ICES Journal of
Marine Science

International Council for
the Exploration of the Sea
Conseil International pour
l'Exploration de la Mer

ICES Journal of Marine Science (2019), doi:10.1093/icesjms/fsz204

## Review article

# Uncovering the relative influences of space and environment in shaping the biogeographic patterns of mangrove mollusk diversity

Guogui Chen[1], Wenqing Wang[1], Yi Liu[1], Yamian Zhang[1], Wei Ma[1], Kun Xin[2], and Mao Wang [1*,‡]

[1]*Key Laboratory of the Coastal and Wetland Ecosystems (Xiamen University) Ministry of Education, College of the Environment & Ecology, Xiamen University, Fujian, Xiamen 361102, China*
[2]*Mangrove Research Center, Research Institute of Tropical Forestry, Chinese Academy of Forestry, Guangdong, Guangzhou 520510, China*

**Corresponding author: tel: +86 13666037893; e-mail: wangmao@xmu.edu.cn.*
*‡Present address: College of the Environment & Ecology, Xiamen University, South Xiang'an Road, Fujian, Xiamen 361102, China.*

Chen, G., Wang, W., Liu, Y., Zhang, Y., Ma, W., Xin, K., and Wang, M. Uncovering the relative influences of space and environment in shaping the biogeographic patterns of mangrove mollusk diversity. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsz204.

Received 25 April 2019; revised 5 October 2019; accepted 7 October 2019.

Determining the relative importance of ecological processes regulating the biogeographic patterns of marine species, especially with respect to α- and β-diversity in multi-habitat communities, is a central goal in marine ecology. We explored the relative contribution of spatial (stochastic processes) and environmental factors (deterministic processes) to the biogeographic patterns of the α- and β-diversity of mangrove mollusks. A total of 16 mangrove areas were sampled in southeast coast China from 18°N to 28°N latitude. The highest mean α-diversity was found at 20°N and that of β-diversity was at 21°N. Both spatial and environmental factors had significant effects on the α- and β-diversity patterns. The environments had greater effects than the spaces on shaping the α-diversity pattern, while the spaces were relatively more important in governing the β-diversity patterns than the environments. Our results suggest that the α-diversity pattern was mainly controlled by deterministic processes (environmental filtering), while β-diversity was primarily shaped by stochastic processes (dispersal-related), although both processes had significant impacts on α- and β-diversity patterns. Identifying the ecological variables and mechanisms that drive variations in α- and β-diversity may help guide the conservation for biodiversity in endangered mangrove ecosystems under anthropogenic and global changes.

**Keywords:** α-diversity, β-diversity, ecological processes, mangrove ecosystem, mangrove mollusk

## Introduction

Stochastic processes and deterministic drivers are the two main ecological processes involved in shaping biogeographic patterns of biodiversity (Hubbell, 2001; Laland *et al.*, 2016). Recently, more focus has been directed towards their relative contribution in different ecosystems. Related studies have been conducted in a wide variety of ecosystems, including tropical rainforests (Ellwood *et al.*, 2009), temperate forests (Furniss *et al.*, 2017), grasslands (Segre *et al.*, 2014), and rocky intertidal ecosystems (Wootton, 2005). However, their application to mangrove ecosystems is limited due to the scarcity of field data, especially for invertebrates (Lee, 2008). This data gap has resulted in a poor understanding of the ecological processes shaping mangrove biodiversity and the lack of a scientific basis for the conservation of biodiversity in mangrove ecosystems (Sarker *et al.*, 2019). Biodiversity is generally described by three levels of diversity (*α*-, *β*-, and *γ*-diversity) over spatial scales (Socolar *et al.*, 2016). Detailed *γ*-diversity might never be measured for most of the globe, especially at regional scales. Most studies in mangrove ecosystem focus on α-diversity (Sarker *et al.*, 2019), which may misrepresent the contributions of *β*-diversity to the mangrove ecosystem. Studies of *β*-diversity can quantify biodiversity loss/gain and inform the placement of reserves (Socolar *et al.*, 2016).

Therefore, the management and conservation of mangrove ecosystems must encompass $\beta$-diversity.

Mangrove ecosystems are found in tropical and subtropical intertidal zones throughout the world (Rajpar and Zakaria, 2014). These ecosystems provide several services to coastal residents, including protection against coastal erosion and the effects of severe weather, such as hurricanes (Rajpar and Zakaria, 2014; Carugati *et al.*, 2018). They are also important nurseries for fishery resources, contain evolutionarily unique resident species, and are inhabited by numerous transient animals that reside in these systems under specific tidal conditions (Manson *et al.*, 2005). However, mangrove ecosystems are highly endangered, suffering global anthropogenic destruction rates of 1–2% of cover loss per year, mainly due to land reclamation and aquaculture (Duke *et al.*, 2007; Thomas *et al.*, 2017). The loss of mangrove forests not only contributes to the rapid loss of global biodiversity but also has a negative impact on ecosystem function. Therefore, it is important to study the biodiversity of the mangrove ecosystem (Friess *et al.*, 2016; Carugati *et al.*, 2018).

Mollusks, which are one of the dominant groups of invertebrate macrofauna found in mangroves, are major contributors to matter and energy cycles in mangrove food webs (Rivera-Monroy *et al.*, 2017). Furthermore, they serve as powerful bio-indicators of mangrove ecosystem health (Veiga *et al.*, 2016). However, there is still a lack of basic information regarding the biogeographic patterns of mollusk biodiversity in mangrove ecosystems (Lee, 2008). Thus, there is an urgent need to advance our understanding of the biogeography of mangrove mollusks.

