Interactome-based abiotic and biotic impacts on biodiversity of plankton communities in disturbed wetlands

Yuzhan Yang | Yangchun Gao | Yiyong Chen | Shiguo Li | Aibin Zhan

Aim: Despite great efforts for conservation, biodiversity in wetland ecosystems is still losing at an alarming rate. Thus, it is crucial to deeply understand ecological processes and mechanisms that potentially affect the loss of biodiversity.

Location: Sanjiang wetland in Sanjiang floodplain, north-east China.

Methods: Biological samples and environmental data were collected from five approximate habitats under different anthropogenic disturbance levels from Sanjiang wetland. Biodiversity of plankton communities (i.e., bacterioplankton and zooplankton) was characterized by high-throughput sequencing-based metabarcoding. Multidisciplinary methods including interactome-based construction of scale-free networks were employed to examine the complex biotic interactions and abiotic influence on plankton biodiversity.

Results: Both environmental variables and community composition of plankton communities varied significantly among five habitats. Environmental filtering was identified as the dominant ecological process that drove the distinct community composition and geographical distribution of biodiversity. However, the significantly influential factors were different for bacterioplankton (e.g., pH and As) and zooplankton communities (e.g., NH\textsubscript{4} and TP). In total, environmental factors could explain approximately 30% of community variation for both types of plankton communities. Based on interactome networks, more organism-associated edges were identified than environment-associated edges. Such a pattern suggests that, in addition to environmental influence, biotic interactions also play a crucial role to shape biodiversity variation.

Main conclusions: Both abiotic factors and biotic interactions largely contributed to the distinct composition and geographical distribution of bacterioplankton and zooplankton communities in Sanjiang wetland. Therefore, the interactome-based investigation is recommended to examine synthesized impacts of abiotic and biotic variables, and such a comprehensive survey can largely facilitate our understanding of ecological processes and associated mechanisms that drive the loss of wetland biodiversity. Results from comprehensive surveys can help identify conservation priorities and improve the predictability of conservation programmes.

KEYWORDS
biodiversity, conservation, interactome, plankton communities, water pollution, wetland
INTRODUCTION

Benefiting from the high productivity and distinct hydrological features, wetlands are considered as one of the most productive ecosystems on the Earth (Gibbs, 2000; Tockner & Stanford, 2002). With less than 3% of the Earth’s surface, wetlands provide habitats for ~20% of known species and contribute more than 40% of the ecosystem services globally (Fang et al., 2006; Finlayson, Davidson, Spiers, & Stevenson, 1999; Zedler & Kercher, 2005). It has been widely acknowledged that the high biodiversity is essential to support and maintain ecosystem services and functioning of wetlands (Fang et al., 2006; Meli, Benayas, Balvanera, & Ramos, 2014; Myers, 1996). However, biodiversity in wetlands, as well as wetland itself, is losing at an unprecedented rate, mainly due to a wide variety of anthropogenic disturbances (An et al., 2007; Erwin, 2009; Hu, Niu, Chen, Li, & Zhang, 2017; Zedler, 2000). Since 1900, 64%-71% of the world’s wetlands have been lost, with a much faster rate during the 20th and early 21st centuries (Davidson, 2014). As a result, severe loss of biodiversity has been reported along with the rapid degradation and loss of wetlands (Davidson, 2014; Fang et al., 2006; Gibbs, 2000). Therefore, effective strategies are urgently needed to conserve and restore wetlands, particularly biodiversity in wetlands.

One crucial prerequisite for conservation is to understand crucial ecological processes, as well as influential factors, that drive the degradation and loss of wetland biodiversity (Chaparro, Horváth, O’Farrell, Ptacnik, & Hein, 2018; Xu et al., 2019). However, most studies focused on the identification of environmental stressors underlying the degradation and loss of wetlands, while paid limited attention to factors that were associated with biodiversity (Meli et al., 2014; Meng et al., 2017). Although threats faced by wetlands could (in)directly affect biodiversity, the investigation of major ecological processes and associated mechanisms has been highly obstructed by complex species-environment and species-species interactions (Bortolotti, Vinebrooke, & Louis, 2016; Mensing, Galatowitsch, & Tester, 1998; Soininen, Kokocinski, Estlander, Kotanen, & Heino, 2007). Such a challenge is further complicated by the increasing anthropogenic disturbances, which could lead to severe fragmentation and excessive heterogeneity of habitats at fine geographical scales, even before significant patterns of large-scale wetland transformation are observed (Fang et al., 2006; Gibbs, 2000; Wang, Fraser, & Chen, 2017; Yang, Deng, & Cao, 2016). All of these challenges call for attention towards the understanding of mechanisms that affect biodiversity in wetlands. As recommended by Zedler (2000), community succession theories can effectively guide practical biodiversity restoration. Thus, comprehensive investigation of factors that influence community succession would benefit the understanding of biodiversity loss, identifying conservation priorities and improving the predictability of conservation programmes.

A majority of literature have documented the influence of environmental factors on wetland biodiversity, such as nutrient enrichment derived from human activities (Fang et al., 2006; Hu et al., 2017; Meng et al., 2017; Tockner, Pushc, Borchardt, & Lorang, 2010). However, recent studies suggest that abiotic impacts alone seem insufficient to explain the biodiversity variation, emphasizing the necessity to investigate biotic impacts (e.g., inter- and intraspecific interactions; Lima-Mendez et al., 2015). Indeed, biodiversity is a combination of biological entities and processes, rather than a simple collection of individual species (Jordan, 2016; Wang & Brose, 2018). Species in a community are involved by a myriad of complex interactions, in the form of predation, competition, mutualism, symbiosis, parasitism and others (Jordan, 2016; Zhou et al., 2010). Thus, species interactions form the architecture of biodiversity and determine ecosystem functioning (Bartomeus et al., 2016). Regarding the high biodiversity in wetland ecosystems, it is reasonable to speculate the existence of highly complex inter- and intraspecific interactions. However, previous studies of wetland biodiversity mainly focused on one single group or several separated groups, while rarely considering biotic interactions (Zhang et al., 2018). One important reason is the impediment to characterize and analyse the complex interactions. Fortunately, with the development of multi-omic techniques and bioinformatic methods, the interactome-based methods have allowed to discover complex species interactions (Bartomeus et al., 2016; Faust, Lahti, Gonze, De Vos, & Raes, 2015). Based on the interactome concept, the complexity of interactions could be well represented and modelled as networks (Layeghifard, Hwang, & Gutman, 2017). A key feature of network theory is that the architectural features of networks appear to be universal to most complex systems (i.e., scale-free), thus paving the way to develop and characterize networks involving both biological and non-biological components (Layeghifard et al., 2017). Henceforth, interactome-based methods have proven to be useful in resolving the succession dynamics of microbiome systems or the marine plankton communities (mainly zooplankton and phytoplankton; Guidi et al., 2016; Layeghifard et al., 2017; Lima-Mendez et al., 2015).

