RESEARCH ARTICLE

Mollusc aquaculture homogenizes intertidal soft-sediment communities along the 18,400 km long coastline of China

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Abstract

Aim: Molluscs are important grazers, filter and deposit feeders, scavengers and predators, which in turn are food for shorebirds, fish and people. Some species, targeted as human food, have been cultured along the Chinese coast for hundreds of years. To examine whether aquacultural practices have meanwhile affected biodiversity gradients, we measured mollusc community structure along the coast of China in habitats which are intensively used by humans.

Location: Chinese coast.

Methods: We sampled 21 intertidal sites spanning 20 latitudinal degrees and 18,400 km of coastline. We assessed alpha diversity to verify whether mollusc communities exhibit the expected biodiversity gradient with latitude and beta diversity gradients with distance. To examine whether human activities such as transportation and culturing could have affected these patterns, we distinguished commercial from non-commercial mollusc species and compared the differences in distribution, density, alpha diversity and beta diversity.

Results: We found non-commercial species showed the expected biodiversity gradients. Commercial species (a) dominated the intertidal mollusc communities at 19 of the 21 sites and compared with non-commercial species, (b) exhibited wider geographical distributions, (c) showed no significant change in Bray-Curtis index (abundance-based beta diversity) with either geographical or climatic distance, (d) exhibited lower average dissimilarities and (e) did not show a decrease in species

richness and Shannon diversity with latitude. Combining all species, trends were the same as for the commercial species.

Main conclusions: A few cultured species dominated the intertidal mollusc communities in high densities along the Chinese coastline, taking over the ecological roles of the native species but not driving them extinct. In this way, aquacultural practices have exerted a homogenizing influence strong enough to erase basic biodiversity gradients. Since molluscs are food for the growing human population and the shrinking populations of migratory animals, coastal planning and management of both intertidal habitats and the exploitative activities employed need to incorporate these dimensions.

KEYWORDS

aquaculture, beta diversity, biotic homogenization, intertidal mudflat, invasion, molluscs

1 | INTRODUCTION

Along shallow coasts with adequate tidal ranges, intertidal shores (e.g. rocky shores, soft sediments, intertidal sand and mudflats) form the link between marine and terrestrial ecosystems (Healy et al., 2002). In many such systems, molluscs occupy a central position in the food web, being the core of a turntable of energy flow and material cycling as they graze the epiphytobenthos and phytoplankton (e.g. Christianen et al., 2017), scavenge putrefied organisms and feed on other benthos (Gosling, 2008), and are fed upon by consumers such as shorebirds, fish and humans (e.g. Mathot et al., 2018). However, with increasing human activities along coastlines (especially land claims), within the past 30 years 16% of the global intertidal mudflats have been lost or altered (Dong et al., 2016; Martin et al., 2005; Murray et al., 2019). The remaining systems have suffered from various disturbances such as farming and harvesting activities (Gentry et al., 2017; Piersma, 2009; Worm et al., 2006).

The dispersal of organisms is usually constrained by natural barriers interacting with dispersal capacities, so that biodiversity tends to become more dissimilar with increasing geographic and climatic distances (Baselga et al., 2013; Kraft et al., 2011; Tobler, 1970). Numerous studies, on a great variety of organisms in all ecosystem types, have shown spatial patterns consistent with these biogeographical "laws" (Baselga et al., 2013; Josefson & Göke, 2013; Socolar et al., 2016). However, impacted by human activities, and the alleviation of dispersal constraints due to the transportation of organisms being one of the underlying causes (Rodrigues et al., 2013), biodiversity gradients have been, and are now being, altered (Millennium Ecosystem Assessment, 2005). For example, ancient agri- and aquaculturists began the cultivation of a few useful edible species, a process continuing today as farmers, fishermen and national and transnational corporations move around the few most productive plants and animals across an increasingly large part of the Earth (Bengtsson et al., 2005; Rodrigues et al., 2013; Socolar et al., 2016).

Stretching 2,500 km from south to north, spanning 20 latitudinal degrees and with a steep climatic gradient (Figure 1), the 18,400 km long coastline of China offers a great diversity of intertidal habitats (Alistair, 2000). Along this lengthy coastline, almost all the inshore intertidal areas, and even many offshore areas, have been altered by aquaculture (Li et al., 2011; Williams et al., 2019). China now produces one-third of the world's reported captures of "fish" (i.e. fish and shellfish), and two-thirds of the world's reported aquaculture production (FAO, 2020). Mollusc aquaculture on intertidal habitats occupies a large part of aquaculture production (Guo et al., 1999), transforming the species composition in coastal ecosystems (Gosling, 2008).

