Linking sediment microbial community traits to environmental changes in the Yarlung Tsangpo River

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Abstract

Knowledge about the ecological patterns of abundant and rare bacteria in regulated river ecosystems, especially with respect to their community traits, is an important but poorly investigated subject. In this study, we examined the community assembly of abundant and rare bacteria, as well as their environmental adaptation, across complex environmental gradients in sediments of the Yarlung Tsangpo River on the Tibetan Plateau. Results showed that abundant taxa exhibited broader environmental thresholds and stronger phylogenetic signals for ecological traits than rare taxa. In contrast, rare taxa were more sensitive to environmental changes and showed stronger phylogenetic clustering. Although both subcommunities exhibited significant distance-decay patterns, the abundant subcommunity was governed primarily by dispersal limitation, while the rare subcommunity was strongly driven by heterogeneous selection. The similar distribution patterns but contrasting assembly mechanisms affecting abundant and rare subcommunities resulted from the differences in environmental adaptation. Forest area and total nitrogen were key factors in determining the stochastic and deterministic assembly for abundant and rare subcommunities, respectively. Additionally, rare taxa might play potential roles in maintaining network stability, although they were less connected and located more peripherally within the network. Collectively, our study provides a new perspective for the ecological significance of abundant and rare bacteria in fluvial sediments, and facilitates the prediction of microbial responses to ongoing environmental changes in the Yarlung Tsangpo River.

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Running title: Sediment bacteria in the Yarlung Tsangpo River

Abstract

Knowledge about the ecological patterns of abundant and rare bacteria in regulated river ecosystems, especially with respect to their community traits, is an important but poorly investigated subject. In this study, we examined the community assembly of abundant and rare bacteria, as well as their environmental adaptation, across complex environmental gradients in sediments of the Yarlung Tsangpo River on the Tibetan Plateau. Results showed that abundant taxa exhibited broader environmental thresholds and stronger phylogenetic signals for ecological traits than rare taxa. In contrast, rare taxa were more sensitive to environmental changes and showed stronger phylogenetic clustering. Although both subcommunities exhibited significant distance-decay patterns, the abundant subcommunity was governed primarily by dispersal limitation, while the rare subcommunity was strongly driven by heterogeneous selection. The similar distribution patterns but contrasting assembly mechanisms affecting abundant and rare subcommunities resulted from the differences in environmental adaptation. Forest area and total nitrogen were key factors in determining the stochastic and deterministic assembly for abundant and rare subcommunities, respectively. Additionally, rare taxa might play potential roles in maintaining network stability, although they were less connected and located more peripherally within the network. Collectively, our study provides a new perspective for the ecological significance of abundant and rare bacteria in fluvial sediments, and facilitates the prediction of microbial responses to ongoing environmental changes in the Yarlung Tsangpo River.

Keywords: Environmental adaptation; Fluvial sediment bacteria; Rare biosphere; Community assembly; Co-occurrence network

1. Introduction

Sediments, serving as sinks or sources for nutrient cycling (Jozsa et al., 2014), are one of the most diverse microbial habitats in aquatic ecosystems (Lozupone and Knight, 2007). Microorganisms attached to the sediments are critical drivers of biogeochemical processes and play a significant role in food webs and the functioning of aquatic ecosystems (Battin et al., 2009; Handley et al., 2013; Nealson, 1997). Meanwhile, sediment microorganisms are sensitive indicators of environmental change in aquatic ecosystems (Liu et al., 2018; Mason et al., 2014). Sediment microbial biodiversity has been shown to be closely correlated with surrounding heterogeneous landscapes, water quality, land uses, and geomorphology (Hu et al., 2014; Ibekwe et al., 2016; Zhang et al., 2021b). Therefore, deciphering the fundamental mechanisms for maintaining and generating sediment microbial biodiversity is critical for predicting the relationships between microbial community function and environmental processes in changing aquatic ecosystems.

In natural ecosystems, microbial communities are often comprised of relatively few abundant taxa co-existing with a large number of rare taxa, the latter often known as the “rare biosphere” (Jia et al., 2018; Pedrós-Alió, 2012). Previous studies have increasingly emphasized the ecological importance of the rare biosphere in community functioning and stability (Jousset et al., 2017; Lynch and Neufeld, 2015). For example, rare taxa can serve as “seed bank” for maintaining microbial diversity (Galand et al., 2009; Shade et al., 2014), and perform a disproportionate amount of work, as compared to their abundance, in regulating ecosystem functioning (Pester et al., 2010). It has previously been observed that abundant and rare taxa have different ecological responses to environmental changes and often show different distribution patterns and functional traits (Jiao and Lu, 2020; Liu et al., 2015; Wan et al., 2021a; Wan et al., 2021b; Wan et al., 2021c; Xue et al., 2018). For instance, recent evidence suggests that in Tibetan Plateau wetland soils, abundant bacteria are primarily influenced by dispersal limitation, while rare bacteria are mainly governed by environmental filtering (Wan et al., 2021a).

It is now well established from a variety of studies, that the biogeographic patterns of abundant and rare microbial taxa are mainly shaped by deterministic and stochastic processes (Ji et al., 2020; Jiao and Lu, 2020; Mo et al., 2018; Wan et al., 2021a; Xue et al., 2018). Traditionally, deterministic processes refer to nonrandom and niche-based mechanisms, including environmental filtering and various biotic interactions (e.g., competition, predation, and mutualism) (Fargione et al., 2003; Stegen et al., 2015). In contrast, stochastic processes emphasize that community structures are independent of species traits and are instead shaped by processes of birth, death, colonization, extinction, and speciation (Volkov et al., 2003; Zhou and Ning, 2017). Data from several studies suggest that rare taxa are shaped to a far greater degree by environmental filtering than abundant taxa in ocean surface waters (Wu et al., 2017) and in agricultural soils (Jiao and Lu, 2020). However, contrasting results were found in a subtropical reservoir (Xue et al., 2018) and Tibetan Plateau grassland soils (Ji et al., 2020), where communities of rare taxa were driven by stochastic processes more than abundant communities. These results indicate that community assembly of the abundant and rare bacteria may vary with ecosystem and organism types. To date, very little is currently known about the relative impacts of deterministic and stochastic processes on microbial communities in plateau river sediments and the underlying factors.