Sanjiang wetland is a promising ecosystem to investigate the biotic interactions and abiotic impacts on biodiversity in wetlands. Sanjiang wetland is located at the Sanjiang floodplain in north-east China, covering an area of 108,900 km². Sanjiang Plain is formed by inundation and exposure of three large rivers—Wusuli, Songhua and Heilong Rivers, and thus providing highly diverse types of habitats. A rich biota has been recorded in Sanjiang wetland, especially endangered and vulnerable waterbirds such as Oriental Stork (Wang et al., 2015). Similar to many wetlands, Sanjiang wetland has been severely degraded and lost, especially in the past few decades. It has been estimated that about 70% of natural wetlands were lost from 1976 to 2005, with more than 90% of area being transformed to croplands (Song et al., 2014). The degradation and loss of wetlands have resulted in the shrinkage of suitable habitats and significant decline of biodiversity (Wang et al., 2015, 2011). In order to facilitate restoration and conservation programmes by the Chinese government (Lu et al., 2016), it is urgent to improve the understanding of processes and mechanisms responsible for biodiversity variability, especially under the severe pressure of anthropogenic disturbances.
In this study, we sampled two types of plankton communities (i.e., bacterioplankton and zooplankton) to investigate the composition and geographical distribution patterns of biodiversity and associated mechanisms responsible for observed patterns in Sanjiang wetland. These plankton communities were chosen as they play vital roles in wetland energy flow, material cycle and ecosystem functioning (Jansson, Andersson, Berggren, & Leonardson, 1994; Soininen et al., 2007). We sampled five locations with different levels of anthropogenic disturbances and habitat types. We characterized the biodiversity of plankton communities by high-throughput sequencing-based metabarcoding and analysed the complex biological interactions based on the interactome concept. We aimed to answer three questions: (a) Would the biodiversity of plankton communities show variability in respect to different habitats at fine geographical scales? (b) What factors drove the variability of community structure and spatial patterns of biodiversity within and among habitats? (c) What was the contribution of biotic and abiotic factors to the observed patterns?

2 | METHODS

2.1 | Collection of biological samples and measurement of physicochemical variables

Samples of bacterioplankton and zooplankton were collected from five habitats in Sanjiang wetland (Figure 1), including one marsh Wetland habitat (MW), one lacustrine Wetland habitat (LW), one paddy Wetland habitat (PW) and two riparian Wetland (RW) habitats. The LW habitat is located at the core area of Sanjiang Wetland National Nature Reserve and is better protected than the other habitats (Zhang et al., 2011). The PW habitat has recently been restored to wetland after decades of agricultural farming. In total, 28 sites were collected, including four, five, five and seven sites in MW, LW, PW, RW1 and RW2, respectively. Geographical location of each site was recorded using a Handheld Garmin GPS Navigator. A total of 500 ml water was collected at each site and filtered through a 0.22-μm membrane to collect microbe cells. Membranes were stored at −80°C until further analyses. A total of 60 L water was filtered through a 35-μm-mesh net to collect zooplankton samples, and all collected animals were immediately preserved in 100% alcohol with a final volume of 100 ml. Another 500 ml water was collected for water physicochemical analysis. Water and biological samples were stored at 4°C before further analyses.

In the field, water quality parameters were measured, including water temperature (T), electric conductivity (EC), pH, oxidation–reduction potential (ORP) and total dissolved solids (TDS) using a multi-parameter water quality sonde (MYRON Company, USA). Dissolved oxygen (DO) and concentration of chlorophyll a (Chl_a) were measured using a portable dissolved oxygen meter (Hach Company, USA) and a Handheld Fluorometer (Turner Designs, USA), respectively. The alkaline potassium persulfate digestion-based UV spectrophotometry, Nessler’s reagent-based spectrophotometry and differential UV spectrophotometry were employed to measure total nitrogen (TN), ammonia (NH₄⁺) and nitrate (NO₃⁻), respectively. The potassium persulfate digestion-based UV spectrophotometry and ammonium molybdate-based spectrophotometry were employed to measure total phosphorous (TP) and soluble reactive phosphorous (SRP). Water samples were pre-processed with digestion kit (HACH Company, USA) and measured using UV spectrophotometry to calculate the concentration of chemical oxygen demand (COD). The concentration of total organic carbon (TOC) was measured using Shimadzu-TC (Shimadzu, Japan). Concentration of potassium (K), calcium (Ca), sodium (Na) and magnesium (Mg) was measured
using the inductively coupled plasma optical emission spectrometry. Concentration of chromium (Cr), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), arsenic (As) and lead (Pb) was measured using the inductively coupled plasma mass spectrometry. These methods of measurement followed the recommendations of Xiong et al. (2016).

2.2 DNA extraction, PCR amplification and high-throughput sequencing

A modified CTAB extraction protocol was employed to extract total genomic DNA of bacteria (Huang et al., 2009; Yang et al., 2016). DNA extracts were then used as PCR templates to amplify the hypervariable V4 region of 16S rDNA with the primer pair of 515F (GTGCCAGCMGCGCGGTAA) and 806R (GGACTACHVGGGTWTCTAAT; Caporaso et al., 2011). Primers were modified with an addition of 12-nucleotide tag at the 5′-end to distinguish samples. The PCR amplification program was 4 min of denaturation at 94°C, 35 cycles of 45 s at 50°C and 90 s at 72°C, followed by a final elongation for 10 min at 72°C. The high-throughput sequencing was performed using the Illumina Miseq PE250 platform.

Total genomic DNA of zooplankton was extracted using the DNeasy Blood and Tissue Kit (Qiagen). DNA extracts were then used as PCR templates to amplify the V4 region of 18S rDNA with the primer pair of Uni18S/Uni18SR, which was specifically designed for zooplankton communities (Zhan et al., 2013). Primer for each sample was labelled with an addition of a unique eight nucleotide tag at the 5′-end to allow pooling all samples together. The PCR amplification program was 5 min of denaturation at 95°C, 35 cycles of 30 s at 95°C, 45 s at 50°C and 90 s at 72°C, followed by a final elongation for 10 min at 72°C. The high-throughput sequencing was performed using the Illumina Miseq PE300 platform.