In a form of aquaculture strongly developed in Asia, especially in China, during the harvest most of the molluscs are taken away, but regular reseeding brings new molluscs to the open intertidal flats (Gosling, 2008; Li et al., 2011; Wang & Wang, 2008). Mollusc aquaculture is an activity by which species are introduced from one community into another, where they may add to, or replace, the local species (Forrest et al., 2009; Lin et al., 2015). Humans routinely collect the juveniles of commercial species of mollusc at one location and transport and spread them to intertidal mudflats elsewhere (Appendix S1: Figure S1; Gosling, 2008; Wang & Zhang, 1995). As a consequence, mollusc species of significant economic importance (human food or aquaculture feed) have been introduced to intertidal soft-sediment flats where they previously did not occur (Guo et al., 1999; Li et al., 2011). Because the commercial species are chosen on the basis of their strong adaptability, such species have quickly become the most abundant in some intertidal areas (Gosling, 2008; Lin et al., 2015). Some of these introduced species, therefore, have been considered invasive, pushing local species to low densities (Du et al., 2011). Noting that other human activities along China's coast may result in direct losses (or sometimes gains) of species, and these include habitat degeneration (e.g. by pollution; Liu & Diamond, 2005), habitat removal (by land claims; Murray et al., 2014; Piersma et al., 2016) and habitat restoration (Fan
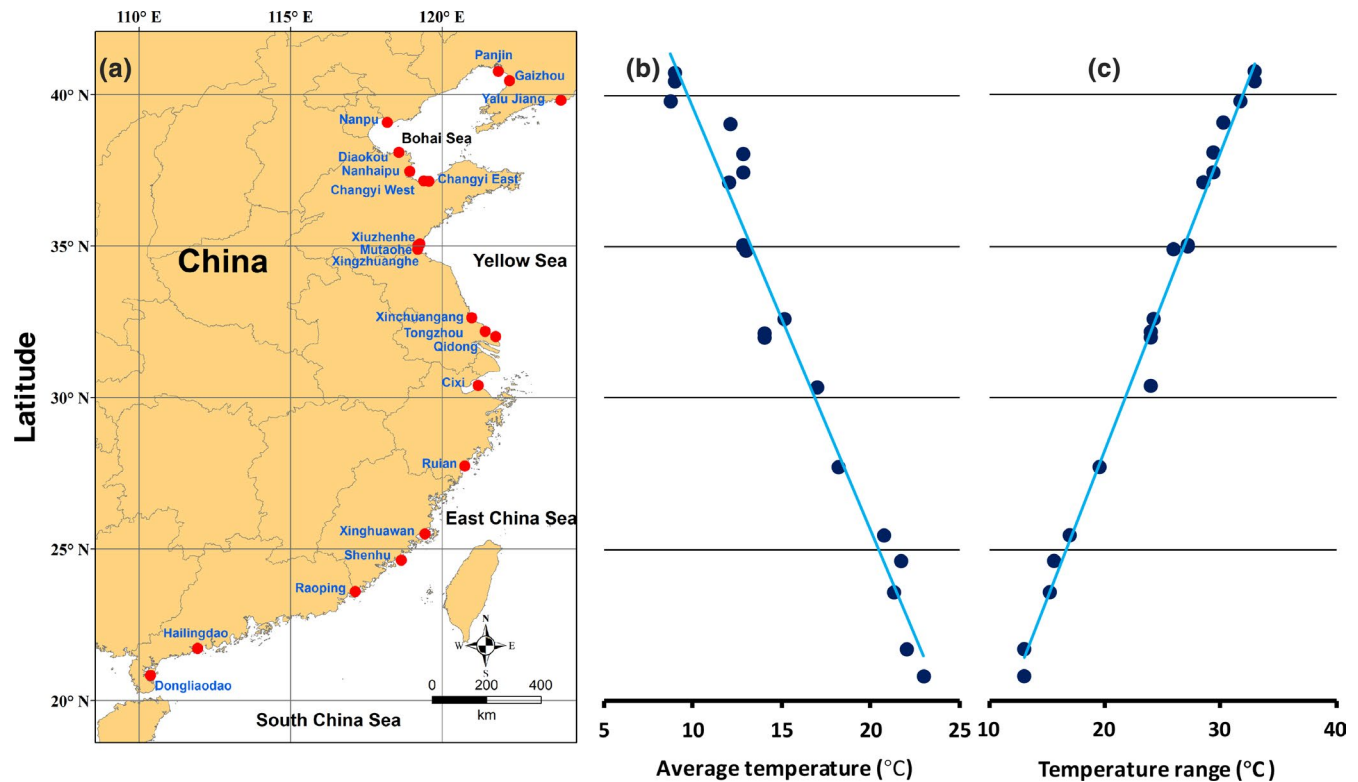
FIGURE 1 Study sites and the climatic gradient along the coast of China. (a) 21 sampling sites (red dots) along the coast. (b) The average temperature decreased with increasing latitude. (c) The local temperature range increased with increasing latitude

et al., 2021), the extent of such ecological effects of intertidal aquaculture, remain to be documented.

Biotic homogenization is the process of species composition at different places becoming more alike (Baiser et al., 2012; Magurran et al., 2015). "Beta diversity" is commonly used in measuring biotic homogenization (Baselga et al., 2013; Kraft et al., 2011; Tobler, 1970) and in evaluating "ecosystem health" (Socolar et al., 2016). Both species composition (represented by Sorensen dissimilarity, hereafter β_{SOR}, incidence-based beta diversity index to summarize changes in the composition of species lists) and species density (represented by Bray-Curtis dissimilarity, hereafter β_{BC}, abundance-based beta diversity index; Cassey et al., 2008) contribute to the variation of beta diversity. However, when communities are affected by invasive species, local species may decrease in density but not go extinct (Gurevitch & Padilla, 2004), so that dissimilarities may decrease especially when taking densities into account. Changes in the Bray–Curtis dissimilarity index indicate "ecological replacement," that is commercial species replacing most of the space previously occupied by the original species, but not driving them extinct as in full replacement.

In this contribution, we aim to investigate whether aquacultural practices have influenced biodiversity gradients in mollusc community structure along the coast of China. In the absence of adequate historical data on mollusc distributions in China, but to still be able to infer whether aquaculture played a role in explaining the biodiversity patterns found, we here distinguished two species categories, one which consists of species not known to be commercially

important nor cultured, the other of species with commercial value known to be cultured. We compared the densities, distributions and the distance decay of similarity indices between non-commercial and commercial species. We examined (a) whether commercial species were more widespread than non-commercial species, (b) whether non-commercial species still kept original biodiversity gradients and showed the distance decay of similarity whereas commercial species were homogenized and thus (c) whether the distance decay of similarity of all coastal mollusc species had been erased. Deviations would reject the null hypothesis of no human effects. Furthermore, with mollusc communities sampled across 20 latitudinal degrees, we are in the position to examine whether latitudinal changes in species richness and Shannon diversity index among the different categories of mollusc (all, non-commercial and commercial species, respectively) vary according to expectation, that is that the highest species diversity occurs in equatorial regions with gradual declines towards higher latitudes (Rex et al., 2000; Willig et al., 2003).

2 | METHODS

2.1 | Study sites and sampling

Sampling was conducted from early April to late May 2018 at 21 sites on intertidal flats along the coastline of China, extending from

Dongliaodao in the far south (20°48′N) to Panjin in the far north (40°48′N) (Figure 1a, Appendix S1: Table S1). For each site, mean annual air temperature and the temperature range (expressed as the difference between the hottest and the coldest average monthly temperature) were taken from www.weatherbase.com. We calculated the average over the past >30 years (weather data available from 30 to 120 years at different sites). The local average temperature decreased with growing latitude (Pearson correlation coefficient = 0.98, $p < .001$, $n = 21$, Figure 1b) and the local temperature range increased with growing latitude (Pearson correlation coefficient = 0.99, $p < .001$, $n = 21$, Figure 1c).

All the sampling stations are located on open "natural" intertidal flats, because this is where mollusc aquaculture is conducted along the coast China. At each site, we sampled across grids (for the rationale; see Bijleveld et al., 2012). Depending on the local situation (e.g. the size of the intertidal flats), gridlines were set either 50 or 500 m apart to cover the area from coast to the low water line (see Sampling sites in Appendix S1). Across the 21 sampling sites, a total of 838 sampling stations were visited. At each sampling station, a sediment core with a surface area of 0.019 m^2 was taken to a depth

of 20 cm and washed over a 0.5 mm sieve. The sieved samples were stored frozen prior to analysis. In the laboratory, molluscs were counted and identified to species level using a dissecting microscope; high density (e.g. 1,000 individuals in one sample) samples were subsampled by a Motodo (1959) before counting.