Environmental filtering is an important determinant in shaping distribution patterns of abundant and rare taxa in aquatic ecosystems (Liu et al., 2019; Liu et al., 2015; Xue et al., 2018). The concept of environmental filtering proposes that changes in species abundances and diversity patterns along environmental gradients, such as sediment pH, temperature, and nitrogen compounds concentration, are based on their traits and adaptations to the prevailing environmental conditions (Wang et al., 2020b; Xiong et al., 2012; Zhang et al., 2021b). It has been reported that abundant taxa exhibit stronger environmental adaptation compared to rare taxa (Jiao and Lu, 2020; Wan et al., 2021a). To be specific, abundant taxa exhibited broader environmental thresholds and stronger phylogenetic signals for ecological preferences across environmental gradients than rare taxa. These studies provided new insights into considering species niche breadth and phylogenetic patterns of microbial response traits for studying the biogeography of abundant and rare taxa and their responses to environmental change. Apart from environmental filtering, biotic interactions are important as a part of deterministic processes in governing distribution patterns and community assemblies of abundant and rare taxa in aquatic ecosystems (Xue et al., 2018; Zhang et al., 2020; Zhou et al., 2020). Analysis of potential interactions between microbial taxa in complex and different microbial communities can help to explore potential functions or environmental niches occupied by microbes (Deng et al., 2012; Hu et al., 2017; Meyer et al., 2020). Furthermore, topology-based analysis of microbial networks is a powerful method for studying the characteristics of co-occurrence patterns at various taxonomic levels and identification of keystone species that play irreplaceable roles in maintaining the stability and function of the microbial community (Ma et al., 2016; Sun et al., 2021).

As the “Water Tower of Asia”, the Tibetan Plateau feeds many large rivers in Asia and benefits billions of people in the surrounding regions (Immerzeel et al., 2010). Among those rivers originating from the Tibetan Plateau, the Yarlung Tsangpo River is the longest plateau river in China. The Yarlung Tsangpo plays an important role in the regional water supply and its annual runoff on the plateau is estimated to be $1.65\text{x } 10^{11}$ m^3 (Liu, 1999). The water resources in this river are vital for sustaining the health of regional socioeconomic developments and ecosystem functioning and peoples’ lives on the Tibetan Plateau. Over the past few decades, the Yarlung Tsangpo River has been experiencing dramatic land surface environment changes under the impact of climate change (e.g., glacier retreat and permafrost degradation) and intensified anthropogenic disturbances (e.g., land use change, wastewater discharge and river damming) (Cui et al., 2006; Wang et al., 2020b; Yao et al., 2010). These changes directly impact the water quality and microbial biodiversity of this river, and finally affect its ecosystem functions and reduce ecosystem services. A few studies have been conducted to elucidate the influences of river damming (Wang et al., 2017; Wang et al., 2020b; Wang et al., 2021) or antibiotic resistance genes (Liu et al., 2021) on the diversity, composition, and function of bacterial communities in the Yarlung Tsangpo River. However, the mechanisms for generating and maintaining microbial diversity remain unclear, particularly those of the abundant and rare taxa in the sediments of the Yarlung Tsangpo River.

To address this gap, we used Illumina sequencing of the V4-V5 region of the 16S rRNA gene to investigate the geographic patterns and underlying mechanisms of abundant and rare bacteria in Yarlung Tsangpo River sediments. The main objectives of this study were to i) evaluate environmental adaptations of abundant and rare bacteria; ii) determine the effects of physicochemical factors and surrounding land use types on the geographic patterns of abundant and rare bacterial taxa; and iii) identify the controlling mechanisms and key environmental variables that influence the geographic patterns of abundant and rare bacterial taxa in sediments of the Yarlung Tsangpo River. Given that the narrow niches and low growth rate of rare taxa (Jousset et al., 2017), we hypothesized that rare bacterial taxa would exhibit weaker environmental adaptation compared with abundant taxa. We also hypothesized that the assembly processes underlying abundant and rare taxa were influenced by different environmental variables.

2. Materials and methods

2.1 Study area and sediment sampling

The Yarlung Tsangpo River is the largest river located on the southern edge of the Tibetan Plateau, with a length of approximate 2,057 km and catchment area of 2.4×10^5 km^2 (Yao et al., 2010). It originates from the Jemayangdrung Glacier on the northern slope of the Himalayas and flows from west to east across the southern region of the Tibetan Plateau. The land use types along the Yarlung Tsangpo River changes from bare land, to grassland, to water and wetland, to infrastructure construction and cropland, and ultimately changes to forest as elevation decreases (Li et al., 2013). The main land use type in the Yarlung Tsangpo River basin is grassland, which accounts for about 60% of the total area of this basin. Grassland is mainly distributed in the middle and upper reaches of the Yarlung Tsangpo River basin, forest land is mainly distributed in the lower reaches of this basin, and urban land and cropland are mainly distributed in the lowland valley area of the Yarlung Tsangpo River basin (Fig. 1). The main channel of the Yarlung Tsangpo River is joined by several major tributaries, including the Lhasa River, the Nyang River, the Nyangqu River, and the Parlung Tsangpo River.

All surface sediment samples were collected in May 2019. The sampling campaign was conducted over the course of two weeks during which no extreme weather (e.g., heavy rainfall or regional debris flow) occurred. A total of 81 sampling sites were chosen. Briefly, 41 sites were sampled along the main channel from Zhongba County to Mainling County (~ 1211 km), 40 sites were selected from three major tributaries: Lhasa River (11 sites), Niyang River (16), and Parlung Tsangpo River (13) (Fig. 1 and Table S1).

At each sampling site, three riparian-zone surface sediments (0-10 cm depth) were randomly collected using a sterilized plastic spoon and mixed thoroughly to form a composite sample. Subsequently, composite samples were stored in sterilized Nasco Whirl-Pak sample bags, sealed, and transported to the laboratory in iceboxes. In the laboratory, subsamples were stored at 4degC for sediment physicochemical characterization and -80degC for genomic DNA extraction.

2.2 Physicochemical analysis

The coordinates (latitude and longitude) of sampling sites were recorded using a Global Positioning System (GPS). Sediment pH and electrical conductivity (EC) were measured using a pH/Conductivity meter (HANNA, HI98129) after creating a slurry, 1:2.5 (v/v) fresh sediment to water ratio. Total carbon (TC) and total nitrogen (TN) contents were measured by a TOC-Vcph analyzer (Shimadzu Corp, Japan). Concentrations of ammonium (NH_4^+-N), nitrite (NO_2^--N), nitrate nitrogen (NO_3^--N), soluble phosphorus (PO_4^{3-}-P), and total phosphorous (TP) were measured with an automatic absorbance microplate reader (Spark 10M, TECAN, Mannedorf, Switzerland) as previously reported (Hernandez-Lopez and Vargas-Albores, 2003). Sediment particle size distribution (e.g., clay, silt, and sand) were measured using particle size analyzer (Mastersizer 2000, Malvern UK). The land use classification and corresponding proportions were derived from National Earth System Science Data Center, National Science & Technology Infrastructure of China (*http://www.geodata.cn*).