2.3 Bioinformatics analyses

Raw data of bacterioplankton were sorted into independent files based on unique tags. Paired-end reads were merged before trimming tags and primers. We discarded low-quality sequences: (a) containing "N"s (undetermined nucleotides); (b) with quality score less than 20 (<Q20); and (c) with length shorter than 200 bp (Yang et al., 2016, 2019). Filtered sequences were clustered into operational taxonomic units (OTUs) at the similarity threshold of 97% using UPARSE pipeline (Edgar, 2013). Using Ribosomal Database Project (RDP) classifier, taxonomic assignment of representative sequences was obtained by searching against the SILVA_128 database at the 85% confidence level (Wang, Garrity, Tiedje, & Cole, 2007). OTUs classified as unknown, archaea and mitochondria were removed from further analyses. To improve normality of sequence data, the OTU table was rarefied down to 19,626 sequences per sample according to the smallest value of total number of sequences. All analyses were conducted using the in-house pipeline Galaxy (http://mem.rccees.ac.cn:8080/root; Feng et al., 2017).

Raw data of zooplankton were processed using the UPARSE algorithm embedded in USEARCH (Edgar, 2010, 2013). Artificial primers and tags were trimmed with Python scripts. We removed sequences: (a) that contained any undetermined nucleotides ("N"s); (b) with quality score lower than 20 (<Q20); and (c) that had the maximum expected error threshold lower than 0.75 (Yang et al., 2016, 2018). Filtered sequences were trimmed to the same length of 225 bp based on the recommendation of Xiong et al. (2017). OTUs were clustered at a similarity threshold of 97% with de-replicated sequences (Xiong & Zhan, 2018; Zhan, Bailey, Heath, & MacIsaac, 2014). By searching against the online nucleotide database of GenBank, taxonomic information of OTUs was obtained. All OTUs and representative sequences were filtered with parameters of e-value < 10^{-10}, minimum query coverage > 80% and similarity > 85% (Zhan et al., 2014). OTUs assigned as metazoan zooplankton were kept for further analyses. For both bacterioplankton and zooplankton, the number of sequences in each OTU was taken as the abundance of OTUs (Zhan et al., 2014).

2.4 Statistical analyses

All the following analyses were performed using R (R Core Team, 2018). Three indices of a-diversity were calculated, namely Shannon index, inverse Simpson index and observed number of OTUs. The variation of community structure in five habitats was compared using analysis of similarity (ANOSIM) and illustrated by non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis distance. The variation of all environmental variables in five habitats was also compared using ANOSIM and illustrated by NMDS based on Euclidean distance. Prior to statistical analyses, environmental variables, except pH, were log_{10}(x + 1) transformed to improve normality and homoscedasticity. To explore the correlation between community dynamics and environmental variables, Mantel test was conducted to select variables which were significantly correlated with community variation. Redundancy analysis (RDA) was conducted to further explore the influence of selected environmental variables on community composition. In addition, forward selection was performed to select relatively more important variables to build a parsimonious RDA model (Blanchet, Legendre, & Borcard, 2008). Spearman’s rank correlation analysis was conducted to further verify the influence of the crucial variables on OTUs which exhibited a high correlation with the first two axes of RDA (i.e., high-fitness OTUs).

2.5 Construction and analysis of co-occurrence networks

To illuminate the relationships between bacterioplankton, zooplankton and environmental variables, a full phylogenetic molecular ecological network (pMEN) was constructed (Deng et al., 2012; Zhou et al., 2010; Zhou, Deng, Luo, He, & Yang, 2011). This method uses the random matrix theory (RMT) to identify the appropriate similarity threshold automatically before network construction. For both communities, only OTUs appearing in >50% of the total samples were used for network computation (Deng et al., 2012; Zhou et al., 2010). The relative abundance of OTUs and environmental variables was log_{10} transformed, and missing values were filled with a very small number (0.01) if paired valid values were available. A symmetric correlation
matrix was calculated by the Spearman’s correlation coefficient. Only the similarity values above a certain threshold were remained for calculating matrix eigenvalues. Random network was generated by a randomization procedure with 100 permutations to evaluate whether or not the constructed network was random (Deng et al., 2012). In the network, positive associations indicate interspecies cross-feeding, co-aggregation or niche overlapping, whereas negative associations suggest competition, or niche portioning and/or resistance to be grazed (Bartomeus et al., 2016; Faust & Raes, 2012). The construction and analysis of network were performed using the pipeline MENA (http://ieg4.rccc.ou.edu/mena; Deng et al., 2012). The statistical results of associations (edges) between bacterioplankton and zooplankton were visualized with the online version of Circos (Krzywinski et al., 2009).

3 | RESULTS

3.1 | Alpha diversity and taxonomic composition of plankton communities

High-throughput sequencing of bacterioplankton community yielded 1,362,628 high-quality sequences, resulting in 7,403 OTUs. Rarefaction curves indicated that current sequencing depth was sufficient to capture most biodiversity (Figure S1a). No significant variation was observed for three $\alpha$-diversity indices across all five habitats (Figure 2a–c). At all sites, the dominant phyla of bacterioplankton were Proteobacteria (Betaproteobacteria [30.96%], Alphaproteobacteria [15.24%], Gammaproteobacteria [4.26%] and Deltaproteobacteria [0.97%]), Actinobacteria (15.79%) and Bacteroidetes (13.86%). Geographical distribution of the observed phyla or classes was uneven in five habitats (Figure 3a). For example, the abundance of Betaproteobacteria was higher in PW and RW2 than that in other habitats, while the abundance of Bacteroidetes was higher in MW, LW and PW than that in other habitats. The abundance of Planctomycetes was highest in MW, and the abundance of Cyanobacteria was lowest in PW. Geographical distribution of lower rank taxa was also uneven in five locations, such as at the family level (Figure S2a). For example, the abundance of Burkholderiaceae (Betaproteobacteria) was higher in PW and RW2 when compared to the other habitats, while the abundance of Chitinophagaceae (Bacteroidetes) was higher in MW and PW than that in the other habitats.

