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Taxonomic dependency and spatial heterogeneity in assembly mechanisms of bacteria across complex coastal waters

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Abstract

Background Understanding community assembly mechanisms across taxa and space is fundamental for microbial ecology. However, the variability and determinants of assembly processes over taxa and space remain unclear. Here, we investigated taxonomic dependency and spatial heterogeneity in bacterial assembly mechanisms across coastal waters in the East China Sea using neutral and null models with customized visualization strategies.

Results Overall, bacterial assembly mechanisms varied across broad taxonomic groups (phyla and proteobacterial classes) and space at the regional scale. A determinism–stochasticity balanced mechanism governed total bacterial assembly, while taxonomic dependency existed in assembly mechanisms and ecological processes. Among community ecological features, niche breadth and negative-to-positive cohesion ratio were strongly associated with the determinism-to-stochasticity ratio of bacterial groups. Bacterial assembly mechanisms commonly exhibited spatial heterogeneity, the extent and determinants of which varied across taxonomic groups. Spatial assembly of total bacteria was directly driven by many environmental factors and potential interactions between taxa, but not directly by geographic factors. Overall, the bacterial groups with higher spatial heterogeneity in assembly mechanisms were more related to environmental and/or geographic factors (except Bacteroidetes), while those with lower heterogeneity were more related to ecological features.

Conclusions Our results confirm the pervasiveness of taxonomic dependency and spatial heterogeneity in bacterial assembly, providing a finer understanding about regulation across complex coastal waters.

Keywords Bacterioplankton, Assembly mechanism, Niche breadth, Null model, Environmental gradient, Biogeography

Background

Understanding assembly mechanisms of microbial community across geographic and taxonomic scales is a fundamental issue of microbial ecology (Zhou and Ning 2017). As the two fundamental theories describing community assembly processes, niche-based theory hypothesizes that deterministic processes such as environmental selection and interspecies interactions govern community assembly (Chesson and Kuang 2008; Letten et al. 2016), while neutral theory assumes that community assemblies are governed by stochastic processes such as dispersal,

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ecological drift (including random birth and death), and speciation/diversification (McGill 2003; Volkov et al. 2003). As the fusion of the two theories has led to the general consensus that both deterministic and stochastic processes contributed to community assembly, the central focus of microbial community assembly mechanisms is to quantify the relative importance of deterministic and stochastic processes (Vellend 2010). As two most popular and influential models specifically developed for microbial communities, Sloan's Neutral Model as a neutral-theory-based process-oriented model (Sloan et al. 2006) and/or Stegen's two-step Null Model based on phylogenetic signal in niche differences between species (Stegen et al. 2013) have been extensively used to infer assembly processes of microbial communities across a broad range of ecosystems or habitats including marine water (Sun et al. 2023; Wu et al. 2020), river (Isabwe et al. 2022; Yang et al. 2023b), lake (Yan et al. 2017; Yang et al. 2023a), soil (Barnett et al. 2020; Tripathi et al. 2018; Xu et al. 2023), human lung (Venkataraman et al. 2015), and aquatic animal (Wang et al. 2020b). Although the core assumptions of the two approaches differ, the deviation of observed patterns from the neutral or null distribution can indicate the extent of determinism relative to stochasticity in shaping microbial communities (Stegen et al. 2012; Venkataraman et al. 2015), thus providing important insights into the balance of ecological processes in governing microbial community assembly. However, given the high diversity and the broad fitness of microbes, quantifying community assembly mechanisms at the whole community level is limited due to the neglect of taxonomically dependent processes, since various ecological processes commonly act on the finer taxonomic levels rather than the whole communities (Nemergut et al. 2013). Previous works based on null models at the community level have reported contrasting assembly mechanisms in global or regional marine waters between microbial domains/kingdoms, including bacteria vs. archaea (Wang et al. 2020a), bacteria vs. protists (Wu et al. 2018), and prokaryotes vs. microeukaryotes (Logares et al. 2020), suggesting the taxonomic dependency at a high taxonomic level. However, assembly mechanisms of different bacterial taxonomic groups across complex coastal waters and their determinants have not been well understood, especially at the regional scale.

According to some previous discussions, including ours, about the pros and cons of neutral and null models (Wang et al. 2020a; Zhou and Ning 2017), we propose that simultaneously considering two methods could improve the inference of the microbial assembly processes. The typical results of either neutral or null models can reflect the general pattern in relative importance of deterministic and stochastic processes (or specific

ecological processes) in shaping microbial communities in the study areas (Logares et al. 2020; Wu et al. 2018; Yan et al. 2017). However, at the larger geographic scale (i.e., regional scale), the understanding of underlying mechanism shaping microbial biogeography could be oversimplified without further characterization of the spatial variability in assembly processes (Wang et al. 2019; Yan et al. 2021). Therefore, evaluating the heterogeneity of assembly processes of microbial communities across space is essential to understanding the mechanism shaping the spatial assembly of microbes, especially at or beyond the regional scale. However, the spatial heterogeneity in the assembly of total bacteria and different taxonomic groups across complex coastal waters at the regional scale has not been comprehensively investigated.

In marine waters, several previous studies have suggested that contrasting community assembly mechanisms of prokaryotes and picoeukaryotes were driven by their differences in dormancy potential and species composition (Kong et al. 2022; Logares et al. 2020), while the distinct assembly mechanisms between bacterial and protist communities depended on niche breadth and cellular size (Wu et al. 2018). Our previous work found that domain-dependency patterns in prokaryotes corresponded to differences in niche breadth and bacteria and archaea population sizes (Wang et al. 2020a). For a finer perspective of sub-communities, most previous efforts compared assembly mechanisms of abundant and rare communities (Alonso-Sáez et al. 2015; Logares et al. 2014; Mo et al. 2018; Wu et al. 2017). For example, taxa abundance and diversity were suggested to contribute to the differences in assembly mechanisms of abundant and rare communities of bacteria in subtropical bays (Mo et al. 2018). However, key factors mediating the taxonomic dependency or spatial variability in assembly processes of marine bacteria have not been extensively revealed. Seawater density and temperature were suggested to be the most important environmental modulators of the balance between stochastic and deterministic assembly processes of prokaryotes along a ~2000-km longitudinal transect (Allen et al. 2020). Our previous work suggested suspended particles as a crucial factor driving the balance between deterministic and stochastic assembly processes of bacteria across the coastal waters in the East China Sea (Wang et al. 2020a). However, determinants of taxonomic dependency and spatial heterogeneity in assembly mechanisms of bacteria across complex coastal waters remain largely unknown.

To characterize taxonomic dependency and spatial heterogeneity in assembly mechanisms of bacteria and their regulation in coastal waters, we used the coastal area of northern Zhejiang, East China Sea, with spatially structured environmental gradients (primarily salinity and

nutrient-related factors including dissolved inorganic nitrogen, phosphate, and suspended particles) (Wang et al. 2015), as a model system. A 16S rRNA microbiome dataset with regionally high coverage was analyzed with both neutral and null models, and with corresponding visualization methods to test three hypotheses: (1) there would be pronounced taxonomic dependency in ecological processes governing bacterial assembly; (2) spatial heterogeneity in assembly processes of bacteria along the environmental gradients would be common across taxonomic groups; and (3) the extent and determinants of spatial heterogeneity would also be taxonomically dependent. Our work could provide a baseline for assessing the impact of regional environmental changes on the mechanisms of maintenance of bacterial diversity and aggregation.

Methods

Sampling scheme, measurements of water physicochemical parameters, 16S rRNA gene amplicon sequencing, and sequence processing

The study area and sampling procedures were described in our previous work (Wang et al. 2015). Briefly, we used a high-coverage sampling scheme at a ~200-km scale across the coastal area of northern Zhejiang Province, China. A total of 95 surface water samples (at 0.5-m depth) were collected from 95 stations, affiliated to eight zones: Hangzhou Bay (HZ), Zhoushan archipelago (ZSI, including three subzones: ZSI_north (northern part of the archipelago), ZSI_mouth (in the mouth of HZ), and ZSI_other (others)), Xiangshan Bay (XS), Sanmen Bay (SM), Shipu (SP), Jiushan (JS), the east boundary of the Island-chain (BIC), and Yushan Reserve (YS) (Additional file 1: Fig. S1). Detailed information of measurements of water physicochemical parameters, 16S rRNA gene amplicon sequencing, and sequence processing can be found in the Supplementary Methods and previous reports (Wang et al. 2015).

This study aims to test taxonomic dependency in assembly processes at the phylum and proteobacterial class levels, since quantifying assembly processes at finer taxonomic levels like genus relies on extremely deep sequencing to obtain sufficient sequences for a given taxon across all the samples, which is limited by the current dataset. A given bacterial phylum (or proteobacterial class) with accumulative reads proportion > 2% in the whole dataset was selected as a dominant taxon for downstream analyses. As the most dominant and diverse bacterial phylum in the marine environment, Proteobacteria (accounting for 40.6% of bacterial sequences in the present study) was conventionally divided into classes when getting involved into the phylum-level analysis with other bacterial phyla (Hoshino et al. 2020; Sunagawa et al.

2015). Separate tables were generated from the total bacterial ZOTU (Zero-radius Operational Taxonomic Unit) table for the above bacterial groups. The Actinobacteria, Gammaproteobacteria, Alphaproteobacteria, Bacteroidetes (aka. Bacteroidota in the GTDB taxonomy), Cyanobacteria, Planctomycetes, and Deltaproteobacteria tables were composed of 574, 1,816, 1,265, 1,297, 93, 1,150, and 1,353 ZOTUs, respectively. To deal with uneven sequence numbers among different taxonomic groups and across different samples, each sub-ZOTU table was normalized by the cumulative sum scaling transformation (Paulson et al. 2013).