A range of abiotic and biotic factors shape mollusk communities and influence their spatial patterns (Pagliosa and Barbosa, 2006). At the local scale such as along a transect (Hortal *et al.*, 2010), the $\alpha$-diversity patterns of mollusks exhibit marked zonation patterns correlated with local environmental conditions, such as mangrove stand age, substrate elevation, salinity, and other physicochemical variables (Underwood and Chapman, 1996; Lee, 2008). At the biogeographic scale (Hortal *et al.*, 2010), the biogeographic patterns of the $\alpha$-diversity of mangrove mollusks should vary because they are scale-dependent (Machac *et al.*, 2018). When investigating spatial patterns of biodiversity, we must face the problem of a lack of information on the effects of spatial differences on species composition, i.e. $\beta$-diversity (Mokany *et al.*, 2011). Spatial-related processes, such as dispersal limiting or the spatial arrangement of environmental conditions, should result in $\beta$-diversity patterns (Mori *et al.*, 2018). Although studies have investigated $\alpha$-diversity in mangrove systems (Lee, 2008), there have been few investigations of mollusks' $\beta$-diversity in these ecosystems, even though both $\alpha$- and $\beta$-diversity are of paramount importance to the investigation of the biogeographic patterns of species and underlying ecological processes (Mori *et al.*, 2018). Most studies of mangrove mollusk assemblages have been conducted only at the habitat scale (Lee, 2008; Li *et al.*, 2012). Therefore, the biogeographic patterns of mangrove mollusks are largely unknown (Lee, 2008). Furthermore, most studies have sampled only the forest floor, despite the fact that many mangrove mollusks are either facultative or obligate arboreal species (Cannicci *et al.*, 2008; Rivera-Monroy *et al.*, 2017).

In China, mangroves are mainly found along the tropical and subtropical intertidal zone of coasts or estuaries between latitudes 18°N and 28°N (Chen *et al.* 2009). In 2015, China's mangrove forests had a total area of 20 303 ha, ∼80% of which was protected in the mangrove nature reserves (Chen *et al.*, 2009, 2017). The mangroves in China, therefore, are one of the most valuable areas for studying conservation of the biodiversity of mangrove ecosystems. From 2007 to 2016, mangrove mollusk assemblages were extensively sampled in both benthic and arboreal habitats of the southeast coast of China. Our objectives were to (i) describe the biogeographic patterns of $\alpha$- and $\beta$-diversity of mangrove mollusks in tropical and subtropical regions and (ii) identify the principal ecological processes responsible for the patterns we observed in the mollusk communities.

## Material and methods

### Study area

Sixteen mangrove forests in both tropical ($n = 11$) and subtropical ($n = 5$) climate zones (18°N–28°N) along the southeast coast of China were selected as study sites (Figure 1). Each study site was located in a mangrove nature reserve where anthropogenic disturbance was minimal. Additional information on each study site is in Supplementary Tables S1 and S2. Sampling was conducted from April 2007 to January 2016 with samples collected in April, July, October, and January corresponding to spring, summer, autumn, and winter, respectively (Supplementary Table S1).

### Sampling and environmental variables

At each site, arboreal mollusks were sampled from one to four parallel transects 100 m apart along an intertidal gradient. Each transect had a length ranging from 100 to 500 m and contained five 5 m × 5 m quadrats. Within the quadrats, mollusks were hand-picked from tree trunks, branches, leaves, and roots, while sessile mollusks, such as mussels and oysters, were collected using sickles. At each site, benthic mollusks were sampled from three parallel transects 100 m apart along the intertidal gradient. Along each transect, three 25 cm ×25 cm quadrats were sampled with a Peterson grab sampler to a depth of 30 cm. Samples were wet sieved in the field through a 1-mm mesh sieve, after which they were fixed in 4% formaldehyde. Within 3 days, samples were washed with water and transferred to 75% ethanol, after which they were sorted according to morphological species (species richness) and counted (abundance). The following environmental variables were measured immediately after taking biological samples in each quadrat during sampling sessions (Supplementary Table S2): water salinity (SAL), which was measured using a hand-held refractometer (three replicates per quadrat); water temperature (WT), which was measured with a thermometer (three measurements per quadrat); latitude and longitude (coordinates), which were determined with a hand-held GPS; canopy closure (CD) of vegetation, which was determined using a digital camera (five photos per quadrat) followed by analysis by the hemispherical photographs technique (Paletto and Tosi, 2009); and vegetation types (FT), which were defined by the dominant mangrove species in each site. The annual average atmospheric temperature (AT) and annual average rainfall (Rain) for each site were based on data from the China Meteorological Data Sharing Service System (http://data.cma.cn/site/index.html). The tidal amplitude (TA) for each site was based on data from the National Marine Science Data Sharing Service Platform (http://mds.nmdis.org.cn). Sediments were sampled to a depth of 30 cm after taking benthic mollusks samples in each quadrat. The sediment characteristics such as the proportion of sand (Sand), clay (Clay), and silt (Silt) were measured using a laser particle size analyser (Mastersizer 2000). The percent organic matter (POM) was