2.2 | Distinguishing between non-commercial and commercial species

To obtain information on the commercial status of each mollusc species, we searched on "Web of Science," "CNKI," "Wanfang Data," "Google scholar" for the scientific name, Chinese name, or English name of species, and combined the word with "aquaculture", "farm", "culture", "养殖" ("culture" in Chinese), "commercial food", "food", "经济物种"("commercial food" in Chinese) or "食物" ("food" in Chinese). With more than 50 years of highly intensive aquaculture practices along the Chinese coast, the cultured commercial species have spread and invaded across a large range. In the absence of historical data, the original distribution of most species will remain unknown.
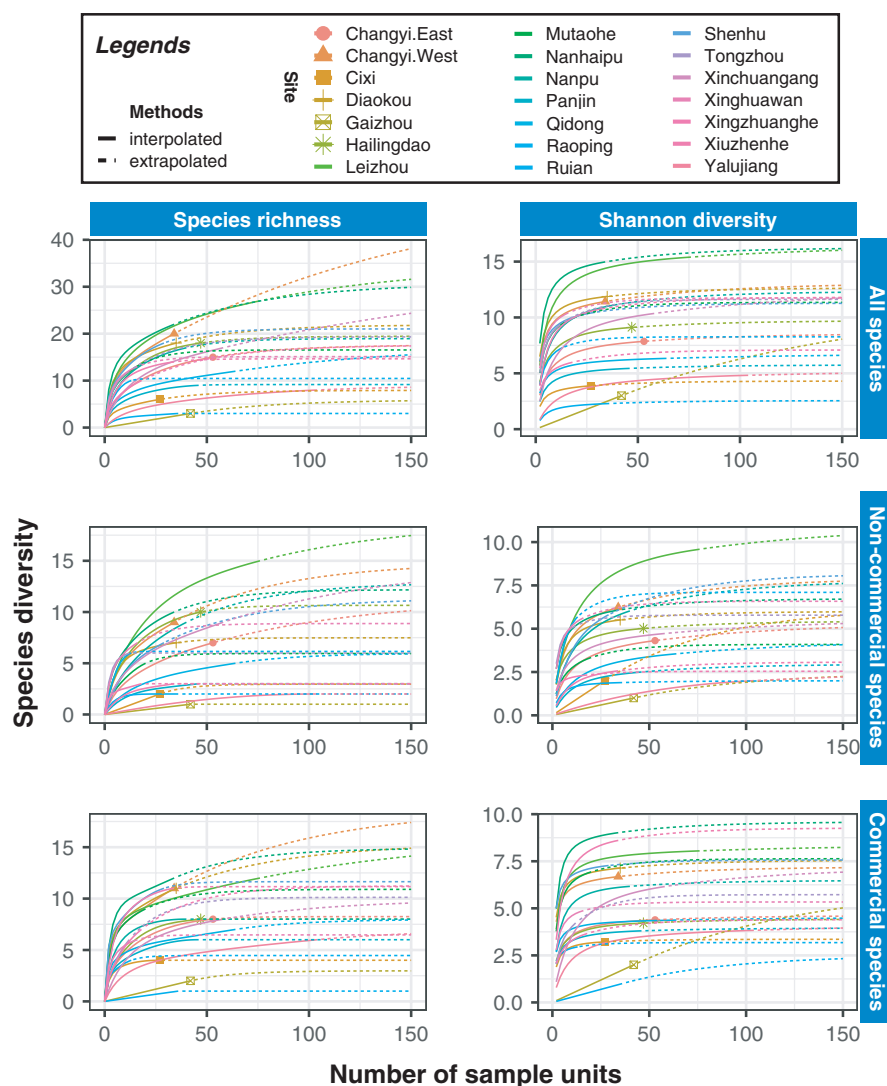
FIGURE 2 Species accumulation curves of shellfish at the 21 sampling sites along the coast of China. Both interpolated values (solid parts of the lines) and extrapolate values (dashed part of the lines) were calculated and established for a sample size of 150

TABLE 1 Mollusc species recorded during benthic sampling along China's coast in 2018. The Brachiopod *Lingula anatina* was included in our analysis, as it can be considered analogous to a bivalve molluscs in terms of ecological role and commercial exploitation

Species	Commercial species	References	Feeding strategy
Bivalvia			
Angulus compressissima	No		Deposit feeder
Coecella formosae	No		Unknown
Codakia golikovi	No		Suspension feeder
Cryptonema producta	No		Suspension feeder
Cyclina sinensis	Yes	Guo et al. (1999)	Suspension feeder
Donax dysoni	No		Suspension feeder
Elachisina ziczac	No		Grazer
Gafrarium pectinaum	No		Suspension feeder
Glauconome chinensis	Yes	Guo et al. (1999); Wang and Deng (1999)	Deposit and suspension feeder
Glauconome primeana	No		Suspension feeder
Gomphina veneriformis	Yes	Guo et al. (1999)	Suspension feeder
Laternula marilina	Yes	Zhuang (2005)	Suspension feeder
Mactra chinensis	Yes	Guo et al. (1999)	Suspension feeder
Mactra veneriformis	Yes	Guo et al. (1999)	Suspension feeder
Meretrix lusoria	Yes	Chen (2003)	Deposit and suspension feeder
Meretrix lyrata	Yes	Chu & Kumar (2008); McCoy and Chongpeepien (1988)	Suspension feeder
Meretrix pethechialis	Yes	Zhang et al. (2016)	Suspension feeder
Moerella iridescens	Yes	Guo et al. (1999)	Suspension feeder
Musculus senhousei	Yes	Guo et al. (1999)	Suspension feeder
Mytilus galloprovincialis[a]	Yes	Guo et al. (2012)	Suspension feeder
Potamocorbula laevis	Yes	Guo et al. (1999); Yang et al. (2016)	Suspension feeder
Pseudopythina Tsurumaru	No		Unknown
Ruditapes philippiarum	Yes	Guo et al. (1999)	Suspension feeder
Scapharca broughtonii	Yes	Guo et al. (1999); Fu et al. (2005)	Suspension feeder
Scapharca subcrenata	Yes	Guo et al. (1999)	Suspension feeder
Sinonovacula constricta	Yes	Guo et al. (1999)	Suspension feeder
Solen strictus	Yes	Chen et al. (2009)	Suspension feeder
Tentidonax kiusiuensis	No		Suspension feeder
Gastropoda			Unknown
Assiminea violacea	No		Suspension feeder
Batillaria zonalis	No		Deposit and suspension feeder
Bullacta exarata	Yes	Guo et al. (1999)	Deposit feeder
Cerithidea cingulata	No		Scavenger, deposit and suspension feeder
Cerithidea sinensis	No		Grazer
Cerithideopsis largillierti	No		Grazer
Laguncula pulchella	No		Predator
Littoraria intermedia	No		Grazer and deposit feeder
Lucidestea matusimana	No		Grazer
Nerita yoldii	No		Grazer