Inference and visualization of assembly processes of bacterial communities from the metacommunity using the neutral model

We used the Sloan Neutral Model to infer assembly processes of bacterial communities from the metacommunity across the study area based on the total bacterial ZOTU table rarefied at 7,140 reads per sample (Sloan et al. 2006). Briefly, the relationship between the frequency of occurrence of ZOTUs in the local communities of 82 stations and their abundance in the metacommunity (estimated by the mean relative abundance across all local communities) was fitted by the neutral model. The model predicts that more abundant species (as referred to ZOTUs here) of a metacommunity will be more ubiquitous across local communities, because of their higher probability to be randomly dispersed and then to colonize in a local community, while less abundant species are more likely to be lost or replaced by others due to ecological drift (Burns et al. 2016). The R code from Burns et al. (2016) was used for the neutral model fitting, the goodness of model fitting was evaluated by R^2 , ranging from ≤ 0 (not fit) to 1 (perfectly fit). The 95% confidence intervals of the model were calculated by bootstrapping with 1,000 replicates. The estimated migration rate (m), presenting the probability that stochastic losses of individuals in local communities replaced by dispersal from the metacommunity, was calculated using a non-linear least-squares fitting with the R package 'minpack.lm' (Burns et al. 2016; Elzhov et al. 2013). This parameter can be considered as an indicator of dispersal limitation, that is, higher m values mean less dispersal limited (Burns et al. 2016).

The ZOTUs that fall within the 95% confidence intervals of the neutral model are considered as neutrally distributed, which are likely assembled into local communities by stochastic dispersal from the metacommunity and ecological drift (Venkataraman et al. 2015). The ZOTUs that were overrepresented compared to the neutral prediction hold a strong probability of preference for certain local conditions, thus being selected

for, while the ZOTUs that were underrepresented compared to the neutral prediction are likely selected against by most of local conditions and/or governed by dispersal limitation from the metacommunity (Venkataraman et al. 2015). The cumulative relative abundances of neutrally distributed and non-neutrally distributed (above and below prediction) species were calculated as a metric to infer the relative influence of dispersal and drift (stochastic processes) and selection (deterministic processes) in governing the assembly of bacteria at the community level (Venkataraman et al. 2015). To assess the taxonomic dependency in relative importance of deterministic and stochastic processes, we calculated the cumulative relative abundance of non-neutrally and neutrally distributed ZOTUs of total bacterial communities and different taxonomic groups. Furthermore, the abundance ratio of non-neutrally and neutrally distributed ZOTUs (hereinafter referred to as non-neutral-to-neutral ratio) of each community at each station was calculated as following:

$$\text{Non-neutral-to-neutral ratio} = \frac{\sum_{i=1}^M \text{Above}_i + \sum_{j=1}^N \text{Below}_j}{\sum_{k=1}^T \text{Neutral}_k} \tag{1}$$

where Above_i , Below_j , and Neutral_k are the relative abundance of overrepresented ZOTU i , underrepresented ZOTU j , and neutrally distributed ZOTU k in a given community, respectively. Then non-neutral-to-neutral ratio of each station was visualized using ArcGIS Desktop 10.4 to evaluate the spatial heterogeneity in assembly processes of bacteria.

Inference and visualization of assembly processes of bacterial communities on between-station basis using the null models

The assembly processes of bacterial communities on the basis of pairwise comparison between stations were inferred using the null models (Stegen et al. 2013). This approach (Stegen et al. 2013) and spatial visualization of assembly processes (Wang et al. 2019) have been described previously. Briefly, the first step of this approach is using the deviation of observed phylogenetic turnover (based on β -Mean Nearest Taxon Distance (βMNTD)) from the null expectation, that is β -Nearest Taxon Index (βNTI), to distinguish deterministic and stochastic processes:

where f_{ik} is the relative abundance of ZOTU i in community k , n_k is the number of ZOTUs in k , and $\min(\Delta_{ikjm})$ is the minimum phylogenetic distance between ZOTU i in community k and all ZOTUs j in community m ;

$$\beta\text{NTI} = \frac{\beta\text{MNTD}_{obs} - \overline{\beta\text{MNTD}_{null}}}{\text{sd}(\beta\text{MNTD}_{null})} \tag{3}$$

where βMNTD_{obs} is phylogenetic distances between two observed communities, $\overline{\beta\text{MNTD}_{null}}$ is that between two randomized communities, $\overline{\beta\text{MNTD}_{null}}$ is the mean βMNTD_{null} from 999 randomization, and $\text{sd}(\beta\text{MNTD}_{null})$ is standard deviations of 999 βMNTD_{null} . The significant difference ($|\beta\text{NTI}| > 2$) indicates the dominance of deterministic processes for a given pair of communities, and $\beta\text{NTI} > +2$ or < -2 suggests that heterogeneous or homogeneous selection governs between-community difference or similarity, respectively. For all the pairs of communities with $|\beta\text{NTI}| < 2$, which suggests stochastic processes, the second step uses Raup–Crick metric based on Bray–Curtis dissimilarity (RC_{bray}) to estimate the standardized deviation of observed ZOTU turnover from the null expectation, thus disentangling various stochastic processes (Chase and Myers 2011; Stegen et al. 2013). When $|\beta\text{NTI}| < 2$, the significant difference, that is $\text{RC}_{bray} > +0.95$ or < -0.95 , suggests that dispersal limitation or homogenizing dispersal governs between-community difference or similarity, respectively, while $|\text{RC}_{bray}| < 0.95$ suggests that the turnover between a given pair of communities is undominated by any processes (Stegen et al. 2015). Subsequently, the spatial distribution of assembly processes of total bacterial communities or different taxonomic groups between stations was visualized using ArcGIS Desktop 10.4 (Yan et al. 2021).

Calculation of niche breadth of bacteria

Levins' niche breadth was used to present habitat specialization and generalization of each bacterial ZOTU, based on the abundance of species in different resource states (Levins 1968). Here, resource states were defined by non-hierarchical clustering as previously described (Wang et al. 2020a; Yan et al. 2022). The ZOTU tables of total bacterial community and different taxonomic groups were then converted into resource matrices (Krebs 2014).

$$\beta\text{MNTD} = 0.5 \left[\sum_{i_k=1}^{n_k} f_{i_k} \min(\Delta_{i_k j_m}) + \sum_{i_m=1}^{n_m} f_{i_m} \min(\Delta_{i_m j_k}) \right] \tag{2}$$

Niche breadth of ZOTUs was calculated and standardized as following (Pandit et al. 2009).

$$\text{Levins' niche breadth index (B)} : B_j = 1 / \sum_{i=1}^N P_{ij}^2, \quad (4)$$

$$\text{Levins' standardized niche breadth (B}_A\text{)} : B_A = (B - 1) / (N - 1), \quad (5)$$

where B_j is the niche breadth of ZOTU j , P_{ij} is the proportion of ZOTU j in resource state i , N is the total number of resource states. The arithmetic average B_A of all ZOTUs in a given bacterial community or groups were calculated as niche breadth at the levels of the total community or taxonomic group (Wu et al. 2018). The habitat specialists and generalists were defined according to B_A value of a given ZOTU as previously described (Liao et al. 2016). Additional details of the threshold of habitat specialists and generalists are provided in Additional file 1.

Inference of potential microbial interactions by association network analysis

Direct microbial associations were inferred using FlashWeave (sensitive=true, heterogeneous=false, alpha=0.001, normalize=true) (Tackmann et al. 2019). FlashWeave was used because of its merits on detecting and removing indirect (i.e., purely correlational) associations to construct direct association networks based on local-to-global learning approach, a constraint-based causal inference framework for the prediction of direct relationships between variables, thus reducing false or suspicious associations. It furthermore allows to estimate influence of environmental factors on microbial associations and then to remove indirect associations driven by them. The total bacterial network with non-environmentally driven edges was generated, and then was divided into sub-networks for seven bacterial groups according to the edges connected to the nodes (ZOTUs) of each bacterial group. Community cohesions and cohesion ratio (|negative cohesion/positive cohesion|), as metrics evaluating the degree of connectivity and relative importance of negative and positive relationships between taxa in a community, were calculated based on the associations revealed in total bacterial network and seven sub-networks as previously described (Hernandez et al. 2021; Herren and McMahon 2017). Furthermore, station-based networks were extracted from the total bacterial network and seven bacterial sub-networks according to the edges connected to the nodes (ZOTUs) present in the local community (Ma et al. 2016) and then topological features including modularity and average degree, as metrics evaluating community stability and potential interaction

strength (Hernandez et al. 2021; Wan et al. 2020), were calculated using the R package “igraph”.