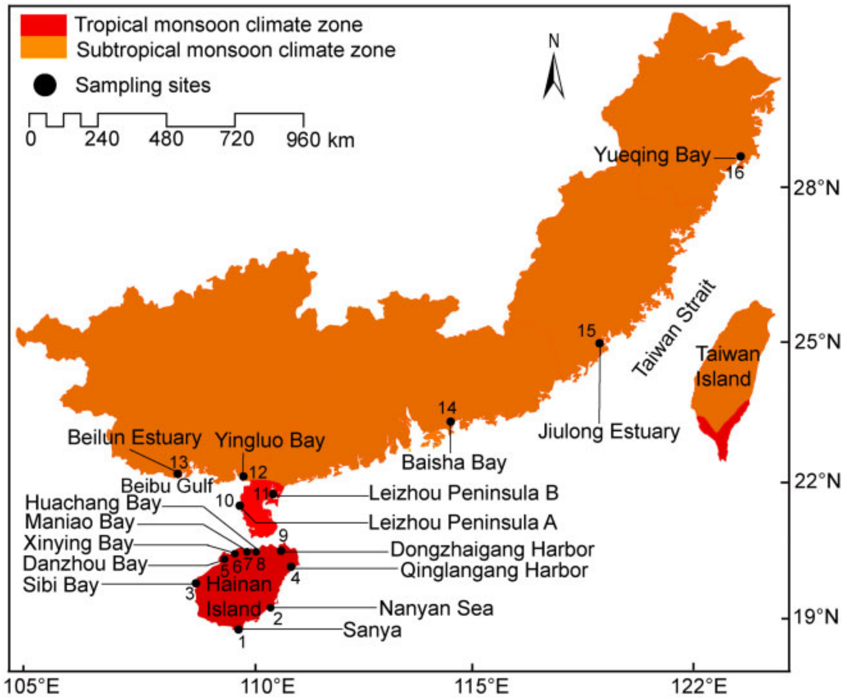

**Figure 1.** Study sites in southeast China. Sites 1 to 16 are in ascending order of latitude from 18°N to 28°N.

obtained through weight differences before and after total combustion at 450°C (Alfaro, 2010).

## Statistical analyses

### *Biogeographic patterns of α- and β-diversity*

Biogeographic patterns of α-diversity were characterized using latitudinal gradients of the Shannon–Wiener diversity (H) and the species richness (i.e. the number of species per quadrat, S). The H of mollusks present in each quadrat was computed with PRIMER v.5 (Clarke and Gorley, 2001). To distinguish the latitude bands in this study, we divided the 16 mangroves into 7 latitudinal bands, 18°N, 19°N, 20°N, 21°N, 22°N, 24°N, and 28°N. To compare α-diversity in each of our latitudinal bands, we used one-way ANOVA and Tukey's HSD post hoc pairwise tests in SPSS Statistics v.21 (IBM) to identify differences in α-diversity along the latitudinal gradient.

The spatial pattern of $\beta$-diversity was determined based on total variations in the mollusk community and the Bray–Curtis index (Tuomisto and Ruokolainen, 2006). We used the ordination methods in the Canoco v.5 platform to examine the total variations in mollusk communities along seven latitudinal bands (Lepš and Šmilauer, 2014). To calculate the differences in mollusk communities between any two quadrats at each latitude, we conducted dissimilarity analyses of mollusk communities based on the Bray–Curtis distance in PRIMER v.5.0. To model the latitudinal trends in the Bray–Curtis index, we conducted linear regression based on Spearman's rank correlations in Origin v.9.1. An analysis of similarity (ANOSIM) was used to test the significant differences among mollusk communities using PRIMER v.5.0. The global R-value in ANOSIM ranges from 0 to 1 and represents a separation degree between latitudinal bands, with $R = 0$ indicating no separation and $R = 1$ indicating complete separation.

### *Relationships among α-diversity and environmental and spatial variables*

Spearman's rank correlation analysis and stepwise multiple linear regression with SPSS v.21 were used to detect congruence between the distribution of α-diversity patterns and the distribution of spatial and environmental factors. Due to multicollinearity among explanatory variables and the lack of ability to detect potential non-linear relationships, the results of the linear regression could not be interpreted with certainty. Therefore, linear regression combined with other approaches was used as an exploratory tool to assess the relative contributions of spatial and environmental variables. The geographic detector method (GDM) created by the GeogDetector software was used as an alternative approach for analysing the relationships among communities, spatial factors, and environmental factors (Wang *et al.*, 2010, 2016). The GDM was selected because it provides several unique data query abilities that make it a valuable tool when used in combination with other statistical approaches for rigorously characterizing factors that contribute to the biogeographic pattern of mangrove mollusks (Wang *et al.*, 2010, 2016). The technique was able to assess both linear and non-linear relationships in the dataset (for more information, see http://www.geodetector.org/ and Supplementary Text S1).

### *Relationships among β-diversity, environmental, and spatial variables*

A distance-based indirect approach was used to establish correlations among the environment, space, and community similarity (Tuomisto and Ruokolainen, 2006). This approach consisted of a multivariate-analysis method using three distance matrices (community similarity, geographic distance, and environmental distance). To calculate the differences in environmental variables between any two quadrats in the seven latitudinal bands, we conducted dissimilarity analyses of environmental factors based on Euclidean distance using PRIMER v.5.0. To compute the geographic distance between any two quadrat locations, we used the *gdistance* package in R (http://www.r-project.org). Finally, the relationships between the matrixes of Bray–Curtis similarity, geographic distance, and Euclidean distance of environmental variability were analysed based on Spearman's rank correlations in Origin v.9.1 (Tuomisto and Ruokolainen, 2006).

The raw-data-based direct approach, which is a multivariate-analysis method in which raw environmental data and spatial $x$–$y$ coordinates are used to analyse changes in the total variations of mollusk community, was applied to community data in this study (Tuomisto and Ruokolainen, 2006). Prior to analysis, all of the variables for statistical tests were ln $(x+1)$ transformed to improve their homoscedasticity and normality. The environmental factors in this analysis represent the local habitat variables. To visualize patterns in the environmental conditions of sites/quadrats, we used Canoco v.5 to conduct PCA of the full suite of normalized environmental variables (Lepš and Šmilauer, 2014). To evaluate the spatial component, we employed principal coordinates of neighbour matrices (PCNMs) analysis. To create the PCNM vectors, we used geographic coordinates to create a distance matrix using Euclidean distances in the Canoco v.5 software (Lepš and Šmilauer, 2014). To maintain the data connection in the PCNM analysis, we used the longest distance set as the distance threshold (Borcard and Legendre, 2002). In addition, only eigenvectors with positive eigenvalues were used in this study.

