



Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv



Different roles for geography, energy and environment in determining three facets of freshwater molluscan beta diversity at broad spatial scales

Yongjiu Cai ^{a,*}, Jun Xu ^{b,*}, Min Zhang ^c, Jianjun Wang ^a, Jani Heino ^d

^a Key Laboratory of Watershed Geographic Sciences, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing 210008, China

^b Donghu Experimental Station of Lake Ecosystems, State Key Laboratory of Freshwater Ecology and Biotechnology of China, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

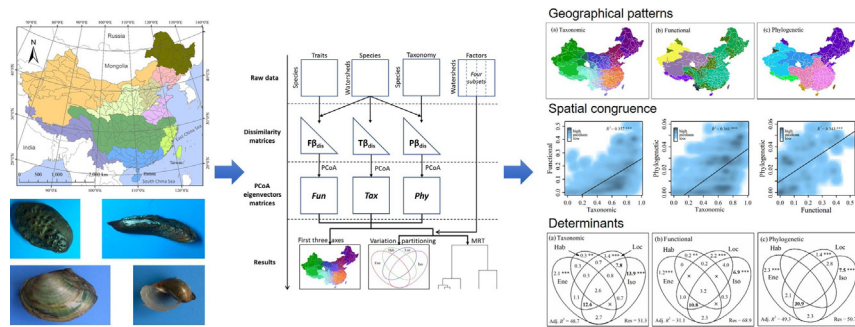
^c College of Fisheries, Huazhong Agricultural University, Wuhan 430070, China

^d Finnish Environment Institute, Biodiversity Centre, Paavo Havaksen Tie 3, FI-90570 Oulu, Finland

HIGHLIGHTS

- We examined patterns and drivers of freshwater molluscan biodiversity across China.
- Taxonomic, functional and phylogenetic beta diversity were considered simultaneously.
- The geographical patterns of the three facets of diversity were only moderately congruent.
- Spatial factors may override environmental filtering in driving molluscan diversity.
- Different ecological drivers were important for each diversity facet.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 27 September 2018
 Received in revised form 10 December 2018
 Accepted 24 December 2018
 Available online 26 December 2018

Editor: Henner Hollert

Keywords:

Community assembly
 Dispersal limitation
 Environmental filtering
 Functional diversity
 Phylogenetic diversity
 Spatial congruence
 Taxonomic diversity

ABSTRACT

Current understanding of different facets of beta diversity and their underlying determinants remains limited at broad scales in the freshwater realm. We examined the geographical patterns and spatial congruence of three beta diversity facets of freshwater molluscs across all of China, and evaluated the relative importance of environmental and spatial factors underlying the observed patterns. Taxonomic (β -TD), functional (β -FD) and phylogenetic (β -PD) beta diversity were calculated for 212 drainage basins belonging to 10 hydrographic regions using compiled occurrence data of 313 molluscan species. Geographical patterns of the three diversity facets were visualized on maps and pairwise spatial congruence among them was evaluated using regression on distance matrices. Variation partitioning and multivariate regression trees were used to assess the relative importance of different factors underlying beta diversity patterns. Beta diversity maps revealed that geographical patterns of β -TD and β -PD showed strong spatial clustering and were well matched with hydrographic regions' boundaries, while β -FD showed only moderate spatial aggregation. The three facets were only moderately congruent, with over 60% of the variation in one facet remaining unexplained by any other facet. Remarkably, all diversity facets were best explained by the spatial factors with considerable unique effects. Environmental filtering associated with energy gradients also made a large contribution, while habitat availability only explained minor fractions of the variation in beta diversity. At the national scale, β -TD and β -PD were more strongly related to spatial processes, whereas β -FD was more strongly associated with energy gradients. Our results suggested that, for freshwater organisms with low dispersal capacity, dispersal processes may override environmental filtering in driving

* Corresponding authors.
 E-mail addresses: caiyj@niglas.ac.cn (Y. Cai), xujun@ihb.ac.cn (J. Xu).

geographical diversity patterns. However, different ecological drivers were important for each diversity facet. Importantly, rather weak spatial congruence among the different diversity facets stresses the need to incorporate functional and phylogenetic facets into the development of conservation planning.

© 2018 Elsevier B.V. All rights reserved.

1. Introduction

Understanding the processes that underlie geographical variation in biodiversity is a central theme in community ecology, macroecology and biogeography (Hortal et al., 2015). Measures of taxonomic diversity (TD), such as species richness, are the most common descriptors of biodiversity in broad-scale studies. However, TD does not account for functional differences and evolutionary relatedness among species, but treats them equivalently and independently, which may hinder generalization of mechanisms underlying the maintenance of biodiversity (Pavoine and Bonsall, 2011). Functional (FD) and phylogenetic (PD) diversity have therefore arisen from the idea that the differences among species in functional and evolutionary relationships can be incorporated into biodiversity measures. FD generally incorporates the variation of biological and ecological traits of organisms that potentially influence ecosystem functioning (Petchey and Gaston, 2006). FD is commonly assumed to be a better predictor of ecosystem productivity, vulnerability and stability than TD (Mouillot et al., 2013; Jourdan et al., 2017; Colin et al., 2018). Phylogenetic diversity reflects variation in evolutionary history, based on the evolutionary relatedness between species in a phylogeny (Webb et al., 2002; Mouquet et al., 2012). Characterizing PD can identify the capacity of an assemblage to generate new evolutionary solutions in the face of environmental change and can account for unmeasured FD (Srivastava et al., 2012). Hence, a combination of the three diversity facets could provide complementary and comprehensive perspectives in revealing different patterns of biodiversity and ecological processes underpinning assemblage assembly (Gianuca et al., 2017; Teichert et al., 2018; Xie et al., 2018). However, current understanding of biodiversity patterns mainly comes from taxonomic studies, while the three facets have not been well explored simultaneously (Devictor et al., 2010; Arnan et al., 2017; Gianuca et al., 2018).

Beta diversity, one intrinsic component of biodiversity (Whittaker, 1960), usually measures the variation in assemblage composition among localities within a geographical area. Several mechanisms have been hypothesized to account for beta diversity patterns. At broad scales, environmental filtering and dispersal limitation are the two main processes in explaining beta diversity patterns (Barton et al., 2013). It is generally assumed that a strong environmental relationship of community similarity denotes strong environmental filtering, whereas a high spatial relationship indicates a strong effect of dispersal limitation or unmeasured spatially-structured environmental variables (Soininen, 2016). Environmental filtering occurs when environmental constraints result in niche differentiation among species, favoring speciation and species turnover (Heino et al., 2013). Usually, the common factors related to environmental filtering across broad geographical gradients are energy availability, water–energy dynamics, and habitat heterogeneity (Field et al., 2009). Dispersal limitation, in turn, is related to speciation, extinction and colonization processes associated with geographical isolation that promote spatial turnover between biological assemblages (Chytrý et al., 2012). Importantly, these two major processes are not mutually exclusive, but often jointly regulate diversity patterns (Heino, 2011). Increasing evidence indicates that their relative roles are dependent on the ecosystem types, spatial scales and taxonomic groups (Soininen, 2016). It is generally believed that the role of dispersal limitation increases, while that of environmental filtering decreases with increasing geographical extent and decreasing dispersal capacity of organisms (Heino, 2011; Soininen, 2016). Moreover, recent findings showed that the relative importance of environmental filtering

and dispersal processes may vary substantially between different facets of beta diversity even if the focus is on the same organism group (Meynard et al., 2011; Cilleros et al., 2016; Gianuca et al., 2017). Thus, considering different facets of diversity simultaneously may help one to disentangle environmental filtering versus dispersal processes in the assembly of biological assemblages.

To date, the majority of studies on beta diversity at broad scales has centered on terrestrial organisms, whereas freshwater organisms have received considerably less attention, except that for fishes (Tyler et al., 2012). Freshwater systems are embedded in relatively independent terrestrial drainage basins where the dispersal among local communities is typically relatively poor. Generally, freshwater organisms show high beta diversity compared with terrestrial organisms (Soininen et al., 2007), and might reasonably be expected to be more closely related to dispersal limitation (Soininen, 2016). Hence, the current understanding of patterns in beta diversity of terrestrial organisms may not be strictly applicable to freshwater organisms (Heino, 2011). In this context, more information on diversity patterns of a variety of freshwater taxa should be examined in testing the generality of ecological theories and geographical patterns. Furthermore, research in freshwater systems is becoming even more urgent as their biodiversity is experiencing dramatic declines due to increasing multiple anthropogenic stressors (Dudgeon et al., 2006). Freshwater molluscs are among the most understudied and threatened freshwater taxa in the world, yet they are responsible for important ecological functions and services (Lopes-Lima et al., 2017). These features of molluscs underscore the importance of gaining more information about their biodiversity patterns to guide conservation at broad scales.