Estimating the direct and indirect effects of different factor categories on bacterial community assembly

Partial least squares path modeling (PLS-PM) (Sanchez et al. 2023) was conducted to obtain a systematic understanding of the direct and indirect effects of factor categories including *Longitude*, *Latitude*, basic abiotic constraints (*Basic*; including pH and DO), inorganic resources (*Inorganic*; including salinity, DIN (dissolved inorganic nitrogen; sum of NO_3 (nitrate), NO_2 (nitrite), NH_4 (ammonium), and PO_4 (phosphate)), organic resources (*Organic*; including SP (suspended particles), COD (chemical oxygen demand), and oil), chlorophyll-*a* (*Chl-a*), niche breadth of bacterial community (*Niche*), bacterial alpha diversity indices (*Diversity*; including phylogenetic diversity, ZOTU richness, and Shannon–Wiener index), relative abundance (*Abundance*), and the features reflecting potential microbial interactions (*Interaction*; including cohesion ratio (|negative cohesion/positive cohesion|), modularity, and average degree) on bacterial community assembly mechanisms (as expressed by the ratio of the relative abundance of non-neutrally ZOTUs to that of neutrally distributed ones) with the R package ‘plsmpm’ (Sanchez et al. 2023). The *GoF* index is regarded as goodness of fit of the entire model. The total effects are the sum of direct and indirect effects. The direct effects are expressed as the path coefficients, and the indirect effects are expressed as the product of the path coefficients by taking an indirect path. Partial least squares path modeling shows the path coefficients (direct effects) of the above ten factor categories, significance of linear model fitting between pairwise factor categories were checked by bootstrap *t*-test.

General statistical analyses

The geo-statistics were performed in ArcGIS Desktop 10.4. Kruskal–Wallis analysis was applied to test the significance of differences in the ecological features including non-neutral-to-neutral ratio, niche breadth, alpha diversity indices, and the features of microbial associations across bacterial communities using IBM SPSS Statistics Version 22.0. Spearman rank correlations between assembly mechanisms (as expressed by non-neutral-to-neutral ratio) of bacterial communities and other community ecological features were tested in IBM SPSS Statistics Version 22.0. Distance-based redundancy analysis (db-RDA) was performed to determine key environmental driver of compositional variation of bacterial communities using the ‘capscale’ function of the R package “vegan”.

Results

Assembly processes of bacterial communities

Our analyses focused on seven bacterial taxonomic groups at the phylum and proteobacterial class levels, accounting for 92.8% of reads of the metacommunity. Overall, the assembly of total bacterial communities fit the neutral model ($R^2 = 0.77$; Additional file 1: Fig. S2). According to the cumulative relative abundance of three categories of ZOTUs (Zero-radius Operational Taxonomic Units) indicating the relative importance of different ecological processes, neutral (stochastic) processes had slightly more contribution to total bacterial community assembly compared with that of selection (deterministic (above or below prediction)) processes (58.4% vs. 41.6%) (Fig. 1A). However, the relative importance of neutral and selection processes was highly variable across the seven bacterial groups, that is, Actinobacteria, Gammaproteobacteria, Alphaproteobacteria, and Cyanobacteria were more dominantly governed by neutral processes; and Bacteroidetes, Planctomycetes, and Deltaproteobacteria were more shaped by selection processes, with more selection against in the assembly of Bacteroidetes and Planctomycetes but more selection for in the assembly of Deltaproteobacteria.

In order to quantify phylogenetic turnover of bacterial communities using the null model based on β NTI (β -Nearest Taxon Index), we first tested for phylogenetic signals for total bacterial community or taxonomic groups (Additional file 1: Fig. S3), and confirmed significant signals across relatively short phylogenetic distances (typically < 13% of the maximum) (Stegen et al. 2012). The null models showed that total bacterial communities were equally governed by deterministic and stochastic

processes (Fig. 1B). Similar to the pattern revealed by the neutral model, Actinobacteria, Gammaproteobacteria, Alphaproteobacteria, and Cyanobacteria were more governed by stochastic processes, of which the relative importance was even higher than that shown by neutral model, while the enhanced stochasticity made Bacteroidetes equally shaped by deterministic and stochastic processes (50.2% vs. 49.8%) (Fig. 1B). However, Planctomycetes and Deltaproteobacteria were governed more by stochastic processes, showing the opposite pattern as revealed by the neutral model. Additionally, we found that all bacterial groups were governed more by deterministic processes when quantifying with RC_{bray} (Raup–Crick metric based on Bray–Curtis dissimilarity) alone than with β NTI alone (Additional file 1: Fig. S4).

Spatial variability of assembly processes of bacterial communities

The ratio of deterministic and stochastic assembly processes at each station quantified by non-neutral-to-neutral ratio was mapped to illustrate the spatial heterogeneity of bacterial community assembly mechanism (Fig. 2). Total bacterial communities were more shaped by deterministic processes (selection) in Hangzhou Bay (HZ) and Yushan Reserve (YS), serving as two ends of multiple environmental gradients (including salinity and nutrient-related factors). In other zones among the intermediate interval of the environmental gradients, stochastic (neutral) processes showed more power in governing the assembly of total bacterial communities. The assembly processes of the seven bacterial groups showed distinct spatial patterns. Bacteroidetes showed a similar pattern as the total bacterial community, with

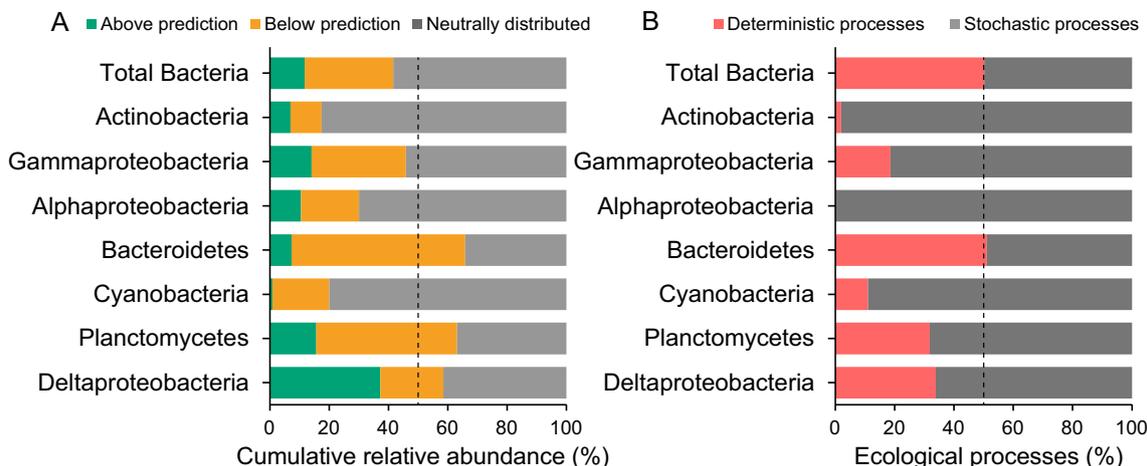


Fig. 1 Relative importance of assembly processes of bacteria using neutral (A) and null models (B). **A** Cumulative relative abundance of bacterial ZOTUs above prediction, below prediction, and neutrally distributed. **B** The percentage of ecological processes governing the spatial turnover of total bacterial communities or seven taxonomic groups in all pairwise comparisons between stations according to β NTI values