TABLE 1 (Continued)

Species	Commercial species	References	Feeding strategy
Mitrella bella	No		Predator and scavenger
Nassarius festiva	No		Scavenger
Nassarius semiplicatus	No		Scavenger
Nassarius sinarus	No		Scavenger
Nassarius variciferus	No		Scavenger
Neverita didyma	No		Predator
Odostomia limpida	No		Predator
Odostomia subangulata	No		Predator
Pseudoliotia pulchella	No		Unknown
Punctacteon yamamurae	No		Predator
Retusa cecillii	No		Scavenger
Retusa minima	No		Scavenger
Stenothyra glabar	No		Grazer
Salinator fragilis	No		Grazer
Terebra bellanodosa	No		Predator
Terebra taylori	No		Predator
Theora lata	No		Unknown
Turbonilla risso	No		Unknown
Umbonium thomasi	Yes	Wang et al. (2016); Zheng and Hu (1991)	Grazer
Brachiopoda			
Lingula anatine	Yes	Printrakoon and Kamlung-ek (2013); McCoy and Chongpeepien (1988)	Suspension feeder

[a]Invasive species along the Chinese coast.

Therefore, we defined commercial species as those mollusc species recorded in publications, reports and books in the context of aquacultural activities and/or common food production. The Brachiopod *Lingula anatina* was included in our analysis, as this species can be considered analogous to bivalve molluscs in terms of both ecological role and commercial exploitation.

## 2.3 | Diversity metrics and statistical analyses

To ascertain the distribution of the molluscs, we estimated the frequency of occurrence of non-commercial and commercial species at two spatial scales. At the local scale (study site), each sampling station was considered a unit and the frequency of occurrence of each species was calculated. These local frequencies of occurrence of non-commercial and commercial species were averaged for each of the 21 sites and compared using paired Student's *t* tests. At the scale of the coast of China, the overall frequency of occurrence used the 21 sites as units.

Latitudinal distribution ranges of each species were calculated from the southern- and northern-most records in this study. If a

species was recorded at a single site only, we recorded the latitudinal range as 0.1 degrees. Independent *t* tests were used to assess the differences between non-commercial and commercial species in overall (the scale of the whole China coast) frequencies of occurrence and latitudinal distribution ranges.

We used beta diversity to assess the dissimilarities between mollusc communities at the 21 sites. Beta diversity between sites was assessed by both the Bray-Curtis (β_{BC}) and Sorensen (β_{SOR}) dissimilarity metrics using R package *betapart* (Baselga & Orme, 2012). The Bray–Curtis diversity (abundance-based) metric takes into account the relative abundances of species and effectively reduces the influence of incomplete sampling (Cassey et al., 2008). In contrast, the Sorensen diversity, which is based on "incidence" (presence or absence at a site), has been more widely used, but is much less informative. To assess the relationships between beta diversity and geographical and climatic distance, nonlinear regression was used to fit exponential curves expressed as $y = a.e_{b.x}$, where *y* is dissimilarity at distance *x*, *a* initial dissimilarity (intercept) and *b* the rate of distance growth (slope, Baselga et al., 2013). Geographical distances between sites (in km) were computed as Euclidian distances between the centroids of sites, climatic distance (in °C) between sites
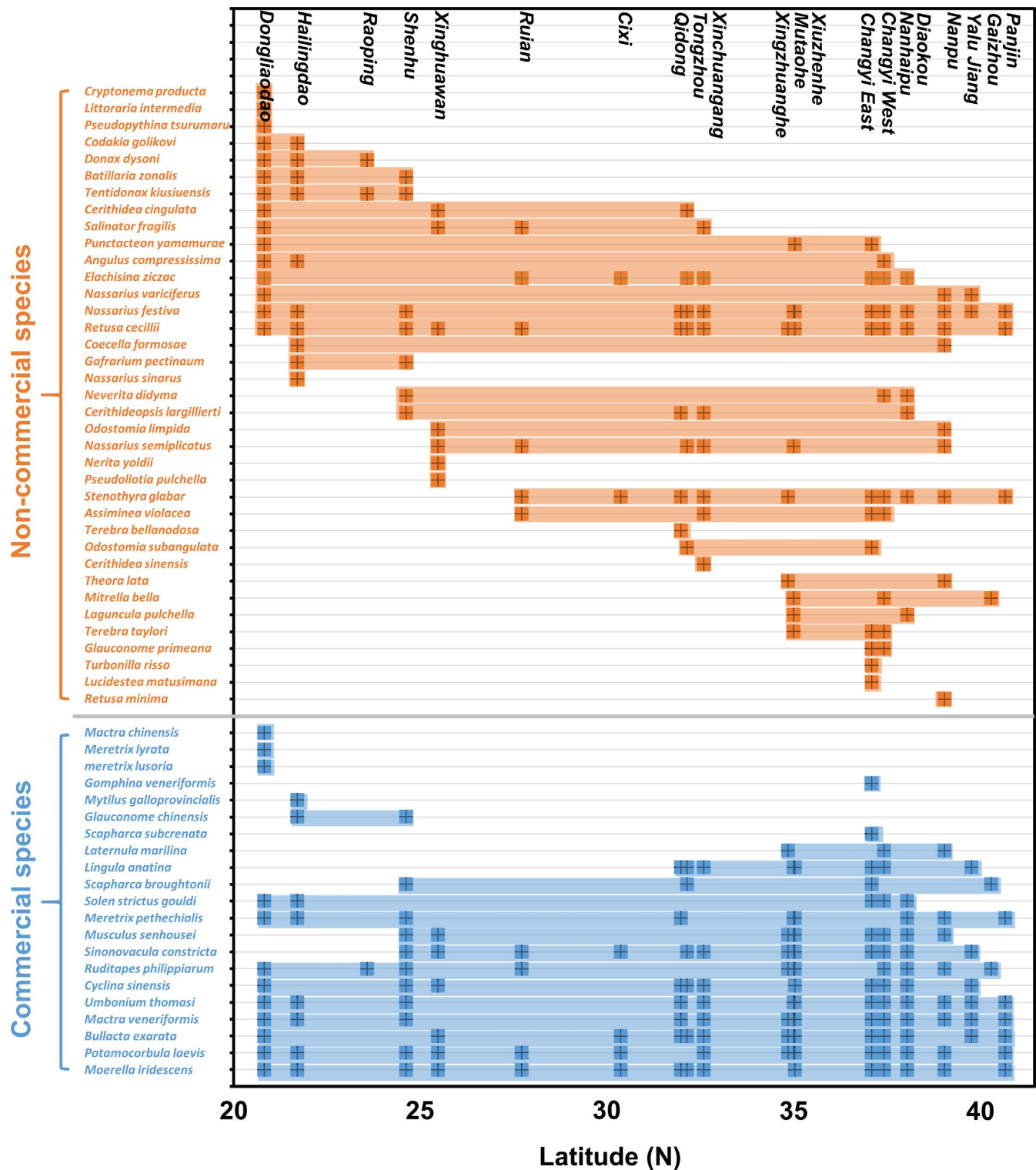
FIGURE 3 Distribution of non-commercial (orange) and commercial (blue) mollusc species at different sites (latitudes). Square symbols represent the records in specific site (latitude), bands show the latitude range (from South to North) of individual species. Sampling sites are located by latitude along the top

were calculated by the differences of the average temperature between sampling sites. To avoid undefined values, an arbitrary small quantity (0.0001) was added to values when climatic distance = 0 (Baselga et al., 2013).