In this study, we examined the spatial congruence and determinants of taxonomic (β -TD), functional (β -FD) and phylogenetic (β -PD) beta diversity of freshwater molluscs across the tributary drainage basins (hereafter called watersheds) of all of China, exhibiting large gradients in primary productivity, temperature, precipitation and topography (Fig. A1). We tested the following two hypotheses. First, both environmental and spatial factors would be related to all facets of beta diversity. However, because of the limited dispersal ability of many molluscs and the broad spatial extent, we expected spatial factors to make a larger contribution (Bohonak and Jenkins, 2003). Second, the role of spatial factors in shaping β -FD should be less important than that for β -TD and β -PD. This is because species identity and evolutionary relatedness should be more affected by dispersal processes and evolutionary divergence (Mouquet et al., 2012), while functional structure should be more influenced by environmental factors owing to trait–environment linkages (Petchey and Gaston, 2006; Heino et al., 2013).

2. Materials and methods

2.1. Spatial grain and molluscs dataset

This study was conducted in 212 watersheds (mean \pm SD watershed area: $(4.46 \pm 6.06) \times 10^4$ km²) based on the national water resources zoning system covering >99% of the land area of China (Fig. 1). Compared with entire river basins, the usage of watershed as a spatial grain will be more appropriate since many molluscs do not inhabit the entire river basins. Watersheds can be considered relatively independent entities separated from each other by geographical barriers (i.e., mountains), which have been documented to be suitable to



Fig. 1. Map showing the 212 watersheds and 10 hydrographic regions across all of China. Hainan Island and Taiwan Island were classified into the Pearl River Basin and Southeast Region, respectively. The upper left map shows the elevation gradient of China.

examine broad-scale diversity patterns of strict freshwater species with low dispersal capacities (Schleuter et al., 2012; Tisseuil et al., 2013).

We compiled presence-absence data of molluscs for each watershed based on a comprehensive review of literature sources, including journal articles and monographs relevant to the distribution, population biology and community ecology of molluscs. Besides, the Chinese biodiversity information system (<http://monkey.ioz.ac.cn/bwg-cciced/english/cesis/csispage.htm>) and the grey research reports were also checked to be sure that the records of freshwater molluscs in China have been fully included. These sources of literature included the related research works from 1960 to 2013. In the first round of collection,

a total of 393 molluscan species was compiled. Second, to retain taxonomic consistency, scientific names were standardized and synonyms were removed (Supplementary material Appendix 1). Third, only native species and subspecies were considered in this study. Finally, 313 species were kept for our analysis, including 227 gastropods and 86 bivalves. The species richness of molluscs for each watershed varied greatly from 8 to 158 with an average value of 56 (Fig. A2). The term assemblage here thus refers to the species composition recorded within a watershed. Since the biases in sampling efforts among watersheds may affect the robustness of results, the number of literature sources (NOL) compiled for each watershed was used to represent the sampling effort.

Pearson correlation analysis showed that species richness was not correlated with NOL ($r = 0.11$, $p = 0.12$, Fig. A3), indicating a weak effect of sampling biases on our results.

2.2. Trait and phylogenetic information

Here, six species traits or grouping features were considered: maximal body size, ratio of shell height to width, respiration, feeding habit, reproduction mode, locomotion and substrate relation (Supplementary material Appendix 2). They are important biological traits of freshwater macroinvertebrates, which are commonly used to reflect different aspects of community function (Usseglio-Polatera et al., 2000).

In the absence of true phylogeny comprising all the molluscs in our data, we used taxonomic hierarchies based on the path lengths in the Linnean taxonomic trees as a proxy for true phylogeny (Clarke and Warwick, 1998). This approach has been commonly used dealing with lack of true phylogeny (Schweiger et al., 2008). We used equal branch lengths and six supra-species taxonomic levels for the calculation of taxonomic distances between species: genus, family, order, subclass, class and phylum (Supplementary material Appendix 1). Although this method has been recently used in similar contexts (e.g., Heino and Tolonen, 2017), one has to keep in mind that taxonomic distances are only proxies of true phylogenetic relatedness and may thus provide inadequate information about phylogenetic beta diversity. However, they do describe coarse patterns in phylogenetic relatedness and can thus be highly useful in broad-scale analyses.

2.3. Explanatory variables

To test the importance of the environmental filtering, two sets of factors related to the energy hypothesis and the habitat availability hypothesis were considered separately (Supplementary material Appendix 3). Typically, energy can regulate biodiversity of consumers by two rather different processes: (1) resources available (i.e. productive energy) for a given assemblage and (2) the physiological limits of the species (i.e. ambient energy) (Field et al., 2009). Here, four common energy variables were considered: annual normalized difference vegetation index (NDVI), mean annual temperature (MAT), mean annual precipitation (MAP) and solar radiation (SOLAR). For testing habitat availability hypothesis, catchment area (CAREA) and water area (WAREA) of each watershed were used (Table 1).

Similarly, to test the role of spatial processes, two types of variables (continuous geographical location and discontinuous geographical groupings) were considered individually (Table 1). At broad scales, beta diversity patterns often vary along a geographical gradient, implying dispersal limitation (Heino, 2011). Here, longitude (LON), latitude (LAT) and altitude (ALT) were considered as one group of variables to distinguish the role of linear and altitudinal geographical gradients from other mechanisms. On the other hand, regional geographical barriers (e.g., insurmountable high mountains) are important factors associated with dispersal processes of freshwater organisms (Schleuter

et al., 2012). We considered two predictors reflecting geographical isolation: (1) region unit identity (RUI), i.e., hydrographic region to which each watershed belongs (Fig. 1); and (2) the degree of watershed isolation characterized by whether or not it is on the land mass, a peninsula or an island (LPI; continental mass = 0; peninsula = 1; island = 2) (Tisseuil et al., 2013).

2.4. Statistical analyses

2.4.1. Measurement of different facets beta diversity

Here, we focused on the overall beta diversity since the nestedness component was minor for β -TD, and there was a similarly very small contribution of the turnover component to β -FD and β -PD. Taxonomic Sorensen dissimilarity matrix among watersheds was calculated in representing β -TD using the function “beta.pair” in the R package *betapart* (Baselga et al., 2017).

To calculate functional dissimilarity matrix, we used the following method proposed by Villéger et al. (2013). We first calculated a trait distance matrix between species based on Gower distance, and then generated Principal Coordinates Analysis (PCoA) trait vectors based on the distance matrix. Gower distance was calculated using the function “gowdis” in the R package FD (Laliberté et al., 2015) and PCoA using the function “pcoa” in the R package *ape*. Mantel analysis showed that Euclidean distance matrix based on the first two functional PCoA vectors was highly correlated to the original trait Gower distance matrix ($r = 0.97$, $p < 0.001$); hence, the first two PCoA vectors were used in the calculation of convex hull volumes shaping any two assemblages in functional space. Then, functional Sorensen dissimilarity matrix was calculated based on site-by-species matrix and functional traits (two PCoA trait vectors) using the function “functional.beta.pair” from the R package *betapart* (Baselga et al., 2017).

We produced phylogenetic dissimilarity matrix using a similar method as for functional beta diversity, but now based on taxonomic distance as proxy for phylogenetic distance. Taxonomic distance between species was calculated using the function “taxa2dist” from the R package *vegan* (Oksanen et al., 2016). Then, the resulting taxonomic distance matrix was used to calculate phylogenetic vectors based on the function “pcoa” in the R package *ape*. Similarly, Euclidean distance matrix based on the first two phylogenetic PCoA vectors also correlated strongly with the original taxonomic distance matrix (Mantel $r = 0.91$, $p < 0.001$). Last, phylogenetic Sorensen dissimilarity matrix was produced based on site-by-species matrix and the two phylogenetic PCoA vectors using the function “functional.beta.pair”.

Spatial congruence between different diversity facets (i.e., dissimilarity matrices) was evaluated using multiple regression on distance matrices, indicated by coefficient of determination. Since the beta diversity indices were dissimilarity matrices, they cannot be used directly as response variables in diversity mapping, constrained ordination and multivariate regression trees. Therefore, we performed a PCoA on each dissimilarity matrix. To deal with negative eigenvalues in the PCoA, a Cailliez correction was used (Cailliez, 1983). The final product is three matrices of orthogonal PCoA eigenvectors, representing β -TD, β -FD and β -PD, respectively (Gianuca et al., 2018).

2.4.2. Mapping beta diversity

To visualize the spatial variation in each beta diversity facet, the scores from the first three PCoA axes were used to assign RGB color values to individual watersheds. The first three axes of PCoA were highly correlated with the original PCoA eigenvectors matrix (Mantel $r: 0.92$ to 0.99 , $p < 0.001$), indicating good representative of beta diversity. The axes 1, 2 and 3 scores were individually rescaled to a range between 0 and 1, and were projected into red-green-blue color space (Thessler et al., 2005). The resulting image can thus be viewed as a color map, in which watersheds of more similar colors have a more similar taxonomic, functional and phylogenetic structure.