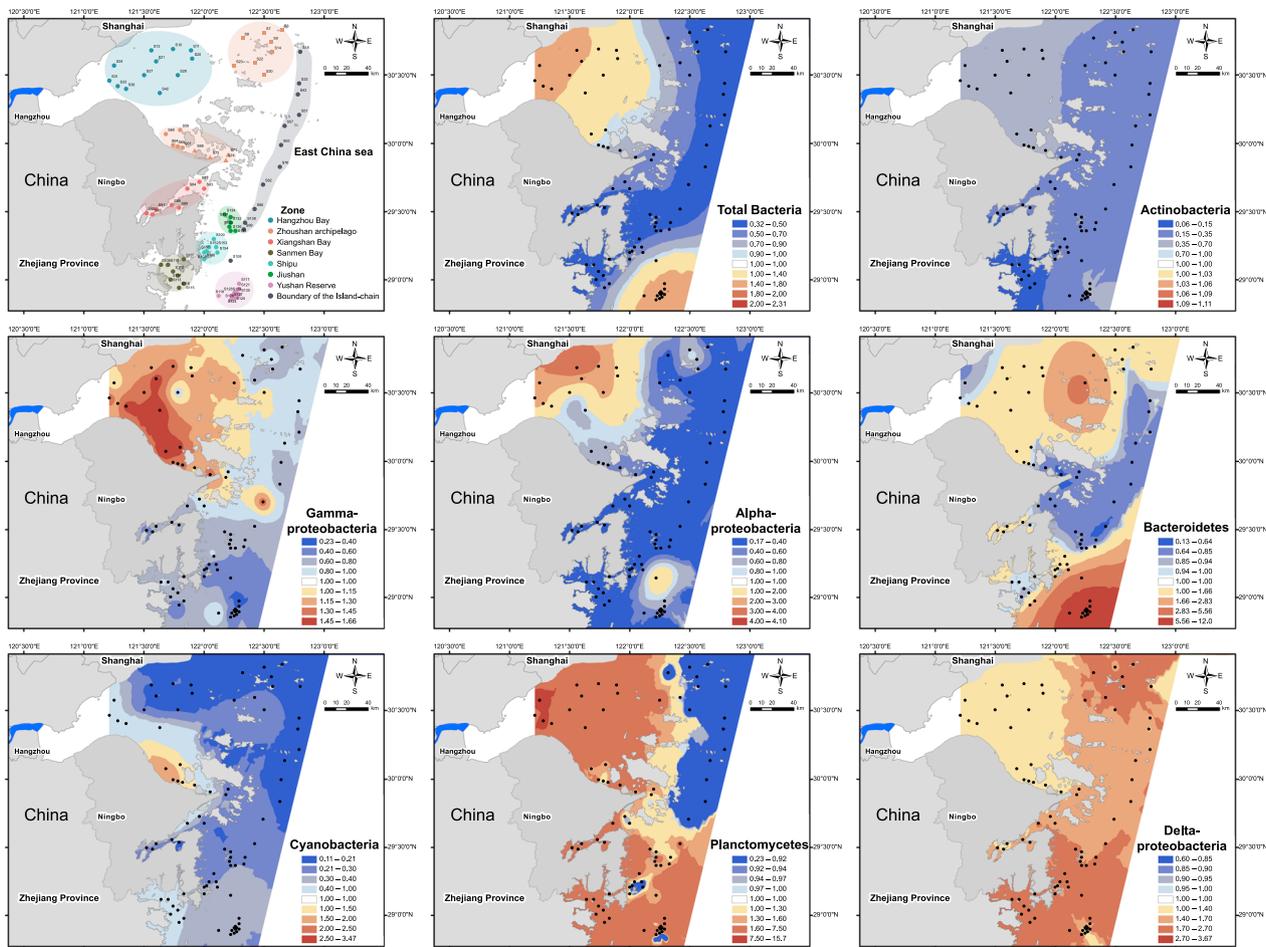


Fig. 2 Kriged maps illustrating the spatial variability of the ratio of relative abundance of non-neutrally (sum of above-prediction and below-prediction) distributed ZOTUs to that of neutrally distributed ZOTUs (defined by the neutral model) in total bacterial communities or seven taxonomic groups. The colors of the stations correspond to different zones, and the stations in the Zhoushan archipelago were grouped into three subzones including ZSI_north (northern part of the archipelago), ZSI_mouth (in the mouth of HZ), and ZSI_other (others), which were shown as square, circle, and triangle symbols, respectively

the zones dominated by determinism extending to the northern part of Zhoushan archipelago (ZSI_north) and Jiushan Islands (JS). The assemblies of Alphaproteobacteria and Gammaproteobacteria were dominantly governed by deterministic processes in HZ, while stochastic processes in other zones. Actinobacteria and Cyanobacteria were generally shaped by stochastic processes across the entire study area (except several HZ stations for Cyanobacteria), while the assembly of Deltaproteobacteria was dominated by deterministic processes. The assembly of Planctomycetes was dominated by deterministic processes in most zones except the east boundary of the Island-chain (BIC). The degree of heterogeneity in assembly mechanisms of bacteria estimated by coefficient of variation (CV) of non-neutral-to-neutral ratio varied from 0.36 to 1.35 (data not shown). Taxonomic groups with higher spatial heterogeneity were Bacteroidetes

(1.35), Alphaproteobacteria (1.18), Cyanobacteria (1.12), and Planctomycetes (1.06), while those with lower heterogeneity were Actinobacteria (0.69), Gammaproteobacteria (0.42), and Deltaproteobacteria (0.36).

From the perspective of pairwise comparisons between zones (as indicated by the ratio of deterministic processes between zones according to β NTI), total bacterial community and taxonomic groups including Bacteroidetes, Deltaproteobacteria, and Planctomycetes showed higher spatial heterogeneity in assembly processes, compared with other taxonomic groups (Fig. 3 and Additional file 1: Fig. S5). The extent of heterogeneity across taxonomic groups overall corresponded to those revealed by the neutral model, except Alphaproteobacteria and Gammaproteobacteria, which showed much less heterogeneity compared with that based on the neutral model. For the total

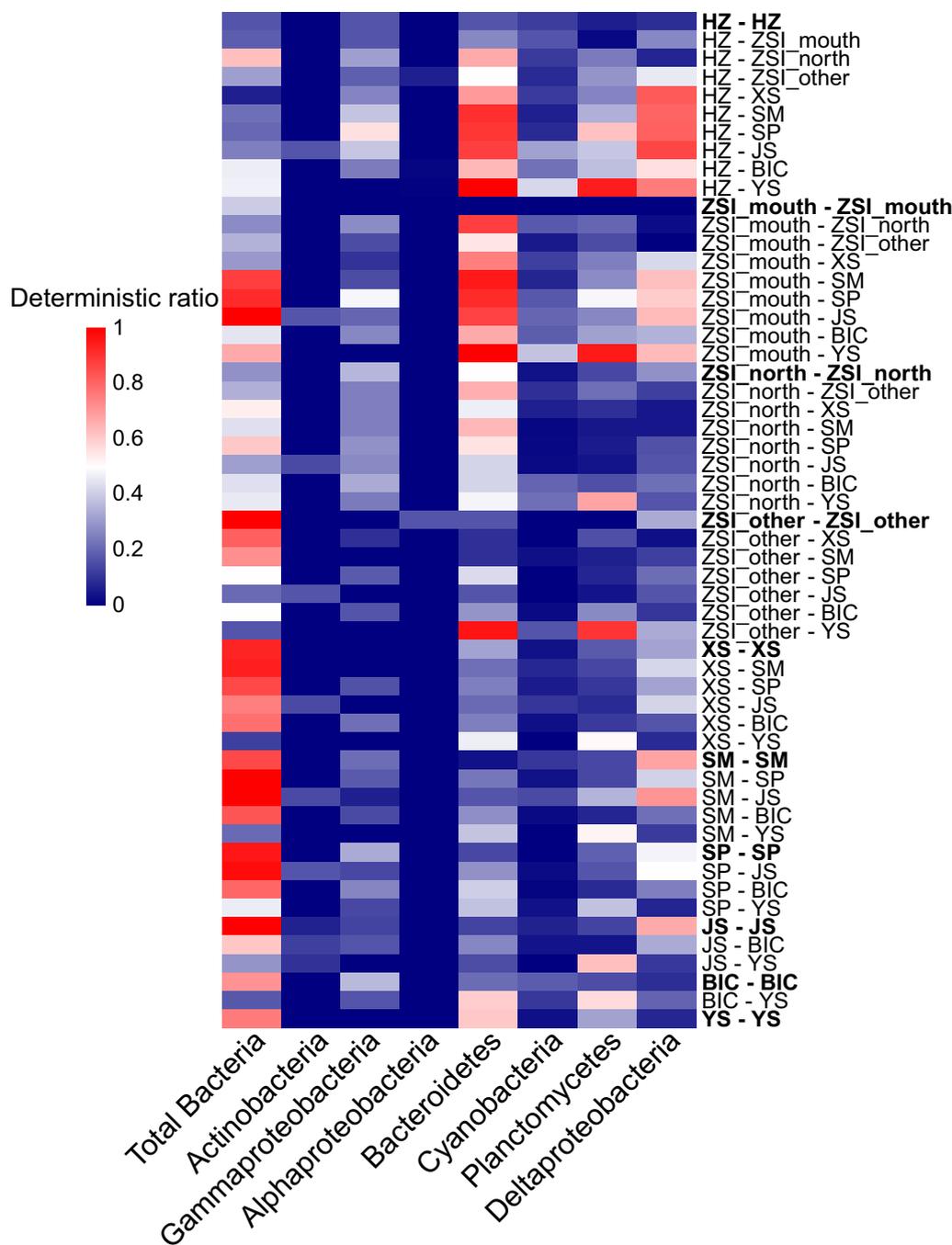


Fig. 3 Heatmap showing deterministic ratio of assembly processes of total bacterial communities and seven taxonomic groups based on pairwise comparisons between zones according to β NTI. Data in bold indicate deterministic ratio of assembly processes within each zone. HZ, Hangzhou Bay; ZSI, Zhoushan archipelago; XS, Xiangshan Bay; SM, Sanmen Bay; SP, Shipu; JS, Jiushan; BIC, the east boundary of the Island-chain; YS, Yushan Reserve. The stations in the ZSI were grouped into three subzones including ZSI_north (northern part of the archipelago), ZSI_mouth (in the mouth of HZ), and ZSI_other (others). Details about the geographic distribution of the ecological processes governing the spatial turnover of bacterial communities between stations according to β NTI and RC_{bray} values are shown in Additional file 1: Fig. S5

bacterial community, a determinism-dominated pattern was more frequently detected between ZSI/Xiangshan Bay (XS)/Sanmen Bay (SM)/Shipu (SP) and other

zones, while a determinism-dominated pattern of Bacteroidetes and Deltaproteobacteria was mainly found between HZ/ZSI_mouth and other zones. Additionally,

the heterogeneous distribution of five specific ecological processes governing the assembly of total bacterial community and bacterial groups was ubiquitous (Additional file 1: Fig. S5).

Associations of community ecological features with assembly mechanism

The optimal number and spatial distribution of resource states are shown in Additional file 1: Fig. S6, then niche breadth was calculated based on the resource matrices. The ecological features including standardized Levins' niche breadth, alpha diversity indices (including phylogenetic diversity, ZOTU richness, and Shannon–Wiener index), relative abundance, and the features of microbial associations (including cohesion ratio (|negative cohesion/positive cohesion|), modularity, and average degree) varied across bacterial groups (Additional file 1: Fig. S7). In the study area, Cyanobacteria possessed the widest niche breadth, followed by Gammaproteobacteria and Actinobacteria, while Deltaproteobacteria with the narrowest niche breadth. In addition, Bacteroidetes had higher proportion of habitat specialists compared with those of the other bacterial groups (Additional file 1: Fig. S8).

