Effects of tourism development on ecological network and function of sediment microbial communities in the urban wetland park

Binhao Wang[1], Kaiming Hu[2], Lin Chen[3,4], Wei Zhang[3,4], Congcong Zhang[3,4], Wenbing Li[1], Hangjun Zhang[1,*]

1 School of Engineering, Hangzhou Normal University, Hangzhou 310018, China
2 School of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou 311121, China
3 Hangzhou Xixi National Wetland Park Ecology & Culture Research Center, Hangzhou 310030, China
4 Zhejiang Xixi Wetland Ecosystem National Observation and Research Station, Hangzhou 310030, China
 * Corresponding author. E-mail: 20080099@hznu.edu.cn (H. Zhang)

ABSTRACT

• Tourism development influenced the ecological network of microbial communities.

• Regulating mechanism of intra- and inter-domain networks was clarified.

• Macrophyte coverage reduces microbial network complexity and stability.

• Landscaping may promote nitrogen and phosphorus cycle in wetland watershed.

Numerous urban wetland parks have been established, yet the understanding of microbial interactions in response to tourism development is still limited. This study aims to elucidate the impact of tourism development on the complexity and stability of molecular ecological networks within the microbial communities of wetland sediments. Through an analysis of sediments properties, microorganism intra- and inter-domain co-occurrence characteristics in three different wetland functional areas (conservation, landscaping, and recreation areas), we found that tourism development influenced sediment physicochemical properties. These changes regulated the diversity and ecological networks of archaeal and bacterial communities. Specifically, areas with landscaping (LA) exhibited reduced network connectivity and robustness, suggesting that macrophyte coverage diminishes the complexity and stability of microbial communities in wetland parks. Notably, the transition from conservation areas (CA) to LA strengthened the correlations between microbial network modules and sediment total nitrogen (TN) and total phosphorus (TP), potentially enhancing the nitrogen and phosphorus cycles in wetlands. Structural equation modeling analysis revealed that both abiotic factors (TC, TP, TN, K, Mg, pH) and biotic factors (archaeal and bacterial α-diversity) can influence interdomain network complexity, accounting for 42% of the variation. Among these factors, sediment TN exerted the largest positive effect on network complexity (37.9%), while Mg had the most negative impact (59.8%). This study provides valuable insights for ecological assessments of urban wetlands and can inform strategies for effective wetland ecosystem management.

Keywords urban wetlands, tourism development, microbial communities, interdomain interactions, network complexity
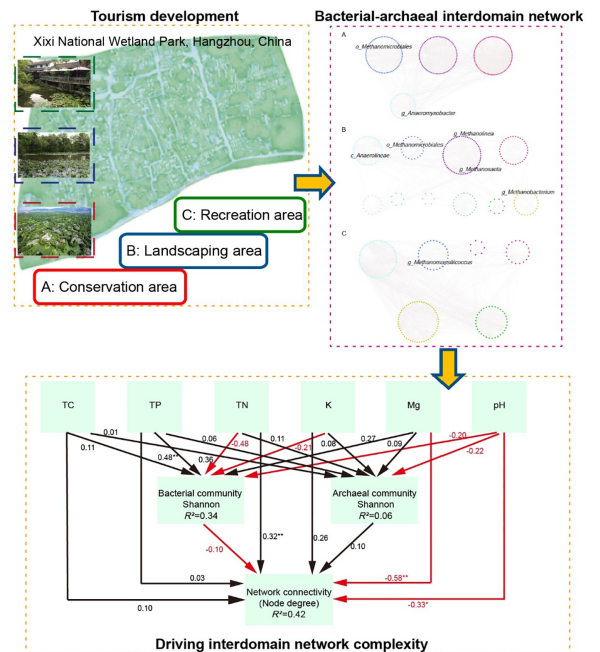
1 Introduction

Urban wetlands offer substantial ecosystem services, encompassing support, regulation, and cultural benefits (Costanza et al., 1997; Russi, 2013; Yu et al., 2018). To maximize their environmental and economic advantages (Sanna and Eja, 2017), a significant number of urban wetland parks have been established globally (Mitsch et al., 2014; Chatterjee et al., 2015; Wahlroos et al., 2015; Arsić

et al., 2018). For instance, by the end of 2022, China had over 1700 wetland parks, with 901 designated as national wetland parks (see the website of National Forestry and Grassland Administrtion, China). The primary goals of these parks are to safeguard wetland resources and to harness their economic potential effectively. Increased tourism in these areas substantially impacts the wetland ecosystem functions mediated by microbes (Wang et al., 2020a; Li et al., 2022; Piano et al., 2023). This is due to the changes in microbial taxa and abundance resulting from the pressure of human activities (Wang et al., 2020b).

In addition to the structure and diversity of microbial communities, there is growing evidence that environmental changes induced by human activities significantly influence microbial co-occurrence networks (Mandakovic et al., 2018; Xue et al., 2022). In freshwater ecosystems, total nitrogen (TN) and total phosphorus (TP) concentrations are key determinants of connectivity within microbial interdomain networks (Wang et al., 2023a). Additionally, plants have been observed to alter microbial communities and their co-occurrence network patterns (Wang et al., 2021b; Zhan et al., 2021). Consequently, both abiotic and biotic conditions shape ecosystem functions by influencing microbial communities, which in turn affect wetland functions (Nelson et al., 2023). The stability of these microbial functional groups also varies in response to environmental changes, impacting co-occurrence patterns (Zhou et al., 2021b). Nevertheless, our comprehension of how microbial ecological networks in human-disturbed wetland parks react to tourism development is still limited (Delgado-Baquerizo et al., 2018; Wagg et al., 2019; Nelson et al., 2023).

Microbial communities are highly complex, characterized by a plethora of biotic interactions (Sun et al., 2022), and they tend to exhibit close associations across domains, rather than acting independently in shaping local ecology (Feng et al., 2019). Prior research has demonstrated that intricate interdomain interactions between bacteria and archaea foster fitness, diversification, and niche adaptations, as each species evolves to thrive within their respective communities (Faust and Raes, 2012). For instance, enhanced direct interspecies electron transfer in bacterial and archaeal consortia has been linked to accelerated methane production, illustrating a key aspect of interdomain interactions (Li et al., 2015, 2021). Moreover, the complexity of the bacteria-archaea interdomain network may mark a significant threshold in the shift from mesotrophic to lightly eutrophic conditions in water bodies (Wang et al., 2023a). Therefore, the response of network complexity to environmental changes can be an indicator of ecosystem health.

Wetland parks are significantly impacted by human activities, such as ecological sightseeing, recreational services, and artificial landscaping, including the planting of aquatic species. These activities influence the composition (Kiersztyn

et al., 2019), diversity (Wan et al., 2017), interactions (Li et al., 2021; Zhou et al., 2021a), and functions (Louca et al., 2018) of microbial communities within these environments. Certain sensitive functional microorganisms, like *Proteobacteria*, *Nitrospirae*, and *Euryarchaeota*, respond actively to environmental changes, leading to shifts in biogeochemical cycles (Sagova-Mareckova et al., 2021). For instance, a study by Peter and Sommaruga (2016) demonstrated that ecosystem functions, particularly those related to carbon, nitrogen, and phosphorus cycling, may shift during transitions from turbid to clear water states. Furthermore, the responsiveness of microorganisms to changes in environmental factors, including pH, concentrations of nitrogen, phosphorus, and other nutrients or pollutants, has been proposed as an effective tool for assessing ecosystem health (Wu et al., 2015, 2016; Zhang et al., 2016). Hence, gaining a comprehensive understanding of the responses of microbial ecological networks and functions to serious anthropogenic disturbances in wetland parks is essential.

Molecular ecological network analysis presents a promising approach for elucidating the interconnections among members of microbial communities (Coux et al., 2016; De Vries et al., 2018). Recently, a workflow utilizing Sparse Correlations for Compositional Data (SparCC) has been employed to construct interdomain bipartite networks, revealing co-occurrence patterns across different domains in various environments (Feng et al., 2019). Employing this method, Yuan et al. (2021b) observed increasingly complex co-occurrence networks between non-mycorrhizal and mycorrhizal fungi-bacteria, corresponding with plant growth. These patterns appear to be influenced by the availability and quality of carbon substrates. In another study, Wang et al. (2023a) reported that mesotrophic wetlands bordering on lightly eutrophic conditions harbored much more intricate bacterial-archaeal interdomain networks. These networks were regulated by factors such as chlorophyll-a, total nitrogen, and total phosphorus. Light eutrophication was found to intensify the network modules' negative associations with organic carbon via certain network hubs, potentially leading to carbon loss in wetlands. This analytical framework is thus pivotal in revealing how microbial interactions respond to environmental pressures caused by tourism development.