High-throughput sequencing yielded 1,109,762 high-quality sequences, resulting in 438 OTUs for metazoan zooplankton. Most samples reached the saturation stage, implying that current sequencing depth was sufficient to capture most biodiversity (Figure S1b). Similarly to bacterioplankton, no significant variation was observed for three $\alpha$-diversity indices across all five habitats (Figure 2d-f). At

![Figure 2](image-url)

**Figure 2** Alpha diversity of bacterioplankton (a–c) and zooplankton (d–f) communities. LW, lacustrine wetland; MW, marsh wetland; PW, paddy wetland; RW, riparian wetland.
all sites, the dominant phyla of zooplankton community were Rotifera (45.52%) and Arthropoda (44.22%). The distribution of zooplankton phyla was uneven in five habitats (Figure 3b). For example, the abundance of Rotifera was higher in MW and RW1 than that in the other habitats, while the abundance of Arthropoda was higher in LW and PW than that in the other habitats. Distribution at lower taxa rank was also uneven in five habitats, such as at the class level (Figure S2b).

3.2 | Variation of plankton community diversity

Bacterioplankton communities in five locations were significantly different from each other (Figure 4a; \( p < 0.05 \), Table S1). The dissimilarity was the smallest between RW1 and RW2 (ANOSIM: \( r = 0.219 \), \( p = 0.019 \)). Venn diagram revealed that only 8.59% OTUs (562/6543) were common among five habitats (Figure S3a). The percentage of unique OTUs was lowest in LW (16.29%) and highest in PW (44.49%). Similarly to bacterioplankton, zooplankton communities in five habitats varied significantly (Figure 4b; \( p < 0.05 \), Table S1). The dissimilarity between RW1 and RW2 was also the smallest (ANOSIM: \( r = 0.222 \), \( p = 0.025 \)). Venn diagram revealed 36.99% OTUs (162/438) were common among five habitats (Figure S3b). The percentage of unique OTUs was lowest in LW (4.20%) and highest in RW1 (7.28%).

3.3 | Influence of environmental variables on community diversity

Similarly to plankton communities, environmental variables in five habitats were significantly different (Figure S4 and Table S2). For example, the concentration of COD, TN and other nutrients was lowest in LW, implying relatively better water quality in this habitat (Table S2). Mantel test indicated that 15 out of 25 environmental variables were significantly correlated with bacterioplankton community. Forward selection further revealed \( pH \) was the most important variable that structured community composition of bacterioplankton, followed by As, TDS, Fe, Mn and Na (Table 1). A parsimonious RDA model was built with these six variables (\( p = 0.001 \); Figure 5a). These selected variables explained 31.4% of the total variation at the OTU level. Correlation analysis indicated that these variables exerted distinct influence on different taxa (Table S3).

Mantel test revealed 14 out of 25 environmental variables were significantly correlated with the composition of zooplankton communities. Forward selection further revealed \( \text{NH}_4 \) as the most important variable to structure zooplankton communities, followed by As, TDS, Fe, Mn and Na (Table 1). A parsimonious RDA model was built on these variables (\( p = 0.001 \); Figure 5b). These five variables explained 29.8% of total community variation. These variables exerted discrepant influence on different taxa (Table S4).

3.4 | Complex interactions depicted by co-occurrence networks

To investigate the association among bacterioplankton, zooplankton and environmental variables, a scale-free network (\( R^2 \) of power law: 0.952) was constructed. Multiple parameters showed that the empirical network was significantly different from relevant random network, suggesting that the observed interactions were non-random (Table 2).
In total, the network was consisted of 373 nodes, including 301 bacterioplankton units, 60 zooplankton units and 12 environmental units. We identified 646 taxon–taxon edges and only 32 environment-associated edges, suggesting that a majority of community variation should be explained by biotic interactions. Among environmental factors, the frequent drivers of network connections were Na, As, pH and TP. Among the taxon–taxon interactions, positive associations (85%) outnumbered the negative exclusions (15%). Besides, we observed a non-random edge distribution with regard to phylogeny (Figure 6). For example, most positive interactions were observed within certain groups, especially for Rotifera and Arthropoda in zooplankton. Positive associations were enriched in Actinobacteria, Alphaproteobacteria and Planctomycetes, which were dominant components of bacterioplankton communities. Although negative associations were also enriched in the three taxa, they were observed mostly between different taxonomic groups. The cross-kingdom association (21/646) between bacterioplankton and zooplankton was less than within-kingdom association (593/646).

4 | DISCUSSION

In order to facilitate the conservation and restoration of wetland biodiversity, it is crucial to deeply investigate potential mechanisms that structure biodiversity in wetlands (Erwin, 2009; Tockner & Stanford, 2002; Xu et al., 2019; Zedler, 2000). In this study, we observed distinct community composition and structure of both bacterioplankton and zooplankton in habitats with varied levels of anthropogenic disturbance (i.e., protection status). The environmental filtering process played an important role in driving the dissimilarity of communities, with environmental variables explaining approximately 30% of community variation (Table 1). Interestingly, the two types of communities were influenced by different factors, suggesting environmental stressors in the same habitat could distinctly influenced different communities (Figure 5; Table 1). The interactome-based analyses added extra explanation for the community variation. Therefore, this study successfully dissected ecological processes and mechanisms which drove the community structure and geographical distributions of plankton biodiversity, and the findings in this study are expected to benefit biodiversity conservation and restoration in wetlands.

4.1 | Variability of plankton communities in different habitats

Characterizing the composition and geographical distribution of communities is fundamental to assess degradation status and to establish rationale targets for wetland biodiversity restoration (Fang et al., 2006; Meli et al., 2014; Zedler & Kercher, 2005). Wetlands naturally present a high level of habitat heterogeneity, and as a result, most local populations of wetland species are small and isolated and thus vulnerable to extinction (Gibbs, 2000). Numerous pioneering studies have revealed that species, especially those flagship species such as waterbirds, were distributed in a few suitable habitats after anthropogenic disturbance (i.e., habitat heterogeneity derived from human activities; Fang et al., 2006; Yang et al., 2016; Wang et al., 2017). However, relatively less attention was paid to the composition and geographical distribution of microscopic communities. Due to the relatively large population size and high dispersal potentials, microscopic organisms have long been considered to be randomly

![Figure 4](image-url)
However, a large number of recent studies have repudiated this old viewpoint by revealing the non-random geographical distribution of these communities (Lindström & Langenheder, 2012; Soininen et al., 2007; Thompson et al., 2017), even in running water ecosystems where significant environmental gradients exist (Peng, Xiong, & Zhan, 2018; Xiong et al., 2017; Yang et al., 2018). Similarly, we also detected significant geographical variability of bacterioplankton and zooplankton communities in Sanjiang wetland in this study (Figure 4). The results indicate that, similarly to many macro-organisms, the microscopic organisms can be largely threatened by anthropogenic disturbances, as environmental factor-induced species sorting promotes the geographical isolation and prohibits possible rescues from neighbouring populations.