2.3 DNA extraction, PCR amplification, and Illumina HiSeq sequencing

Total DNA was extracted from 0.5 g of sediment using the FastDNA(r) Spin kit (MP Biomedicals, Santa Ana, CA) following the manufacturer's protocol. The extracted DNA was re-suspended into 100 μL of nuclease-free water and quantified using a Qubit 4.0 fluorometer with the dsDNA Broad Range assay kit (Invitrogen, Singapore).

The V4-V5 region of the bacterial 16S rRNA gene was amplified using a universal primer pair 515F (5'-GTG YCA GCM GCC GCG GTA-3') and 907R (5'-CCG YCA ATT YMT TTR AGT TT-3') (Quince et al., 2011). PCR reaction was performed under the condition of 95°C for 3 min, followed by 25 cycles of 95°C for 45 s, 50°C for 60 s, 72°C for 90 s and a final cycle of 10 min at 72degC. Each sample was amplified in triplicate and pooled prior to purification with Agencourt AMpure XP beads and quantification with a Quant-iT dsDNA HS Assay Kit (Invitrogen, Carlsbad, CA, USA). Finally, PCR products were sequenced on the Illumina NovaSeq 6000 platform at Magigene (Guangzhou, China) using the PE250 strategy.

2.4 Sequence analysis

Raw sequences were assembled using FLASH (v1.2.11) with default settings (Magoč and Salzberg, 2011). The assembled files were subsequently demultiplexed, quality filtered using the quantitative insight into microbial ecology (QIIME) pipeline v1.9.0 (Caporaso et al., 2010). Operational taxonomic units (OTUs) were clustered with 97% similarity cutoff using UPARSE algorithm (Edgar, 2013). Taxonomic assignment was performed by RDP Classifier (Wang et al., 2007) against the SILVA 132 NR database (Quast et al., 2012) at a bootstrap cutoff of 80%. OTUs that were affiliated with chloroplast, archaeal, and unclassified sequences (not affiliated with Bacteria) were removed from subsequent analysis. To ensure that rare bacteria were not the result of sequencing errors, OTUs that present in <10 samples and/or possessing <10 sequences were discarded. All further data analyses were based on the rarefied OTU table at 18799 reads per sample, which was created according to the minimum sequence number of 16S rRNA gene amplicon reads per sample.

2.5 Definition of abundant and rare OTUs

In this study, OTUs were classified as abundant or rare in relation to their relative abundances. Briefly, the OTUs with a relative abundance of $> 0.1\%$ in all samples were defined as abundant taxa (AT), whereas the OTUs with a relative abundance of $< 0.01\%$ in all samples were defined as rare taxa (RT) (Jiao and Lu, 2020; Wan et al., 2021a). Those OTUs with a relative abundance between 0.01% and 0.1% in all samples were defined as intermediate taxa.

2.6 Statistical analyses

Alpha diversity metrics, including the Shannon index and Pielou's evenness, were used to estimate the community diversity of abundant and rare taxa. Faith's phylogenetic diversity (PD) was used to estimate the phylogenetic community diversity of abundant and rare taxa. Shannon index, Pielou's evenness, and Faith's PD index were calculated using the "diversity" function in R package "vegan" (Oksanen et al., 2015). Further, the standardized index of effect size measure of the mean nearest-taxon distance (SES.MNTD) was applied to evaluate the phylogenetic clustering of abundant and rare taxa. The SES.MNTD index was calculated using the "ses.mntd" function with the mean of the null distribution (null.model = 'taxa.labels' in 'ses.MNTD', 999 randomizations) in the R package "picante" (Kembel et al., 2010). Statistical differences in the above diversity indices were determined using Wilcoxon rank-sum test in SPSS 22.0 (IBM, Armonk, NY, USA).

The community composition and phylogenetic variations of abundant and rare taxa were calculated based on the Bray–Curtis dissimilarity matrices and the beta mean nearest taxon distance (βMNTD). The Bray–Curtis dissimilarity was calculated using the "vegdist" function in R package "vegan" (Oksanen et al., 2015), whereas the βMNTD distance was calculated using the function "comdistnt" the R package "picante" (Kembel et al., 2010).

Pairwise geographic distance was determined based on the latitude and longitude of each site using the function "distGeo" in R package "geosphere" (Hijmans et al., 2016). Linear regression was used to assess the relationships between bacterial community similarity (1 - Bray–Curtis dissimilarity) or phylogenetic similarity (1 - βMNTD) and geographic distance. Variation partitioning analysis (VPA) was used to tease apart the pure effects of physicochemical factors, land use types, and space on the variation of abundant and rare taxa. Spatial variables in the VPA were calculated using principal coordinates of neighbor matrices (PCNM) analysis and calculated in the"vegan" R package with the "pcnm" function (Borcard and Legendre, 2002; Oksanen et al., 2015).

Threshold indicator taxa analysis (TITAN) was carried out to detect and interpret biodiversity and environmental thresholds of abundant and rare taxa by using the R package "TITAN2" (Baker and King, 2010). Briefly, the sums of indicator taxa scores for bacterial OTUs were used to determine lower and upper thresholds of changes in abundant and rare taxa based on each environmental variable (Jiao and Lu, 2020; Wan et al., 2021a; Wan et al., 2021b).

Phylogenetic signal is tendency for related species to resemble each other more than they resemble species drawn at random from the phylogenetic tree (Blomberg and Garland Jr, 2002). Before testing for phylogenetic signals, we firstly obtained potential trait information about both abundant and rare taxa via the Spearman's correlations between the relative abundances of OTUs and environmental variables (Oliverio et al., 2017). The OTUs that showed significant associations (positive or negative) with a given environmental variable were identified as species with a preference for that environmental variable. For example, the OTUs positively or negatively correlated with pH were identify as "alkaline-preferred taxa" or "acid-preferred taxa". Subsequently, phylogenetic signals for the environmental preference of abundant and rare taxa were calculated via Blomberg's K statistic approach using the "multiPhylosignal" function in the "picante" R package (Kembel et al., 2010). The Blomberg's K statistic approach tests whether the observed trait variation across a phylogeny is smaller than expected according to a Brownian motion model of trait evolution (Blomberg et al., 2003). K values higher than 1 implies strong phylogenetic signals and conservatism of traits, while K values closer to zero indicate a random or convergent pattern of evolution.