In this research, our objectives were to: (i) examine the impact of tourism development on microbial composition and ecological network attributes; (ii) identify the mechanisms driving the complexity and stability of archaeal-bacterial interdomain networks under varying disturbance conditions; and (iii) uncover the main effects of interdomain interactions on ecosystem functions. To investigate how tourism development affects sediment microbial networks and their ecological functions, we employed a combination of high-throughput sequencing and network analysis. This approach was applied to 54 sediment samples collected from three

functional regions within Xixi National Wetland Park, China. The study offers valuable insights into the dynamics of microbial ecological network under different levels of tourism disturbances and contributes to enhancing the ecological assessment and conservation of wetland parks.

2 Materials and methods

2.1 Sampling procedures and physicochemical measurements

To investigate the effects of tourism development on microbial interdomain network complexity and ecological function, we focused on three distinct functional regions within Xixi National Wetland Park (30°15.39′ N–30°16.96′ N, 120°03.16′ E–120°04.94′ E), Hangzhou, China. Spanning 11.5 km^2, more than half of its area is water-covered. The park features a humid subtropical monsoon climate, characterized by hot, wet summers and dry winters with low precipitation. Our study consists of three areas: conservation areas (CA), landscaping areas (LA), and recreation areas (RA), each subject to different management practices and possessing different physicochemical characteristics, as detailed in our previous paper (Wang et al., 2020a). In May 2018, a total of 54 sediment samples were collected. Each sample was divided into two parts: one subsample was immediately stored at −80°C for DNA extraction, while the other was kept at 4°C for subsequent chemical analysis. The sediment samples were dried to constant weight at 30°C, and their physicochemical characteristics, including total nitrogen (TN), total carbon (TC), total phosphorus (TP), potassium (K), magnesium (Mg), and pH, were measured using standard methods previously described (Wang et al., 2020a). Our physicochemical analysis (Fig. S1) revealed that TP concentrations in the three functional regions ranged from 0.18 to 2.32 g kg^{-1}, while TN and TC varied widely, from 0.69 to 7.98 g kg^{-1} and 8.37 to 65.03 g kg^{-1}, respectively.

2.2 DNA extraction and 16S rRNA gene sequences analysis

The process of DNA extraction, purification, amplification and sequencing refered to our previous paper (Wang et al., 2020a). Raw FASTQ files were processed using the DADA2 pipeline to generate amplicon sequence variants (ASVs). This involved denoising the 16S V3-V4 amplicon data (Callahan et al., 2016), with taxonomic assignment based on the GreenGenes database (see the website of Greegenes) (Tromas et al., 2017), utilizing the RDP classifier algorithm. During our analysis, ASVs mapping to mitochondria and chloroplasts were excluded to maintain data accuracy. To mitigate the impact of sequencing depth variability on the

assessment of treatment effects, we normalized the sequence depth across all samples. Following this, ASVs with a total abundance below 0.000 1 across all samples were removed. The resulting filtered abundance table was then used to calculate alpha diversity metrics.

2.3 Network construction and analysis

(i) To investigate potential interactions between archaeal and bacterial communities, we utilized Sparse Partial Correlation Coefficients (SPRCC) to construct a coexistence network. Our analysis was focused on ASVs present in over 80% of the samples. To evaluate the significance of sparse correlations between genera within our dataset, we computed pseudo-P-values through 100 bootstrap iterations. Only correlations that met a specific threshold ($r \geqslant 0.6$, $P \leqslant 0.05$) were considered for network construction.

(ii) To further explore interactions between bacterial and archaeal communities, we constructed interdomain ecological networks (IDENs) following the methodology outlined by Feng et al. (2019). Here, only ASVs found in more than 80% of all samples were included. For these IDENs, 100 rewired networks were generated to evaluate the topological properties of each index (Deng et al., 2012). The differences between the observed IDENs and their corresponding random networks were assessed using one-sample Student's t-tests.

Network topological properties, such as complexity and modularity, have proven effective in predicting the stability of microbial networks (Coux et al., 2016; De Vries et al., 2018). To determine whether and how tourism development impacts the stability of these ecological networks, network robustness was used as a measure of stability and the resilience of its constituent members (Yuan et al., 2021a). Network robustness is defined as the proportion of remaining species in the network after random or targeted node removal (Montesinos-Navarro et al., 2017). The final visualizations of these networks were created using Cytoscape.

2.4 Statistical analysis

Data analyses were mainly performed using R version 4.0.2 with software packages. Non-metric multidimensional scaling (NMDS) was performed based on the Bray−Curtis distances of microbial communities with a vegan package (R Development Core Team, 2014). We incorporated a second matrix of the sediment physicochemical variables (TN, TC, TP, K, Mg, and pH) into the NMDS using the *envfit* function.

To further explain linkages among the physicochemical parameter, microbial community composition, and interdomain network stability, a structural equation modelling approach (SEM) was employed with improved model fit assessed based on reduced χ^2 and Akaike information crite-

ria (*sem* function; *lavaan* package) (Mamet et al., 2017, 2019).

3 Results

3.1 Variations in microbial diversity and community composition

The high-quality sequences from all the 54 sediment samples were assigned to 774 and 1752 amplicon sequence variants (ASVs) from archaea and bacteria, respectively. The α-diversity indices (richness) varied widely, ranging from 176 to 442 for archaea and from 211 to 938 for bacteria, as illustrated in Figure S2. Notably, the richness of archaea was relatively higher in conservation areas (CA) compared to landscaping areas (LA) and recreation areas (RA), with a significant difference ($P < 0.05$) (Fig. S2). Similarly, both richness and shannon indices for bacteria were higher in CA than in RA ($P < 0.05$) (Fig. S2). The predominant archaeal phyla were *Euryarchaeota* and *Crenarchaeota*, while *Proteobacteria* and *Chloroflexi* were the dominant bacterial phyla (Fig. S3). Although the dominant phyla of microbial communities were similar across the three functional regions (Fig. S4), significant differences ($P < 0.05$) in the relative abundances of some dominant archaeal and bacterial phyla were observed among them (Fig. S4). The relative abundance of *Proteobacteria* and *Actinobacteria* was higher in recreational areas compared to other areas. β-diversity also demonstrated clustering by site (Fig. S5). Using NMDS, shifts in microbial community composition among the three functional regions were detected, indicating that archaeal and bacterial communities formed distinct clusters influenced by tourism development, as shown by stress values of 0.1432 and 0.1424, respectively (Fig. S5). Total nitrogen (TN) was significantly ($P < 0.05$) correlated with the NMDS axis, highlighting its substantial impact on the structure of archaeal and bacterial communities (Table S1).

3.2 Archaeal and bacterial network characteristics

We examined the co-occurrence patterns of archaeal and bacterial communities using network analysis, which revealed significant clustering within the networks (Fig. 1). For the archaeal ecological network (Fig. 1A−C), frequent co-occurrences of genera such as *Methanosaeta* were identified. In the LA, the network comprised 112 nodes and 276 edges, exhibiting the lowest average degree (*avgK*, 4.93), geodesic efficiency (*GE*, 0.32), and the highest average path distance (*GD*, 3.88) compared to other areas. In contrast, CA had 128 nodes and 567 edges, with *avgK* at 8.86, *GE* at 0.39, and *GD* at 3.05, whereas RA had the

fewest nodes (106), with *avgK* at 10.36, *GE* at 0.44, and *GD* at 2.62 (Fig.1). The average betweenness centrality values showed that CA (0.06) was higher than RA (0.04), but lower than LA (0.18). To understand the topological roles of taxa within these networks, we categorized nodes into four types based on their within-module (Zi) and among-module (Pi) connectivity values. ASVs serving as network hubs were designated as keystone taxa, with threshold values for Zi and Pi set at 2.50 and 0.62, respectively. According to the Zi-Pi plots, two keystone taxa were detected in both CA and RA (Fig. 2A−C): ASV1221 (belonging to *Methanosaeta*) with a relative abundance of 1.1%, and ASV215 (belonging to *Thermoplasmata*) with a relative abundance of 1.0%. To further explore network topology characteristics across different sediment samples, network connectivity was calculated, representing network stability (Fig. 2D). The network connectivity varied from 4.6 to 10.5, with an average of 7.44. Notably, the network complexity in RA was higher than in other areas, suggesting a more complex archaeal network in RA compared to CA or LA (Fig. 2D).