The degree of association between beta diversity and geographical or climatic distance was computed as a Pearson correlation (r), after linearizing the increase curves through log-transformation (Baselga et al., 2013). Mantel tests were used to assess the

TABLE 2 The observed densities, species richness and frequency of occurrence of non-commercial (non-comm.) and commercial (comm.) species at each sampling site

Sampling Sites	Density (Individuals per m^2)		Observed Species Richness		Frequency of Occurrence (%)	
	$\overline{x}_{Non-Comm.}$	$\overline{x}_{Comm.}$	$\overline{x}_{Non-Comm.}$	$\overline{x}_{Comm.}$	$\overline{x}_{Non-Comm.}$	$\overline{x}_{Comm.}$
Panjin	25	232	3	6	8 ± 5	23 ± 24
Gaizhou	1	3	1	2	3	3 ± 0
Yalu Jiang	2	48	2	6	2 ± 0	7 ± 8
Nanpu	53	3,690	9	8	8 ± 8	23 ± 16
Diaokou	133	1,301	7	11	18 ± 14	32 ± 31
Nanhaipu	1,011	1,266	10	12	19 ± 21	30 ± 23
Changyi West	739	1,964	9	11	12 ± 11	30 ± 32
Changyi East	82	231	7	8	8 ± 9	17 ± 23
Xiuzhenhe	17	347	3	11	11 ± 7	20 ± 14
Mutaohe	60	2,471	5	9	15 ± 17	27 ± 20
Xingzhuanghe	220	4,101	3	7	24 ± 27	26 ± 34
Xinchuangang	61	55	9	8	9 ± 13	7 ± 6
Tongzhou	495	503	6	6	32 ± 19	22 ± 23
Qidong	15	285	5	7	6 ± 6	27 ± 27
Cixi	4	483	2	4	3 ± 0	28 ± 21
Ruian	106	836	6	4	15 ± 5	39 ± 33
Xinghuawan	135	1,087	7	6	23 ± 16	30 ± 20
Shenhu	52	2,058	7	11	8 ± 6	34 ± 32
Raoping	57	1	2	1	21 ± 10	3
Hailingdao	265	4,435	10	8	7 ± 5	29 ± 33
Dongliaodao	237	404	15	12	6 ± 7	20 ± 18

significance of r values using package *vegan*. An increase of dissimilarity index with growing distance means that similarity decays with growing distance. We tested the slope differences between beta diversity index and distance measures among three species categories (commercial, non-commercial and all species) by bootstrapping using the *boot* package (Canty & Ripley, 2008) with 1,000 bootstrap samples. Package *ggplot2* and *gridExtra* were used for graphs.

Two measures of alpha diversity were used to describe the latitudinal diversity gradient of molluscs along China's coast: observed diversity (species richness) given the same number of samples taken at each site, and the expected diversity (Shannon diversity) considered both the number of rare species and their relative densities within a sample (Chao et al., 2014). Considering the differences in sampling intensity among sites, we used the "extrapolated" total species richness and Shannon metrics (Chao et al., 2014). The extrapolated species richness and Shannon metrics were estimated using Hill's numbers (i.e. estimation of the effective number of species, (Chao et al., 2014; Hill, 1973)). The Hill number q weighs the sensitivity of the measure to relative abundance, where $q = 0$ is simply species richness; $q = 1$ is the exponential form of Shannon diversity. These metrics were computed with the R package *iNEXT* (Chao et al., 2014; Hsieh et al., 2016) using a fixed sample size of 150 (Figure 2). Linear regression model was used to evaluate whether (extrapolated) species richness and (extrapolated) Shannon diversity of three categories decreased with growing latitude. In order to test for slope and

intercept differences between alpha diversity index and latitude among species categories, the frequency distributions of the slopes were estimated by bootstrapping ($n = 1,000$ bootstraps) using the *boot* package (Canty & Ripley, 2008). When examining a parameter markedly larger in one species category than another, the possibility of obtaining the opposite result by chance was empirically computed by comparing the bootstrap parameter distributions.

All analyses were run in R Studio version 1.1.383 in Mac (R Core Team, 2018). We used $\alpha < 0.1$ (Type II error) to establish statistical significance. Means are reported ± *SD*.