Table 1
The explanatory variables used to test for the different hypotheses.

Category	Variables	Abbreviation
Energy	Mean annual temperature (°C)	MAT
	Mean annual precipitation (mm)	MAP
	Solar radiation (W·h/m ² /day)	SOLAR
	Annual normalized difference vegetation index	NDVI
Habitat availability	Catchment area of each watershed (km ²)	CAREA
	Water area within each watershed (km ²)	WAREA
Geographical location	Longitude (°)	LON
	Latitude (°)	LAT
	Altitude (m)	ALT
Geographical isolation	Hydrographic region unit identity	RUI
	Land Peninsula Island	LPI

2.4.3. Determinants of beta diversity

Two methods, redundancy analysis (RDA) in combination with variation partitioning (Peres-Neto et al., 2006) and multivariate regression tree (MRT) analyses (De'ath, 2002), were used to disentangle the drivers of beta diversity patterns. As measures of beta diversity, we used the PCoA eigenvectors representing β -TD, β -FD and β -PD (see above).

For final variation partitioning analysis, we first selected predictor variables in the RDA models of each set of explanatory variables using a conservative forward selection method (Blanchet et al., 2008). Forward selection was conducted with two stopping rules: either exceeding the critical p value ($p = 0.05$) or the adjusted R^2 value of the reduced model exceeded that of the global model. This procedure was employed using the function “ordiR2step” in the R package *vegan* (Oksanen et al., 2016). We next used variation partitioning to reveal the pure and shared effects of the four explanatory variable groups on each beta diversity facet (Peres-Neto et al., 2006). Variation partitioning analyses were conducted using the function “varpart”. Adjusted R^2 values were reported, which are unbiased estimates of explained variation since they are corrected for the number of explanatory variables (Peres-Neto et al., 2006).

To evaluate the hierarchical importance of ecological factors in structuring beta diversity patterns, we employed the MRT analysis (De'ath,

2002). MRT, a method of constrained clustering, forms clusters of watersheds by repeatedly splitting the watersheds into two homogenous groups. At each split, the explanatory variable was selected to minimize the dissimilarity of watersheds within each group. MRT finally produces a tree whose terminal watershed groups (i.e. leaves) are composed of subsets of watersheds that are formed to minimize the within-group sums of squares. Each successive splitting of data is defined by a threshold value or a state of one of the explanatory variables. This method is particularly useful as it can deal with a wide variety of situations, such as both continuous and categorical explanatory variables, and nonlinear assemblage–environment relationships. Two criteria we applied to prune the fine tree: (1) constrained partitioning of the data, and (2) cross-validation of the results (De'ath, 2002). Here, we chose the ‘best’ tree with the minimum cross-validated error (CVRE, 1000 times). MRTs were constructed using the R package *mvpart* (Therneau and Atkinson, 2012) and *MVPARTwrap* (Ouellette and Legendre, 2012).

Detailed analytical procedures of the measurements and drivers of beta diversity can be found in Fig. 2 and Figs. A4, A5, A6. Furthermore, to evaluate the effects of sampling efforts on the results, the watersheds with NOL <6 were arbitrarily defined as undersampled watersheds. Additional RDA and variation partitioning analyses were performed based the sub-dataset (167 watersheds) after removing undersampled watersheds. The results were compared with those based on all watersheds.

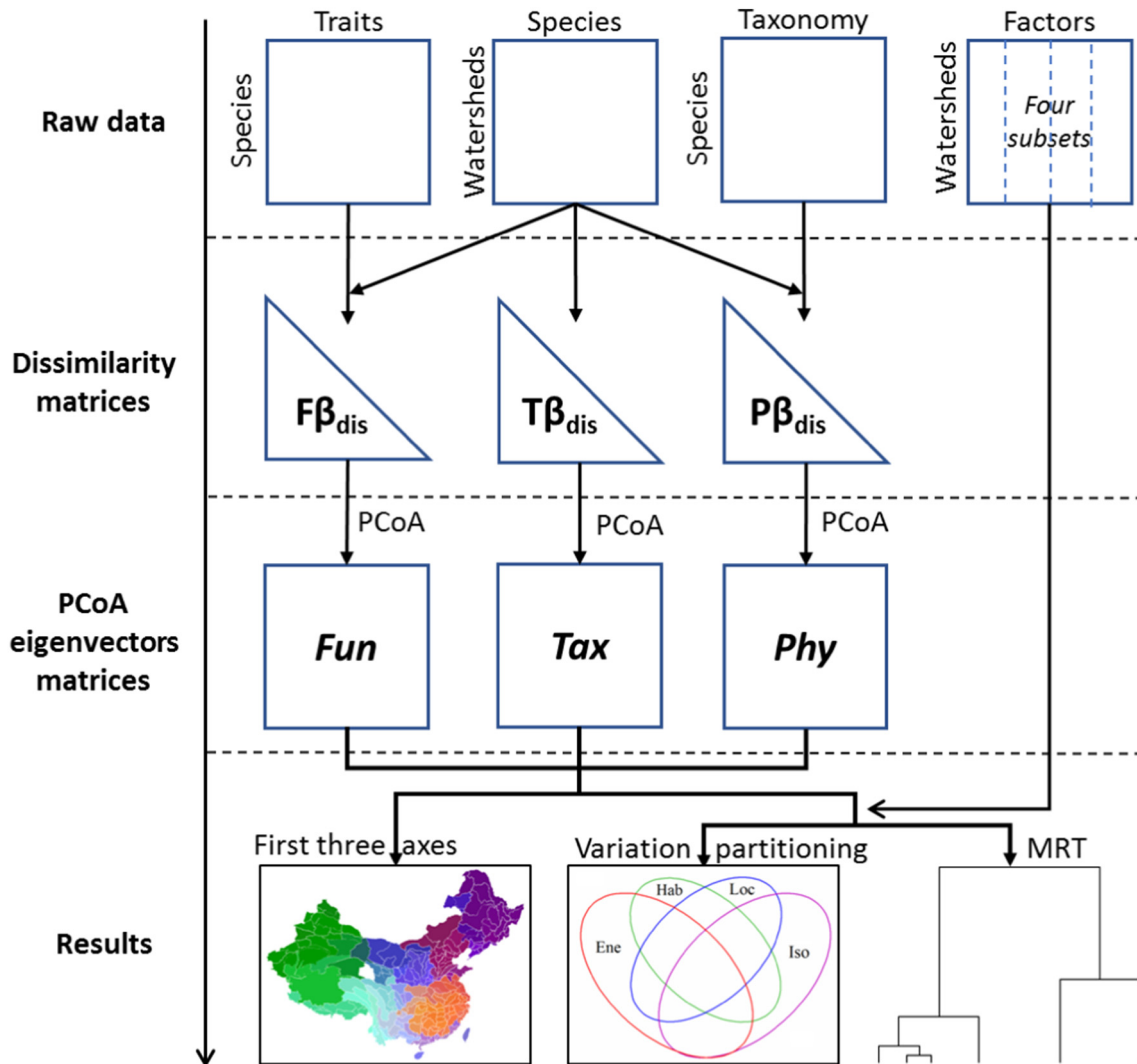


Fig. 2. A brief flow chart of the statistical analyses sequence employed in this study. For detailed descriptions and procedures, see the main text and Figs. A4, A5, A6. Abbreviations: $T\beta_{dis}$, $F\beta_{dis}$ and $P\beta_{dis}$ represent taxonomic, functional and phylogenetic dissimilarity matrices among watersheds, respectively; Tax, Fun and Phy represent taxonomic, functional and phylogenetic PCoA eigenvectors' matrices, respectively.

3. Results

3.1. Geographical patterns of beta diversity

Average between-watershed dissimilarities varied considerably among the three facets. While the β -TD median value was 0.67 (max: 0.97), and the β -FD median value was 0.09 (max: 0.51), the β -PD median value was 0.02 (max: 0.06). Overall, all three facets of beta diversity were significantly positively related to each other: β -TD vs. β -FD ($R^2 = 0.357$, $p < 0.001$); β -TD vs. β -PD ($R^2 = 0.361$, $p < 0.001$); β -FD vs. β -PD ($R^2 = 0.343$, $p < 0.001$, Fig. A7). These results showed, however, that over 60% of the variation in one facet remained unexplained by any other diversity facet.