Among observed ecological features, niche breadth of bacterial community/groups showed strong negative correlations ($\rho = -0.477$, $P < 0.001$) with the

non-neutral-to-neutral ratio (as an indicator of community assembly mechanisms; Table 1). For alpha diversity, Shannon–Wiener index and ZOTU richness showed positive correlations with the non-neutral-to-neutral ratio ($\rho_{\text{Shannon}} = 0.500$, $\rho_{\text{Richness}} = 0.244$, both $P < 0.001$), while the phylogenetic diversity was not significantly correlated. Relative abundance showed a negative correlation with the non-neutral-to-neutral ratio ($\rho = -0.355$, $P < 0.001$). Furthermore, cohesion ratio, |negative cohesion|, and modularity of community showed positive correlations with the non-neutral-to-neutral ratio ($\rho = 0.406$, 0.381 , and 0.381 , respectively, all $P < 0.001$), while positive cohesion was negatively correlated with the non-neutral-to-neutral ratio ($\rho = -0.384$, $P < 0.001$).

Effects of different factor categories on spatial variability in assembly processes of bacteria

Spatial variability of environmental conditions across the study area was extensively found previously (Wang et al. 2015). The distance-based redundancy analysis (db-RDA) plots revealed that environmental conditions [commonly including salinity, dissolved oxygen (DO), pH, and nutrient-related factors such as nitrate, phosphate, and suspended particles (SP)] largely drove the similar patterns of compositional variation of total bacterial community and seven bacterial groups across zones (Additional file 1: Fig. S9). As for the ecological features, niche breadth, Shannon–Wiener index, and average degree showed overall stronger spatial variability compared with other features (Fig. 4 and Additional file 1: Fig. S7). After screening strongly correlative factors corresponding to each factor category (latent variables) for partial least squares path modeling (PLS-PM) (Fig. 5), the final PLS-PM showed that basic abiotic constraints (*Basic*), inorganic resources (*Inorganic*), and *Chl-a* directly shaped, while geographic factors (*Longitude* and/or *Latitude*) indirectly shaped spatial variability of assembly mechanisms of total bacterial communities via the aforementioned three factor categories (Fig. 6). Furthermore, potential microbial interactions (*Interaction*) also showed a direct effect for the total bacterial community but not for the seven bacterial groups. The combination of factors that drove spatial heterogeneity in the assembly mechanisms of bacteria varied across taxa. Geographic factors (*Longitude* and/or *Latitude*) only directly mattered for Planctomycetes, but indirectly influenced all bacterial groups via environmental factors (*Basic*, *Inorganic*, organic resources (*Organic*), and/or *Chl-a*) and/or the ecological features (niche breadth (*Niche*), alpha diversity (*Diversity*), and/or relative abundance (*Abundance*)) of bacteria. *Basic* directly shaped the spatial assembly patterns of Alphaproteobacteria, Planctomycetes, and Deltaproteobacteria. Spatial assembly of Actinobacteria and

Table 1 Spearman rank correlations of the ratio of relative abundance of non-neutrally distributed (sum of above-prediction and below-prediction) ZOTUs to that of neutrally distributed ZOTUs (defined by the neutral model) with niche breadth, alpha diversity indices (including phylogenetic diversity, ZOTU richness, and Shannon–Wiener index), relative abundance of bacteria groups, and the features of microbial associations (including |negative cohesion|, positive cohesion, cohesion ratio (|negative cohesion/positive cohesion|), modularity, and average degree)

Ecological features	Non-neutral-to-neutral ratio	
	ρ	P
Niche breadth	-0.477	<0.001
Phylogenetic diversity	-0.014	0.740
ZOTU richness	0.244	<0.001
Shannon–Wiener index	0.500	<0.001
Relative abundance	-0.355	<0.001
Negative cohesion	0.381	<0.001
Positive cohesion	-0.384	<0.001
Cohesion ratio	0.406	<0.001
Modularity	0.381	<0.001
Average degree	-0.150	0.008

Data in bold indicate significant correlations ($P < 0.001$)

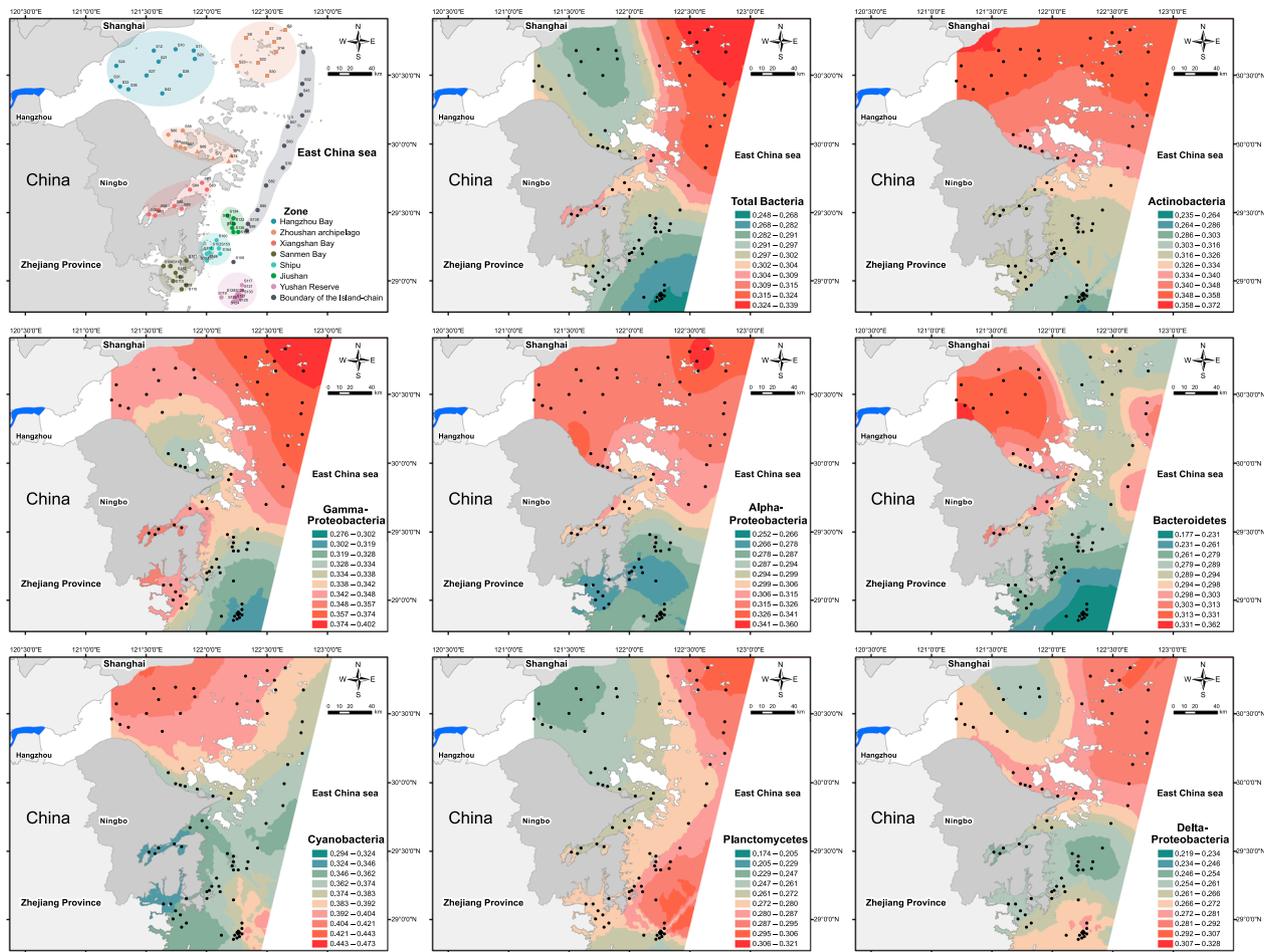


Fig. 4 Kriged maps showing the geographic distribution of the standardized Levins' niche breadth (B_{com}) of the total bacterial communities or the seven taxonomic groups. The scale of color bar varies with panel

Cyanobacteria were directly and positively influenced by *Organic*, while *Inorganic* had a direct and positive effect only on Alphaproteobacteria. Chlorophyll-*a* directly shaped spatial assembly pattern of Planctomycetes, and indirectly shaped that of Gammaproteobacteria via *Niche*. As for the internal ecological features of bacterial communities, *Diversity* directly and positively affected the spatial assembly patterns of Actinobacteria and Gammaproteobacteria, but negatively affected those of Planctomycetes and Deltaproteobacteria. Furthermore, *Abundance* directly mattered for the spatial assembly patterns of Bacteroidetes, Planctomycetes, and Deltaproteobacteria, while *Niche* only directly mattered for Gammaproteobacteria and Deltaproteobacteria.