3 | RESULTS

At the 21 sites visited, a total of 58 mollusc species were recorded (Table 1). Locally, the number of species varied between 3 and 27 (mean = 14 ± 6, Appendix S1: Table S2). Of the mollusc species recorded, 37 were considered to be non-commercial and 21 as commercial (Table 1). The distribution ranges of non-commercial species (average 6.6 ± 7.0 latitudinal degrees) were much narrower than that of commercial species (11.8 ± 8.6 latitudinal degrees, independent *t* test, $t = 2.14$, $df = 56$, $p = .04$, Figure 3). Non-commercial species occurred at 17% (± 16%) of the sites, while commercial species occurred at 37% (± 27%) (independent *t* test, $t = 3.7$, $df = 56$, $p < .001$, Figure 3). At 14 of the 21 sites, the commercial species (with an average of 6 species)
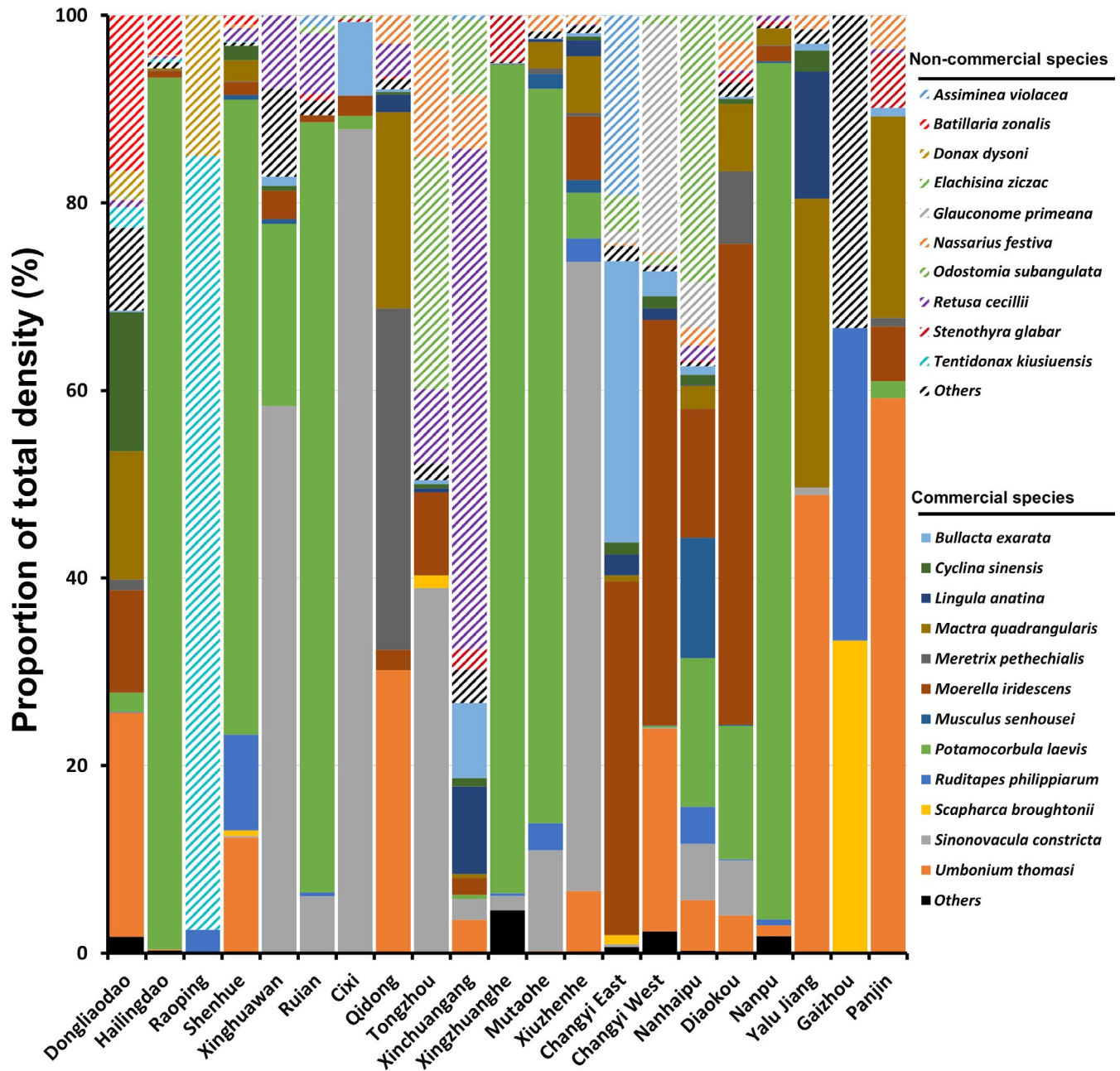
FIGURE 4 Proportion of density of mollusc species at each site. Textured squares represent non-commercial species and filled squares represent commercial species. Only species that reached 5% of local total density are shown, others are grouped into two "Others" categories of non-commercial and commercial species, respectively

outnumbered the non-commercial species (average of 7 species, paired Student's t test, $t = 1.87$, $df = 20$, $p = .08$, Table 2). Non-commercial species occurred on average at 12% ($\pm$ 8%) of the sampling stations, whereas commercial species occurred at 23% ($\pm$ 10%) of the stations (paired Student's t test, $t = 4.15$, $df = 20$, $p < .001$, Table 2). The overall densities of commercial species were higher than non-commercial species at 19 of the total 21 sites (Table 2, Figure 4).

The dissimilarity index accounting for the abundances of the non-commercial species β_{BC} was positively correlated with both geographical and climatic distance (Figure 5), while in the commercial species β_{BC} did not significantly increase with either measure

(Figure 5, Appendix S1: Table S3). For all species combined, the dissimilarity metric β_{BC} did not significantly correlate with the two measures either (Figure 5, Appendix S1: Table S3). Pairwise comparisons on bootstrapped intercepts in β_{BC} between the commercial species, non-commercial species, and all species exhibited no significant differences between the groups (Appendix S1: Figure S2, Appendix S1: Table S3), but there were marked differences in the slopes of β_{BC} on distance between the groups (Appendix S1: Figure S3, Appendix S1: Table S3, non-commercial species > all species > commercial species, $p < .001$ for all). By contrast, β_{SOR} in all the three categories increased with both distance measures (Figure 5); there were
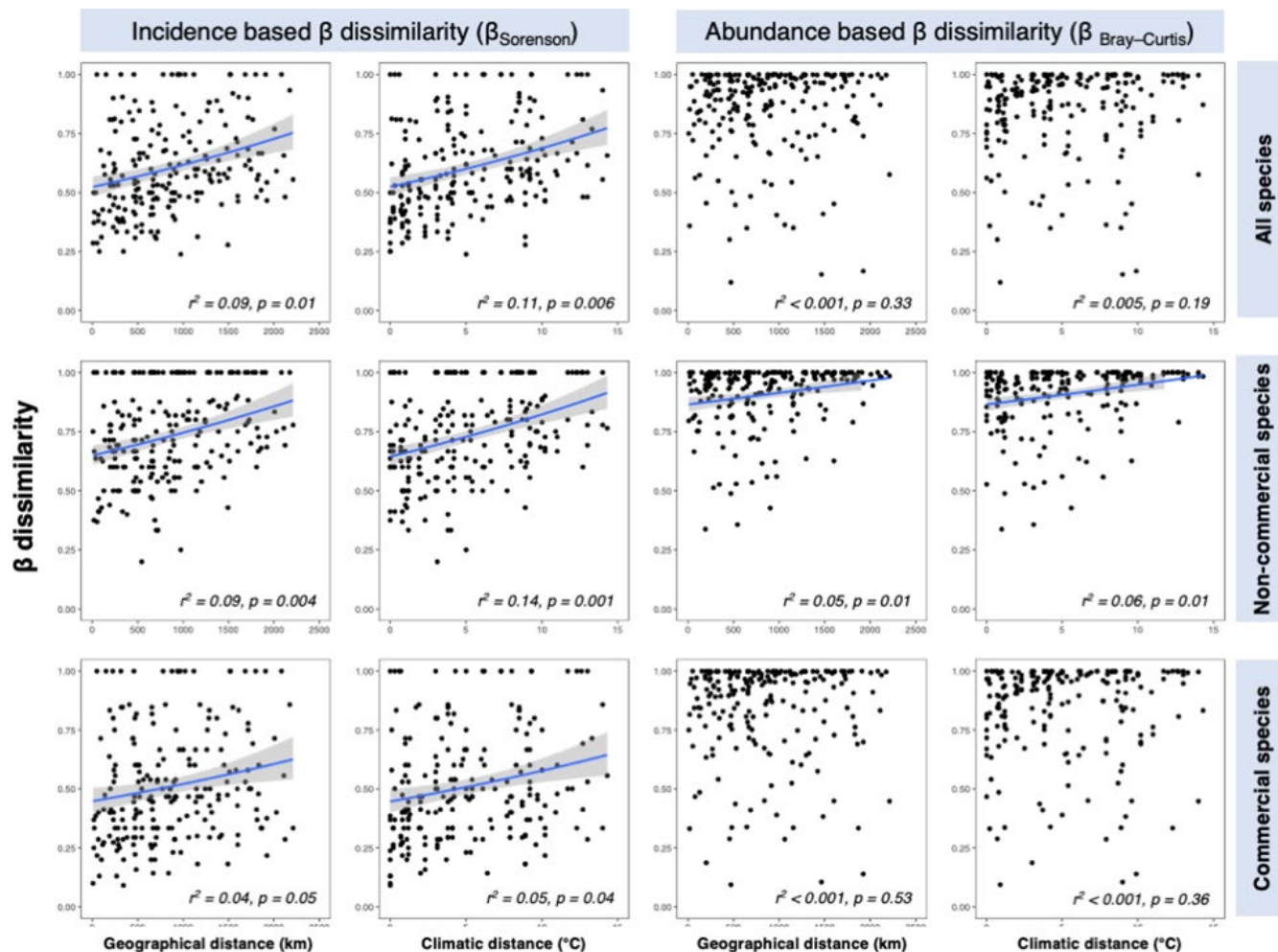
FIGURE 5 Distance effect of dissimilarity of mollusc assemblages along China's coast for all species (top row), non-commercial species (middle row) and commercial species (bottom row). Both geographical and climatic distances are used for the distance, β_{SOR} and β_{BC} are used for dissimilarity metrics, exponential curves are shown with 95% confidence interval. Only trends with a tendency towards type II error significance ($p < .1$) are shown

