pool are cosmopolitan, with 25% of all species being Asian endemic species. Selective colonisation may hence play less of a role in macrophyte distributions at the national scale than it does for fish (Ricklefs, 2007; Ricklefs & Schluter, 1993; Tisseuil et al., 2013).

Dispersal limitation was the most consistent and strongest determinant of variation in taxonomic and functional total dissimilarity, including its turnover and nestedness components. Assemblages of strict freshwater species with low dispersal capacities via riverine corridors, such as fish, receive new colonists so rarely that immigration and speciation processes often occur on similar time scales and can be considered as specific to each catchment (Cai et al., 2018; Reyjol et al., 2007; Schleuter et al., 2012; Tisseuil et al., 2013). Macrophytes, despite having high dispersal capacities mediated by flows, birds, or winds, have been demonstrated to have important historical levels of taxonomic dissimilarity between assemblages at regional scales (Zhang et al., 2018). Therefore, our results, which hold for both fishes and macrophytes, despite major differences in their dispersal capacities and other biological traits, stress the importance of dispersal limitation in explaining cross-taxon congruence patterns (Baselga, 2010; Leprieur et al., 2011; Qian & Ricklefs, 2012) and reinforce recent evidence on the role of distance decay relationships in understanding diversity patterns in freshwater systems (Leprieur et al., 2011; Villéger et al., 2014). Furthermore, our findings also highlight the role of connectivity in highly spatially structured systems, such as hydrological networks, where long-distance dispersal may be easily disrupted, preventing freshwater taxa from tracking other environmental gradients (Heino et al., 2015; Tonkin et al., 2018), in contrast to many marine and terrestrial taxa (Dobrovolski et al., 2012).

Locally, aquatic plants can affect fish diversity by altering the abundance and composition of prey, by adjusting prey behaviour in refugia as a response to fish, by directly influencing predator–prey interactions (herbivory by fish and its prey), and by increasing the reproductive success of some fish species through providing attachment of eggs and protection for young fish from predation (Diehl & Kornijów, 1998; Maceina, Cichra, & Betsill, 1992). However, energy and environmentally-related factors still can play an important role in driving patterns of diversity at broad geographic scales (Hawkins et al., 2003). In this study, we found that broad-scale climatic and environmental factors, either directly or indirectly via productivity, together with dispersal-related geographic gradients were important in explaining existing macroecological congruence patterns in species richness and composition across China. A recent study on forest communities found that when compared with the effect of fine-scale determinants directly or indirectly related to forest structure (e.g. microclimatic conditions, occurrence of specific elements), the inclusion of a wider extent and, consequentially, broader ecological gradients, increased congruence for all pairs of taxa (Burrascano et al., 2018). Thus, the congruence we observed suggests that fish diversity may be predicted by aquatic plant diversity at broad scales, but the local ecological preferences of the species should also be assessed to preserve their habitats and ecological interactions between macrophytes and fish.

To conclude, our analysis strongly suggests that the processes associated with the *energy*, *area/environmental heterogeneity*, and *dispersal* hypotheses have all played important roles in determining the diversity patterns of fish and macrophyte assemblages across

the catchments examined in this study. Nonetheless, our results also provide strong evidence of the existence of consistent cross-taxon congruence patterns in multiple facets of diversity between fishes and macrophytes, driven by underlying variation in environmental drivers. Cross-taxon congruence studies can provide valuable information for predicting assemblage patterns across multiple taxonomic groups at broad spatial scales. Such studies should be of interest to ecologists, conservation biologists and environmental managers aiming to understand anthropogenic effects on species diversity and to prioritise large-scale conservation efforts.

ACKNOWLEDGMENTS

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.