The detrended correspondence analysis showed that the longest gradient length was shorter than 3.0, indicating that redundancy analysis (RDA), a constrained ordination method, was suitable to investigate the relationships among mollusk communities and spatial and environmental factors (Canoco v.5; Lepš and Šmilauer 2014). Prior to variation partitioning, we used global-RDA to test the correlations among mollusk communities, environmental factors, and spatial factors (PCNM vectors), after which the environment factors and spatial factors were individually filtered and examined for significance at $p < 0.05$. A forward selection and Monte Carlo randomization test with 999 unrestricted permutations were conducted to select significant explanatory variables ($p < 0.05$). Finally, variation partitioning analysis (VPA) with adjusted $R^2$ coefficients was used to evaluate the relative contribution of the spatial and environmental variables to the total variations in mollusk communities ($\beta$-diversity). This analysis isolated the variations into the pure components of spatial factors (i.e. spatial distance, S|E), environmental factors (i.e. environmental filtering, E|S), and their shared contribution (the intersection not the interaction, S∩E) to the explanation of $\beta$-diversity. The residual variation (1− S|E−E|S−S∩E) was not explained by the variables used.

# Results

## Diversity of mollusks

We found 556 mollusk taxa from 105 families and 5 classes exhibiting wide variation in taxonomic relationships. The majority of the mollusks were gastropods (50%) and bivalves (47%). Additionally, there were a total of 55 arboreal and 501 benthic mollusk species (Supplementary Table S3 and Figure S1).

## Biogeographic patterns of α- and β-diversity

The mean α-diversity indexes (H and S) for both arboreal and benthic mollusks decreased significantly with increasing latitude ($p < 0.05$; Figure 2). However, these trends showed some variation, increasing from 18°N to 20°N, then decreasing significantly from 20°N to 28°N ($p < 0.05$; Figure 2).

The mean Bray–Curtis index decreased with increasing latitude, but this trends also varied, increasing from 18°N to 21°N, then decreasing significantly from 21°N to 28°N (Figure 3a and b). The ANOSIM between mollusk communities in distinct latitudes showed that the community similarity of both arboreal and benthic mollusks differed greatly between any two latitudes (Figure 3c and d).

The Spearman correlations between the Bray–Curtis community similarity and geographic distance showed significant negative correlations, although the correlation coefficients were low ($p < 0.01$; Figure 4a). Environmental distances exhibited positive significant relationships with geographic distances (arboreal mollusk: $r = 0.54$, $p < 0.01$; benthic mollusk: $r = 0.95$, $p < 0.01$), but they were negatively correlated with the community similarity (arboreal mollusk: $r = -0.29$, $p < 0.01$; benthic mollusk: $r = -0.21$, $p = 0.09$; Figure 4c).

## Environmental and spatial factors related to the biogeographic patterns of α- and β-diversity

Both spatial and environmental factors were related to the species richness and Shannon–Wiener diversity in arboreal and benthic mollusks (Figure 5a). The data show positive relationships between mollusk communities and three environmental factors (SAL, WT, and AT; Figure 5a). The POM, Clay, and Silt were also positively correlated with benthic communities (Figure 5a). Negative correlations were found between mollusk communities and two spatial factors (Lat. and Lon.) and the remaining four environmental factors (TA, FT, CD, and Rain; Figure 5a). The benthic mollusk community was negatively correlated with the proportion of sand (Figure 5a). According to the results of GDM, all of the spatial factors (S), environmental factors (E), and their interactions (i.e. E∩S and E∩E except for S∩S) passed the significance test ($p < 0.05$; Figure 5b). The paired factors explained more of the observed trends than any individual factor alone (Supplementary Table S4). The interactions of environmental factors were identified as the most relevant to the total variation of species richness and the Shannon–Wiener index (i.e. E∩E) were identified as the most relevant to the total variation of species richness and the Shannon–Wiener index (Figure 5b). Most interaction contributions were found to be bi-linear (or bi-nonlinear) enhancements that were less (or more) than the summed contributions of the individual factors (Supplementary Table S4). These suggest that the geographic distribution of mollusks' α-diversity resulted from the interaction of spatial and environmental factors rather than mutually independent and were mainly controlled by the environmental conditions.

The local environmental factors showed considerable variation across the study area (Supplementary Figure S2a). The total variations of both arboreal and benthic mollusk communities across the seven latitudinal bands were strong (Supplementary Figure S2b). All of the environmental and spatial factors were significantly related to the total variation of both arboreal (9 factors) and benthic (12 factors) mollusks ($p < 0.05$; Supplementary Table S5). Therefore, based on the forward selection results, all of the environmental variables significantly influenced the variations of arboreal and benthic mollusks ($p < 0.05$; Supplementary Figure S2b). Nine spatial factors (PCNMs 1–6, 8, 9, and 11; Supplementary Figure S2b) showed striking effects on the arboreal mollusk community ($p < 0.05$), whereas seven spatial variables (PCNMs 3, 4, 5, 6, 7, 8, and 9; Supplementary Figure S2b) exhibited significant effects on variations in the benthic mollusks.