For bacterial communities from LA, the network had 285 nodes and 1123 edges with the lowest average degree (*avgK*, 7.88), betweenness centrality (*CB*, 0.05) and geodesic efficiency (*GE*, 0.31), and highest average path distance (*GD*, 3.74) than other araes, where CA had 166 nodes and 749 edges with *avgK* at 9.57, *CB* at 0.07, *GE* at 0.36 and *GD* at 3.26, and RA with the lowest number of nodes (87), *avgK* at 10.46, *CB* at 0.14, *GE* at 0.42 and *GD* at3.02 (Fig. 1D−F). As for topological roles of taxa (Fig. 2E−H), our results showed that LA had a higher proportion of module hubs than other areas, which meant more interactions within modules but less outside modules among bacterial communities in LA. These keystones are ASV14278, ASV2748 and ASV21796 in CA, and ASV11883, ASV18076, ASV9373, ASV5228, ASV3278, ASV2275 in LA. Comparing sequences of keystone ASVs at GreenGenes database indicates that these keystones were mostly belonged to *Proteobacteria, Firmicutes, Bacteroidetes, Acidobacteria* and *Nitrospirae*. Meanwhile, we observed the bacterial network connectivity varied between 5.7 and 10.8, with the highest mean value of 8.70 in RA (Fig. 2H).

3.3 Microbial interdomain ecological network characteristics

To investigate potential microbial interactions, archaeal and bacterial Interdomain ecological networks (IDENs) were constructed based on SparCC correlations among ASVs. The three networks we developed exhibited distinct structural and topological characteristics, as depicted in Fig. 3A−C and detailed in Table S2. Our analysis revealed that the linkage density and nestedness of bacterial-archaeal IDENs were highest in the RA. When compared to randomly generated bipartite networks, the rewired network checkerboard
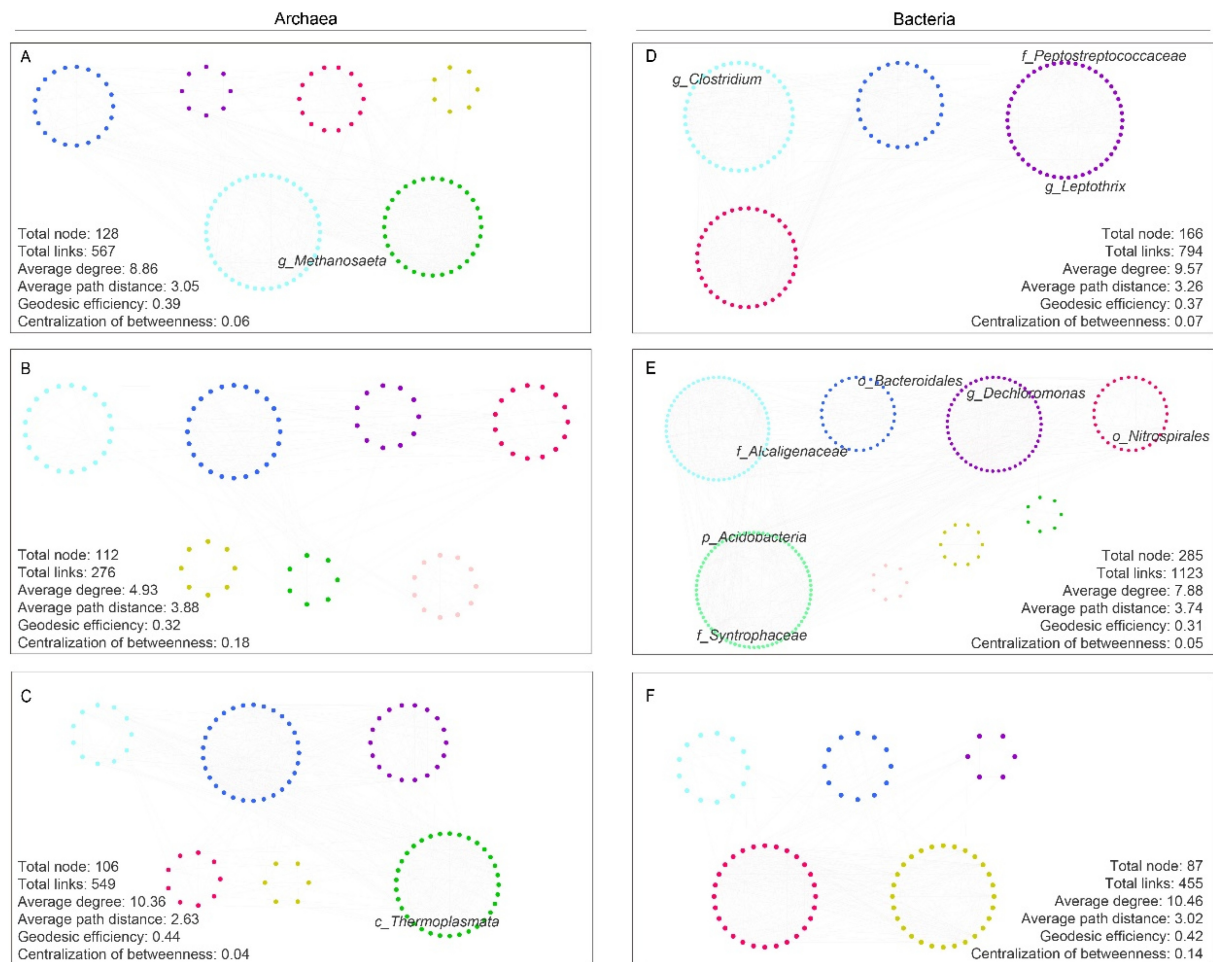
Fig. 1 Ecological network of archaeal and bacterial ASVs detected in conservation areas (A and D), landscaping areas (B and E) and recreation area (C and F). Each node corresponds to an ASV, and different colors represent different modules, where large modules with ⩾5 nodes are shown.

scores for archaea and bacteria were significantly lower ($P <$ 0.05) than those of the observed networks. This indicates nonrandom patterns in the observed bacterial-archaeal networks (Table S3). Based on the Zi-Pi plots, two archaeal and seven bacterial taxa were identified as keystone taxa across the three functional regions. Network connectivity, as represented by node degree, and network robustness was notably lower in the LA (3.67 and 0.22, respectively) compared to CA and RA (8.57 and 8.58, 0.25 and 0.25, respectively) (Fig. 4D−E).

3.4 Linking environmental factors, microbial community, and network complexity

Spearman correlation analysis was conducted to explore the relationships between environmental parameters and the complexity of microbial communities, as depicted in Figure S6. We found that the complexity of both archaeal and bacterial communities was significantly negatively correlated with pH ($r = -0.33$ and -0.34, respectively) and magnesium (Mg) ($r = -0.30$ and -0.27, respectively) ($P <$ 0.05). To

further examine the association between these environmental factors and the complexity of bacterial-archaeal interdomain networks, linear regression analysis was performed (Fig. 5). The complexity of the interdomain ecological networks also exhibited significant negative correlations with pH and Mg ($P <$ 0.05).

To further reveal the relationships between bacterial-archaeal interactions and phosphorus, nitrogen and carbon cycling, we used a module-eigenvalue analysis to link the network modules to the TP, TN and TC (Fig. 6). Within the bacterial-archaeal network, one module in CA, five modules in LA, and one module in RA were significantly correlated with TP ($P <$ 0.05). One module in CA and three in LA showed significant correlations with TN ($P <$ 0.05), while no modules in RA were associated with TN. Three modules in each region were also linked to TC, with specific modules (#CA3 with 73 nodes, #LA2 with 10 nodes, and #RA2 with 18 nodes) demonstrating significant negative associations with water TC ($P <$ 0.05).