Beta diversity maps revealed substantial geographical variation in taxonomic, functional and phylogenetic composition across China. Overall, geographical pattern of β -TD was well matched with hydrographic regions' boundaries, as evidenced by the distinct assemblage types between regions, while having highly similar composition within each of them (Fig. 3a). Similarly, β -PD also presented several distinct 'evolutionary assemblage types' distributed across China, with the watersheds of the same hydrographic region usually being spatially structured (Fig. 3c). In contrast, β -FD presented at best moderate spatial aggregation, with some watersheds similar with functional composition being patchily distributed among different hydrographic regions (Fig. 3b). Notably, the two islands, Hainan and Taiwan, usually showed distinct assemblage structure compared with neighboring mainland watersheds for all beta diversity facets.

3.2. Variation partitioning

The total percentage of variations in beta diversity explained were similar between β -TD ($R^2 = 48.7\%$) and β -PD ($R^2 = 49.3\%$), and lower for β -FD ($R^2 = 31.1\%$) (Fig. 4). In all the three diversity facets, the observed variations were best explained by geographical isolation (26.5%–43.6%), followed by geographical location (20.5%–37.2%) and energy variables (18.0%–37.6%). Habitat availability variables only accounted for 5.1% and 2.7% of β -TD and β -FD, respectively, while they were not important in explaining variation in β -PD (Table A2). Of the unique effects (Fig. 4), geographical isolation variables were clearly the most important ones (6.9%–13.9%), while other unique fractions only explained a small amount of the total variations (0.2%–3.4%). Clearly, there was a large amount of shared effects (20.8%–30.8%) among energy, geographical location and isolation variables in explaining all beta diversity facets, which typically overcame the unique effects of each variable group. Moreover, geographical location and isolation variables also jointly explained considerable amounts of the variations (2.8%–7.8%).

Of the variables selected in the final RDA models, highly similar sets of significant variables were observed for all beta diversity facets (Table A2). Generally, almost all of the three sets of variables (excluding habitat availability variables) were retained in the forward selection with similar order. The results of variation partitioning for well-sampled watersheds were similar to those of all watersheds, with the explained variation increasing slightly (Table A3, Fig. A8).

3.3. Multivariate regression tree

The final MRT of β -TD comprised 15 nodes and 16 leaves, and explained 60% of variation in total (Fig. 5). The first node was related to the categorical variable RUI, which explained 14.22% of the variation. Of the remaining 14 nodes, nine of them were related to geographical location (six were related to longitude), three were related to MAP and two were related to RUI. Generally, longitude was an important contributor to the few first several nodes, accounting for 2.43% to 10.43% of the variation, while MAP was responsible for the last nodes and only explained 1.14% to 1.28% of the variation.

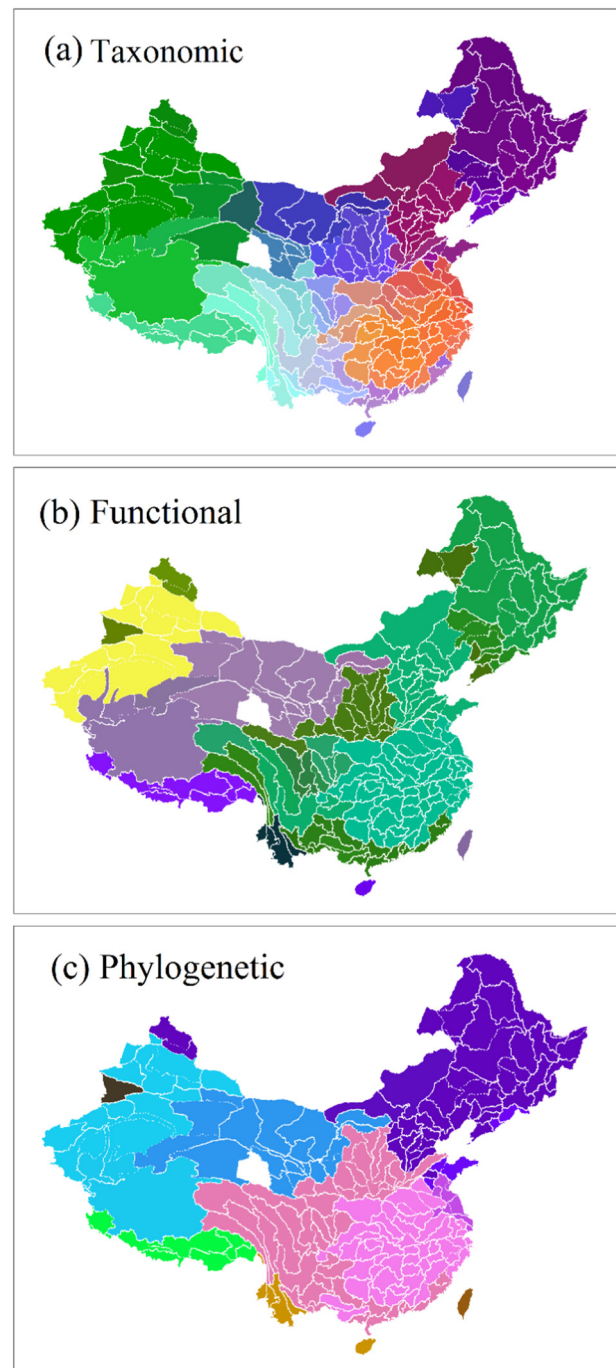


Fig. 3. Maps of beta diversity among watersheds across China for different facets: (a) taxonomic; (b) functional; (c) phylogenetic. Similar colors indicate similar composition for each facet of beta diversity. White color: no data.

For β -FD, MAP was associated with the strongest breakpoint and alone accounted for 15.87% of variation, followed by RUI (5.29%), longitude (1.39%, 2.96%), latitude (1.71%, 2.64%) and altitude (2.44%). These other variables had much weaker contributions to the total explained variation of 32.3% than MAP (Fig. 6).

For β -PD, there were five nodes in the final MRT which accounted for 54.3% of variation (Fig. 7). Only two geographical location variables, latitude and longitude, were selected as best predictors. The first node was related to latitude (31.07%), accounting for over half of the total explained variation. The second and the third nodes were both related to

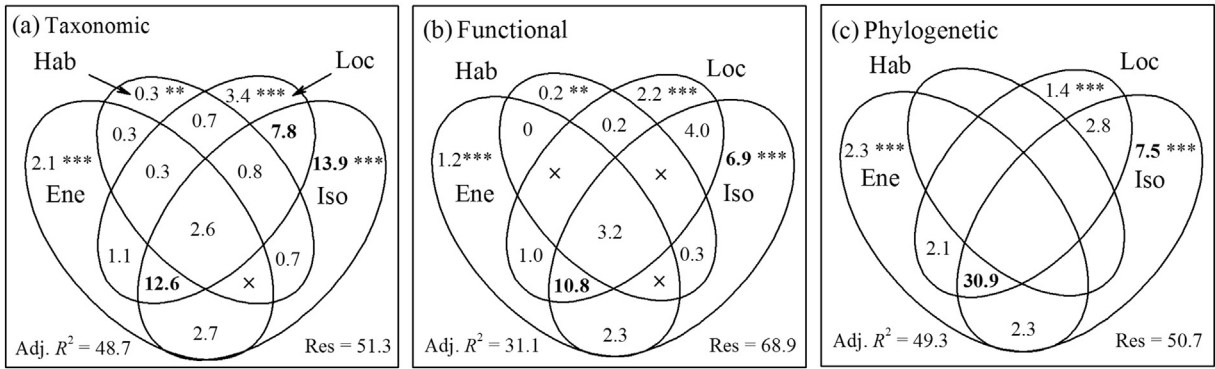


Fig. 4. Results of variation partitioning, illustrating the contributions of different factors to (a) taxonomic, (b) functional, and (c) phylogenetic beta diversity. All fractions are based on adjusted R_2 values shown as percentages of total variation. The significance of unique fractions was tested based on 999 permutations (**, $p < 0.01$; ***, $p < 0.001$). The components higher than 5% are in bold font. Negative values are shown as “x”. Total adjusted R_2 and residuals (Res) are shown in the lower left and right corners, respectively. Abbreviations: Ene = energy; Hab = habitat availability; Loc = geographical location; Iso = Geographical isolation.