Discussion

Taxonomic dependency in bacterial assembly processes and its determinants

Our results suggested high taxonomic dependency in assembly processes within the domain Bacteria across the coastal waters at the regional scale. The assembly mechanisms of the dominant bacterial groups, including Actinobacteria, Gammaproteobacteria, Alphaproteobacteria, Bacteroidetes, and Cyanobacteria, derived from both neutral and null models, were overall similar, in terms of relative importance of determinism to stochasticity. Among these five taxonomic groups, only Bacteroidetes was more dominantly governed by determinism, while the other bacterial groups were more governed by

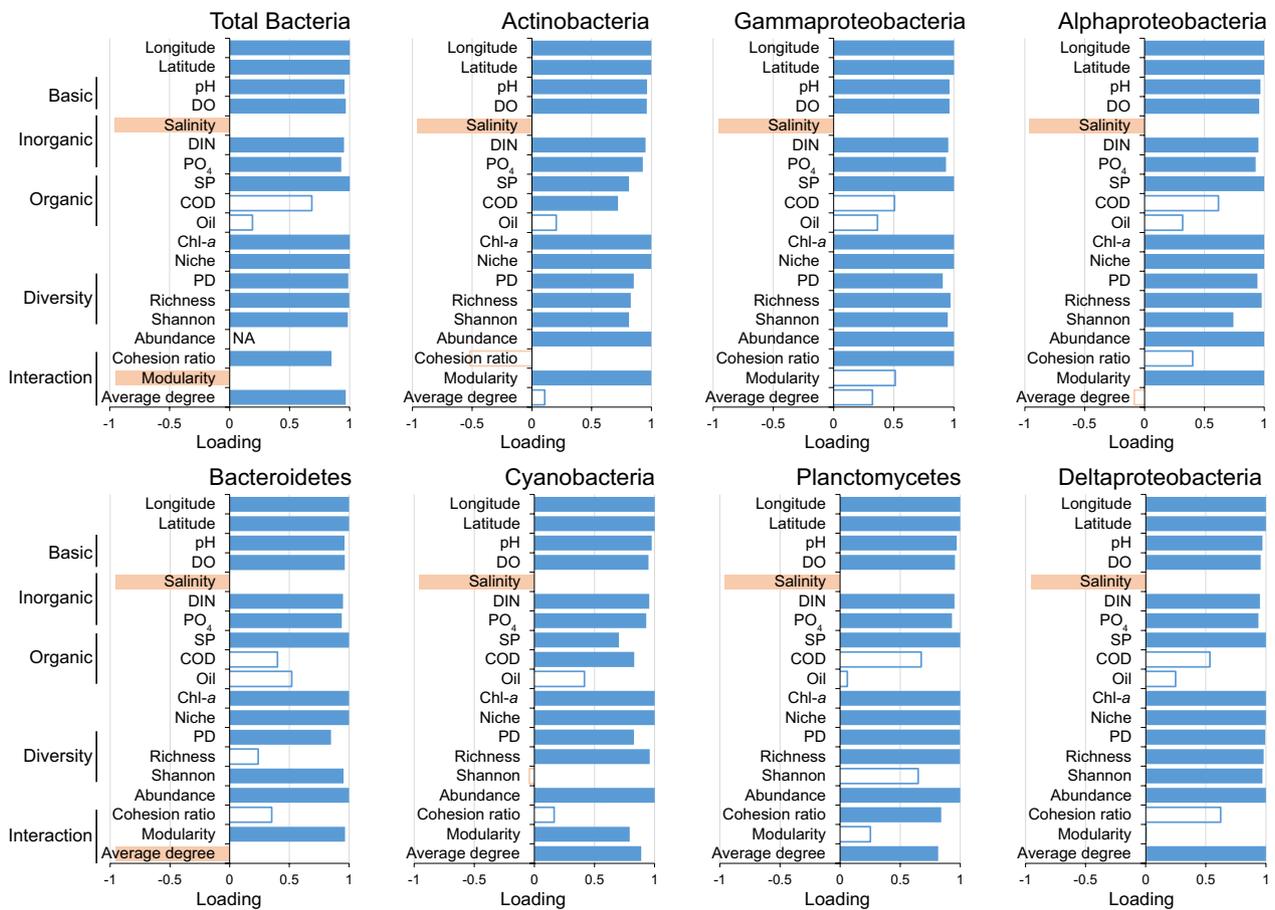


Fig. 5 Bar plots showing the loadings between observed factors and corresponding factor categories (latent variables) according to partial least squares path modeling (PLS-PM). The factors with empty bars were below the loading threshold (<0.7) to the corresponding factor category, and thus were not used in the final PLS-PM. Relative abundance of total bacteria was marked as NA (not applicable) due to that all values are same as 1 thus being forbidden by PLS-PM. DO, dissolved oxygen; DIN, dissolved inorganic nitrogen; SP, suspended particles; COD, chemical oxygen demand; Chl-*a*, chlorophyll-*a*; PD, phylogenetic diversity; Richness, ZOTU richness; Shannon, Shannon–Wiener index; Abundance, relative abundance; Cohesion ratio, [negative cohesion/positive cohesion]

stochastic mechanisms, among which Gammaproteobacteria was more influenced by deterministic processes compared with others. This is consistent with the previous report suggesting that Bacteroidetes were more shaped by deterministic processes compared with Alphaproteobacteria and Cyanobacteria in the ocean surface

via null model based metrics (net relatedness and nearest taxa indices) (Barberán and Casamayor 2010; Webb 2000). On the other hand, we found inconsistency in the dominant assembly mechanisms of bacterial groups inferred by neutral and null models for certain groups like Planctomycetes and Deltaproteobacteria. Moreover,

(See figure on next page.)

Fig. 6 Partial least squares path modeling (PLS-PM) showing path coefficients (direct effects) of factor categories on spatial variability in assembly mechanisms of total bacterial community and seven taxonomic groups (expressed by the ratio of the relative abundance of non-neutrally ZOTUs to that of neutrally distributed ones). The overall prediction performance of the models was assessed using goodness of fit (*GoF*) statistic. Blue and red lines present significant positive and negative effects, respectively (only significant effects were shown, $P < 0.01$), and the thickness of lines indicated direct effect strength (as data on the lines). Basic: basic abiotic constraints including pH, and DO; Inorganic: inorganic resources including salinity, DIN (sum of NO_3 , NO_2 , and NH_4), and PO_4 ; Organic: organic resources including SP, COD, and oil; Chl-*a*: chlorophyll-*a*; Diversity: alpha diversity indices including phylogenetic diversity, ZOTU richness, and Shannon–Wiener index; Niche: niche breadth of bacteria at the community level; Interaction: potential bacterial interactions inferred by the features of microbial associations including cohesion ratio (|negative cohesion/positive cohesion|), modularity, and average degree

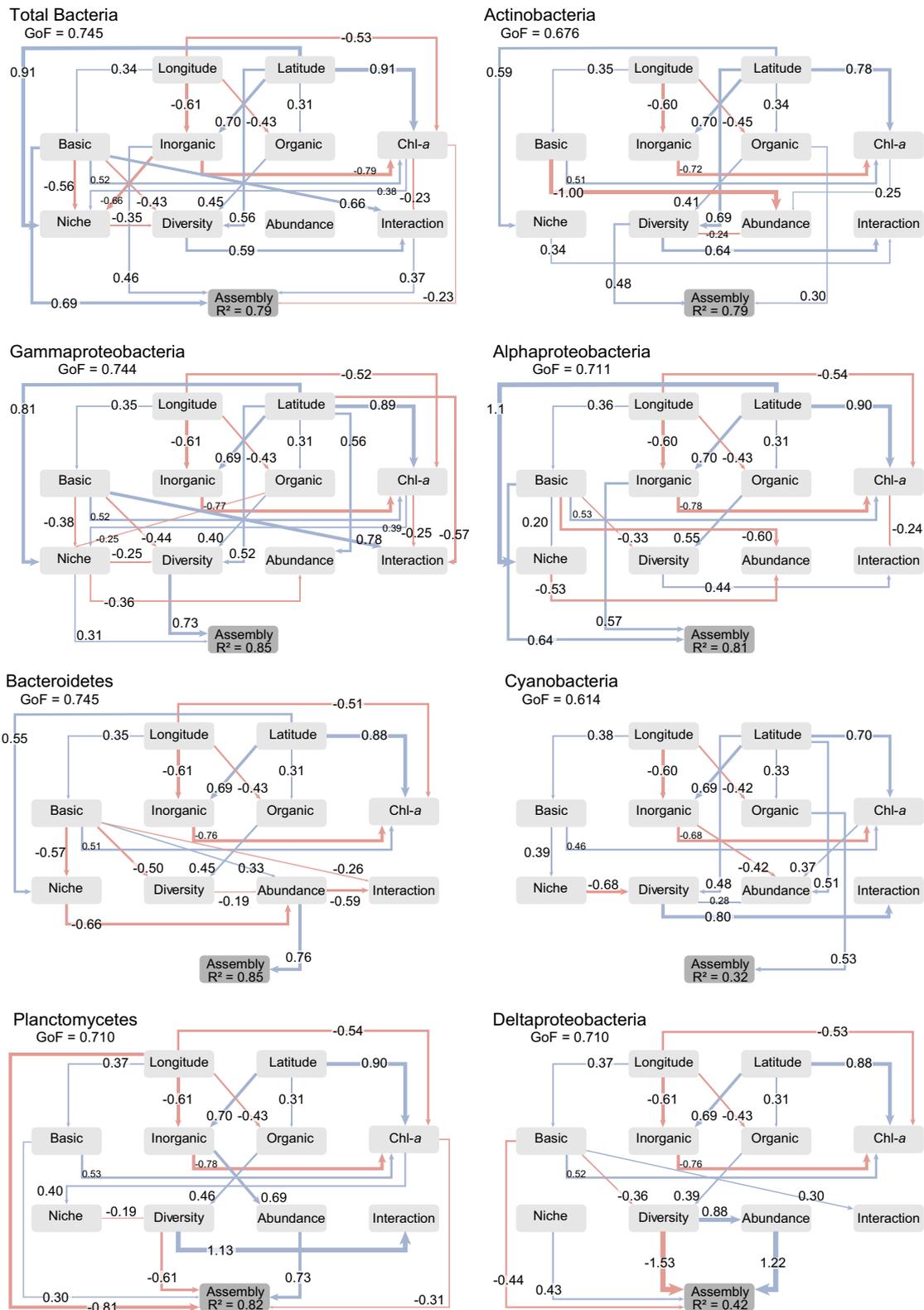


Fig. 6 (See legend on previous page.)

the null model seems to introduce a higher proportion of stochasticity compared with the neutral model for any given bacterial group. The following reasons may explain the extra randomness introduced by the current null model. First, the null model based on phylogenetic metrics can result in higher proportion of stochastic processes compared with the one based on taxonomic-abundance metrics (Stegen et al. 2013), which was confirmed by the comparison between the results derived from β NTI and from RC_{bray} alone, while the neutral model is a special form of taxonomic-abundance based null model (Hubbell 2001; Sloan et al. 2006). The second possible explanation could be the endogenous difference in the basis for inferring community assembly process, that is the local-metacommunity relationship of each species for the neutral model and pairwise comparison between local communities based on community-level metrics for the null model. These results emphasize the necessity of using different models to complementarily interpret assembly mechanisms of microbial communities, especially for taxonomic groups with lower relative abundance, since conflicting results from the two models were more likely to occur in bacterial groups with lower relative abundance. Despite that, both models confirmed that taxonomic dependencies exist in the assembly mechanisms of bacterial groups in terms of dominant assembly mechanisms and specific ecological processes. Due to the limitation of sequencing depth and unevenness in sequences and coverage across taxonomic scales for different samples, our analyses did not expand to the finer taxonomic resolutions. Future efforts should be made to assess taxonomic scale dependency and hierarchical determinants of bacterial assembly mechanisms.