Finally, we employed structural equation modeling (SEM) to identify both direct and indirect associations between
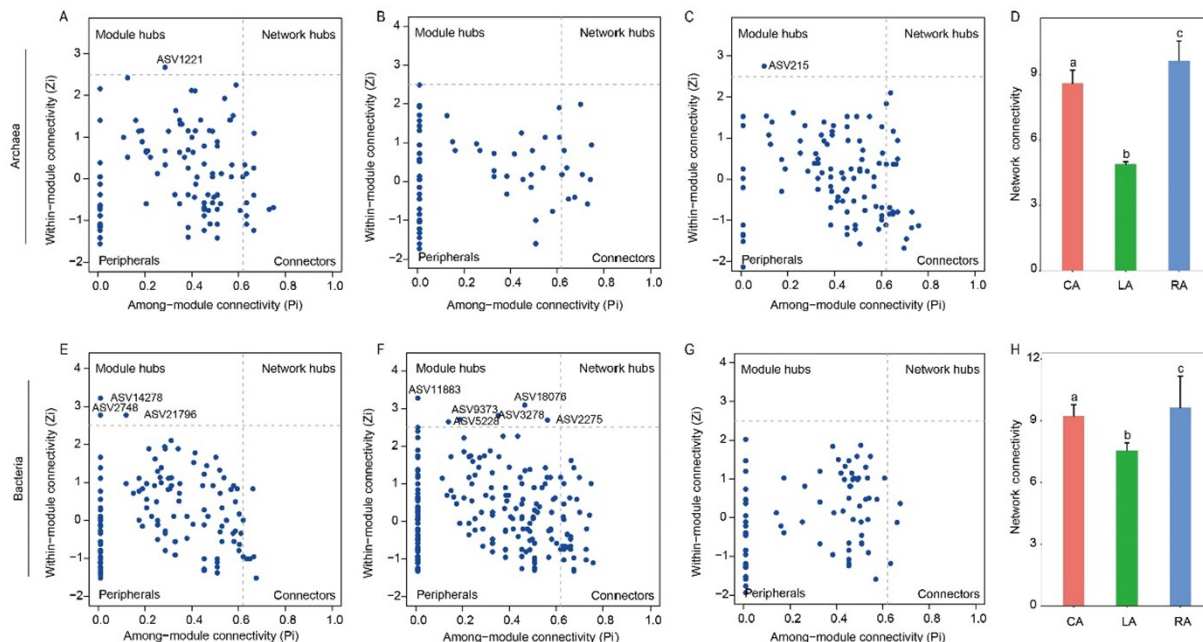
Fig. 2 Network topological properties of archaeal and bacterial communities. Zi–Pi plots (A−C for archaea and E−G for bacteria) showed the distribution of ASVs based on their topological roles in six networks. Threshold values of Zi and Pi for categorizing OTUs were 2.5 and 0.62, respectively. Network connectivity in sediments is represented by node degree for individual pond and was calculated by subsetting the networks of two pond groups (D and H). Different letters above the error bar indicate statistical difference among the three functional area. Groups are as follows: conservation areas (CA), landscaping areas (LA) and recreation area (RA).

physicochemical parameters and the stability of bacterial-archaeal interdomain networks (Fig. 7). The SEM analysis revealed that 42% of the variance in network complexity was directly explained by abiotic factors (TC, TP, TN, K, Mg, pH) and biotic factors (represented by bacterial and archaeal α-diversity, as measured by their shannon index values). Among these, sediment TN exerted the largest positive effect on network complexity (37.9%), while Mg had the most substantial negative impact (59.8%).

4 Discussion

Understanding the impacts of wetland tourism development on microbial ecological network and ecosystem functioning is an important topic in ecology and environmental management (Arif et al., 2022). Here we show that wetland parks under different tourism development harbor distinct microbial communities with varying network complexity and stability. Regardless of whether it is an intra-domain or an inter-domain network, sediments in LA displayed lower network complexity and stability compared to those in CA. Notably, the interdomain network complexity in CA and RA was twice as high as that in LA sediments. These variations are primarily influenced by physicochemical properties and microbial diversity, which are associated with tourism development. Importantly, plants cultivation strengthened the network modules' associations with TN and TP through

methanogenic archaea hub taxa, which might promote nitrogen and phosphorus cycles in wetlands (Zeng et al., 2021). These findings not only provide new insights into microbial interactions in response to tourism development, but also provide guidance for monitoring the wetland ecosystem stability.

Our findings reveal that tourism development significantly influences the overall structure and network topological properties of microbial communities in wetland sediments. This observation aligns with previous ecosystem studies (Li et al., 2022; Piano et al., 2023). Notably, both archaeal and bacterial ecological networks in LA exhibit lower complexity and stability. The same phenomenon was shown for the interdomain network complexity in LA compared to the results observed in the three functional areas. These changes in microbial community structure and interaction patterns partly explain this phenomenon (Deng et al., 2012). In LA, the growth and decay of macrophytes modify the surrounding environment, acting as a nutrient source for microbes (Mentes et al., 2018), and facilitating the colonization of functional bacteria. We observed a decrease in the relative abundance of *Actinobacteria*, whereas *Acidobacteria*, known for their adaptability to harsh environments (Ji et al., 2021), showed increased abundance under macrophyte coverage. If macrophytes are not timely harvested and managed, they contribute to nutrient enrichment through the decomposition of plant litter (Heilmayr, 2014; Wang et al., 2018). *Nitrospirae*, a phylum involved in nitrogen
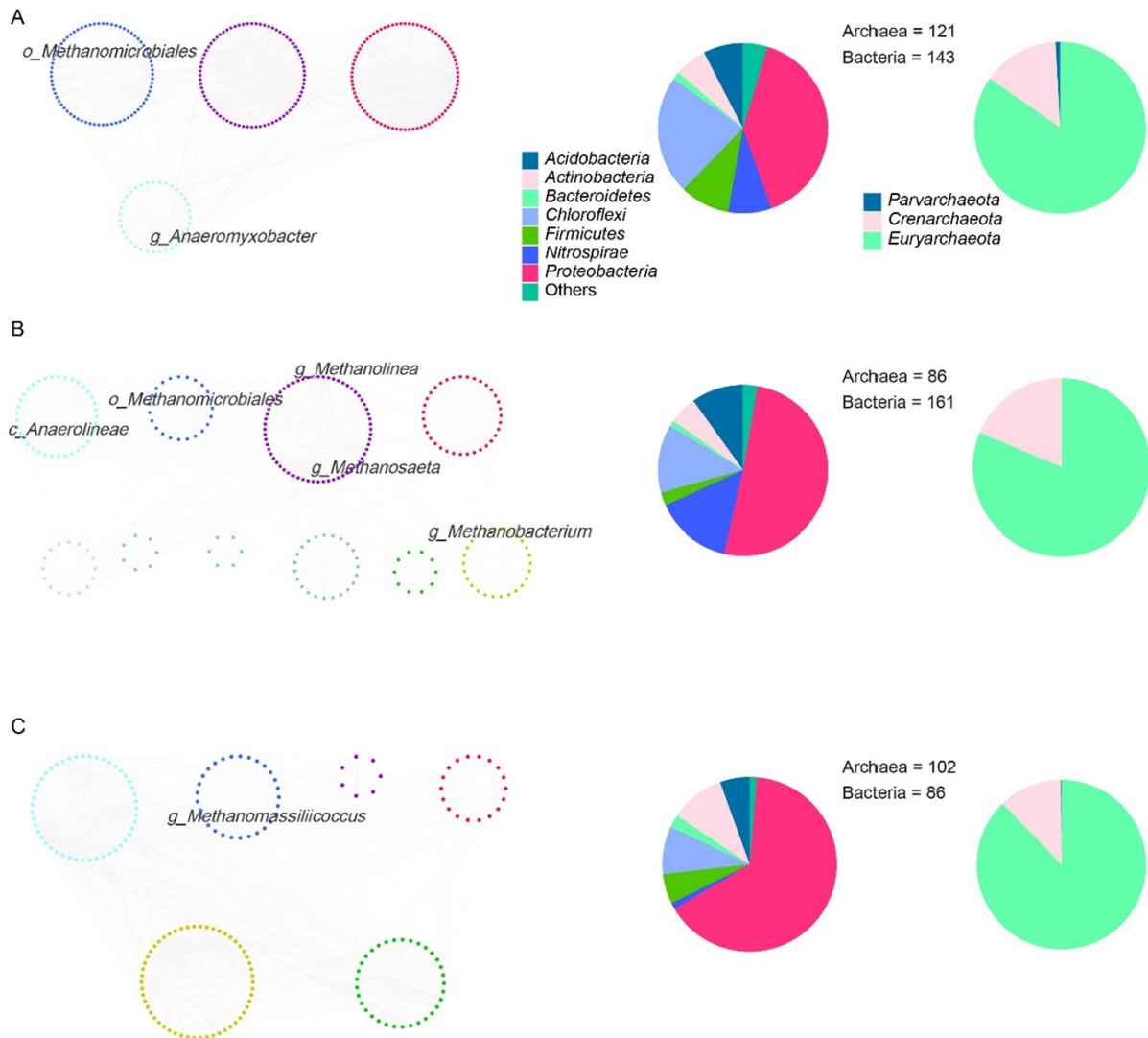
Fig. 3 The observed interdomain (archaea-bacteria) ecological networks for conservation areas (A), landscaping areas (B), and recreation area (C). Only large modules with ⩾5 nodes are shown in different colors. Relative abundances of bacterial and archaeal phyla within the corresponding networks were showed in each panel (right). Details of network topological attributes are listed in Supplementary Tables 2 and 3.

cycling, was prevalent in areas with plant coverage, aligning with previous studies (Pang et al., 2016; Wang et al., 2017; Yun et al., 2017). Furthermore, enhanced synergistic resource utilization among archaeal and bacterial taxa could result in altered ecological network characteristics (Spribille et al., 2016).