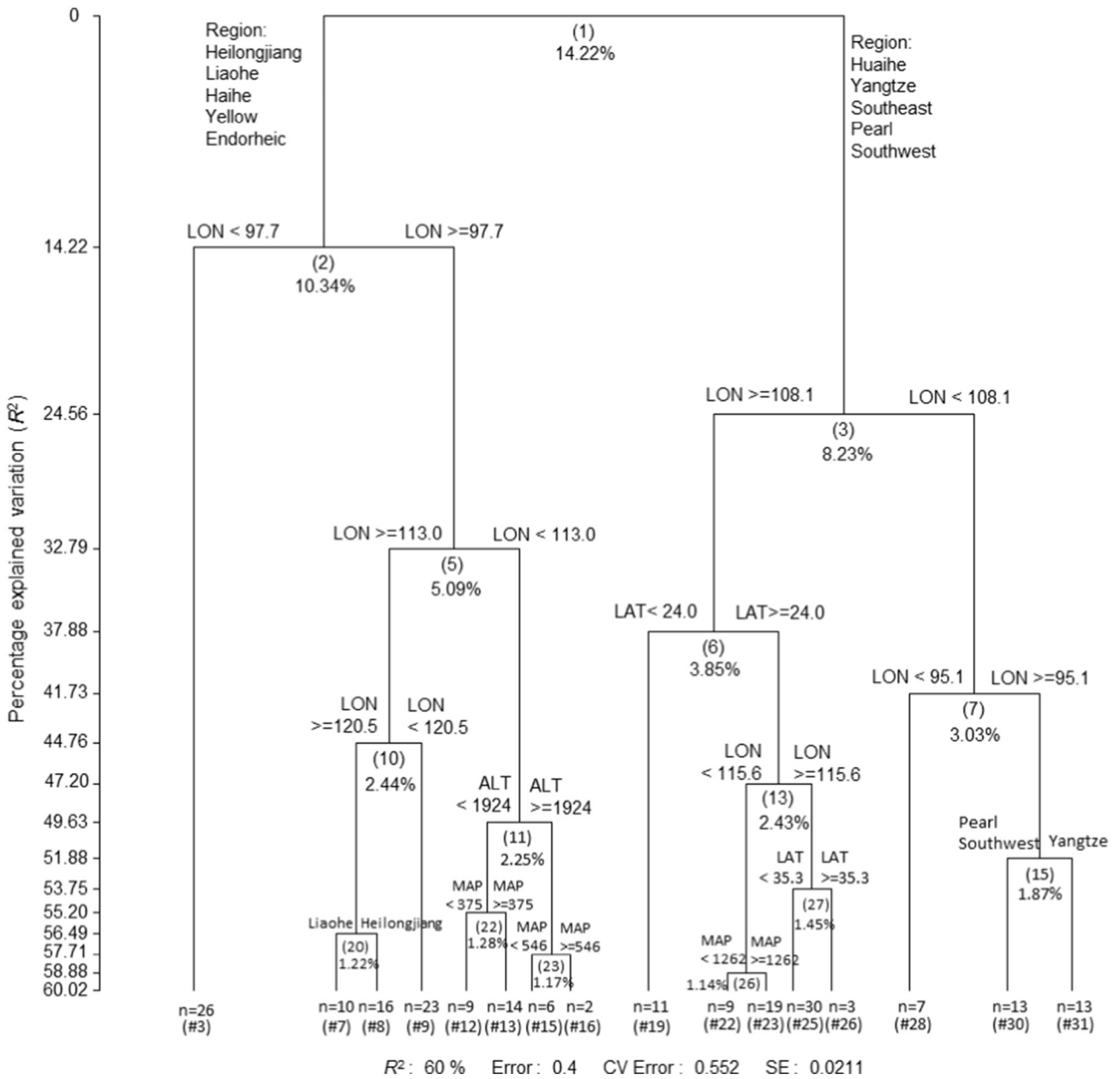


Fig. 5. Multivariate regression tree of taxonomic beta diversity. The percentage of improvement in model performance given by each node, the environmental variable discriminating each node and the threshold are shown. Numbers at the bottom of the tree indicate the number of watersheds classified at each leaf. CV Error = cross-validated mean error; SE = standard error. For abbreviations of explanatory variables, see Table 1.

longitude, which accounted for 7.78% and 10.68% of variation, respectively. The fourth (2.75%) and ninth nodes (2.05%) were weak contributors to the total explained variation.

4. Discussion

4.1. Beta diversity patterns and their spatial congruence

Our results showed that β -TD, β -FD and β -PD of freshwater molluscan assemblages across China were only moderately congruent. Over 60% of the variation in one facet cannot be predicted by any other facet. Increasing numbers of studies showed that the relationships between the three facets diversity are very complex, which are dependent on spatial scale, geographical isolation, environmental gradients and dispersal capacities of organisms (Graham and Fine, 2008; Tucker and Cadotte, 2013; Monnet et al., 2014). Generally, broad spatial extent, high degrees of isolation, strong environmental gradients and limited dispersal ability may weaken the degree of congruence (Graham and Fine, 2008; Tucker and Cadotte, 2013). In this regard, it is not surprising that only moderate congruence was observed since we focused on molluscs with weak dispersal ability across geographically and environmentally heterogeneous China.

Weinstein et al. (2014) proposed eight possible combinations of high versus low β -TD, β -FD and β -PD between assemblages. In some cases, β -TD, β -FD and β -PD are congruent (i.e., all low or all high) across a region due to phylogenetic constraints on niche and trait evolution (Mouquet et al., 2012; Srivastava et al., 2012). Specifically, biological assemblages in similar environments with no or weak dispersal limitation will lead to low β -TD, low β -FD and low β -PD, while assemblages in distinct environments isolated by geographic and historical barriers will result in a pattern of high β -TD, high β -FD, and high β -PD. Both these two types of patterns will appear as high between-facet congruence. However, different beta diversity facets may be more likely to be decoupled. Weinstein et al. (2014) pointed out that the decoupling associated with β -PD to be most influenced by historical connectivity or environmental stability, and decoupling associated with β -FD resulting from environmental filtering. For example, recent geographic isolation of historically connected (i.e., short evolutionary time) assemblages in similar environments may result in high β -TD, low β -FD and low β -PD. Likewise, if these assemblages are recent and historically geographically isolated, they may contain long branch lengths among species, leading to high β -TD and high β -PD but low β -FD due to convergent adaptation of traits to environmental factors (Graham and Fine, 2008; Weinstein et al., 2014). Although we did not evaluate the relative prevalence of the eight combinations in our study, comparison of beta diversity maps revealed substantially consistent and inconsistent geographical variations of taxonomic, functional and phylogenetic structure of freshwater molluscan fauna across China. For example, we indeed found that some molluscan assemblages within a hydrographic region (e.g., Yangtze River Basin) presented high similarities of taxonomic, functional and phylogenetic structure (Fig. 3), implying low beta diversity among these assemblages based on all the three facets. Correspondingly, some assemblages belonging to distant and isolated hydrographic regions (e.g., endorheic region vs. Yangtze River Basin) demonstrated strong divergence, resulting in high beta diversity of the three facets. These concurrent changes may contribute to the observed moderate congruence. On the other hand, considerable inconsistent geographical variations in taxonomic, functional and phylogenetic structure were also evidenced in beta diversity maps (Fig. 3). For instance, some assemblages with similar functional structure were patchily distributed in geographically isolated watersheds that differed greatly in species identity and evolutionary relatedness. Hence, such various inconsistent changes may be responsible for the high amount of unexplained variation in the relationships between different beta diversity facets.

4.2. Relative importance of environmental filtering and dispersal processes

In line with our first hypothesis, we found that environmental and spatial factors jointly shaped the three facets of beta diversity, with considerable shared components of energy, geographical location and isolation variables. This finding is not surprising since energy gradients are often spatially structured at broad scales. Moreover, geographical isolation variables (mainly due to hydrographic region identity) played a large role with considerable unique fractions, implying dispersal limitation may have a strong effect on the three beta diversity facets. In this study, the large hydrographic regions (of which six are large river basins) are often strongly separated from each other by barriers (i.e. mountains, dry land or seawater) and are therefore similar to the large river basins or biogeographic realms in previous studies (Schleuter et al., 2012; Tisseuil et al., 2013). Thus, the 10 hydrographic regions are highly independent entities that present formidable barriers for freshwater molluscs, and can be considered as 'biogeographical islands' which constrain dispersal among regions (Hugueny et al., 2010; Schleuter et al., 2012). In this context, dispersal effects via watercourses are more likely happen within such hydrographic regions than among them, as evidenced by the strong matches between beta diversity maps and hydrographic regions' boundaries, especially for β -TD and β -PD. The hydrographic regions thus define a species pool from which watershed-level assemblages are drawn. Interestingly, β -FD was also more related to dispersal limitation than environmental filtering, contrasting with the general contention that functional structure should be weakly related to dispersal processes (Heino et al., 2013). One probable reason was that the dispersal capacities of molluscs are dependent on some important traits (e.g., body size, reproduction mode). Specifically, freshwater molluscs in our study generally include two groups of species with different dispersal capacities, i.e. large bivalves with glochidia, and the small bivalves and gastropods combined. The former are mostly spread by fish via water courses, while the latter group can be more effectively dispersed by active vectors such as water birds, amphibians and mammals (Kappes and Haase, 2011). On the other hand, some functional traits may also be evolutionarily conserved, i.e., closely-related species have more similar traits (Webb et al., 2002). Our results agree with two previous studies (Meynard et al., 2011; Arnan et al., 2015), suggesting that dispersal limitation strongly structures patterns of β -TD, β -FD, and β -PD in western and central European communities and French bird communities, respectively. Dispersal limitations are potentially much more important in freshwater molluscs than in terrestrial organisms (e.g. ants and birds). Accordingly, we found a stronger effect of spatial variables on the beta diversity of freshwater molluscs. For these reasons, it is reasonable that all the three diversity facets were more influenced by dispersal limitation. Furthermore, β -FD responded less strongly to geographical isolation than either β -TD or β -PD did, which moderately supported our second hypothesis. This finding is not surprising due to the fact that functional traits of a species mainly regulate whether it will successfully overcome multi-scale environmental filters (Pavoine and Bonsall, 2011; Heino et al., 2013).