Ecological community assembly analyses were performed by applying the null model within the framework described by Stegen et al. (2013). Network analysis was constructed based on the Spearman's rank correlations as described by Hu et al. (2017). Detailed descriptions of the ecological community assembly and network analyses were summarized in supplementary material.

3. Results

3.1 Diversity and community compositions

After quality filtering and reads control, a total of 1,522,719 quality sequences were obtained from 81 samples and clustered into 9797 OTUs at the cutoff of 97% sequence identity. Among the 9,797 OTUs obtained, 132 (1.3%) abundant taxa with 555,761 (36.5%) sequences and 8,182 (83.5%) rare taxa with 398,356 (26.2%) sequences were identified (Table S2). Both abundant ($R^2 = 0.097$, $P < 0.001$) and rare ($R^2 = 0.617$, $P < 0.001$) taxa showed significantly positive abundance-occupancy relationships (Fig. S1a). The abundant taxa were more widespread geographically than rare taxa, with 99% of the abundant OTUs being detected in more than 50% of sites. In contrast, only 4% of rare taxa existed in more than 50% of sites. Taxonomic analyses revealed that Proteobacteria (39%), Bacteroidetes (19%), Firmicutes (17%), and Actinobacteria (14%) were the most abundant bacterial phyla, together accounting for 89% of the total sequences of abundant taxa (Fig. S1b). The rare taxa were dominated by Proteobacteria (40%), followed by Actinobacteria (13%) and Bacteroidetes (12%). Some phyla, such as Acidobacteria, Chloroflexi, and Planctomycetes were present at high abundances in rare taxa.

Alpha diversity metrics, including the Shannon, Pielou's evenness, and Faith's PD, of rare taxa were significantly higher than those of abundant taxa (Wilcoxon rank sum test, $P < 0.001$, Fig. S2a-c). However, SES.MNTD was significantly higher for abundant taxa than for rare ones (Wilcoxon rank-sum test, $P < 0.001$, Fig. S2d), indicating that rare taxa were more closely clustered phylogenetically than abundant taxa.

3.2 Geographic distribution patterns

The taxonomic and phylogenetic similarities of both abundant and rare taxa exhibited significantly negative relationships with corresponding geographic distance (all $P < 0.05$, Fig. 2a and 2b). However, the slopes of distance-decay of compositional and phylogenetic similarity were steeper for abundant taxa (Bray-Curtis, 0.0084; βMNTD, 0.0013) than those for rare taxa (Bray-Curtis, 0.0038; βMNTD, 0.0003), indicating a stronger influence of dispersal limitation for abundant taxa. Moreover, significantly higher taxonomic and phylogenetic β-diversity values were found in rare taxa than for the corresponding abundant taxa (Wilcoxon rank-sum test, $P < 0.001$, Fig. 2c and 2d). Additionally, significant correlations between community composition and phylogeny were observed in both the abundant and rare subcommunities (all $P < 0.001$, Fig. S3). The correlation in the rare subcommunity ($R^2 = 0.829$) was much stronger than that in the abundant subcommunity ($R^2 = 0.149$).

VPA results revealed that the pure effect of spatial variables was consistently higher than that of environmental factors for both the abundant (16.9% versus 3.5%) and rare (7.9% versus 1.5%) subcommunities (Fig. S4). The pure effect of land use types accounted for the smallest portions of the variability in both the abundant and rare subcommunities. However, of all the environmental variables and land use types examined, forest area by itself explained 7.7% of the variation in the abundant subcommunity, more than any of the other individual sediment variables (Table S3).

3.3 Environmental responses of abundant and rare taxa

Environmental threshold analysis indicated that abundant taxa showed a broader range of environmental thresholds than rare taxa for almost all of the environmental and land use types examined (Fig. 3a). Further, Blomberg's K statistic revealed that abundant taxa exhibited stronger phylogenetic signals for almost all tested variables compared with the corresponding rare taxa (Fig. 3b). In addition, we examined the potential ecological preferences for the top 30 abundant and rare OTUs, respectively, and found that abundant taxa exhibited stronger environmental associations than rare taxa (Fig. 3c). This suggests that closely correlated taxa in the abundant subcommunity exhibited more similar ecological preferences to the measured environmental factors than those in the rare subcommunity.

3.4 Disentangling the community assembly processes of abundant and rare taxa

The values of βNTI varied partly from -2 to +2 for abundant taxa, while rare taxa exhibited βNTI values higher than 2 (Fig. 4a). Null model analysis revealed that stochastic processes, especially dispersal limitation (DL, 84%) were the most important processes responsible for the community assembly of abundant taxa, followed by heterogeneous selection (HeS, 15%) (Fig. 4b). By contrast, the deterministic processes were largely responsible for the community assembly of rare taxa (79%), of which the greatest contributor was HeS (77%, Fig. 4b). Taken together, these results suggest that rare taxa are more environmentally constrained and less limited by dispersal than their abundant counterparts.

Mantel tests were performed to examine the relationships between βNTI and the variation of environmental variables in order to infer the relative influences of deterministic and stochastic assembly processes in the abundant and rare subcommunities. Results of Mantel tests demonstrated that forest area and TN were the most important variables associated with βNTI of the abundant ($r = 0.116$, $P = 0.005$) and rare ($r = 0.171$, $P = 0.002$) subcommunities, respectively (Table 1). Furthermore, the changes in forest area and TN were significantly correlated with pairwise comparisons of βNTI of the abundant ($R^2 = 0.029$, $P < 0.001$, Fig. S5a) and rare ($R^2 = 0.041$, $P < 0.001$, Fig. S5b) subcommunities, respectively. Despite the βNTI values of the abundant subcommunity being significantly related to differences in forest area, the distribution of βNTI values were mainly in the region of stochastic assembly ($-2 < \beta\text{NTI} < +2$). Yet the distribution of βNTI values of the rare subcommunity were mainly in the region of HeS ($\beta\text{NTI} > +2$) with the changes in sediment TN content.