The keystone taxa of module hubs and network hubs are highly connected groups that considerably influence microbial community structure and interactions regardless of their abundance (Banerjee et al., 2018). In landscaping areas, we identified a notable presence of such hub taxa, including *Methanolinea, Methanosaeta and Methanobacterium* at the genus level. This prominence may be attributed to the anaerobic conditions created by plant litter, where these archaea thrive (Wang et al., 2023b; Zhu et al., 2023). However, this environment also leads to a reduction in non-

anaerobic bacteria that coexist with them, resulting in lower network complexity compared to other areas (Wang et al., 2021a). Environmental filtering serves as another pivotal mechanism shaping microbial interdomain interactions. Our study indicates that pH and TN are key drivers of microbial community dynamics, significantly impacting microbial ecological networks. An optimal level of pH and nitrogen is beneficial for microbial growth and metabolism (Sims et al., 2013; Kuypers et al., 2018). Our findings reveal that network connectivity is significantly influenced by pH levels. Low pH often leads to changes in selective pressure and niche adaptation, typically diminishing microbial diversity and, consequently, reducing network connectivity (Guo et al., 2022). Decreased node connectivity can lead to weakened network stability (Banerjee et al., 2019; Yuan et al., 2021a). Therefore, the observed decrease in the stability of microbial
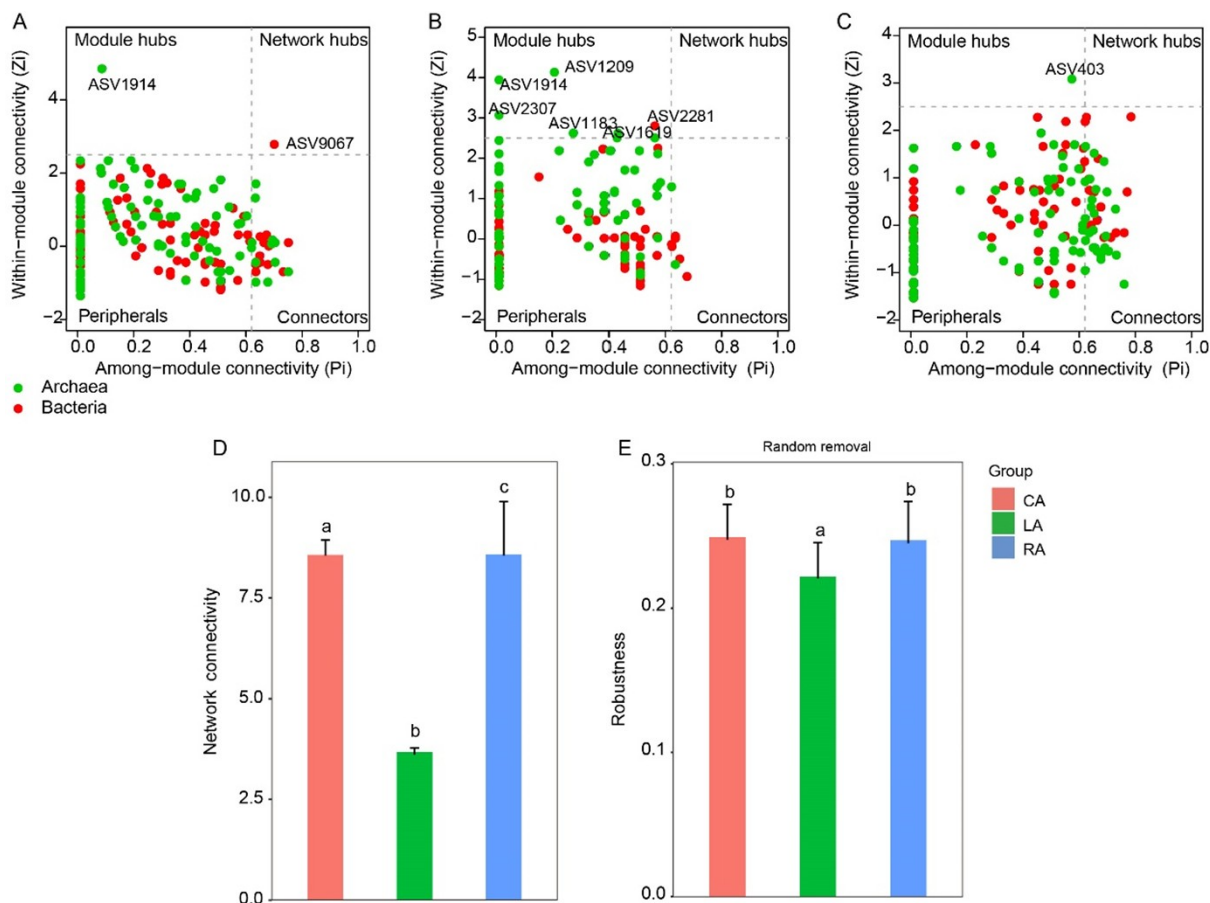
Fig. 4 Topological properties of interdomain ecological network. Node topologies (A−C), network connectivity (D). Network robustness as measured by the proportion of taxa that remain after 50% of the network nodes were randomly removed from each of the empirical molecular ecological networks (E). Different letters above the error bar indicate statistical difference among the three functional area ($P < 0.05$). Conservation areas, CA; Landscaping areas, LA; Recreation areas, RA.
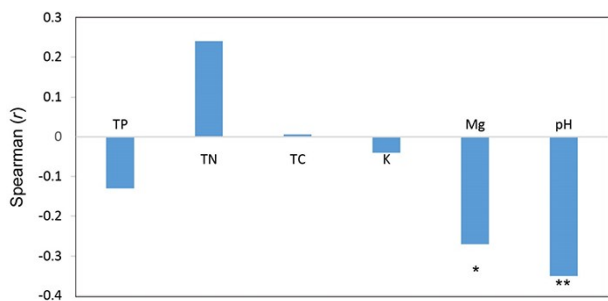

Fig. 5 Relationships between sediment physicochemical parameters and network connectivity. The correlation coefficient (r) is determined by Spearman. Significance: *, < 0.05, **, < 0.01.

communities in LA might be an adaptive response to macrophyte coverage.

Changes in interdomain interactions could further affect ecological nitrogen and phosphorus cycles. We found that the modules showed strong correlations with TN and TP under landscaping, suggesting that these taxa consume an amount of nutrient elements derived from decomposition products of plant litter. Specifically, aquatic plants contribute

organic matter and oxygen (through root exudates and photosynthesis), which enhances microbial activity. This heightened activity accelerates the decomposition of organic matter, thus expediting the nitrogen cycling process (Raza et al., 2023). Furthermore, aquatic plants increase the availability of substrates for nitrification and denitrification processes undertaken by microbial communities (Fu et al., 2020). Macrophyte debris and root exudates can serve as sources of organic nitrogen, fostering these microbial processes. The root zone of aquatic plants creates microenvironments with varying oxygen levels, influencing both aerobic (nitrification) and anaerobic (denitrification) nitrogen-transforming processes (Wu et al., 2021). As with nitrogen, aquatic plants affect microbial processes involved in phosphorus cycling, such as mineralization and immobilization (Zhang et al., 2023; Zhao et al., 2023).