no significant differences in bootstrapped slopes between the three groups (Appendix S1: Figure S3, Appendix S1: Table S3). However, pairwise comparisons of bootstrapped intercepts showed marked differences between categories: non-commercial species > all species > commercial species ($p < .001$ for all, Figure 5, Appendix S1: Figure S2 and Table S3), so that the average dissimilarities were the highest in non-commercial species and the lowest in the commercial species for both β_{SOR} and β_{BC} (Figure 5).

Non-commercial species richness ($R^2 = .13$, $F = 3.0$, $df = 19$, $p = .1$) and the Shannon diversity index ($R^2 = .15$, $F = 3.4$, $df = 19$, $p = .08$) exhibited the expected decrease with growing latitude, but in commercial species there was no significant change in species richness with growing latitude ($R^2 = .002$, $F = 0.03$, $df = 19$, $p = .85$) nor in the Shannon diversity index ($R^2 = .05$, $F = 0.09$, $df = 19$, $p = .77$; Figure 6). For all species combined, there were no significant correlations between species richness or Shannon diversity index and latitude either (species richness: $R^2 = .04$, $F = 0.7$, $df = 19$, $p = .41$, Shannon diversity index: $R^2 = .05$, $F = 0.09$, $df = 19$, $p = .77$; Figure 6). The bootstrapped slopes of all species were markedly steeper than

the slopes of commercial species, but flatter than the slope of non-commercial species (Appendix S1: Figure S4). The extrapolated alpha diversity index exhibited similar trends (Figure 2, Appendix S1: Figures S4 and S5), except that the extrapolated species richness of non-commercial species did not significantly decrease with growing latitude (Appendix S1: Figure S5).

4 | DISCUSSION

In this study, it was discovered that commercial species of intertidal soft-sediment living molluscs (and a brachiopod), animals which have been deliberately and intensively transported to be reseeded and cultured over at least the past 50 years (Cao et al., 2015; Guo et al., 1999; Li et al., 2011), generally occurred in much higher densities (Figure 4), had wider distributions (Table 2, Figure 3) and showed larger latitudinal ranges than non-commercial species (Figure 3). For the non-commercial species, the expected geographical patterns of decay of similarity with growing distance (at least in the

FIGURE 6 Diversity gradients of mollusc assemblages along China's coast. The relationship between mollusc species richness and Shannon diversity with growing latitudes. Only trends with a tendency towards type II error significance (*p* < .1) are shown
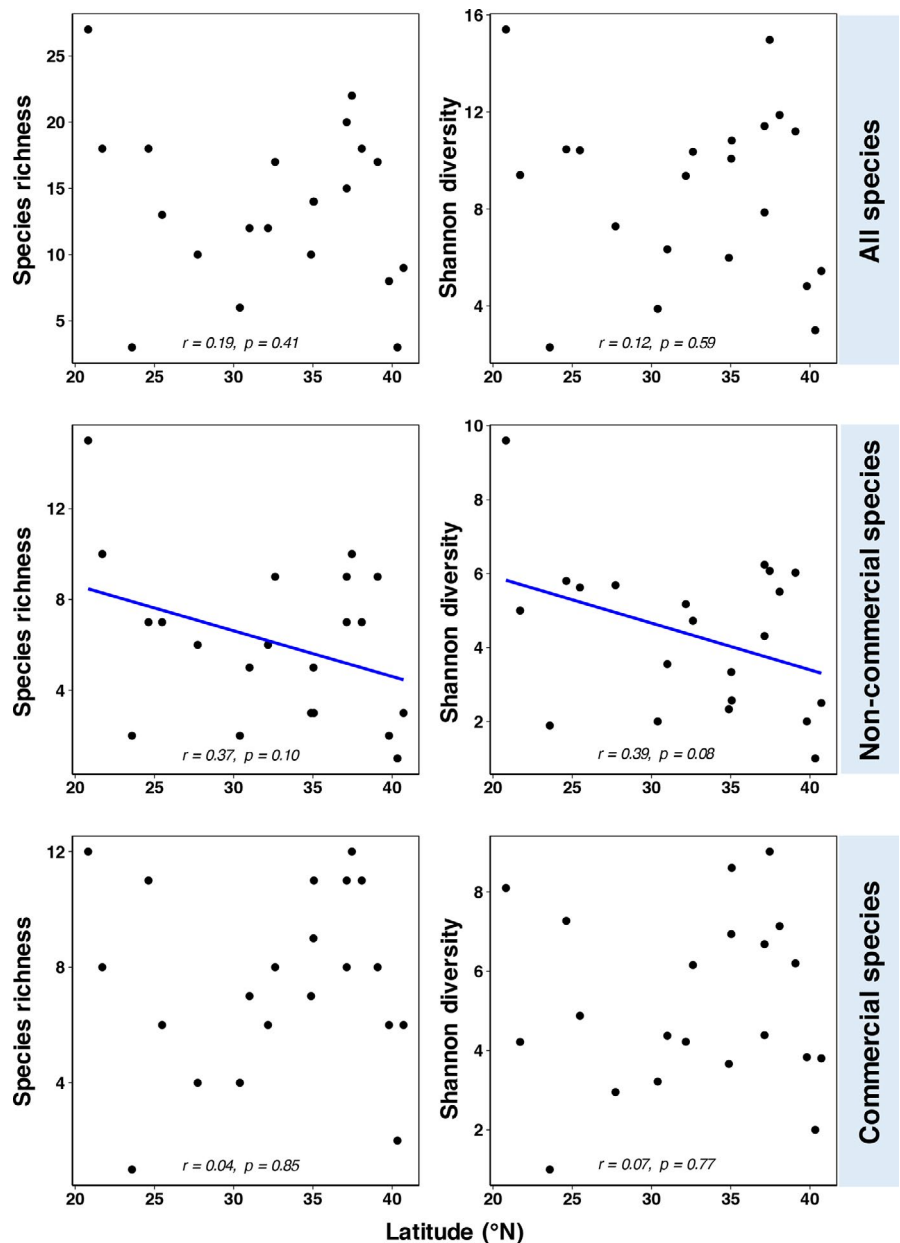
abundance-based dissimilarity index β$_{BC}$) and the decrease with growing latitude, were still recognizable along the coast of China. These gradients were undetected in the β$_{BC}$ and latitudinal biodiversity gradients of commercial species and all the species combined (Figure 6). Although incidence-based dissimilarity index β$_{SOR}$ still exhibited similar trends of increase with growing distance in the three categories, the original high dissimilarities among communities (reflected by non-commercial species) have been weakened by low dissimilarities of commercial species (Figure 5). All these results suggest that commercial aquaculture activities have homogenized mollusc communities along the long and varied coast of China, erasing the expected biodiversity gradients.