3.5 Species co-occurrence patterns

The co-occurrence network consisted of 3,705 associations among 1,100 OTUs (Table 2 and Fig. 5). The high power-law coefficient ($R^2 = 0.994$) and modularity value (0.759) of the co-occurrence network indicated that the organization of the ecological network was not randomly connected and had modular structure (Table 2). The topological properties, such as average clustering coefficient and average path length in the empirical network were higher than those in the respective Erdös-Rényi random networks. Meanwhile, the small-world coefficient (46.136 ± 6.809) of the co-occurrence network was much greater than 1, suggesting that the co-occurrence network had a 'small-world' property.

Within the co-occurrence network, we identified 108, 616 and 376 OTUs for abundant, intermediate and rare taxa, respectively (Fig. 5a). There were 660 associations between abundant and intermediate taxa, and 674 links between rare and intermediate taxa. However, only 133 edges connected abundant and rare taxa. These results indicated that rare taxa frequently interacted more with intermediate taxa and themselves than with abundant taxa. In addition, both the degree and betweenness centrality values of abundant taxa were significantly higher than those of rare taxa (Fig. 5b).

The co-occurrence network was clearly divided into 8 major modules (Fig. 5c). Many of these modules were comprised of a group of OTUs that were phylogenetically close and belonged to the same clade (Fig. 5d). For example, modules 2 and 8 were predominated by OTUs belonging to Firmicutes and Actinobacteria, respectively. Moreover, the results of incidences of observed (O) and random (R) co-occurrence between all pairwise OTUs indicated that OTUs within the same phylum, including Verrucomicrobia, Firmicutes, Chloroflexi, Bacteroidetes, Actinobacteria, and Acidobacteria, tended to co-occur more often than expected by chance (with O/R ratios > 2.0, Table S4).

There were 28 module hubs and 10 connectors in the co-occurrence network (Fig. S6). According to the definition of keystone taxa as described in the Materials and Methods section, these module hubs and connectors can be regarded as keystone taxa. Of the 28 module hubs, 9 belonged to abundant taxa and 4 belonged to rare taxa, which were mainly affiliated with the phyla Acidobacteria, Bacteroidetes, Chloroflexi, Proteobacteria, and Verrucomicrobia (Table S5). 8 of the 10 connectors belonged to the intermediate taxa. The only connector from the abundant taxa belonged to Proteobacteria and the only connector from the rare taxa was affliated to Actinobacteria.

4. Discussion

4.1 Different diversity patterns of abundant and rare bacteria

In this study, we found that bacterial α-diversity was significantly higher in the rare subcommunity than in the abundant subcommunity (Fig. S2). This result supports the notion that rare taxa play the role of "seed bank" in maintaining microbial diversity (Lynch and Neufeld, 2015; Shade et al., 2014). Our results also showed that the rare subcommunity displayed higher β-diversity than the abundant subcommunity in fluvial sediments (Fig. 2). This finding suggests that differentiation of the rare subcommunity along environmental gradients is higher than the abundant subcommunity. Variations in β-diversity generally depend on the interaction of species traits (e.g., ability to disperse and niche width) and characteristics of the environmental conditions (e.g., environmental heterogeneity and topographic complexity) (Maloufi et al., 2016; McKnight et al., 2007). In virtue of the rare and abundant subcommunities being subjected to the same environmental conditions, the higher β-diversity of the rare subcommunity may partly be attributable to the potential of some rare taxa could be actively growing or waking up from dormancy and present in the currently active community (Jiao et al., 2017; Pedrós-Alió, 2012).

4.2 Broader environmental adaptations of abundant bacteria

The current study found that abundant taxa were ubiquitous in more than half of sediment samples, while most rare taxa occurred only in a few samples (Fig. S1a). These results are in line with previous studies where abundant taxa with high local abundance have a widespread or ubiquitous distribution in terrestrial (Ji et al., 2020; Jiao and Lu, 2020; Wan et al., 2021a) and aquatic (Liu et al., 2015; Mo et al., 2018; Wan et al., 2021b) ecosystems. It is possible that abundant taxa may grow on a wider array of substrates and occupy a broader niche compared with rare taxa, hence supporting their persistence at higher abundance in a wider range of sites (Hambright et al., 2015). Indeed, our environmental threshold analysis further corroborated this assumption that abundant taxa exhibited potential broader response thresholds to the environmental variables compared to rare ones (Fig. 3a). For example, abundant taxa exhibited broader nutrient utilization potential than rare taxa, especially for TC, TN, NH_4-N, and NO_3-N.

Our results further demonstrated that abundant taxa displayed stronger phylogenetic signals for environmental preferences compared with rare taxa (Fig. 3b). This indicates closely related taxa in the abundant subcommunity exhibit more similar ecological preferences across environmental gradients than taxa in the rare subcommunity. Several recent reports have shown that the stronger phylogenetic signals for a given microbial community of environmental preferences, the greater the phylogenetic niche conservatism in the evolutionary history of environmental adaptation (Jiao and Lu, 2020; Wan et al., 2021a). Thus, the stronger phylogenetic signals of abundant taxa for environmental preferences may explain why they have broader environmental breadths than their rare counterparts. In addition, our results revealed that the correlation between community composition and phylogeny in the rare subcommunity was stronger than that in the corresponding abundant subcommunity. This finding implies that abundant taxa are better in maintaining ecological niches than rare taxa under altered environmental conditions (Ji et al., 2020). Together, the above findings indicated that abundant bacterial taxa possessed stronger adaptations to various environmental conditions than rare bacteria in sediments of the Yarlung Tsangpo River.