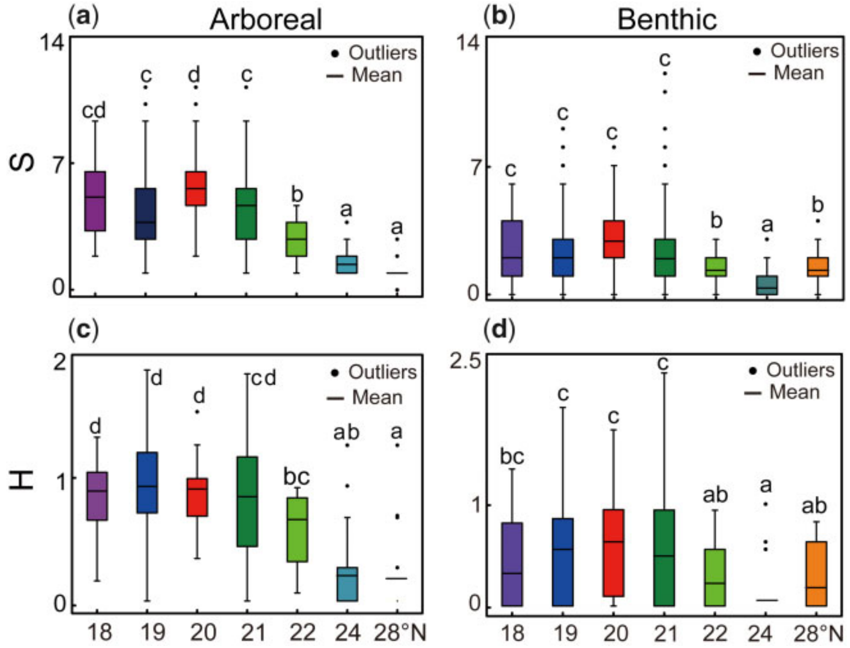

**Figure 2.** Geographic patterns of mollusk $\alpha$-diversity across 16 coastal estuaries in China. (a), (b), (c), and (d) The pairwise comparison of species richness (S) and Shannon–Wiener diversity (H) of mollusks between different latitude bands. The top and bottom boundaries of each box indicate the 75th and 25th quartile values, respectively, and lines within each box represent the mean values. Different letters above bars indicate a significant difference of the mean value at the $p < 0.05$ level according to one-way ANOVA.

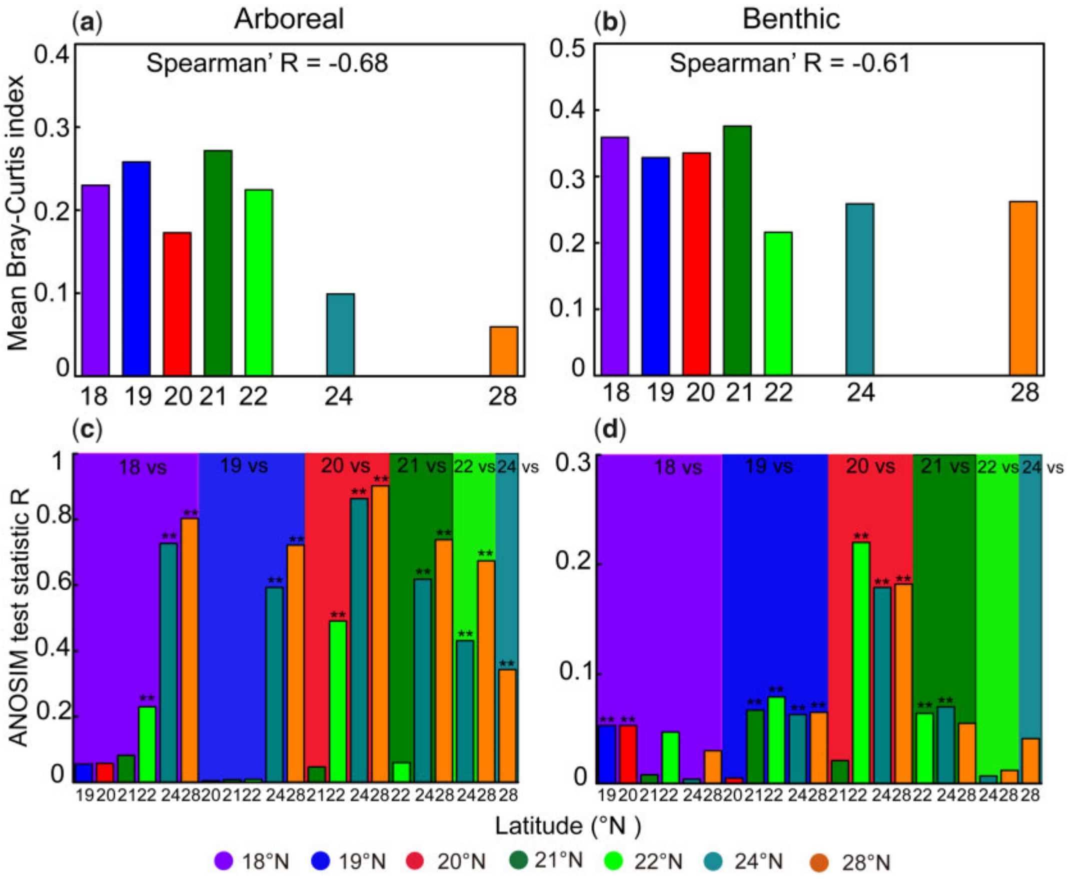

**Figure 3.** The biogeographic pattern of $\beta$-diversity of mollusks. (a) and (b) The latitudinal trend of mean Bray–Curtis index across the seven latitude bands. (c) and (d) ANOSIM test for differences between any two latitudes, $^*p < 0.05$ and $^{**}p < 0.01$.