The energy variables used here were strongly correlated to the three beta diversity facets. These results corroborate the energy hypothesis that has been extensively documented at large scales (Meynard et al., 2011; Barton et al., 2013), and it has been linked to energetic constraints as well as to environmental filtering at the assemblage level. MAP, often positively correlated with the diversity of flow regime and habitats, was the most important variable first entered into the RDA models. This finding agrees with the results of Kang et al. (2014) and MCGarvey and Terra (2016), who found that factors related to flow regime are the primary drivers shaping fish diversity and assemblage composition. MAT and NDVI also explained a considerable amount of the variation in the three beta diversity facets. The results are not surprising since the two factors are strongly coupled with genetic divergence, speciation and species coexistence (Whittaker et al., 2001). We found only weak

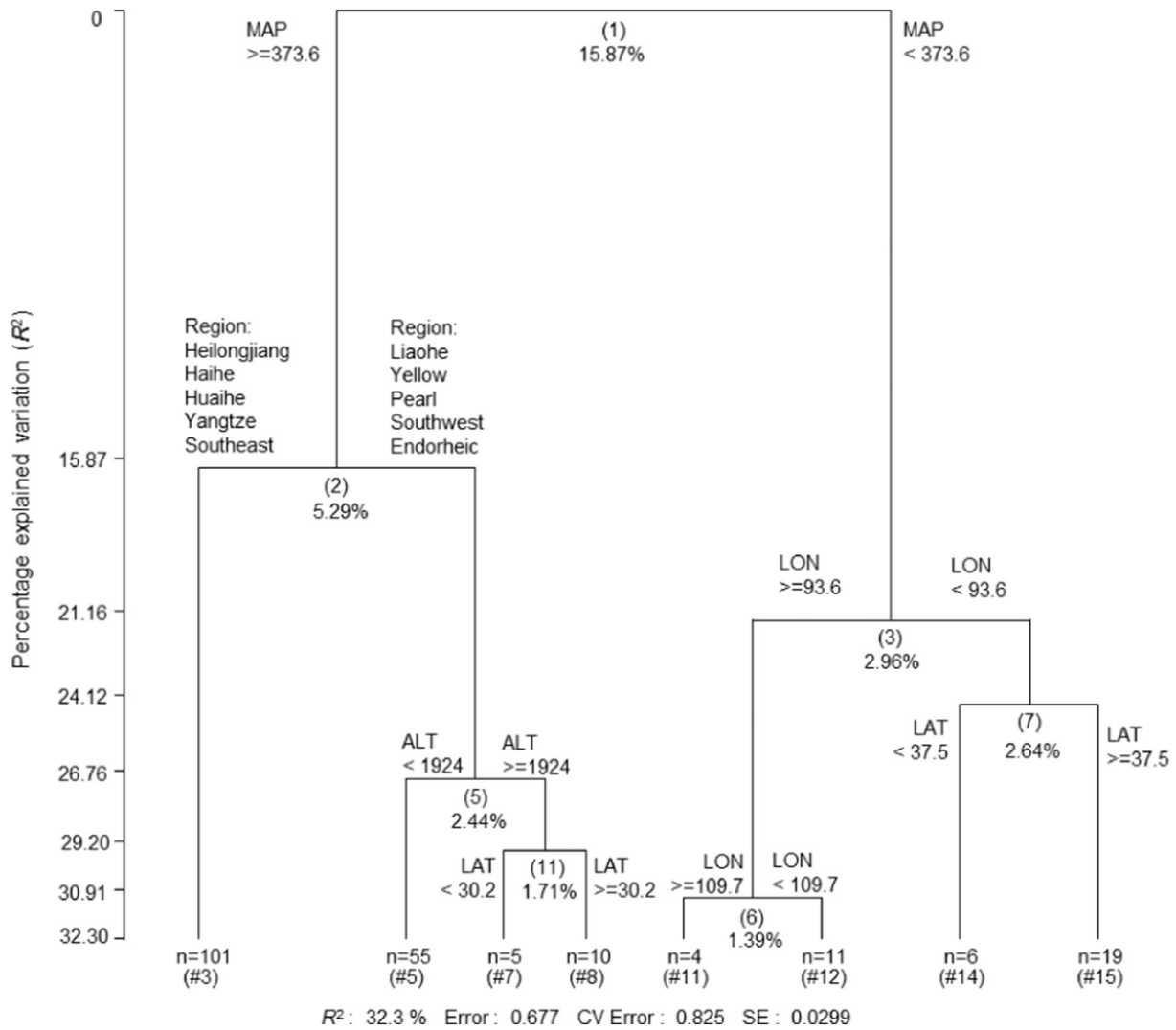


Fig. 6. Multivariate regression tree of functional beta diversity. The percentage of improvement in model performance given by each node, the environmental variable discriminating each node and the threshold are shown. Numbers at the bottom of the tree indicate the number of watersheds classified at each leaf. CV Error = cross-validated mean error; SE = standard error. For abbreviations of explanatory variables, see Table 1.

evidence for the habitat availability hypothesis, with area variables only explaining a small amount of the variation in β -TD and β -FD. A possible reason might be that catchment area and water area are not good surrogates of the diversity and total amounts of habitats available for freshwater molluscs. In more detail, different freshwater systems such as lakes, wetlands, rivers and streams play different roles in maintaining freshwater biodiversity (Dehling et al., 2010). In this context, lack of these data may weaken the role of habitat availability hypothesis in our study.

In community ecology, biogeography and macroecology, it is well established that beta diversity is regulated by many hierarchical coexistence mechanisms, with their importance being highly dependent on spatial scale (Barton et al., 2013). Moreover, the beta diversity scaling relationships also vary widely across disparate organism groups (Hortal et al., 2015). The results of the MRT analyses showed that the scale-dependence of drivers shaping beta diversity may also vary greatly for different beta diversity facets. Specifically, we found that geographical isolation and location variables were important in driving β -TD at national and broad regional scales and accounted for 56.41% of the variation, whereas one energy variable (i.e., MAP) only explained 3.59% of the variation of smaller sets of watersheds. Also, it has to be noted that only geographical location variables were selected in the

MRT of β -PD. These results reinforce the findings of variation partitioning that dispersal limitation plays a preponderant role in structuring β -TD and β -PD. In contrast, β -FD at national scale was best explained by MAP that was also strongly related to geographical location at various minor nodes of the MRT analysis, and presented almost equal contributions (15.87% vs. 16.43%). The results indicated that environmental filtering and dispersal limitation jointly shape the β -FD of molluscan assemblages across China. This reasoning was strongly supported by the β -FD map that matched well with some hydrographic regions, but functional assemblage types were sometimes patchily distributed (Fig. 3).