For both types of communities in Sanjiang wetland, the species richness (i.e., α-diversity) did not significantly vary among habitats (Figure 2), while the species composition and relative abundance (i.e., β-diversity) varied greatly (Figure 3). The provision of ecosystem services is supported not just by species richness, but also by species abundance and geographical distribution (Meli et al., 2014). Therefore, a comprehensive assessment of different biodiversity components is recommended to reflect the succession dynamics of wetland biodiversity. Regarding community composition at the OTU level, the percentage of unique OTUs in each habitat was smallest in lacustrine wetland (LW) habitat for both bacterioplankton and zooplankton communities (Figure S3). The lower level of uniqueness of OTUs in LW suggests a higher level of migration to surrounding areas and thus LW has the potential to serve as crucial seed banks for biodiversity restoration. This result also indicates that nature reserves are crucial to maintain biodiversity, since LW habitat sits at the core of Sanjiang Wetland National Nature Reserve and is under better protection than the...
other habitats. Significant variation was also observed at the taxonomic level, such as the reverse relationship between Rotifera and Arthropoda (mostly crustaceans; Figure 3b). Such a reverse relationship was common in aquatic ecosystems (Xiong et al., 2017; Yang et al., 2018) and was mainly related to interspecific interactions, such as competition or predation (Laxson, McPhedran, Makarewicz, Telesh, & Maclsaac, 2003; Meyer, Hampton, Ozersky, Rusanovskaya, & Woo, 2017).

4.2 | The importance of environmental filtering

Studies have summarized that abiotic factors impact community composition and geographical distribution mainly through two ecological processes—environmental filtering and dispersal limitation (Heino, Melo, & Bini, 2015; Leibold et al., 2004; Soininen et al., 2007). In this study, several environmental variables were identified to drive the distinct community composition of plankton communities in Sanjiang wetland (Figure 5; Table 1), stressing the importance of environmental filtering. The strength of environmental filtering depends largely on the length of environmental gradient (Heino et al., 2015; Xiong et al., 2017). In Sanjiang wetland, the environmental gradient mainly comes from the significantly different water quality in five habitats, which was mainly derived from varied levels of anthropogenic disturbances. Due to long-term reclamation, large area of natural wetlands has been transformed to croplands, resulting in severe degradation and loss of wetlands (Song et al., 2014; Wang et al., 2015). Newly launched protection programmes, such as the establishment of nature reserves, have been beneficial to conservation of wetlands. For example, the relatively better water quality of LW habitat results from the better protection status (Table S2). However, the other habitats are suffering from different levels of anthropogenic disturbance, such as ongoing reclamation in riparian wetlands (RW1 and RW2 habitats), and low efficiency of restoration from croplands (PW habitat; Song et al., 2014; Wang et al., 2015). Therefore, it still remains a great challenge to restore and conserve the biodiversity of Sanjiang wetland.

4.3 | The complex interactions of biotic and abiotic factors on biodiversity

Our results showed that the two types of communities responded differently to environmental stressors in the same habitats (Figure 5; Table 1). This discrepancy might be owing to physiological features of different organisms and, in turn, reflect their varied tolerance to exterior environmental stressors. For example, in freshwater ecosystems, most microbial cells could only stand within 1 pH unit of neutral; therefore, acidic or alkaline habitats may disturb their metabolism, restrict their growth and consequently alter community composition (Niño-García, Ruiz-González, & del Giorgio, 2016; Ren et al., 2015). While for zooplankton communities, the impacts of nutrient (e.g., nitrogen and phosphorous) enrichment may function dialectically. The high concentration of nutrients can directly facilitate zooplankton growth by providing adequate food or growth elements to primary producers, although too high concentration could definitely poison these animals, leading to significant changes of community composition (Palmer & Yan, 2013; Xiong et al., 2017). Despite the strong environmental selection pressure, abiotic variables could only explain a fraction (approximately 30%) of community variation (Table 1). The incomplete measurement of all abiotic and the biotic variables might be one of the reasons. However, similar to other studies (Fang et al., 2006; Soininen et al., 2007; Xiong et al., 2016; Xu et al., 2019), as we have considered the dominant and well-known potential abiotic variables, the limited explanation might be derived from an overlooked factor, biotic interactions.

To deeply investigate the complex interactions between abiotic and biotic impacts and biodiversity of plankton communities, we built scale-free co-occurrence networks. Interestingly, the environment-associated edges were far less than the taxon-taxon edges, suggesting that only a minority of network associations could be explained by environmental variables. This was consistent with the above-mentioned incompleteness of environmental variables to explain the variation of communities. Consistent with other interactome-based studies, this finding highlighted the necessity to take biotic interactions into consideration to analyse succession

| Network properties       | Indexes        |
|--------------------------|---------------|
| Empirical network        |               |
| Number of nodes          | 373           |
| Number of links          | 678           |
| Positive biotic edges (%)| 549 (84.98%)  |
| Similarity threshold     | 0.730         |
| $R^2$ of power law       | 0.952         |
| Average connectivity (avgK)| 3.635   |
| Geodesic distance (HD)   | 3.966         |
| Average clustering coefficient (avgCC)| 0.251 |
| Modularity               | 0.713         |
| Random network           |               |
| Geodesic distance (HD)   | 3.677 ± 0.040 |
| Average clustering coefficient (avgCC)| 0.021 ± 0.006 |
| Modularity               | 0.529 ± 0.007 |

**TABLE 2** Topological properties of the scale-free networks and relevant random networks
Moreover, the taxon–taxon associations across functional types and taxonomic groups were non-randomly distributed on the network. Most of the interactions were positive (85%), suggesting that species mutualism or parasitism might be the dominant processes to regulate ecosystem functioning in Sanjiang wetland. Interestingly, positive interactions mostly occurred within each kingdom. Species with close phylogenetic relationship are supposed to share similar biological functions or occupy similar niches, and thus facilitate the uptake and metabolism of resources (Deng et al., 2012; Faust & Raes, 2012). However, negative interactions occurred mainly between bacterioplankton and zooplankton or within zooplankton. As some taxa of zooplankton could feed on bacteria or small-bodied zooplankton, grazing or predation might play important roles (Baltar et al., 2016; Fermani et al., 2013). In return, bacteria could release some secondary metabolites, such as Shiga toxin, to defend the predation of zooplankton (Jousset, 2012; Matz et al., 2008). Therefore, the complex interactions, especially taxon–taxon associations, contributed to the variation of both bacterioplankton and zooplankton communities.