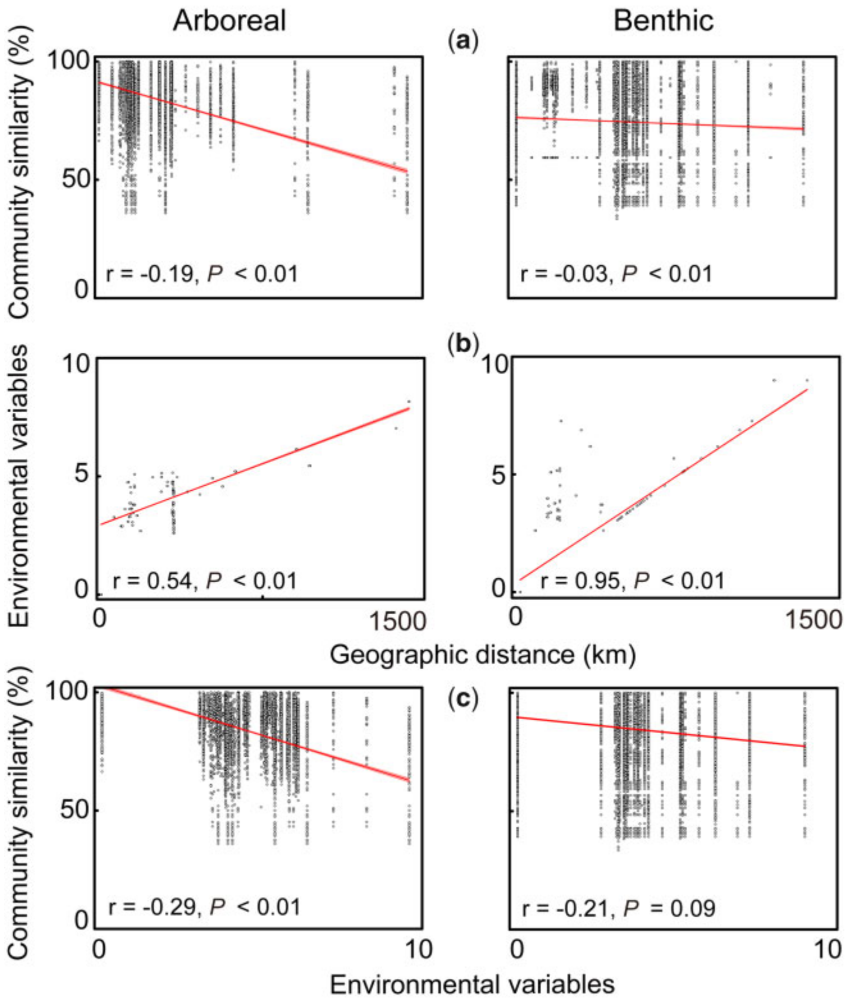

**Figure 4.** Relationships among β-diversity and geographic distance and environmental factors. (a) Spearman's rank correlations between similarities mollusk communities and geographic distance. (b) Spearman's rank correlations between the Euclidean distance of environmental variables and geographic distance. (c) Spearman's rank correlations between the community similarity and the Euclidean distance of environments.

VPA revealed that the proportion of purely spatial variation in mollusk community compositions (benthic mollusks: 15.4%, arboreal mollusks: 12.9%) tended to be higher than purely environmental factors (benthic mollusks: 10.1%, arboreal mollusks: 9.4%; Figure 5c). The shared spatial and environmental factors were responsible for 27.6% of the variation in the arboreal community and 21.1% of the variation of benthic taxa (Figure 5c). Remarkably, much of the variation in the mollusk communities (53.4% for benthic mollusks, 50.1% for arboreal mollusks) was not influenced by the spatial and environmental variables investigated (Figure 5c).

## Discussion

### Environmental factors are more important than spatial factors in shaping the latitudinal gradient of α-diversity

α-Diversity measures how diversified the species is within a local site; hence, its distribution pattern should mainly be influenced by local environmental conditions (Mokany *et al.*, 2011). Our analysis suggests that the environmental factors used were correlated with α-diversity (Figure 5a). Both the individual effects of environments (E, after controlling for variation due to the spatial variables) and the interactive effects of environments (E∩E) had obvious effects on the α-diversity (Figure 5b; Supplementary Table S4). At broad biogeographic scales, as in this study, species can also be affected by dispersal dynamics. For marine species that have limited dispersal abilities, such as adult mollusks, dispersal limitation would play a major role in biogeographic distribution (Johnson *et al.*, 2001). This is likely to be one of the causal factors behind the marked latitudinal pattern of α-diversity. Our results revealed that spatial variables were significantly influential in explaining the variations of α-diversity at the biogeographic scale (Figure 5b).

One intriguing result of our study is that local variables were more important descriptors of variation in α-diversity than the spatial variables—a conclusion that is completely different from that observed for benthic α-diversity in the Norwegian continental shelf (Ellingsen and Gray, 2002). Environmental and spatial variables cannot by themselves increase or decrease local α-diversity (Wiens and Donoghue, 2004). Both the presence and persistence of local α-diversity of marine invertebrates depend on successful colonization and subsequent coexistence (Dethier *et al.*, 2003). In general, local environmental conditions determine the successful colonization and coexistence of species and