Interestingly, different from the abundance-based index (β$_{BC}$), the decay of similarity with growing distance was present in the incidence-based index (β$_{SOR}$) in all three species categories

(commercial, non-commercial, and all). This resulted from the different contributions of mollusc species on either the incidence-based or the abundance-based diversity indices. For example, the single commercial species *Potamocorbula laevis* contributed >95% of the total density in Hailingdao (Figure 4), but they only contributed 1 of 18 species in the local species list. These indicate that ecological rather than full replacement occurs when commercial species expand in the places of introduction. Apparently, commercial species do not generally drive local species to extinction.

Although this appears to be the first study reporting the homogenization by aquaculture of marine biodiversity gradients, the loss of these biodiversity gradients along the coast of China should not come as a surprise. As commercial species are chosen for high economic value and adaptability, they tend to become dominant in a short time (Gosling, 2008; Lin et al., 2015).

For example, when the snail *Bullacta exarata* was introduced from Jiangsu Province into Laizhou Bay (Shandong Province) for aquaculture, soon it occupied more than 80% of the intertidal mudflats (Du et al., 2011).

In addition to being outcompeted by introduced commercial competitors (Lin et al., 2015), stocks of local species in some cases are deliberately reduced by humans (Forrest et al., 2009; Gosling, 2008; NBSO, 2010; Wang & Zhang, 1995). For example, before reseeding with the spat of commercial species, native species with low economic value, especially those which are potential predators or competitors to commercial species, are routinely removed with poisons (Li et al., 2011; Melville et al., 2016). Reseeding is also facilitated by nets, wood frames and low banks constructed in intertidal areas, leading to transformation of sediments, which may negatively affect native species (Guo et al., 1999; Wang & Wang, 2008). More seriously, engineering projects (e.g. land claims, construction of ports; Dong et al., 2016; Murray et al., 2014), pollution (e.g. from sewage, industrial effluent, agricultural wastewater, Cao & Wong, 2007) and other disturbances to intertidal sediments will result in species losses (Islam & Tanaka, 2004) or benefit several species (Dong et al., 2016). All these can affect mollusc communities.

The biotic homogenization of the biodiversity gradient and the loss of the latitudinal biodiversity gradient of intertidal mollusc communities in China, which we argue is mainly the result of intense and widespread aquacultural practices, is probably not exceptional. Agriculture, urbanization, aquaculture, overfishing and deforestation have caused the extinction or rarity of many taxonomic groups, altering biodiversity gradients in numerous ecosystems (Baiser et al., 2012; Diana, 2009; Magurran et al., 2015; Socolar et al., 2016). With the increasing demand for seafood (Cao et al., 2015; Li et al., 2011; Naylor et al., 2000), development of mollusc aquaculture in coastal and offshore areas have been strongly promoted (Gentry et al., 2017). This will further aggravate biotic homogenization in coastal communities in the future.

There is increasing awareness of, and concern about, potential ecological impacts of long-distance mollusc introductions (Brenner et al., 2014; Muehlbauer et al., 2014). Long-distance transport of molluscs will facilitate the spread of pathogens or parasites, which may infest native species and result in the outbreak of diseases (Ruesink et al., 2005). Changes in biodiversity will also affect ecosystem properties and services such as energy transfer and nutrient retention (Worm et al., 2006). A decrease or disappearance of native mollusc species will have cascading effects, in some cases causing the collapses of other species (Loreau et al., 2001). In addition, pollution and disturbances along with aquaculture will negatively affect marine biodiversity. Protocols to assess and manage such risks have been developed in Europe (Brenner et al., 2014; Muehlbauer et al., 2014). In China, as yet there are no such safeguards.

Nevertheless, it is important to note that commercial mollusc species may also benefit some species, especially the molluscivores among the migratory shorebird species (Yang et al., 2013, 2016; Zhang et al., 2019). For example, the high densities of the commercial species *Potamocorbula laevis* at Nanpu, one of the study sites, have supported an increasing number of staging red knots *Calidris canutus* when nearby intertidal habitats were lost (Yang et al., 2016). In this light, restoration of coastal ecosystems by simply stopping intertidal mollusc aquaculture may include unintended negative consequences for the overall community structure and ecosystem functioning, including their role as refuelling areas for shorebirds (Choi et al., 2019; Ma et al., 2014). Clearly, future coastal management and conservation plans should carefully explore changes in intertidal community composition and assess, or possibly control and mitigate, the pressures from expanding aquaculture.

CONFLICT OF INTERESTS

The authors declare no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Depository: (https://doi.org/10.5061/dryad.stqjq2c3d).

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BIOSKETCH

HE-BO PENG is working to understand how current aquacultural practices in coastal intertidal area affect the biodiversity of macrobenthos communities and the further impacts on other associated species (e.g. migratory shorebirds).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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