Human activities, such as tourism development, significantly alter the construction and functionality of microbial communities (Boetius, 2019; Thackeray and Hampton, 2020). To our knowledge, research on the impacts of tourism development on microorganisms has primarily
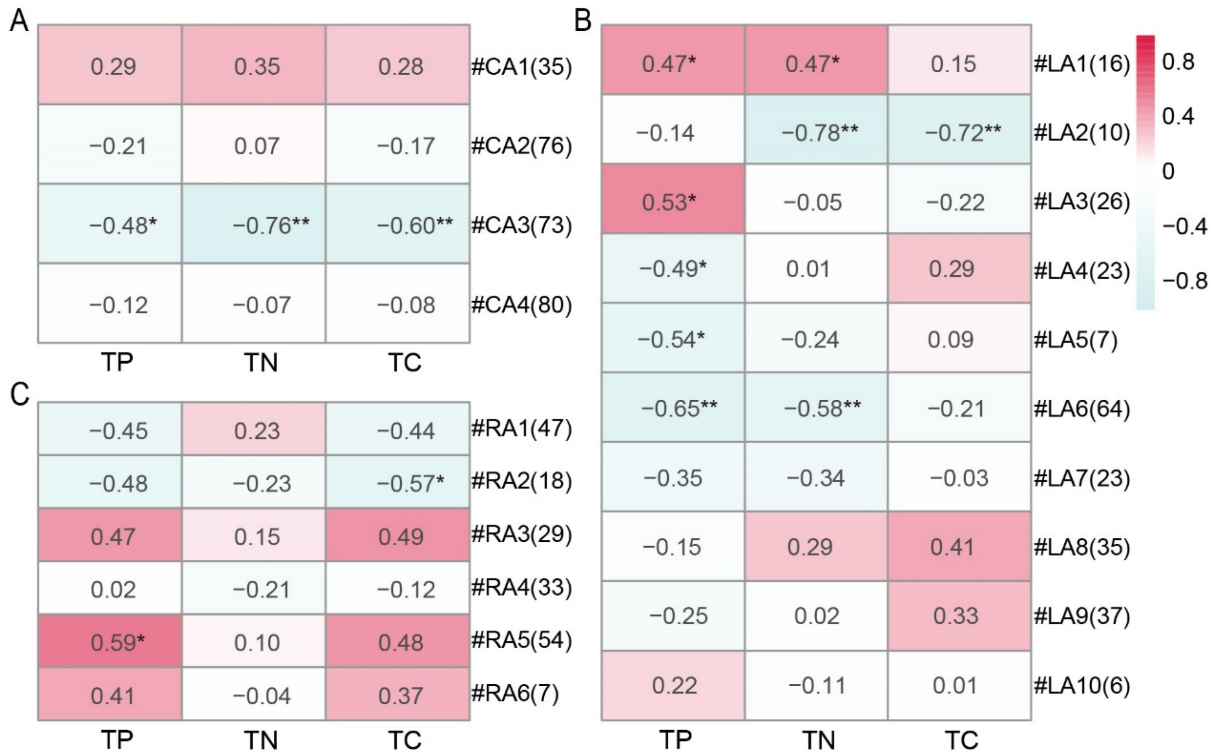
Fig. 6 Correlations between network module eigenvalues (excluding modules with < 5 nodes) and TP, TN and TC for conservation areas (A), landscaping areas (B), and recreation areas (C). The number in parentheses indicates the number of nodes in each module. Significance: *, < 0.05; **, < 0.01.
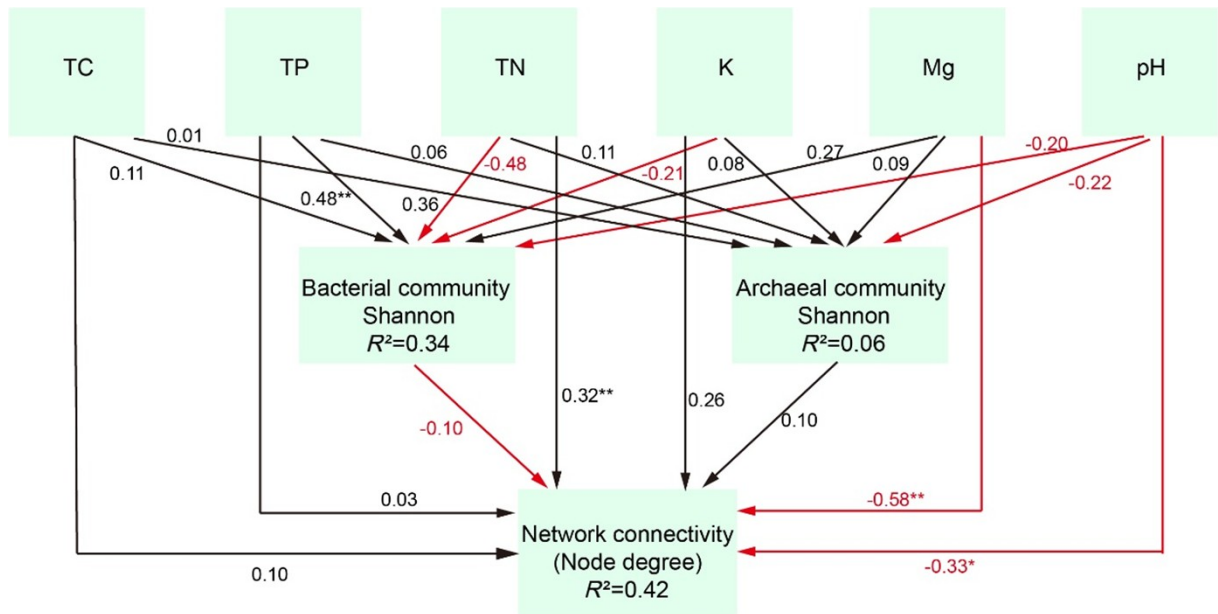

Fig. 7 Structural equation modelling showing significant relationships ($P < 0.01$) between sediment abiotic/biotic factors and microbial network complexity. R^2 values denote the amount of variance explained by the model for the response variables. The overall SEM model fit was satisfactory ($\chi^2 = 2.07$, $P = 0.15$; SRMR = 0.042)

focused on species abundance and diversity. However, there is a notable gap in research concerning the characteristics of microbial ecological networks, particularly interdomain networks. While many studies concentrate on single domain such as archaea, bacteria, or fungi (Li et al., 2021),

our study extends this scope by considering the influence of tourism development from an interdomain perspective. We discovered that the archaea-bacteria network characteristics respond significantly to tourism development, with marked changes observed from conservation areas to landscaping

areas to recreation areas. These changes can serve as indicators of broader ecosystem shifts to some extent. This insight is vital for effective wetland management, particularly in the context of long-term ecological monitoring (Haase et al., 2018; Sagova-Mareckova et al., 2021).

5 Conclusions

In summary, our research established that tourism development in urban wetlands impacts the structure and ecological functions of archaeal and bacterial communities. This impact leads to alterations in the topological properties of both intra-domain and inter-domain networks. We determined that 42% of the variance in the complexity of interdomain networks can be directly attributed to abiotic factors (TC, TP, TN, K, Mg, and pH) as well as biotic factors (bacterial and archaeal α-diversity). Changes of water environment caused by tourism development also influence microbial functions, particularly evident in the transition from conservation areas to landscaping areas. This transition amplifies the correlations between microbial network modules and sedimentary TN and TP, potentially enhancing the cycling of elements in wetlands. Our findings suggest that the construction and functional stability of microbial communities may be jeopardized by the tourism development.

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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.

Electronic supplementary material

Supplementary material is available in the online version of this article at https://doi.org/10.1007/s42832-024-0249-z and is accessible for authorized users.

References

Arif, M., Behzad, H.M., Tahir, M., Li, C.X., 2022. Nature-based tourism influences ecosystem functioning along waterways: Implications for conservation and management. Science of the Total Environment 842, 156935.

Arsić, S., Nikolić, D., Mihajlović, I., Fedajev, A., Živković, Ž., 2018. A new approach within ANP-SWOT framework for prioritization of ecosystem management and case study of National Park Djerdap, Serbia. Ecological Economics 146, 85–95.

Banerjee, S., Schlaeppi, K., Van Der Heijden, M.G.A., 2018. Keystone taxa as drivers of microbiome structure and functioning. Nature Reviews Microbiology 16, 567–576.

Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A.Y., Gattinger, A., Keller, T., Charles, R., Van Der Heijden, M.G.A., 2019. Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. The ISME Journal 13, 1722–1736.

Boetius, A., 2019. Global change microbiology-big questions about small life for our future. Nature Reviews Microbiology 17, 331–332.

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: High-resolution sample inference from Illumina amplicon data. Nature Methods 13, 581–583.

Chatterjee, K., Bandyopadhyay, A., Ghosh, A., Kar, S., 2015. Assessment of environmental factors causing wetland degradation, using Fuzzy Analytic Network Process: A case study on Keoladeo National Park, India. Ecological Modelling 316, 1–13.

Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., Van Den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260.

Coux, C., Rader, R., Bartomeus, I., Tylianakis, J.M., 2016. Linking species functional roles to their network roles. Ecology Letters 19, 762–770.

De Vries, F.T., Griffiths, R.I., Bailey, M., Craig, H., Girlanda, M., Gweon, H.S., Hallin, S., Kaisermann, A., Keith, A.M., Kretzschmar, M., Lemanceau, P., Lumini, E., Mason, K.E., Oliver, A., Ostle, N., Prosser, J.I., Thion, C., Thomson, B., Bardgett, R.D., 2018. Soil bacterial networks are less stable under drought than fungal networks. Nature Communications 9, 303.

Delgado-Baquerizo, M., Reith, F., Dennis, P.G., Hamonts, K., Powell, J.R., Young, A., Singh, B.K., Bissett, A., 2018. Ecological drivers of soil microbial diversity and soil biological networks in the Southern Hemisphere. Ecology 99, 583–596.

Deng, Y., Jiang, Y.H., Yang, Y.F., He, Z.L., Luo, F., Zhou, J.Z., 2012. Molecular ecological network analyses. BMC Bioinformatics 13, 113.

Faust, K., Raes, J., 2012. Microbial interactions: from networks to models. Nature Reviews Microbiology 10, 538–550.

Feng, K., Zhang, Y.G., He, Z.L., Ning, D.L., Deng, Y., 2019. Interdomain ecological networks between plants and microbes. Molecular Ecology Resources 19, 1565–1577.