In common with macroecological studies in general, the sampling bias among watersheds may weaken the strength of our findings. Overall, our data were geographically biased towards eastern China owing to the fact that most scientific studies tend to focus on specifically selected or relatively easily accessible regions. We, however, believe that this spatial sampling bias does not account for the high power in the variation partitioning and MRT analyses because the ecological drivers were highly plausible as evidenced by the beta diversity maps. Also, we found almost the same results after removing undersampled watersheds, suggesting that any potential sampling bias in the entire dataset did not affect beta diversity patterns and our understanding of the

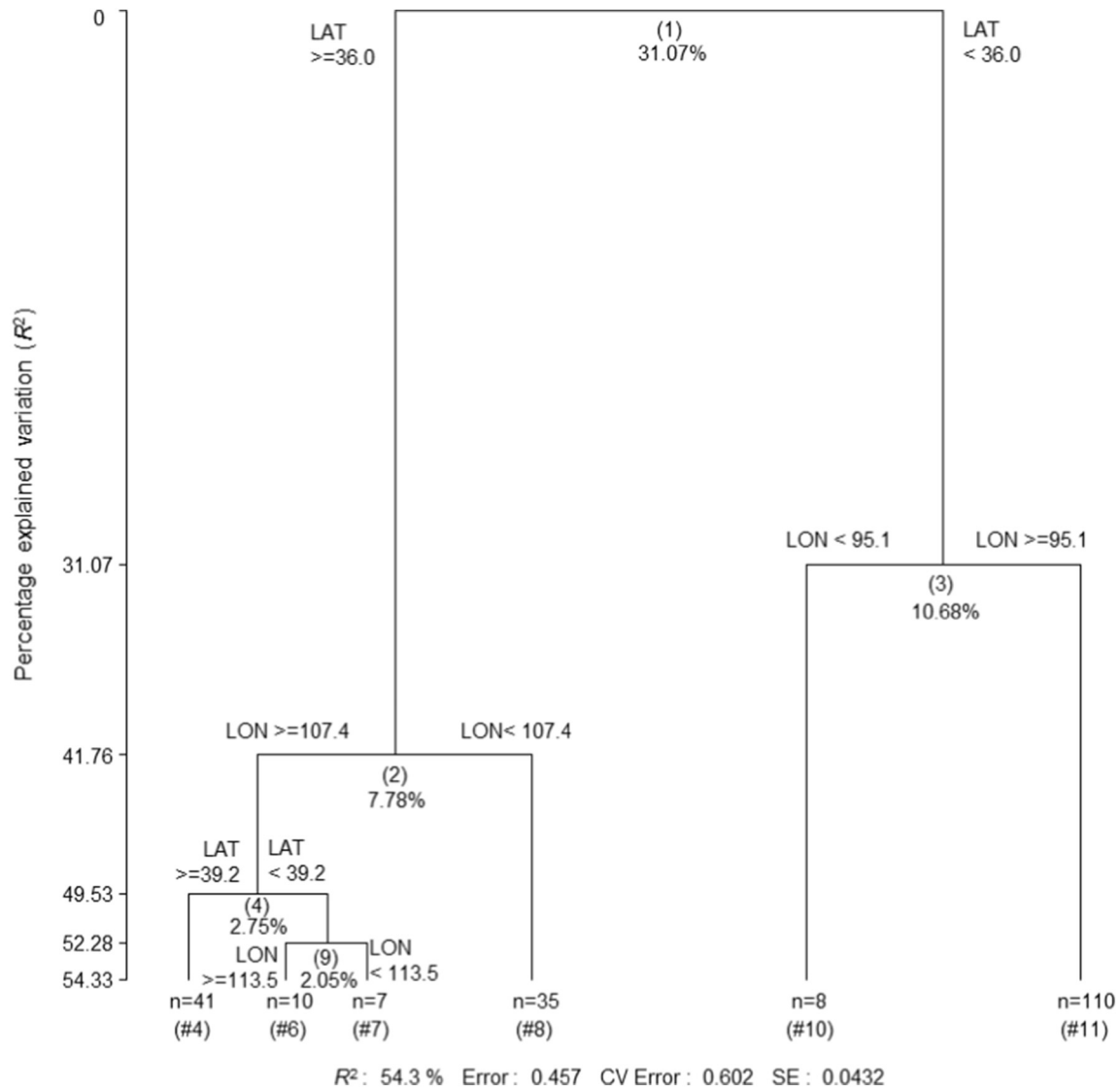


Fig. 7. Multivariate regression tree of phylogenetic beta diversity. The percentage of improvement in model performance given by each node, the environmental variable discriminating each node and the threshold are shown. Numbers at the bottom of the tree indicate the number of watersheds classified at each leaf. CV Error = cross-validated mean error; SE = standard error. For abbreviations of explanatory variables, see Table 1.

underlying mechanisms. Additionally, lack of true phylogeny is a drawback of this work, which might weaken the robustness of the findings for phylogenetic beta diversity (Schweiger et al., 2008).

5. Conclusions

Overall, we found that molluscan beta diversity patterns across all of China, whether β -TD, β -FD, or β -PD, were jointly driven by environmental filtering and spatial factors. However, spatial factors related to dispersal processes played a more prominent role as evidenced by strong spatial matches between beta diversity maps and hydrographic regions' boundaries, in particular for β -TD and β -PD. Environmental filtering was mainly associated with energy gradients, while the habitat availability hypothesis was only weakly supported. Moreover, the relative importance of different mechanisms varied greatly among different facets of beta diversity. Specially, at the national scale, β -TD and β -PD were more related to dispersal limitation, while β -FD was rather strongly regulated by energy gradients. Different hydrographic regions harbor distinct assemblages suggests that dispersal limitation may be an important driver of molluscan beta diversity. The results indicate that conservation networks could better focus on multiple spatially

disjunct reserves over China to maximize conservation of total biodiversity. Lastly, the result of moderate spatial congruence among different diversity facets urges paying attention to the conservation dilemma of which facet should be favored (Devictor et al., 2010). Since β -TD was weakly congruent with β -FD and β -PD, it is critically important to re-examine the performance of existing reserve networks in protecting multiple diversity facets of freshwater molluscs and other organisms. We also suggest that how different facets of biodiversity relate to each other should be incorporated into conservation planning, with a view to clarify when and where functional and phylogenetic need to be considered. For example, beta diversity patterns may be used to identify variations in taxonomic, functional and phylogenetic assemblage structures among hydrographic regions and watersheds, while more specific gamma and alpha diversity patterns may be used to highlight the watersheds showing particularly high levels of biodiversity and facilitating conservation decisions (Socolar et al., 2016).

Acknowledgements

We are grateful to Yingying Chen, Yi Yang, Xiaohu Huang for data compiling and to Kai Peng for assistance in drawing beta maps. This

work was supported by the National Key R&D Program of China (2018YFD0900904), the National Natural Science Foundation of China (31670466), the Major Science and Technology Program for Water Pollution Control and Treatment (2017ZX07301-001), Key Research Program of Frontier Sciences, Chinese Academy of Sciences (QYZDB-SSW-DQC043) and the Science and Technology Service Network Initiative Project of Chinese Academy of Sciences (KFJ-STS-ZDTP-011).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.12.373>.