4.3 Distinct assembly processes underlie similar biogeography of abundant and rare bacteria

Disentangling the biogeography and community assembly of abundant and rare microbial taxa is essential for understanding microbe-driven ecosystem processes and functions in the Yarlung Tsangpo River. We observed that both abundant and rare bacteria exhibited significant distance-decay relationships (Fig. 2), which was consistent with previous studies (Ji et al., 2020; Jiao et al., 2017; Mo et al., 2018). Although both subcommunities yielded similar biogeographic patterns, we found that the relative contributions of ecological processes to the assembly of abundant and rare subcommunities were different (Fig. 4b). Null model showed that the assembly of abundant subcommunity was dominated by dispersal limitation (84%), and is in line with previous investigations on inland lakes (Liu et al., 2015), epipelagic waters (Wu et al., 2017), and agricultural soils (Jiao and Lu, 2020). This result may be due to the strong environmental adaptation of abundant taxa as mentioned above, which make them less sensitive to environmental filtering and thus being more influenced by dispersal limitation. Additionally, the VPA results in our study indicated the pure effect of spatial variables surpassed those of environmental factors and land use types for abundant taxa, suggesting the greater significance of dispersal limitation in the abundant subcommunity assembly (Fig. S4). By contrast, assembly of the rare subcommunity was dominated by heterogeneous selection (77%), which was contradictory to previous findings that the rare subcommunity was primarily controlled by homogeneous selection (Jiao and Lu, 2020; Zhang et al., 2021a). Heterogeneous selection refers to selection under heterogeneous abiotic and biotic environmental conditions leading to more dissimilar structures among communities (Zhou and Ning, 2017). These discrepancies may be ascribed to the environmental heterogeneity in fluvial sediments. Due to the interplay of climate change, increasing anthropogenic, and complex geomorphologies, the water quality and biogeochemical nutrients in the Yarlung Tsangpo River were suspected to be highly variable over time and space (Wang et al., 2017; Wang et al., 2020b; Zhang et al., 2021c). Therefore, we would expect a strong heterogeneous selection on rare taxa in the investigated fluvial sediments.

4.4 Discerning drivers of abundant and rare community assembly

Revealing the factors affecting the relative influences of deterministic and stochastic ecological processes is important for deeper understanding of community assembly (Tripathi et al., 2018). In this study, we found that forest area had a greater association with the abundant subcommunity assembly than other factors, while TN was more closely correlated with the rare subcommunity assembly (Table 1). The strong associations of βNTI values of abundant and rare subcommunities with differences in forest area and TN, respectively, further suggesting that forest area and TN were the key factors shaping the stochastic and deterministic assembly for abundant and rare subcommunities, respectively (Fig. S5). In recent decades, deforestation is one of the most visible land use changes in the Yarlung Tsangpo River basin (Hao et al., 2021; Harris, 2010). Deforestation, combined with climate-induced soil erosion are the main sources of suspended sediment in the river flow (Shi et al., 2018; Wang et al., 2020a). On the one hand, soil erosion can transfer substantial amounts of nutrients (e.g., TN and NH_4-N) into the fluvial sediments to support bacterial growth (Quinton et al., 2010). More importantly, surrounding soil derived bacteria inputs can directly affect bacterial composition and diversity in the fluvial sediments (Crump et al., 2012; Ruiz-González et al., 2015). Thus, our findings reveal the important linkage between land use types and community assembly processes, which might influence the microbial diversity and fluvial sediment ecosystem processes. This is an important issue in need of further research. Future work to explore the precise role of land use types for sediment bacterial community assembly processes, providing scientific support for environmental regulation and ecological security maintenance in the Yarlung Tsangpo River basin is needed.

4.5 Roles of abundant and rare taxa in mediating interspecific interactions

Network analysis can improve our understanding on the potential roles of abundant and rare taxa in the complex interaction webs of fluvial sediments. Our results illustrated that the co-occurrence network had non-randomly connected properties and closely related taxa tended to be interconnected and clustered together within the network, suggesting that taxonomic relatedness plays a key role in determining the network modular structure. This non-random pattern may reflect the effects of environmental filtering and niche differentiation among species in the Yarlung Tsangpo River sediments (Hu et al., 2017; Ju and Zhang, 2015).

Our results revealed that rare taxa rarely coexisted with abundant taxa within the fluvial sediment network (Fig. 5a). This result may be explained by the fact that abundant and rare taxa occupy different ecological niches and respond differently to environmental variables (Jiao et al., 2017). The topological properties of the network can also reflect interactions between species (Xue et al., 2018). Previous research has revealed that abundant taxa, with higher degree and betweenness centrality values, are more connected with each other and more often located in central positions, than rare taxa within the network (Jiao et al., 2017; Zhang et al., 2021a). Our results showed that the values of degree and betweenness centrality for abundant taxa were significantly higher compared with rare taxa, implying that abundant taxa may play a more important role in maintaining the co-occurrence network than rare taxa (Rottjers and Faust, 2018). However, rare species might be keystone taxa. In our study, five rare OTUs were identified as underlying keystone taxa in the co-occurrence network (Table S5 and Fig. S6). Considering the importance of keystone taxa in mediating interspecific interactions (Sun et al., 2021), our results thus indicated the potential roles of those rare keystone bacteria in maintaining ecosystem stability in sediments of the Yarlung Tsangpo River. Our results also showed that intermediate taxa had the most interactions with both abundant and rare taxa, and more than half of the module hubs and connectors belonged to intermediate taxa, indicating that intermediate taxa may act as bridges between rare and abundant taxa within the co-occurrence network.

5. Conclusions

In summary, the present study systematically investigated the biogeographic patterns, environmental adaptations, assembly processes, and co-occurrence patterns of abundant and rare bacteria in the sediments of the Yarlung Tsangpo River. The present work linked abundant and rare bacterial community traits, including phylogenetic clustering, environmental thresholds, and phylogenetic signals of ecological preferences to different environmental conditions, and revealed the factors mediating community assembly processes. We found that abundant taxa had stronger environmental adaptation and exhibited ubiquitous distribution, whereas rare taxa were more sensitive to environmental changes and exhibited restricted distribution. Forest area and TN were the major factors mediating the balance of stochastic and deterministic assembly processes in the abundant and rare subcommunities, respectively. Although the rare taxa were less connected and located more peripherally within the co-occurrence network compared with abundant taxa, both played important roles in maintaining network stability. These results expand our understanding of the mechanisms underlying the maintenance of microbial diversity and predicting microbial responses to environmental perturbation caused by climate change and human activities in the Yarlung Tsangpo River.

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author Contributions

This work was conceived by KSL, YQL, and AYH. Field work was done by AYH, LPZ, and QTZ. Laboratory work was done by LPZ, QTZ, and FW. Analysis was carried out by KSL, QY, ZHZ, XX, and JZL. The manuscript was written by KSL and AYH. Manuscript editing was done by AYH and YQL.

Data Accessibility Statement

All raw sequences data from this study have been submitted to the NCBI Sequence Read Archive (SRA) database under project PRJNA790017.