Fu, G.P., Wu, J.F., Han, J.Y., Zhao, L., Chan, G., Leong, K., 2020. Effects of substrate type on denitrification efficiency and microbial community structure in constructed wetlands. Bioresource Technology 307, 123222.

Fuhrman, J.A., 2009. Microbial community structure and its functional implications. Nature 459, 193–199.

Guo, Y.P., Song, B., Li, A.Q., Wu, Q.L., Huang, H.L., Li, N., Yang, Y., Adams, J.M., Yang, L., 2022. Higher pH is associated with

enhanced co-occurrence network complexity, stability and nutrient cycling functions in the rice rhizosphere microbiome. Environmental Microbiology 24, 6200–6219.

Haase, P., Tonkin, J.D., Stoll, S., Burkhard, B., Frenzel, M., Geijzendorffer, I.R., Häuser, C., Klotz, S., Kühn, I., McDowell, W.H., Mirtl, M., Müller, F., Musche, M., Penner, J., Zacharias, S., Schmeller, D.S., 2018. The next generation of site-based long-term ecological monitoring: Linking essential biodiversity variables and ecosystem integrity. Science of the Total Environment 613–614, 1376–1384.

Heilmayr, R., 2014. Conservation through intensification? The effects of plantations on natural forests. Ecological Economics 105, 204–210.

Ji, M.K., Williams, T.J., Montgomery, K., Wong, H.L., Zaugg, J., Berengut, J.F., Bissett, A., Chuvochina, M., Hugenholtz, P., Ferrari, B.C., 2021. *Candidatus* eremiobacterota, a metabolically and phylogenetically diverse terrestrial phylum with acid-tolerant adaptations. The ISME Journal 15, 2692–2707.

Kiersztyn, B., Chróst, R., Kaliński, T., Siuda, W., Bukowska, A., Kowalczyk, G., Grabowska, K., 2019. Structural and functional microbial diversity along a eutrophication gradient of interconnected lakes undergoing anthropopressure. Scientific Reports 9, 11144.

Kuypers, M.M.M., Marchant, H.K., Kartal, B., 2018. The microbial nitrogen-cycling network. Nature Reviews Microbiology 16, 263–276.

Li, C., Hambright, K.D., Bowen, H.G., Trammell, M.A., Grossart, H.P., Burford, M.A., Hamilton, D.P., Jiang, H.L., Latour, D., Meyer, E.I., Padisák, J., Zamor, R.M., Krumholz, L.R., 2021. Global co-occurrence of methanogenic archaea and methanotrophic bacteria in *Microcystis* aggregates. Environmental Microbiology 23, 6503–6519.

Li, H.J., Chang, J.L., Liu, P.F., Fu, L., Ding, D.W., Lu, Y.H., 2015. Direct interspecies electron transfer accelerates syntrophic oxidation of butyrate in paddy soil enrichments. Environmental Microbiology 17, 1533–1547.

Li, Q.J., Dai, M.Q., Luo, F., 2022. Influence of tourism disturbance on soil microbial community structure in Dawei Mountain national forest park. Sustainability 14, 1162.

Louca, S., Polz, M.F., Mazel, F., Albright, M.B.N., Huber, J.A., O'Connor, M.I., Ackermann, M., Hahn, A.S., Srivastava, D.S., Crowe, S.A., Doebeli, M., Parfrey, L.W., 2018. Function and functional redundancy in microbial systems. Nature Ecology & Evolution 2, 936–943.

Mamet, S.D., Lamb, E.G., Piper, C.L., Winsley, T., Siciliano, S.D., 2017. Archaea and bacteria mediate the effects of native species root loss on fungi during plant invasion. The ISME Journal 11, 1261–1275.

Mamet, S.D., Redlick, E., Brabant, M., Lamb, E.G., Helgason, B.L., Stanley, K., Siciliano, S.D., 2019. Structural equation modeling of a winnowed soil microbiome identifies how invasive plants restructure microbial networks. The ISME Journal 13, 1988–1996.

Mandakovic, D., Rojas, C., Maldonado, J., Latorre, M., Travisany, D., Delage, E., Bihouée, A., Jean, G., Díaz, F.P., Fernández-Gómez, B., Cabrera, P., Gaete, A., Latorre, C., Gutiérrez, R.A., Maass, A., Cambiazo, V., Navarrete, S.A., Eveillard, D.,

González, M., 2018. Structure and co-occurrence patterns in microbial communities under acute environmental stress reveal ecological factors fostering resilience. Scientific Reports 8, 5875.

Mentes, A., Szabó, A., Somogyi, B., Vajna, B., Tugyi, N., Csitári, B., Vörös, L., Felföldi, T., 2018. Differences in planktonic microbial communities associated with three types of macrophyte stands in a shallow lake. FEMS Microbiology Ecology 94, fix164.

Mitsch, W.J., Cronk, J.K., Zhang, L., 2014. Creating a living laboratory on a college campus for wetland research–the olentangy river wetland research park, 1991–2012. Ecological Engineering 72, 1–10.

Montesinos-Navarro, A., Hiraldo, F., Tella, J.L., Blanco, G., 2017. Network structure embracing mutualism–antagonism continuums increases community robustness. Nature Ecology & Evolution 1, 1661–1669.

Nelson, C.E., Kelly, L.W., Haas, A.F., 2023. Microbial interactions with dissolved organic matter are central to coral reef ecosystem function and resilience. Annual Review of Marine Science 15, 431–460.

Pang, S., Zhang, S.H., Lv, X.Y., Han, B., Liu, K.H., Qiu, C.H., Wang, C., Wang, P.F., Toland, H., He, Z.L., 2016. Characterization of bacterial community in biofilm and sediments of wetlands dominated by aquatic macrophytes. Ecological Engineering 97, 242–250.

Peter, H., Sommaruga, R., 2016. Shifts in diversity and function of lake bacterial communities upon glacier retreat. The ISME Journal 10, 1545–1554.

Piano, E., Biagioli, F., Nicolosi, G., Coleine, C., Poli, A., Prigione, V., Zanellati, A., Addesso, R., Varese, G.C., Selbmann, L., Isaia, M., 2023. Tourism affects microbial assemblages in show caves. Science of the Total Environment 871, 162106.

R Development Core Team, 2014. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Raza, T., Qadir, M.F., Khan, K.S., Eash, N.S., Yousuf, M., Chatterjee, S., Manzoor, R., Rehman, S.U., Oetting, J.N., 2023. Unrevealing the potential of microbes in decomposition of organic matter and release of carbon in the ecosystem. Journal of Environmental Management 344, 118529.

Russi, D., Brink, P.T., Farmer, A., Badura, T., Coates, D., Förster, J., Kumar, R., Davidson, N., 2013. The economics of ecosystems and biodiversity for water and wetlands. IEEP, London and Brussels, 78.

Sagova-Mareckova, M., Boenigk, J., Bouchez, A., Cermakova, K., Chonova, T., Cordier, T., Eisendle, U., Elersek, T., Fazi, S., Fleituch, T., Frühe, L., Gajdosova, M., Graupner, N., Haegerbaeumer, A., Kelly, A.M., Kopecky, J., Leese, F., Nõges, P., Orlic, S., Panksep, K., Pawlowski, J., Petrusek, A., Piggott, J.J., Rusch, J.C., Salis, R., Schenk, J., Simek, K., Stovicek, A., Strand, D.A., Vasquez, M.I., Vrålstad, T., Zlatkovic, S., Zupancic, M., Stoeck, T., 2021. Expanding ecological assessment by integrating microorganisms into routine freshwater biomonitoring. Water Research 191, 116767.

Sanna, S., Eja, P., 2017. Recreational cultural ecosystem services: How do people describe the value? Ecosystem Services 26, 1–9.

Sims, A., Zhang, Y.Y., Gajaraj, S., Brown, P.B., Hu, Z.Q., 2013. Toward the development of microbial indicators for wetland assessment. Water Research 47, 1711–1725.

Spribille, T., Tuovinen, V., Resl, P., Vanderpool, D., Wolinski, H., Aime, M.C., Schneider, K., Stabentheiner, E., Toome-Heller, M., Thor, G., Mayrhofer, H., Johannesson, H., Mccutcheon, J.P., 2016. Basidiomycete yeasts in the cortex of ascomycete macrolichens. Science 353, 488–492.

Sun, P., Wang, Y., Huang, X., Huang, B.Q., Wang, L., 2022. Water masses and their associated temperature and cross-domain biotic factors co-shape upwelling microbial communities. Water Research 215, 118274.

Thackeray, S.J., Hampton, S.E., 2020. The case for research integration, from genomics to remote sensing, to understand biodiversity change and functional dynamics in the world's lakes. Global Change Biology 26, 3230–3240.