The current knowledge about taxonomic dependency determinants in community assembly mechanisms is scarce. Niche breadth at the community level has been proposed as a major determinant of differences in assembly mechanisms across microbial domains (Logares et al. 2020; Wang et al. 2020a; Wu et al. 2018), since microorganisms with wider niche breadths are less sensitive to environmental changes and are less governed by environmental selection, thus leading to stronger stochastic assembly relative to deterministic assembly (Jiao et al. 2020; Liao et al. 2016). In this study, we also found that niche breadth showed a strong negative correlation with the determinism-to-stochasticity ratio in the assembly of bacterial groups, suggesting this principle could also apply to taxonomic dependency in assembly mechanisms within the domain Bacteria. Furthermore, the relative abundance of habitat specialists and generalists (as defined by the range of niche breadth) in a given community could also determine its assembly mechanism, and the community with higher proportion or abundance of

specialists tends to be more governed by selection (Mo et al. 2020). Therefore, the higher abundance of specialists in Bacteroidetes compared with those of other bacterial groups corresponded to the determinism-dominated assembly mechanism of Bacteroidetes assemblages. We also found that bacterial groups with higher alpha diversity tended to have a higher determinism-to-stochasticity ratio. Similarly, previous studies found that the bacterial communities with higher alpha diversity were more deterministically assembled in wetlands (Yang et al. 2022) and tropical ocean water ecosystems (Kong et al. 2022), suggesting that bacterial groups with higher species diversity could possess more diverse metabolic potential to cope with the broader spectrum of environmental selection. On the contrary, the bacterial groups with lower species diversity were more governed by stochastic processes. In the case of Cyanobacteria with the lowest diversity here, stochasticity-dominance could be due to the broad range of growth conditions even within a particular cyanobacterial genus or species (Ferris and Palenik 1998), leading to niche complementarity and subsequently the resistance to environmental selection during the assembly. Biotic interactions are often considered as a part of selection, thus being deterministic in governing community assembly (Faust and Raes 2012; Lin et al. 2024); however, others proposed that biotic interactions do not necessarily impose deterministic assembly (Zhou and Ning 2017). We found considerable positive effects of negative-to-positive cohesion ratio, negative cohesion strength, and modularity on the determinism-to-stochasticity ratio, while positive cohesion showed the opposite effect. These results suggested that negative cohesion, with its ratio to positive cohesion reflecting the relative importance of potential competitive relationships to cooperative relationships between taxa (Danczak et al. 2018), could impose a more selective pressure to govern deterministic community assembly (Wu et al. 2023b), while higher positive cohesion reflecting more extensive microbial cooperative interactions may increase the flexibility during community assembly thus increasing stochasticity (Wang et al. 2023). Furthermore, negative-to-positive cohesion ratio and modularity were considered as good indicators to reflect community stability (Hernandez et al. 2021; Yuan et al. 2021), and higher community stability should be largely archived by more deterministic assembly processes. The average degree reflecting potential interaction strength showed a weak correlation with assembly mechanism, suggesting that the relative importance of microbial interaction types, not microbial interaction strength, might be the key determinant of taxonomic dependency in the assembly mechanisms of bacteria. Notably, the relative abundance of a given taxonomic group, reflecting its population size

within the bacterial community, showed a negative association with determinism-to-stochasticity ratio. Theoretically, however, a given taxa with smaller population size is more vulnerable to ecological drift (caused by random birth and death of individuals) and thus tends to be more stochastically assembled (Kong et al. 2022). Our previous work demonstrated that archaea with lower abundance relative to bacteria were more strongly governed by stochasticity at a similar regional scale (Wang et al. 2020a). Some other studies comparing assembly mechanisms of abundant and rare bacterial communities also reported inconsistent results, where rare bacterial sub-communities were more governed by stochastic processes relative to abundant sub-communities in many bays across China's coastline (Mo et al. 2018). Despite the inconsistency, the importance of niche breadth, diversity, relative abundance, and potential interactions of bacterial taxa in driving taxonomic dependency in assembly mechanisms of marine bacteria could be general patterns, worthy of further testing across various temporal and spatial scales.

Spatial heterogeneity of bacterial assembly mechanisms and its key determinants

During the past decade, the vision of microbial biogeography has evolved from patterns to processes (Hanson et al. 2012; Vellend 2010; Zhou and Ning 2017). However, most of the studies interpreted microbial community assembly mechanisms in a general manner across various geographic scales (Cheng et al. 2023; Logares et al. 2020; Wu et al. 2018). The spatial variability or heterogeneity of community assembly mechanisms of microorganisms has been neglected for a long time. Our previous work has demonstrated the remarkable spatial variability of community assembly processes of total archaea and the dominant archaeal groups (Marine Groups I and II) (Wang et al. 2019). We also found that the extent of spatial heterogeneity of microbial assembly mechanisms might largely depend on the range of environmental gradients across similar geographic scales, that is, broader environmental gradients led to higher spatial heterogeneity of assembly mechanisms (Wang et al. 2019, 2020a). In this study, by using customized spatial visualization methods for both neutral and null models, we confirmed the prevalence of spatial heterogeneity in assembly processes of total bacterial community and taxonomic groups, and the differences in the degree of spatial heterogeneity in assembly processes across the seven bacterial groups suggested taxonomic dependency in spatial heterogeneity of assembly mechanisms. As the two ends of the environmental gradients (including salinity and nutrients) in our study area, the Hangzhou Bay (HZ) and Yushan Reserve (YS) served as the only two hot spots of determinism-dominated mechanism for the total

bacterial community. This corresponded to the stronger selection triggered by more extreme local environmental conditions in these two zones, which harbored very distinct community composition compared with those in the other zones (Wang et al. 2015). As one of the most eutrophic coastal area in China, the study area forms a strong-to-weak gradient of anthropogenic/terrestrial disturbances from HZ to YS (MEE 2023), due to the emissions from the intensive economic development of the big/mega cities surrounding HZ and the terrestrial runoffs from the Qiantang River (Chen et al. 2009; Sun et al. 2013; Yang et al. 2012). The stochasticity-dominated assembly mechanism of the total bacterial community found in the zones across the intermediate range of gradients suggests that intermediate anthropogenic/terrestrial disturbances could lead to more stochastic assembly of bacteria. These results indicate an 'intermediate disturbance hypothesis' (Connell 1979) of heterogeneity in microbial community assembly mechanisms. This has been shown in a soil ecosystem/microcosm experiment where stochasticity overwhelmed determinism in bacterial community assembly processes at neutral pH/moderate disturbance conditions but showed the opposite pattern at two poles of pH value/disturbance frequency (Santillan et al. 2019; Tripathi et al. 2018).

Although the degree of heterogeneity varied across bacterial groups, HZ served as the hot spot of determinism-dominated mechanisms for more than half of the taxonomic groups including Alphaproteobacteria, Gammaproteobacteria, Planctomycetes, and Bacteroidetes, emphasizing that these bacterial taxa tend to be more deterministically assembled under more intensive disturbances. Several previous studies also found enhanced determinism (niche selection) coupled with more intensive perturbation such as anthropogenic activities and extreme climates like heavy rain and desiccation across various ecosystems including freshwater lakes (Obieze et al. 2022; Wu et al. 2023a), rock pools (Vass et al. 2020), and coastal sediments (Valverde et al. 2014). Furthermore, eutrophic waters in HZ could increase the proportion of deterministic processes of these taxa as other researchers found that planktonic *Vibrio* communities were more deterministically assembled in eutrophic waters compared with those in mesotrophic waters in a marine subtropical gulf (Li et al. 2020). Furthermore, YS also served as the hot spot of determinism-dominated mechanisms for Bacteroidetes, which corresponded to the dominant Bacteroidetes likely triggered by the phytoplankton bloom in this zone as previously reported (Wang et al. 2015). Collectively, spatial heterogeneity in the assembly mechanisms of bacteria was prevalent across the study area.