References

- Arnan, X., Cerda, X., Retana, J., 2015. Partitioning the impact of environment and spatial structure on alpha and beta components of taxonomic, functional, and phylogenetic diversity in European ants. *PeerJ* 3, e1241.
- Arnan, X., Cerda, X., Retana, J., 2017. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. *Ecography* 40, 448–457.
- Barton, P.S., Cunningham, S.A., Manning, A.D., Gibb, H., Lindenmayer, D.B., Didham, R.K., 2013. The spatial scaling of beta diversity. *Glob. Ecol. Biogeogr.* 22, 639–647.
- Baselga, A., Orme, D., Villeger, S., de Bortoli, J., Leprieux, F., 2017. betapart: partitioning beta diversity into turnover and nestedness components. R package version 1.4-1. <http://CRAN.R-project.org/package=betapart>.
- Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. *Ecology* 89, 2623–2632.
- Bohonak, A.J., Jenkins, D.G., 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecol. Lett.* 6, 783–796.
- Cailliez, F., 1983. The analytical solution of the additive constant problem. *Psychometrika* 48, 305–308.
- Chytrý, M., Lososová, Z., Horská, M., Uher, B., Čejka, T., Danihelka, J., Fajmon, K., Hájek, O., Juříčková, L., Kintrová, K., Láňková, D., Otyčková, Z., Řehořek, V., Tichý, L., 2012. Dispersal limitation is stronger in communities of microorganisms than macroorganisms across Central European cities. *J. Biogeogr.* 39, 1101–1111.
- Cilleros, K., Allard, L., Grenouillet, G., Brosse, S., 2016. Taxonomic and functional diversity patterns reveal different processes shaping European and Amazonian stream fish assemblages. *J. Biogeogr.* 43, 1832–1843.
- Clarke, K., Warwick, R., 1998. A taxonomic distinctness index and its statistical properties. *J. Appl. Ecol.* 35, 523–531.
- Colin, N., Villéger, S., Wilkes, M., De Sostoa, A., Maceda-Veiga, A., 2018. Functional diversity measures revealed impacts of non-native species and habitat degradation on species-poor freshwater fish assemblages. *Sci. Total Environ.* 625, 861.
- De'ath, G., 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology* 83, 1105–1117.
- Dehling, D.M., Hof, C., Brändle, M., Brandl, R., 2010. Habitat availability does not explain the species richness patterns of European lentic and lotic freshwater animals. *J. Biogeogr.* 37, 1919–1926.
- Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.* 13, 1030–1040.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81, 163–182.
- Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Turner, J.R.G., 2009. Spatial species-richness gradients across scales: a meta-analysis. *J. Biogeogr.* 36, 132–147.
- Gianuca, A.T., Declerck, S.A.J., Cadotte, M.W., Souffreau, C., De Bie, T., De Meester, L., 2017. Integrating trait and phylogenetic distances to assess scale-dependent community assembly processes. *Ecography* 40, 742–752.
- Gianuca, A.T., Engelen, J., Brans, K.I., Hanashiro, F.T.T., Vanhamel, M., van den Berg, E.M., Souffreau, C., Meester, L.D., 2018. Taxonomic, functional and phylogenetic metacommunity ecology of cladoceran zooplankton along urbanization gradients. *Ecography* 41, 183–194.
- Graham, C.H., Fine, P.V., 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecol. Lett.* 11, 1265–1277.
- Heino, J., 2011. A macroecological perspective of diversity patterns in the freshwater realm. *Freshw. Biol.* 56, 1703–1722.
- Heino, J., Tolonen, K.T., 2017. Ecological drivers of multiple facets of beta diversity in a lentic macroinvertebrate metacommunity. *Limnol. Oceanogr.* 62, 2431–2444.
- Heino, J., Schmera, D., Erős, T., 2013. A macroecological perspective of trait patterns in stream communities. *Freshw. Biol.* 58, 1539–1555.
- Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., Ladle, R.J., 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu. Rev. Ecol. Syst.* 46, 523–549.
- Hugueny, B., Oberdorff, T., Tedesco, P.A., 2010. Community ecology of river fishes: a large-scale perspective. *Am. Fish. Soc. Symp.* 73, 29–62.
- Jourdan, J., O'Hara, R.B., Bottarin, R., Huttunen, K.L., Kuemmerlen, M., Monteith, D., Muotka, T., Ozoliņš, D., Paavola, R., Pilotto, F., 2017. Effects of changing climate on European stream invertebrate communities: a long-term data analysis. *Sci. Total Environ.* 621, 588.
- Kang, B., Deng, J., Wu, Y., Chen, L., Zhang, J., Qiu, H., Lu, Y., He, D., 2014. Mapping China's freshwater fishes: diversity and biogeography. *Fish. Fish.* 15, 209–230.
- Kappes, H., Haase, P., 2011. Slow, but steady: dispersal of freshwater molluscs. *Aquat. Sci.* 74, 1–14.
- Laliberté, E., Legendre, P., Shipley, B., 2015. FD: measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. Package 1.0-12. <https://CRAN.R-project.org/package=FD>.
- Lopes-Lima, M., Sousa, R., Geist, J., Aldridge, D.C., Araujo, R., Bergengren, J., Bessalaya, Y., Bodis, E., Burlakova, L., Van Damme, D., Douda, K., Froufe, E., Georgiev, D., Gumpinger, C., Karatayev, A., Kebapci, U., Killeen, I., Lajtner, J., Larsen, B.M., Lauceri, R., Legakis, A., Lois, S., Lundberg, S., Moorkens, E., Motte, G., Nagel, K.O., Ondina, P., Outeiro, A., Paunovic, M., Prie, V., von Proschwitz, T., Riccardi, N., Rudzite, M., Rudzitis, M., Scheder, C., Seddon, M., Sereflisan, H., Simic, V., Sokolova, S., Stoeckl, K., Taskinen, J., Teixeira, A., Thielen, F., Trichkova, T., Varandas, S., Vicentini, H., Zajac, K., Zajac, T., Zogaris, S., 2017. Conservation status of freshwater mussels in Europe: state of the art and future challenges. *Biol. Rev.* 92, 572–607.
- Mcgarvey, D.J., Terra, B.D.F., 2016. Using river discharge to model and deconstruct the latitudinal diversity gradient for fishes of the Western Hemisphere. *J. Biogeogr.* 43, 1436–1449.
- Meynard, C.N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F., Mouquet, N., 2011. Beyond taxonomic diversity patterns: how do α , β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Glob. Ecol. Biogeogr.* 20, 893–903.
- Monnet, A.C., Jiguet, F., Meynard, C.N., Mouillot, D., Mouquet, N., Thuiller, W., Devictor, V., 2014. Asynchrony of taxonomic, functional and phylogenetic diversity in birds. *Glob. Ecol. Biogeogr.* 23, 780–788.
- Mouillot, D., Graham, N.A., Villeger, S., Mason, N.W., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28, 167–177.
- Mouquet, N., Devictor, V., Meynard, C.N., Munoz, F., Bersier, L.F., Chave, J., Coutron, P., Dalecky, A., Fontaine, C., Gravel, D., 2012. Ecophylogenetics: advances and perspectives. *Biol. Rev.* 87, 769–785.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. Vegan: community ecology package. R package version 2.4-1. <https://cran.r-project.org/web/packages/vegan/index.html>.
- Ouellette, M.H., Legendre, P., 2012. MVPARTwrap: additional functionalities for package mvpart. - R package ver. 0.1-9. <https://cran.r-project.org/src/contrib/Archive/MVPARTwrap/>.
- Pavoine, S., Bonsall, M.B., 2011. Measuring biodiversity to explain community assembly: a unified approach. *Biol. Rev.* 86, 792–812.
- Peres-Neto, P., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625.
- Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9, 741–758.
- Schleuter, D., Daufresne, M., Veslot, J., Mason, N.W., Lanoiselée, C., Brosse, S., Beauchard, O., Argillier, C., 2012. Geographic isolation and climate govern the functional diversity of native fish communities in European drainage basins. *Glob. Ecol. Biogeogr.* 21, 1083–1095.
- Schweiger, O., Klotz, S., Durka, W., Kühn, I., 2008. A comparative test of phylogenetic diversity indices. *Oecologia* 157, 485–495.
- Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How should beta-diversity inform biodiversity conservation? *Trends Ecol. Evol.* 31, 67–80.
- Soininen, J., 2016. Spatial structure in ecological communities - a quantitative analysis. *Oikos* 125, 160–166.
- Soininen, J., Lennon, J., Hillebrand, H., 2007. A multivariate analysis of beta diversity across organisms and environments. *Ecology* 88, 2830–2838.
- Srivastava, D.S., Cadotte, M.W., MacDonald, A.A.M., Marushia, R.G., Mirotnich, N., 2012. Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.* 15, 637–648.
- Teichert, N., Lepage, M., Lobry, J., 2018. Beyond classic ecological assessment: the use of functional indices to indicate fish assemblages sensitivity to human disturbance in estuaries. *Sci. Total Environ.* 639, 465–475.
- Therneau, T.M., Atkinson, B., 2012. Mvpart: multivariate partitioning. - R package ver. 1.6-0. <https://cran.r-project.org/src/contrib/Archive/mvpart/>.
- Theessler, S., Ruokolainen, K., Tuomisto, H., Tomppo, E., 2005. Mapping gradual landscape-scale floristic changes in Amazonian primary rain forests by combining ordination and remote sensing. *Glob. Ecol. Biogeogr.* 14, 315–325.
- Tisseuil, C., Cornu, J.F., Beauchard, O., Brosse, S., Darwall, W., Holland, R., Hugueny, B., Tedesco, P.A., Oberdorff, T., 2013. Global diversity patterns and cross-taxa convergence in freshwater systems. *J. Anim. Ecol.* 82, 365–376.
- Tucker, C.M., Cadotte, M.W., 2013. Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. *Divers. Distrib.* 19, 845–854.
- Tyler, E.H.M., Somerfield, P.J., Berghe, E.V., Bremner, J., Jackson, E., Langmead, O., Palomares, M.L.D., Webb, T.J., 2012. Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. *Glob. Ecol. Biogeogr.* 21, 922–934.
- Usseglio-Polatera, P., Bournaud, M., Richoux, P., Tachet, H., 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshw. Biol.* 43, 175–205.
- Villéger, S., Grenouillet, G., Brosse, S., 2013. Decomposing functional β -diversity reveals that low functional β -diversity is driven by low functional turnover in European fish assemblages. *Glob. Ecol. Biogeogr.* 22, 671–681.

- Webb, C.O., Ackerly, D.D., McPeck, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Evol. Syst.* 33, 475–505.
- Weinstein, B.G., Tinoco, B., Parra, J.L., Brown, L.M., McGuire, J.A., Stiles, F.G., Graham, C.H., 2014. Taxonomic, phylogenetic, and trait Beta diversity in South American hummingbirds. *Am. Nat.* 184, 211–224.
- Whittaker, R.H., 1960. Vegetation of the Siskiyou mountains, Oregon and California. *Ecol. Monogr.* 30, 279–338.
- Whittaker, R.J., Willis, K.J., Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *J. Biogeogr.* 28, 453–470.
- Xie, G., Lundholm, J.T., Scott Macivor, J., 2018. Phylogenetic diversity and plant trait composition predict multiple ecosystem functions in green roofs. *Sci. Total Environ.* 628, 1017–1026.