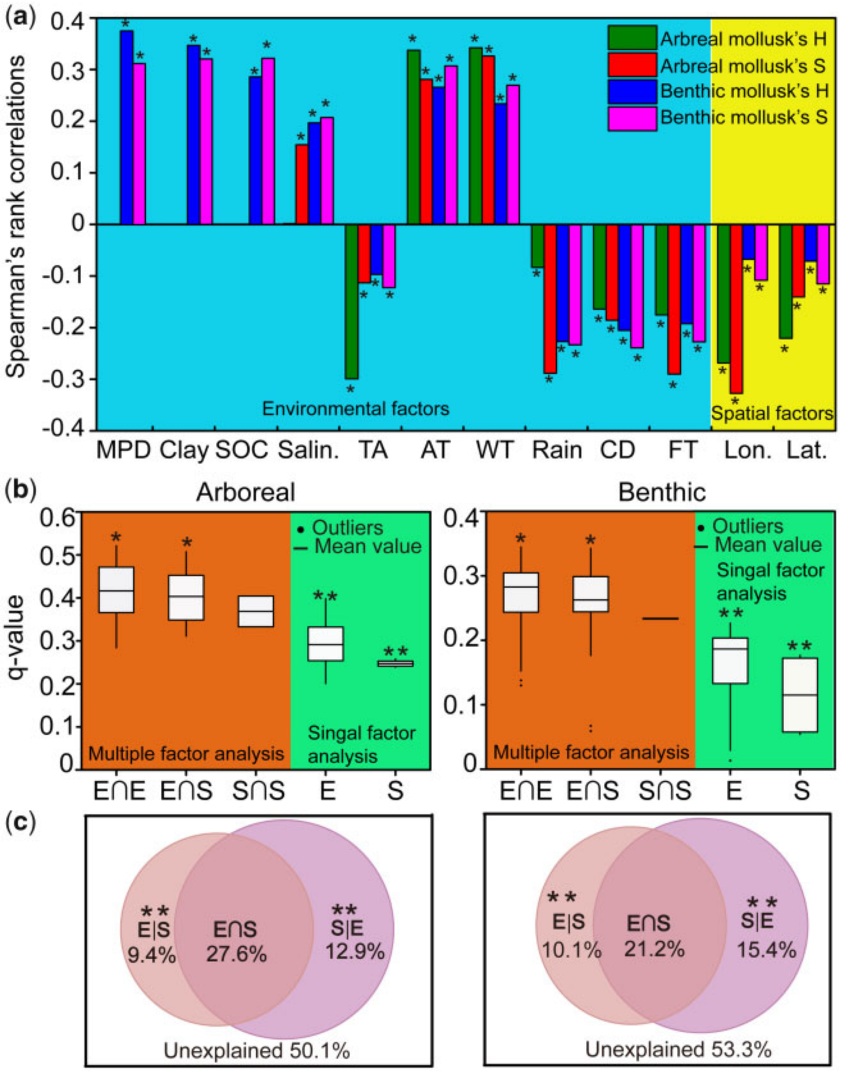

**Figure 5.** Variations in the geographic patterns of α- and β-diversity of mollusks explained by spatial and environmental variables. *$p < 0.05$ and **$p < 0.01$. (a) Spearman's rank correlations between α-diversity of mollusks and spatial and environmental factors. S, sample species richness; H, sample Shannon–Wiener diversity; POM, percent organic matter; Sand, the proportion of sand; Clay, the proportion of clay; Silt, the proportion of silt; SAL, water salinity; TA, tidal amplitude; AT, average annual atmospheric temperature; WT, water temperature; Rain, average annual rainfall; CD, canopy closure; FT, vegetation types; Lon., longitude; Lat., latitude. Negative $R$ value indicates a negative correlation between α-diversity and factor. The sediment characteristics such as Sand, Clay, Silt and POM are only used to explain the α-diversity of benthic mollusk. (b) Effects of interactions among environmental and spatial factors and their individual roles in α-diversity. E∩E, interactive effects between any two environmental factors; E∩S, the interaction between spatial and environmental factors; S∩S, the interaction between spatial factors; E, individual role of environmental factors; S, individual effects of spatial factors. (c) Variation partitioning-based Venn diagrams showing facets of β-diversity variation explained by unique and joint effects of local environmental and spatial variables. S|E, pure spatial variation; E|S, pure environmental variation; E∩S, intersection of variation explained by space and environment; 1−S|E−E|S−S∩E, unexplained variation.

generate large-scale biogeographic patterns in α-diversity (Dethier *et al.*, 2003; HilleRisLambers *et al.*, 2012).

## The relative influences of spatial and environmental factors in governing the biogeographic pattern of β-diversity

β-Diversity measures species composition diversity among quadrats within a region (Tuomisto and Ruokolainen, 2006). It can provide information on marine area relationships or connectivity, reflecting the processes operating in those areas (Mori *et al.*, 2018). It is considered to be essential in environmental and conservation-based censuses and for the establishment of nature reserves (Tuomisto and Ruokolainen, 2006; Mori *et al.*, 2018). β-Diversity incorporates the decay of community similarity with geographic distance known as the distance–decay relationship, which reflects patterns of geographic distribution and autocorrelation (Morlon *et al.*, 2008). It is sensitive to key spatial processes and environmental heterogeneity (Morlon *et al.*, 2008; Perez Rocha *et al.*, 2018). Therefore, the relationships between community similarity, geographic distances, and environmental distances can be used to reveal underlying ecological processes (Morlon *et al.*, 2008). A Spearman analysis examines linear relationships between community similarity and other factors. The coefficients of Spearman's correlation in this study were very low (Figure 4a) indicating that the linear effects of dispersal limitation and environmental filtering on the biogeographic pattern of mollusks community were relatively weak. However, this does not mean that the mollusk communities were not affected by strong dispersal limitation and environmental filtering. Nonlinear relationships are ubiquitous in the natural world and dispersal limitation might override environmental selection under certain conditions, such as at increasing spatial scales of observation (Smith and Lundholm, 2010; Schuldt *et al.*, 2015).

A fraction of pure environmental variation (E|S) separated by VPA indicates that the pure non-spatially structured environment explained a significant portion of the geographic distributions of mollusk communities. In other words, the $\beta$-diversity of mollusks was under strong environmental selection (Smith and Lundholm, 2010). The significant pure spatial variation (S|E) indicates that the biogeographic patterns of mollusk communities were markedly influenced by stochastic processes. Since the dispersal abilities of adult mollusks are limited, distance or spatial components should be important factors influencing their biogeographic distribution (Becking *et al.*, 2006). Although adult mobility seems to be crucial to the distribution of marine mollusks, the larvae may also exert a strong influence. For instance, the numerous small larvae of some marine species would be expected to spend a large amount of time within the water column, thus being transported long distances to colonize distant habitats by random dispersal (Cowen and Sponaugle, 2009; D'Aloia *et al.*, 2015). Recent work, however, has indicated that the dispersal distances of marine larval are limited by conditions in nearshore waters and the effects of pollution (Becking *et al.*, 2006; Cowen and Sponaugle, 2009). Therefore, mollusk larvae within mangrove ecosystems should also be limited by dispersal and distance. The intersection of variation explained by spatial and environmental variability (E∩S) indicates that mollusk communities can be shaped by spatial processes as well as environmental filtering (Smith and Lundholm, 2010). The large fraction of unexplained variation observed in this study appears to be common in many ecosystem taxa, such as bacterioplankton communities in marine ecosystems and plant communities in terrestrial ecosystems (Mo *et al.*, 2018). Unexplained variation can be caused by noise in species data, unmeasured environmental variables, and biological stochastic processes, such as dispersal and mortality (Smith and Lundholm, 2010; Mo *et al.*, 2018). The fraction of variation that is unexplained is usually a measure of ecological drift (Smith and Lundholm, 2010). Therefore, the $\beta$-diversity of mollusks may be also influenced by ecological drift.