Our understanding of the determinants of spatial heterogeneity in bacterial assembly mechanisms in marine waters is poor at best. Some studies have demonstrated that temperature was the major factor mediating the balance between stochastic and deterministic assembly processes of bacteria in the sediments of hot springs (He et al. 2021) and in the oligotrophic ocean at a ~2,000-km scale (Allen et al. 2020). Our previous study across coastal waters at a ~300-km scale found that suspended particles (SP) and phosphate had a great impact on spatial variability of bacterial assembly processes (Wang et al. 2020a), while salinity largely regulated that along an exorheic river (Shi et al. 2023). Here, we found that environmental determinants including pH, dissolved oxygen (DO), salinity, dissolved inorganic nitrogen (DIN), and phosphate directly affected the spatial heterogeneity of the determinism-to-stochasticity ratio of total bacterial community. Among them, the nutrient concentrations (mainly DIN and phosphate) formed a high-to-low gradient from HZ to YS, while salinity and pH showed a high-to-low gradient from YS to HZ, corresponding to the determinism-dominance in total bacterial assembly in these two zones, but stochasticity-dominated pattern in other zones as discussed above. Besides strong environmental constraints on total bacterial community assembly mechanisms over space, potential interactions between taxa also contributed to spatial assembly patterns of total bacteria, emphasizing the role of specific microbial interactions in enhancing deterministic community assembly as we discussed above.

In general, many factors could affect the spatial assembly of multiple bacterial groups, but how they acted on distinct communities subtly differed. As we hypothesized, the determinants of spatial heterogeneity in assembly mechanisms were also taxonomically dependent. Similar to the total bacterial community, spatial variability in the assembly mechanism of Alphaproteobacteria was strongly and directly affected by basic abiotic constraints and inorganic resources. But the underestimation of a key alphaproteobacterial group (Pelagibacterales, aka. SAR11 clade) by the current primer set could influence the assessment of processes and determinants of Alphaproteobacteria assembly, which should be evaluated in the future with the modified primer set. Bacteroidetes was strongly and directly affected by its relative abundance, corresponding to its thriving following a phytoplankton bloom in YS as mentioned above. It is well known that the spatial distribution of abundance and diversity of marine Cyanobacteria is mainly driven by the combination of light, temperature, and inorganic nutrients including N, P, and Fe (Cunningham and John 2017; Flombaum et al. 2013), but the factors determining the spatial variability in its assembly processes are barely

known. We found that spatial heterogeneity in the assembly of Cyanobacteria was directly regulated by organic resources including SP and chemical oxygen demand (COD), enforcing determinism-dominance in the mouth of HZ, which may reflect underlying cruciality of light and nutrients. Given the importance of Cyanobacteria in marine endogenous organic carbon flux, this association between cyanobacterial assembly and exogenous organic matter indicates the complex roles of cyanobacteria in organic carbon turnover in the transitional zone between land and sea. Among all the tested bacterial groups, only the assembly of Planctomycetes was simultaneously and directly controlled by geographic, environmental, and community ecological features. This suggests complexity in the mechanisms governing the spatial assembly of Planctomycetes. Given that longitude showed the strongest effect on Planctomycetes, we speculated that unmeasured factors such as water temperature highly associated with longitude might be the actual drivers, which deserves further investigation.

Compared with the above bacterial groups, the assembly mechanism of Gammaproteobacteria, Actinobacteria, and Deltaproteobacteria showed much lower spatial heterogeneity. The spatial heterogeneity in assembly mechanism of Gammaproteobacteria was strongly and directly affected by its alpha diversity, which was largely conditioned by environmental and geographic factors, suggesting diversification as a force in governing deterministic assembly in HZ. Alpha diversity also directly influence spatial assembly patterns of Actinobacteria and Deltaproteobacteria but with opposite manners and different co-factors, suggesting distinct mechanisms underlying the observed patterns. Collectively, the degree and determinants of spatial heterogeneity in community assembly mechanisms varied across bacterial groups. The ones with higher heterogeneity in assembly mechanism were more related to environmental and/or geographic factors (except Bacteroidetes), while those with lower heterogeneity were more related to community ecological features.

Conclusions

This study systematically tested the existence and extent of taxonomic dependency and spatial heterogeneity in assembly mechanisms of marine bacteria in a coastal ecosystem with spatially structured regional environmental gradients. Our results confirmed the variability of assembly processes of bacteria with taxonomic group and with space. The assembly of total bacterial communities was balancedly governed by deterministic and stochastic processes, while only the Bacteroidetes were dominated by determinism among the seven dominant bacterial

groups. The taxonomic dependency of bacterial assembly processes was mainly related to the differences in niche breadth and negative-to-positive cohesion ratio, followed by alpha diversity and relative abundance of bacterial taxa. The spatial distribution patterns of assembly processes commonly varied across bacterial groups, and were driven by various combinations of factors, suggesting that spatial heterogeneity of assembly processes of bacteria also exhibited taxonomic dependency. Collectively, this work assessed the pervasiveness of taxonomic dependency and spatial heterogeneity in bacterial community assembly from the perspectives of one-station (local-community) basis and pairwise between-station comparisons, providing a comprehensive understanding of the regulation of bacterial community assembly across taxa and space.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-023-00480-7>.

Additional file 1: Supplementary methods. Figure S1. The map of sampling stations from eight coastal zones. The colors of the stations correspond to different zones, and the stations in the Zhoushan archipelago were grouped into three subzones including ZSI_north (northern part of the archipelago), ZSI_mouth (in the mouth of HZ), and ZSI_other (others), which were shown as square, circle, and triangle symbols, respectively. **Figure S2.** Fit of the neutral model for bacterial ZOTUs with bacterial metacommunity across the sampling zones as the source. R^2 values present the goodness of fit of the neutral model, ranging from 0 (no fit) to 1 (perfect fit). The ZOTUs that occurred more frequently than predicted by the model are shown in green, while those occurred less frequently than predicted are shown in orange (A). The ZOTUs are colored by their taxonomy at the phylum level and at the class level for the phylum Proteobacteria (B). Dashed lines represent 95% confidence intervals around the model prediction and the ZOTUs fall within the confidence intervals were considered as neutrally distributed. **Figure S3.** Mantel correlograms showing significant phylogenetic signal in between-ZOTU niche differences across short phylogenetic distances for total bacterial and key bacterial communities. Solid and open symbols present significant ($P < 0.05$ after Holm correction, 999 permutations) and non-significant Pearson correlations between niche differences and phylogenetic distances, respectively, across phylogenetic distance classes. Absent circle symbols indicate that no phylogenetic distance value is assigned to the corresponding distance class. **Figure S4.** The percentage of ecological processes governing the spatial turnover of total bacterial communities or seven taxonomic groups in all pairwise comparisons between stations according to β NTI or RC_{bray} values. **Figure S5.** The geographic distribution of the ecological processes governing the spatial turnover of total bacterial community and seven taxonomic groups in all pairwise comparisons between stations according to β NTI and RC_{bray} values. Each column corresponds to a specific ecological process as noted at the top. **Figure S6.** The optimal number of resource states when setting different number of groups for the partition based on the simple structure index (SSI) using K -means partitioning (1,000,000 iterations) (A). Spatial distribution of the resource states determined by K -means partitioning based on water environmental conditions (B). The colors of the stations correspond to different resource states. **Figure S7.** Box plots illustrating the ecological features of total bacterial community and seven taxonomic groups, including ratio of relative abundance of non-neutrally distributed ZOTUs to that of neutrally distributed ZOTUs, standardized Levins' niche breadth, alpha diversity indices including phylogenetic diversity, ZOTU richness, and Shannon–Wiener index, relative abundance, and the features of microbial associations including cohesion ratio (negative cohesion/positive cohesion), modularity, and

average degree across sampling stations. Different communities sharing the same letter above the boxes are not significantly different from each other, whereas two communities with different letters are significantly different (multiple comparisons after Kruskal–Wallis test, $P < 0.05$). **Figure S8.** Cumulative relative abundance of habitat specialists and generalists in the total bacterial community and the seven taxonomic groups. ZOTUs with standardized niche breadth (B_A) value > 0.5 were regarded as habitat generalists, and ZOTUs with $B_A < 0.05$ were defined as specialists. This criterion was chosen according to the frequency distribution of B_A value for all ZOTUs. **Figure S9.** Distance-based redundancy analysis (db-RDA) plots based on Bray–Curtis dissimilarity illustrating environmental constraints of compositional variation of total bacterial communities and seven bacterial groups. Environmental variables were normalized to reduce the effect of unit differences. The “vif.cca” and “envfit” functions of the “vegan” package in R environment were used to identify nonredundant (variance inflation factors < 10) and significant ($P < 0.05$) constraints for generating the final ordinations. DO, dissolved oxygen; SP, suspended particle; COD, chemical oxygen demand; Chl-*a*, chlorophyll-*a*. HZ, Hangzhou Bay; ZSI, Zhoushan archipelago; XS, Xiangshan Bay; SM, Sanmen Bay; SP, Shipu; JS, Jiushan; YS, Yushan Reserve; BIC, the east boundary of the Island-chain. **Dataset S1.** Numbers of reads and ZOTUs of dominant bacterial taxa (cumulative proportion of reads $> 2\%$ in the whole dataset).

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Author contributions

DZ and KW: designed the study; KW: proposed the data analysis strategy; HY, DL, and KW: analyzed the data; GG, YH, XH, ZY, and DH: assisted with the analytic tools; HY and KW: wrote the manuscript; BJC: revised the manuscript. All the authors reviewed and approved the manuscript.

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Availability of data and materials

The sequence data are available under accession number DRA002865 in the Sequence Read Archive of DDBJ (<http://ddbj.nig.ac.jp/DRAsearch>) (Wang et al. 2015).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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