5 | CONCLUSIONS

Effective conservation of wetland biodiversity is hampered by the lack of a comprehensive understanding of ecological processes and mechanisms that influence biodiversity. In this study, we found complex interactive effects of abiotic and biotic factors to drive the distinct distribution patterns of plankton communities in Sanjiang wetland. The selective strength of abiotic variables was mainly derived from different levels of anthropogenic disturbances. Interestingly, bacterioplankton and zooplankton communities responded differently to variables in the same habitats, suggesting that a comprehensive survey is needed to take diverse organisms into consideration when restoration programmes are established. Furthermore, the incompleteness of abiotic variables to predict community dynamics was partially supplemented by the integration of biotic interactions, calling for attention towards the interactome-based framework to examine the synthesizing impacts of both abiotic and biotic variables. Outcomes from comprehensive surveys can help identify conservation priorities and improve the predictability of conservation programmes.

ACKNOWLEDGEMENTS

This work was supported by the National Key R&D Program of China [grant no.: 2016YFC0500406], National Natural Science Foundation of China [grant no.: 31800419], the Innovation in Cross-functional Team Program of the Chinese Academy of Sciences [grant no.: 2015], Chinese Academy of Science [grant no.: ZDRW-ZS-2016-5], the State Key Joint Laboratory of Environment Simulation and Pollution Control [RCEES, Chinese Academy of Sciences; grant no.: 15K01ESPCR] and the Water Pollution Control and Treatment Special Project [grant no.: 2015ZX07201-008-09].

DATA ACCESSIBILITY

These sequence data have been submitted to the GenBank Sequence Read Archive under the accession numbers PRJNA 542032 (zooplankton) and PRJNA 542034 (bacterioplankton).

ORCID

Aibin Zhan https://orcid.org/0000-0003-1416-1238
REFERENCES

An, S., Li, H., Guan, B., Zhou, C., Wang, Z., Deng, Z., ... Li, H. (2007). China’s natural wetlands: Past problems, current status, and future challenges. *AMBIO: A Journal of the Human Environment, 36,* 335–343. https://doi.org/10.1579/0044-7447(2007)36[335:CNWPPC]2.0.CO;2

Baltar, F., Palou-Puig, J., Unrein, F., Catala, P., Horrak, K., Šimek, K., ... Pinhasi, J. (2016). Marine bacterial community structure resilience to changes in protist predation under phytoplankton bloom conditions. *The ISME Journal, 10,* 568. https://doi.org/10.1038/ismej.2015.135

Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M. (2016). A common framework for identifying linkage rules across different types of interactions. *Functional Ecology, 30,* 1894–1903.

Blanchet, F. G., Legende, P., & Borcard, D. (2008). Forward selection of explanatory variables. *Ecology, 89,* 2623–2632. https://doi.org/10.1890/07-0986.1

Bortolotti, L. E., Vinebrooke, R. D., & St. Louis, V. L. (2016). Prairie wetland communities recover at different rates following hydrological restoration. *Freshwater Biology, 61,* 1874–1890. https://doi.org/10.1111/fwb.12822

Caporaso, J. G., Lauber, C. L., Walters, W. A., Berg-Lyons, D., Lozupone, C. A., Turnbaugh, P. J., ... Knight, R. (2011). Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. *Proceedings of the National Academy of Sciences of the United States of America, 108,* 4516–4522. https://doi.org/10.1073/pnas.1000081017

Chaparro, G., Horváth, Z., O’Farrell, I., Ptacnik, R., & Hein, T. (2018). Prairie biodiversity and species competition regulate the resilience of microbial biofilm community. *Bioinformatics, 34,* 111. https://doi.org/10.1101/113076

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics, 26,* 2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Edgar, R. C. (2013). UPARSE: Highly accurate OTU sequences from microbial amplicon reads. *Nature Methods, 10,* 996–998. https://doi.org/10.1038/nmeth.2604

Erwin, K. L. (2009). Wetlands and global climate change: The role of wetland restoration in a changing world. *Wetlands Ecology and Management, 17,* 71. https://doi.org/10.1007/s11273-008-9119-1

Fang, J., Wang, Z., Zhao, S., Li, Y., Tang, Z., Yu, D., ... Zheng, C. (2006). Biodiversity changes in the lakes of the Central Yangtze. *Frontiers in Ecology and the Environment, 4,* 369–377. https://doi.org/10.1890/1540-9295(2006)004[0369:BFICI]2.0.CO;2

Fang, J., Wang, Z., Zhao, S., Li, Y., Tang, Z., Yu, D., ... Zheng, C. (2006). Biodiversity changes in the lakes of the Central Yangtze. *Frontiers in Ecology and the Environment, 4,* 369–377. https://doi.org/10.1890/1540-9295(2006)004[0369:BFICI]2.0.CO;2

Faust, K., Lahti, L., Gessner, Morris O., & Raes, J. (2016). Metagenomics meets time series analysis: Unraveling microbial community dynamics. *Current Opinion in Microbiology, 25,* 56–66. https://doi.org/10.1016/j.mib.2015.04.004

Faust, K., & Raes, J. (2012). Microbial interactions: From networks to models. *Nature Reviews Microbiology, 10,* 538–550. https://doi.org/10.1038/nrmicro2832

Finlayson, C. M., Davidson, N. C., Spiers, A. G., & Stevenson, N. J. (1999). Global wetland inventory-current status and future priorities. *Marine and Freshwater Research, 50,* 717–727. https://doi.org/10.1071/MF99098

Gibbs, J. P. (2000). Wetland loss and biodiversity conservation. *Conservation Biology, 14,* 314–317. https://doi.org/10.1111/j.1523-1739.2000.98608.x

Guidi, L., Chaffron, S., Bittner, L., Evellard, D., Larhlimi, A., Roux, S., ... Gorsky, G. (2011). plankton networks driving carbon export in the oligotrophic ocean. *Nature, 532,* 465. https://doi.org/10.1038/natur e16942

Heino, J., Melo, A. S., & Bini, L. M. (2015). Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshwater Biology, 60,* 223–235. https://doi.org/10.1111/fwb.12502

Hu, S., Niu, Z., Chen, Y., Li, L., & Zhang, H. (2017). Global wetlands: Potential distribution, wetland loss, and status. *Science of the Total Environment, 586,* 319–327. https://doi.org/10.1016/j.scitotenv.2017.02.001

Huang, W. E., Ferguson, A., Singer, A. C., Lawson, K., Thompson, I. P., Kain, R. M., ... Whiteley, A. S. (2009). Resolving genetic functions within microbial populations: In situ analyses using rRNA and mRNA stable isotope probing coupled with single-cell Raman-fluorescence in situ hybridization. *Applied and Environmental Microbiology, 75,* 234–241. https://doi.org/10.1128/AEM.01861-08

Jansson, M., Andersson, R., Berggren, H., & Leonardson, L. (1994). Prairie wetlands as nitrogen traps. *AMBIO: A Journal of the Human Environment, 23,* 320–325.