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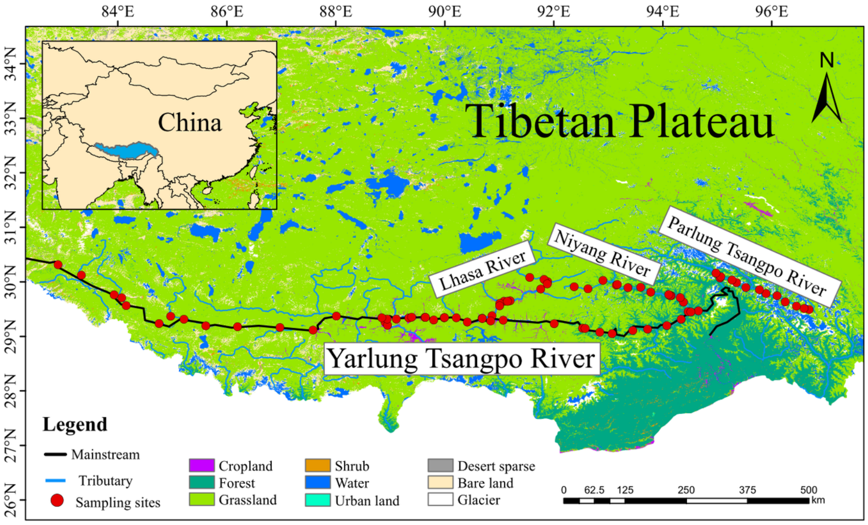

Fig. 1. Overview of the sampling sites and their geographic locations along the Yarlung Tsangpo River. Red circles present the sampling sites of our study. Black lines and blue lines indicate mainstreams and tributaries of the Yarlung Tsangpo River, respectively.

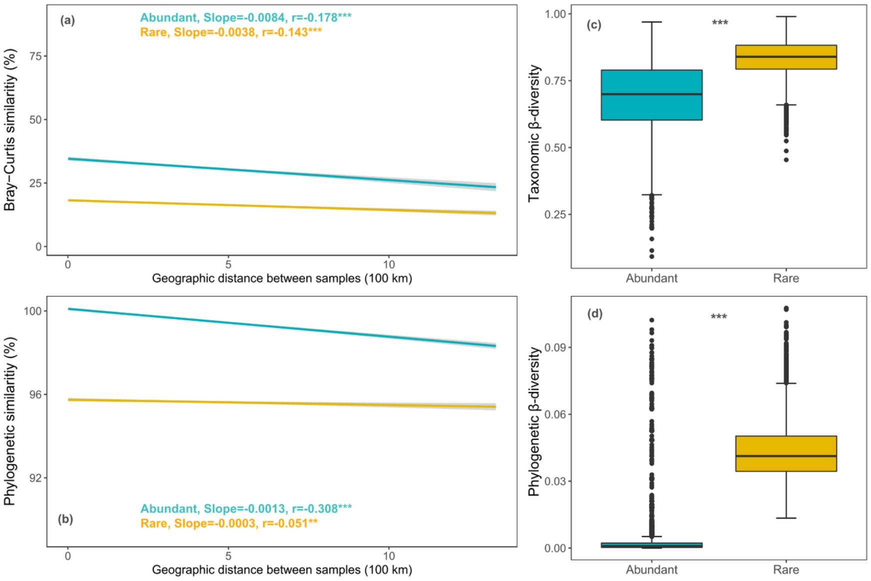

Fig. 2. Patterns of abundant and rare taxa based on compositional and phylogenetic similarities. Distance-decay curves of compositional similarity (a, Bray–Curtis similarity) and phylogenetic similarity (b, 1-βMNTD) for abundant and rare taxa; Differences in community distance (c, Bray–Curtis dissimilarity) and phylogenetic distance (d, βMNTD dissimilarity) between abundant and rare taxa. Gray shaded areas in the plots (a and b) denote 95% confidence intervals. Asterisks indicate significance (***, $P < 0.001$) according to nonparametric Wilcoxon rank-sum test.

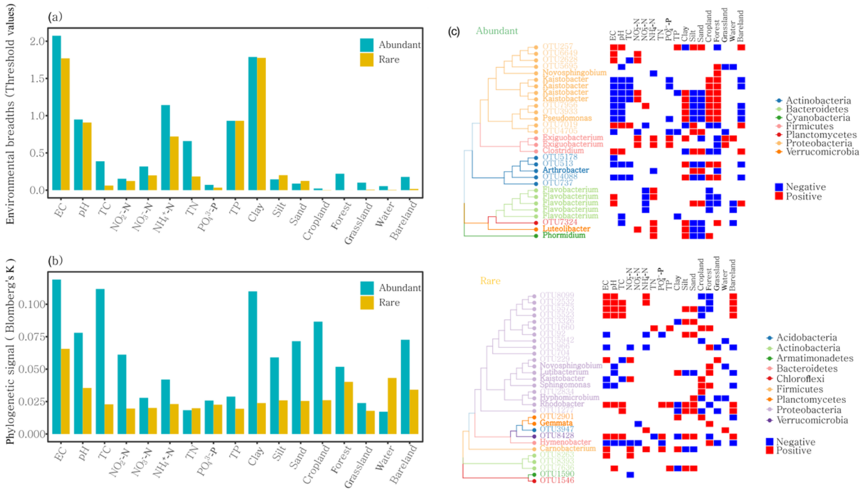

Fig. 3. Environmental adaptation of abundant and rare taxa in sediments. (a) Environmental breadth estimated by the threshold values of abundant and rare taxa in response to environmental variables calculated using TITAN. The threshold values were log-transformed [by log (X +1)]. (b) Phylogenetic signal showing the trait conservatism for environmental preferences of the abundant and rare taxa based on Blomberg's K statistic. (c) Phylogenetic distribution of the top 30 most abundant taxa in the abundant and rare subcommunities and their environmental preferences. Note that taxa that could be assigned to genus level are shown as genus, otherwise as OTU ID.

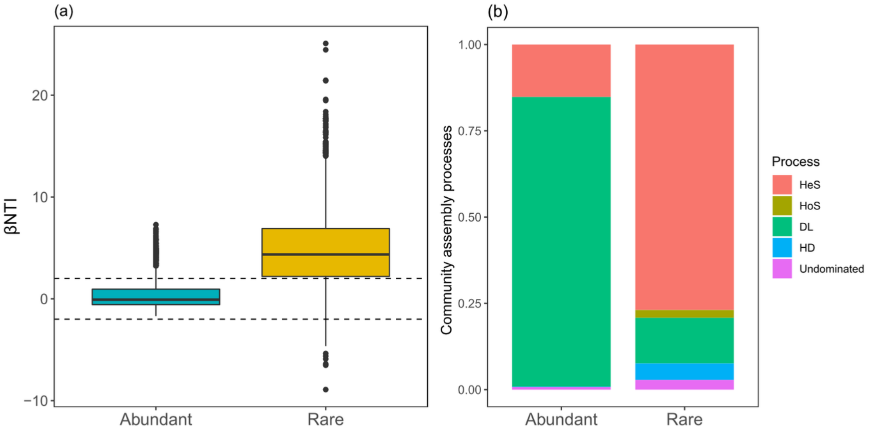

Fig. 4. Community assembly processes of abundant and rare taxa. (a) Patterns of the beta nearest taxon index (βNTI) for the abundant and rare taxa. The horizontal dashed lines represent upper and lower significance thresholds at βNTI = +2 and -2, respectively. (b) Depiction of the contribution of the ecological

processes that determine community assembly of the abundant and rare taxa. Heterogeneous selection (HeS), homogeneous selection (HoS), dispersal limitation (DL), homogenizing dispersal (HD), and Undominated.