Tromas, N., Fortin, N., Bedrani, L., Terrat, Y., Cardoso, P., Bird, D., Greer, C.W., Shapiro, B.J., 2017. Characterising and predicting cyanobacterial blooms in an 8-year amplicon sequencing time course. The ISME Journal 11, 1746–1763.

Wagg, C., Schlaeppi, K., Banerjee, S., Kuramae, E.E., van der Heijden, M.G.A., 2019. Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. Nature Communications 10, 4841.

Wahlroos, O., Valkama, P., Mäkinen, E., Ojala, A., Vasander, H., Väänänen, V.M., Halonen, A., Lindén, L., Nummi, P., Ahponen, H., Lahti, K., Vessman, T., Rantakokko, K., Nikinmaa, E., 2015. Urban wetland parks in Finland: improving water quality and creating endangered habitats. International Journal of Biodiversity Science, Ecosystem Services & Management 11, 46–60.

Wan, Y., Ruan, X.H., Zhang, Y.P., Li, R.F., 2017. Illumina sequencing-based analysis of sediment bacteria community in different trophic status freshwater lakes. MicrobiologyOpen 6, e00450.

Wang, B.H., Ma, B., Stirling, E., He, Z.L., Zhang, H.J., Yan, Q.Y., 2023a. Freshwater trophic status mediates microbial community assembly and interdomain network complexity. Environmental Pollution 316, 120690.

Wang, B.H., Stirling, E., He, Z.L., Ma, B., Zhang, H.J., Zheng, X.F., Xiao, F.S., Yan, Q.Y., 2021a. Pollution alters methanogenic and methanotrophic communities and increases dissolved methane in small ponds. Science of the Total Environment 801, 149723.

Wang, B.H., Zheng, X.F., Zhang, H.J., Xiao, F.S., Gu, H., Zhang, K.K., He, Z.L., Liu, X., Yan, Q.Y., 2020a. Bacterial community responses to tourism development in the Xixi National Wetland Park, China. Science of the Total Environment 720, 137570.

Wang, B.H., Zheng, X.F., Zhang, H.J., Xiao, F.S., He, Z.L., Yan, Q.Y., 2020b. Keystone taxa of water microbiome respond to environmental quality and predict water contamination. Environmental Research 187, 109666.

Wang, B.H., Zheng, X.F., Zhang, H.J., Yu, X.L., Lian, Y.L., Yang, X.Q., Yu, H., Hu, R.W., He, Z.L., Xiao, F.S., Yan, Q.Y., 2021b. Metagenomic insights into the effects of submerged plants on functional potential of microbial communities in wetland sediments. Marine Life Science & Technology 3, 405–415.

Wang, C., Liu, S.Y., Zhang, Y., Liu, B.Y., He, F., Xu, D., Zhou, Q.H., Wu, Z.B., 2018. Bacterial communities and their predicted func-

tions explain the sediment nitrogen changes along with submerged macrophyte restoration. Microbial Ecology 76, 625–636.

Wang, C., Liu, S.Y., Zhang, Y., Liu, B.Y., Zeng, L., He, F., Zhou, Q.H., Wu, Z.B., 2017. Effects of planted versus naturally growing Vallisneria natans on the sediment microbial community in west lake, China. Microbial Ecology 74, 278–288.

Wang, T., Zhumabieke, M., Zhang, N., Liu, C., Zhong, J.C., Liao, Q.J.H., Zhang, L., 2023b. Variable promotion of algae and macrophyte organic matter on methanogenesis in anaerobic lake sediment. Environmental Research 237, 116922.

Wu, H.P., Hao, B.B., Cai, Y.P., Liu, G.H., Xing, W., 2021. Effects of submerged vegetation on sediment nitrogen-cycling bacterial communities in Honghu Lake (China). Science of the Total Environment 755, 142541.

Wu, H.P., Zeng, G.M., Liang, J., Chen, J., Xu, J.J., Dai, J., Li, X.D., Chen, M., Xu, P., Zhou, Y.Y., Li, F., Hu, L., Wan, J., 2016. Responses of bacterial community and functional marker genes of nitrogen cycling to biochar, compost and combined amendments in soil. Applied Microbiology and Biotechnology 100, 8583–8591.

Wu, H.P., Zeng, G.M., Liang, J., Guo, S.L., Dai, J., Lu, L.H., Wei, Z., Xu, P., Li, F., Yuan, Y.J., He, X.X., 2015. Effect of early dry season induced by the Three Gorges Dam on the soil microbial biomass and bacterial community structure in the Dongting Lake wetland. Ecological Indicators 53, 129–136.

Xue, P.P., Minasny, B., McBratney, A.B., 2022. Land-use affects soil microbial co-occurrence networks and their putative functions. Applied Soil Ecology 169, 104184.

Yu, X.F., E, M.J., Sun, M.Y., Xue, Z.S., Lu, X.G., Jiang, M., Zou, Y.C., 2018. Wetland recreational agriculture: Balancing wetland conservation and agro-development. Environmental Science & Policy 87, 11–17.

Yuan, M.M., Guo, X., Wu, L.W., Zhang, Y., Xiao, N.J., Ning, D.L., Shi, Z., Zhou, X.S., Wu, L.Y., Yang, Y.F., Tiedje, J.M., Zhou, J.Z., 2021a. Climate warming enhances microbial network complexity and stability. Nature Climate Change 11, 343–348.

Yuan, M.M., Kakouridis, A., Starr, E., Nguyen, N., Shi, S.J., Pett-Ridge, J., Nuccio, E., Zhou, J.Z., Firestone, M., 2021b. Fungal-bacterial cooccurrence patterns differ between arbuscular mycorrhizal fungi and nonmycorrhizal fungi across soil niches. mBio 12, e03509–20.

Yun, J.L., Deng, Y.C., Zhang, H.X., 2017. Anthropogenic protection alters the microbiome in intertidal mangrove wetlands in Hainan Island. Applied Microbiology and Biotechnology 101, 6241–6252.

Zeng, L.P., Dai, Y., Zhang, X.M., Man, Y., Tai, Y.P., Yang, Y., Tao, R., 2021. Keystone species and niche differentiation promote microbial N, P, and COD removal in pilot scale constructed wetlands treating domestic sewage. Environmental Science & Technology 55, 12652–12663.

Zhan, P.F., Liu, Y.S., Wang, H.C., Wang, C.L., Xia, M., Wang, N., Cui, W.Z., Xiao, D.R., Wang, H., 2021. Plant litter decomposition in wetlands is closely associated with phyllospheric fungi as revealed by microbial community dynamics and co-occurrence network. Science of the Total Environment 753, 142194.

Zhang, C., Nie, S., Liang, J., Zeng, G.M., Wu, H.P., Hua, S.S., Liu, J.Y., Yuan, Y.J., Xiao, H.B., Deng, L.J., Xiang, H.Y., 2016. Effects

of heavy metals and soil physicochemical properties on wetland soil microbial biomass and bacterial community structure. Science of the Total Environment 557–558, 785–790.

Zhang, Z.Q., Yu, H.W., Tao, M., Lv, T., Li, D.X., Yu, D., Liu, C.H., 2023. Shifting enzyme activity and microbial composition in sediment coregulate the structure of an aquatic plant community under polyethylene microplastic exposure. Science of the Total Environment 901, 166497.

Zhao, J.S., Yang, P., Lin, Y.Y., Zhu, X.Y., Wang, J.X., Gan, X.Y., Zheng, X.Y., Zhao, M., Fan, C.Z., Du, L.N., Miu, H.Y., 2023. The effect of underwater supplemental light on the growth of *V.spinulosa Yan* and the restoration process of water. Process Safety and Environmental Protection 169, 328–336.

Zhou, L., Zhou, Y.Q., Tang, X.M., Zhang, Y.L., Zhu, G.W., Székely, A.J., Jeppesen, E., 2021a. Eutrophication alters bacterial co-occurrence networks and increases the importance of chro-mophoric dissolved organic matter composition. Limnology and Oceanography 66, 2319–2332.

Zhou, Y.Q., Sun, B.Y., Xie, B.H., Feng, K., Zhang, Z.J., Zhang, Z., Li, S.Z., Du, X.F., Zhang, Q., Gu, S.S., Song, W., Wang, L.L., Xia, J.Y., Han, G.X., Deng, Y., 2021b. Warming reshaped the microbial hierarchical interactions. Global Change Biology 27, 6331–6347.

Zhu, J.L., Li, Y.H., Huang, M.H., Xu, D., Zhang, Y., Zhou, Q.H., Wu, Z.B., Wang, C., 2023. Restoration effects of submerged macro-phytes on methane production and oxidation potential of lake sediments. Science of the Total Environment 866, 161218.