Jordan, P. (2016). Chasing ecological interactions. *PLoS Biology, 14,* e1002559. https://doi.org/10.1371/journal.pbio.1002559

Jousset, A. (2012). Ecological and evolutionary implications of bacterial defences against predators. *Environmental Microbiology, 14,* 1830–1843. https://doi.org/10.1111/j.1462-2927.2011.02627.x

Krzywiniski, M., Schein, J., Birol, I., Connors, J., Gascoyne, R., Horsman, D., ... Marra, M. A. (2009). Circos: An information aesthetic for comparative genomics. *Genome Research, 19,* 1639–1645. https://doi.org/10.1101/gr.092759.109

Laxson, C. L., McPhedran, K. N., Makarewicz, J. C., Telesh, I. V., & MacIsaac, H. J. (2003). Effects of the non-indigenous cladoceran Cercopagis pengoi on the lower food web of Lake Ontario. *Freshwater Biology, 48,* 2094–2106. https://doi.org/10.1111/j.1365-2427.2003.01154.x

Layeghifard, M., Hwang, D. M., & Guttman, D. S. (2017). Disentangling interactions in the microbiome: A network perspective. *Trends in Microbiology, 25,* 217–228. https://doi.org/10.1016/j.tim.2016.11.008

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., ... Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters, 7,* 601–613. https://doi.org/10.1111/j.1462-2920.2004.00608.x

Lima-Mendez, G., Faust, K., Henry, N., Decelle, J., Colin, S., Carcillo, F., ... Raes, J. (2015). Determinants of community structure in the global plankton interactome. *Science, 348,* 1262073. https://doi.org/10.1126/science.1262073

Lindström, E. S., & Langenheder, S. (2012). Local and regional factors influencing bacterial community assembly. *Environmental Microbiology Reports, 4,* 1–9. https://doi.org/10.1111/j.1758-2229.2011.00257.x

Lu, C., Wang, Z., Li, L., Wu, P., Mao, D., Jia, M., & Dong, Z. (2016). Assessing the conservation effectiveness of wetland protected areas in Northeast China. *Wetlands Ecology and Management, 24,* 381–398. https://doi.org/10.1007/s11273-015-9462-y

Martiny, J. B. H., Bohannan, B. J. M., Brown, J. H., Colwell, R. K., Fuhrman, J. A., Green, J. L., ... Staley, J. T. (2006). Microbial biogeography: Putting microorganisms on the map. *Nature Reviews Microbiology, 4,* 102. https://doi.org/10.1038/nrmicro1341
Matz, C., Webb, J. S., Schupp, P. J., Phang, S. Y., Penesyan, A., Egan, S., ... Kjelleberg, S. (2008). Marine biofilm bacteria evade eukaryotic predation by targeted chemical defense. PLoS ONE, 3, e2744. https://doi.org/10.1371/journal.pone.0002744

Meli, P., Benayas, J. M. R., Balvanera, P., & Ramos, M. M. (2014). Restoration enhances wetland biodiversity and ecosystem service supply, but results are context-dependent: A meta-analysis. PLoS ONE, 9, e93507. https://doi.org/10.1371/journal.pone.0093507

Meng, W., He, M., Hu, B., Mo, X., Li, H., Liu, B., & Wang, Z. (2017). Status of wetlands in China: A review of extent, degradation, issues and recommendations for improvement. Ocean and Coastal Management, 146, 50–59. https://doi.org/10.1016/j.ocecoaman.2017.06.003

Mensing, D. M., Galatowitsch, S. M., & Tester, J. R. (1998). Anthropogenic effects on the biodiversity of riparian wetlands of a northern temperate landscape. Journal of Environmental Management, 53, 349-377. https://doi.org/10.1016/j.jema.1998.02.015

Meyer, M. F., Hampton, S. E., Ozersky, T., Rusanovskaya, O. O., & Woo, K. H. (2017). Vulnerability of rotifers and copepod nauplii to predation by Cyclops kolensis (Crustacea, Copepoda) under varying temperatures in Lake Baikal, Siberia. Hydrobiologia, 796, 309–318. https://doi.org/10.1007/s10750-016-3005-2

Myers, N. (1996). Environmental services of biodiversity. Proceedings of the National Academy of Sciences of the United States of America, 93, 2764–2769. https://doi.org/10.1073/pnas.93.7.2764

Niño-García, J. P., Ruiz-González, C., & del Giorgio, P. A. (2016). Fine-scale environmental gradients drive bacterial communities in running water ecosystems. Aquatic Biology, 27, 43–53. https://doi.org/10.3354/ab06065

R Core Team (2018). A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Ren, L., Jeppesen, E., He, D., Wang, J., Liboriussen, L., Xing, P., & Wu, Q. (2015). pH influences the importance of niche-related versus neutral processes in lacustrine bacterioplankton assembly. Applied and Environmental Microbiology, 81, 3104–3114.

Soininen, J., Kokocinski, M., Estlander, S., Kotanen, J., & Heino, J. (2007). Neutrality, niches, and determinants of plankton metacommunity structure across boreal wetland ponds. Ecology, 14, 146–154. https://doi.org/10.2980/1195-6860(2007)14[146:NNADOP]2.0.CO;2

Song, K., Wang, Z., Du, J., Liu, L., Zeng, L., & Ren, C. (2014). Wetland degradation: Its driving forces and environmental impacts in the Sanjiang Plain, China. Environmental Management, 54, 255–271. https://doi.org/10.1007/s00267-014-0278-y

Thompson, L. R., Sanders, J. G., McDonald, D., Amir, A., Ladau, J., Loecey, K. J., ... Knight, R. (2017). A communal catalogue reveals Earth's multiscale microbial diversity. Nature, 551, 457. https://doi.org/10.1038/nature24621

Tockner, K., Pusch, M., Borchardt, D., & Lorang, M. S. (2010). Multiple stressors in coupled river-floodplain ecosystems. Freshwater Biology, 55, 135–151. https://doi.org/10.1111/j.1365-2427.2009.02371.x

Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: Present state and future trends. Environmental Conservation, 29, 308–330. https://doi.org/10.1017/S037689290200022X

Wang, Q., Garrity, G. M., Tiedje, J. M., & Cole, J. R. (2007). Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. Applied and Environmental Microbiology, 73, 5261-5267. https://doi.org/10.1128/AEM.00062-07

Wang, S., & Brose, U. (2018). Biodiversity and ecosystem functioning in food webs: The vertical diversity hypothesis. Ecology Letters, 21, 9–20. https://doi.org/10.1111/ele.12865

Wang, W., Fraser, J. D., & Chen, J. (2017). Wintering waterbirds in the middle and lower Yangtze River floodplain: Changes in abundance and distribution. Bird Conservation International, 27, 167–186. https://doi.org/10.1017/S0959270915000398

Wang, Z., Mao, D., Li, L., Jia, M., Dong, Z., Miao, Z., ... Song, C. (2015). Quantifying changes in multiple ecosystem services during 1992–2012 in the Sanjiang Plain of China. Science of the Total Environment, 514, 119–130. https://doi.org/10.1016/j.scitotenv.2015.01.007

Wang, Z., Song, K., Ma, W., Ren, C., Zhang, B., Liu, D., ... Song, C. (2011). Loss and fragmentation of marshes in the Sanjiang Plain, Northeast China, 1954–2005. Wetlands, 31, 945–954. https://doi.org/10.1007/s13157-011-0209-0

Xiong, W., Li, J., Chen, Y., Shan, B., Wang, W., & Zhan, A. (2016). Determinants of community structure of zooplankton in heavily polluted river ecosystems. Scientific Reports, 6, 22043. https://doi.org/10.1038/srep22043

Xiong, W., Ni, P., Chen, Y., Gao, Y., Shan, B., & Zhan, A. (2017). Zooplankton community structure along a pollution gradient at fine geographical scales in river ecosystems: The importance of species sorting over dispersal. Molecular Ecology, 26, 4351–4360. https://doi.org/10.1111/mec.14199

Xiong, W., & Zhan, A. (2018). Testing clustering strategies for metabarcoding-based investigation of community-environment interactions. Molecular Ecology Resources, 18, 1326–1338. https://doi.org/10.1111/1755-0998.12922

Xu, Y., Si, Y., Yin, S., Zhang, W., Grischchenko, M., Prins, H. H. T., ... de Boer, W. F. (2019). Species-dependent effects of habitat degradation in relation to seasonal distribution of migratory waterfowl in the East Asian-Australasian Flyway. Landscape Ecology, 34, 243–257. https://doi.org/10.1007/s10980-018-00767-7

Yang, Y., Deng, Y., & Cao, L. (2016). Characterising the interspecific variations and convergence of gut microbiota in Anseriformes herbivores at wintering areas. Scientific Reports, 6, 32655. https://doi.org/10.1038/srep32655

Yang, Y., Gao, Y., Huang, X., Ni, P., Wu, Y., Deng, Y., & Zhan, A. (2019). Adaptive shifts of bacterioplankton communities in response to nitrogen enrichment in a highly polluted river. Environmental Pollution, 245, 290–299. https://doi.org/10.1016/j.envpol.2018.11.002

Yang, Y., Ni, P., Gao, Y., Xiong, W., Zhao, Y., & Zhan, A. (2018). Geographical distribution of zooplankton biodiversity in highly polluted running water ecosystems: Validation of fine-scale species sorting hypothesis. Ecology and Evolution, 8, 4830–4840. https://doi.org/10.1002/ece3.4037

Zedler, J. B. (2000). Progress in wetland restoration ecology. Trends in Ecology and Evolution, 15, 402–407. https://doi.org/10.1016/S0169-5347(00)01959-5

Zedler, J. B., & Kercher, S. (2005). Wetland resources: Status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources, 30, 39–74. https://doi.org/10.1146/annurev.energy.30.050504.144248

Zhan, A., Bailey, S. A., Heath, D. D., & MacIsaac, H. J. (2014). Performance comparison of genetic markers for high-throughput sequencing-based biodiversity assessment in complex communities. Molecular Ecology Resources, 14, 1049–1059. https://doi.org/10.1111/1755-0998.12254

Zhan, A., Hulak, M., Sylvester, F., Huang, X., Adebayo, A. A., Abbott, C. L., ... MacIsaac, H. J. (2013). High sensitivity of 454 pyrosequencing for detection of rare species in aquatic communities. Methods in Ecology and Evolution, 4, 558–565. https://doi.org/10.1111/2041-210X.12037

Zhang, C., Robinson, D., Wang, J., Liu, J., Liu, X., & Tong, L. (2011). Factors influencing farmers' willingness to participate in the conversion of cultivated land to wetland program in Sanjiang National Nature
Reserve, China. Environmental Management, 47, 107–120. https://doi.org/10.1007/s00267-010-9586-z

Zhang, Y., Cioffi, W., Cope, R., Daleo, P., Heywood, E., Hoyt, C., ... Silliman, B. (2018). A global synthesis reveals gaps in coastal habitat restoration research. Sustainability, 10, 1040. https://doi.org/10.3390/su10041040

Zhou, J., Deng, Y., Luo, F., He, Z., Tu, Q., & Zhi, X. (2010). Functional molecular ecological networks. mBio, 1, e00169-10. https://doi.org/10.1128/mBio.00169-10

Zhou, J., Deng, Y., Luo, F., He, Z., & Yang, Y. (2011). Phylogenetic molecular ecological network of soil microbial communities in response to elevated CO₂. mBio, 2, e00122-11. https://doi.org/10.1128/mBio.00122-11

**BIOSKETCH**

Yuzhan Yang is a postdoctoral researcher in Zhan Lab at Research Center for Eco-Environmental Sciences, Chinese Academy of Science. Her research focuses on ecology and evolution of aquatic microorganisms in highly disturbed and polluted water ecosystems.

Aibin Zhan’s research group is interested in a variety of questions pertaining to molecular and evolutionary ecology in biological invasions and water pollution.

Author contributions: A.Z. and Y.Y. conceived and designed this study; Y.Y., Y.G., Y.C. and S.L. conducted the experiments; Y.Y. analysed the data; Y.Y. and A.Z. wrote the manuscript; and all authors reviewed and commented on the manuscript.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Yang Y, Gao Y, Chen Y, Li S, Zhan A. Interactome-based abiotic and biotic impacts on biodiversity of plankton communities in disturbed wetlands. Divers Distrib. 2019;25:1416–1428. https://doi.org/10.1111/ddi.12949