Temporal fluctuations in biotic and abiotic factors are also important for the regulation of biodiversity dynamics (Kalyuzhny *et al.*, 2014). However, the biogeographic patterns in this study were treated as predominantly atemporal, due to the use of single survey data and time-averaged data. Ignoring temporal factors may inadvertently weaken the interpretation of ecological processes that shape biogeographic patterns (Kalyuzhny *et al.*, 2014). Therefore, if temporal fluctuations (e.g. interannual and seasonal dynamics) were more thoroughly investigated and analysed along with the deterministic factors (e.g. environmental factors, such as species traits and interspecies interactions) and stochastic variables (e.g. colonization, birth, death, extinction, drift, and speciation), the unexplained proportion of the variation would decrease, and the proportion that is explained by environmental and spatial factors would increase.

Our results on the relative contributions of spatial versus environmental variables in shaping mollusks' $\beta$-diversity confirmed that stochastic processes could have a stronger effect on the $\beta$-diversity of mollusks than environmental filtering. Although environmental heterogeneity allows species to co-exist in local habitats (Laland *et al.*, 2016), evidence suggests that community structuring can be constrained by spatial-related processes (e.g. dispersal limitation) at the biogeographic scale (Perez Rocha *et al.*, 2018). Moreover, dispersal limitation might override environmental selection under increasing spatial scales of observation (Smith and Lundholm, 2010).

## Integrating β-diversity and ecological processes into the conservation of mangrove ecosystem biodiversity

In the light of the lack of funding for marine conservation, site selection for protected areas (i.e. priority conservation) is an exercise of optimization in marine conservation planning (Edwards *et al.*, 2010). A successful priority protected area must capture the landscapes with the highest biodiversity along spatial or environmental gradients. Most previous studies to select priority protected areas for marine biodiversity conservation generally used $\alpha$-diversity measures (McAfee *et al.*, 2016). Selecting regions based solely on $\alpha$-diversity is not sufficient for capturing alterations of ecosystems, because $\alpha$-diversity does not reflect complementarity (Mori *et al.*, 2018). As another dimension of diversity, $\beta$-diversity can quantify biodiversity loss/gain and inform the placement of reserves (Socolar *et al.*, 2016). More importantly, our results revealed that the regions with the highest level of $\alpha$-diversity (20°N) are different from the regions with highest $\beta$-diversity (21°N). Thus, a sole focus on $\alpha$- or $\beta$-diversity is not sufficient to measure the biodiversity of mangrove ecosystems.

Biodiversity measures are an essential component of selecting conservation sites, but the conservation of these sites will not be effective in the long term unless the ecological processes that sustain such assets are well maintained (Edwards *et al.*, 2010). Stochastic (neutral) and deterministic (niche) processes shape biodiversity and are complementary in their consequences for biological conservation. Niche theories mainly lead to a focus on deterministic factors, such as interactions of species with the environment and with other species (Laland *et al.*, 2016). In this study, environmental filtering significantly affected the pattern of $\alpha$- and $\beta$-diversity of mangrove mollusks, leading to a recommendation for environmental protection to maintain the biodiversity of mangrove mollusks. Although in China the conversion of mangroves to aquaculture/agriculture is no longer a major threat to mangroves, other complicated environmental problems such as wastewater, oil pollution, and climate change are serious threats to mangrove ecosystems (Chen *et al.* 2009). Neutral perspectives ignore such deterministic processes and highlight similarities between species and the influence of stochastic processes (Hubbell, 2001). Therefore, neutral theories promote an explicit consideration of spatial processes and stochasticity at the community level in conservation. This study suggests that a certain amount of protected areas and maintaining connectivity between these areas should be effective in maintaining the biodiversity of mangrove mollusks, which were significantly affected by stochastic processes.

The protection of single species (e.g. flagship species) and niches (e.g. environments and habitats) should be a priority initiative in strongly niche-structured communities (Laland *et al.*, 2016). In a community where spatiality and stochasticity are significant, neutral approaches can lead managers to protect the community and ecological process instead of single species and niches (Hubbell, 2001). Therefore, to ensure that the biodiversity of mangrove ecosystems is adequately protected, both deterministic and stochastic processes should be considered in conservation planning.

## Conclusions

Understanding the biogeographical patterns of marine species can help marine biologists, ecologists, and fisheries managers to better carry out relevant research and protection efforts. In this study, we saw a distinct hump-shaped pattern in the latitudinal gradients of mollusk $\alpha$- and $\beta$-diversity from 18°N to 28°N. The highest mean $\alpha$-diversity was found at 20°N and the highest mean of $\beta$-diversity was at 21°N. Therefore, both $\alpha$- and $\beta$-diversity should be integrated into the research and management of mangrove ecosystem. Furthermore, we found that environmental and spatial variables were important drivers of the biodiversity patterns of mangrove mollusks at the biogeographic scale. While local environmental variables were more important than spatial factors to $\alpha$-diversity, spatial components made a greater contribution to $\beta$-diversity than local conditions. Therefore, neutral and deterministic theory could help improve the conservation of biodiversity in mangrove ecosystems.

## Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

## Acknowledgements

We also thank Xueqin Gao, Haifeng Fu, Xinghai Ao, Chaoyi Tang for their assistance during the field investigation, and Gianluca Polgar for his assistance during the writing.

## Funding

We thank the Programs of Science and Technology on Basic Resources Survey for the Ministry of Science and Technology of China (No. 2017FY100701), and the National Natural Science Foundation of China (No. 31670490) for our research grant.

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*Handling editor: Howard Browman*