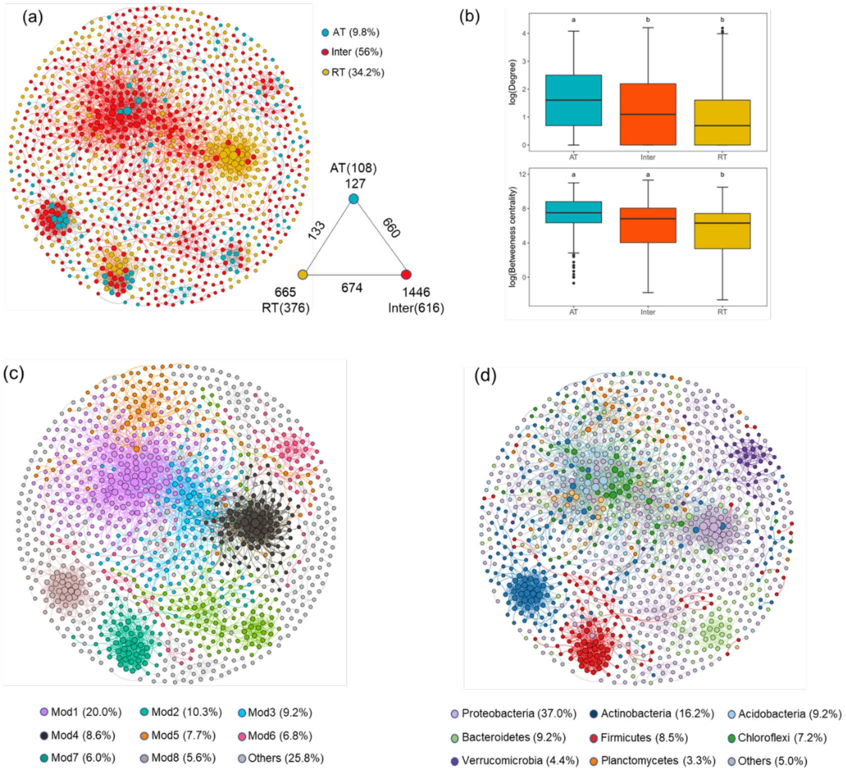

Fig. 5. The co-occurrence patterns among OTUs revealed by network analysis. (a) OTUs coloured by different subcommunities. AT: abundant taxa, RT: rare taxa, Inter: intermediate taxa. A connection indicates a very strong (Spearman's r [?] 0.7) and significant (FDR-adjusted P -value < 0.01) correlation. The size of each node is proportional to the number of connections (i.e., degree). Numbers inside parentheses represent the number of nodes belonging to the corresponding subcommunity. Numbers adjacent to nodes indicate the intra-associations within each subcommunity and numbers adjacent to edge connections represent inter-associations between different subcommunities. (b) Comparison of node-level topological features between different subcommunities. Different letters indicate the significant level at $P < 0.05$ level according to nonparametric Wilcoxon rank-sum test. OTUs coloured by (c) module and (d) phylum-level taxonomy. Percentages within parentheses indicate percent of nodes belong to each group.

Table 1 Mantel tests for the correlation between environmental variables and βNTI of abundant and rare taxa.

Variables	Abundant	Abundant	Rare	Rare
	r	P	r	P
EC	-0.024	0.720	**0.104**	**0.019**
pH	-0.061	0.975	**0.123**	**0.002**
TC	0.002	0.468	-0.094	0.959
NO_2^--N	-0.024	0.702	**0.120**	**0.015**
NO_3^--N	**0.112**	**0.008**	0.005	0.456
NH_4^+-N	**0.107**	**0.014**	0.045	0.202

Variables	Abundant	Abundant	Rare	Rare
TN	-0.053	0.862	**0.171**	**<0.001**
PO_4^{3-}-P	0.010	0.405	0.058	0.140
TP	-0.011	0.588	0.011	0.401
Clay	-0.016	0.663	**0.119**	**0.004**
Silt	-0.050	0.854	**0.117**	**0.022**
Sand	-0.025	0.695	0.073	0.085
Cropland%	-0.024	0.781	**0.076**	**0.024**
Forest%	**0.116**	**0.005**	0.066	0.091
Grassland%	-0.071	0.971	0.019	0.322
Water%	-0.007	0.547	0.044	0.170
Bare land%	-0.088	0.989	0.034	0.224

The abbreviations of the environmental factors listed are defined in Materials and Methods.

Mantel tests are performed using Spearman's rank correlations.

The significances were tested based on 9999 permutations, and bold values indicate $P < 0.05$.

Table 2 Topological properties of the empirical ecological network of riverine bacterial communities and their associated random network.

	Topological properties	Metacommunity
Empirical network	Nodes	1100
	Edges	3705
	Modularity[a]	0.759
	Average clustering coefficient[b]	0.447
	Average path length[c]	6.290
	Average degree[d]	6.736
	Power- law R^2	0.994
Erdős-Rényi random network	Modularity	0.291 (± 0.007)
	Average clustering coefficient	0.006 (± 0.001)
	Average path length	3.884 (± 0.005)
	Small-word coefficient[e]	46.136 (± 6.809)

[a] Modularity >0.4 suggests that the network has a modular structure.

[b] How nodes are embedded in their neighborhood, and the degree to which nodes tend to cluster together.

[c] The average number of steps along the shortest paths for all possible pairs of network nodes.

[d] Node connectivity showing how many connections (on average) each node has to the other nodes in the network.

[e] Small-word coefficient >1 indicates "small-world" properties, that is, high interconnectivity and high efficiency.

The number in the brackets indicates the standard deviation of topological properties of the 1000 Erdös-Rényi random networks.