

# Change of the structure and assembly of bacterial and photosynthetic communities by the ecological engineering practices in Dianchi Lake

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## Research Article

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# Abstract

**Background:** Cyanobacterial bloom challenges the aquatic ecosystem and ecological restoration is an effective approach for cyanobacterial bloom control, but the change of aquatic community after ecological restoration is still unclear. Dianchi Lake is a eutrophic lake with frequent cyanobacterial blooms in China, and recent ecological restoration projects in Caohai (north part) have a satisfactory performance. In this study, we collected 249 water samples at 23 sites from Dianchi Lake to explore the relationships between water physiochemical variables and aquatic microbial communities.

**Results:** Water physicochemical variables in Waihai (south part) intensively changed along time, whereas those in Caohai did not. Photoautotrophic communities were significantly divergent between Caohai and Waihai. Waihai had a lower diversity of photoautotrophic community, containing higher abundance of *Cyanophyceae* (89.9%) than Caohai (42.7%). Nutrient level and *Cyanophyceae* only exhibited strong correlations in Waihai ( $p < 0.05$ ). Redundancy analysis and microbial ecological network suggested that microbial communities in Caohai had a higher stability. Deterministic process dominated the microbial assembly (50-80% for bacteria and >90% for photoautotrophs), and particularly in Caohai.

**Conclusions:** Our results unraveled that the structure and assembly of bacterial and photoautotrophic communities significantly changed after ecological restoration, offering valuable suggestions that photosynthetic diversity should be focused for other ecological restoration projects.

## 1. Background

Cyanobacterial bloom is one of the most critical environmental problems in surface water ecosystems around the world [1–5], particularly in eutrophic lakes and reservoirs [6, 7]. The proliferation of harmful algae greatly damages the ecological functions and landscape of recreational waters, and cyanotoxins and fishy odors directly threaten the municipal drinking water safety and aquatic ecosystems [8–10]. Cyanobacterial bloom is closely related to the eutrophic degree of lakes, which is affected by the input of nitrogen and phosphate [11]. Additionally, cyanobacterial bloom is named as species belonging to *Cyanobacteria* like *Microcystis aeruginosa* [12], *Anabaena flos-aquae* [12, 13], *Aphanizomenon flos-aquae* [14], and *Cylindrospermopsis raciborskii* [15] dominate the algal community. Those cyanobacterial lineages have relatively higher growth rates and distinct adaptive mechanisms at high temperatures [16, 17], capable of dominating aquatic ecosystems and forming cyanobacterial bloom in warm water environments [18]. Thus, cyanobacterial bloom often shows seasonal variations responsive to annual temperature cycle and is hard to prevent and control [4, 7, 19], attracting many attentions for its occurrence and control strategy in the last decades.

The outbreak of cyanobacterial bloom is closely related to water physicochemical variables. Nutrient level, particularly phosphorus (P) and nitrogen (N), is considered as the key factor for cyanobacterial bloom [20]. Substantial studies have pointed out that phosphorus is the most critical limiting nutrient for aquatic organisms in freshwater systems, as phosphorus has no gaseous atmospheric cycle and

appreciable internal compensation [20–23]. A large-scale European Water Ecology Survey shows that the risk of cyanobacterial bloom increases when total phosphorus concentrations exceed 10–20 µg/L [24]. When the phosphorus supply is sufficient, nitrogen becomes a key factor in the size and duration of cyanobacterial bloom, *e.g.*, Erie Lake, Taihu Lake and New York Lake [25–28]. Some other variables influencing cyanobacterial bloom include illumination [29], temperature [16] and turbidity [20]. Those variables normally co-occur or interact synergistically to shape cyanobacterial growth and activities [4]. Therefore, it is critical to explore the relationship between environmental restriction factors and cyanobacterial blooms for effective eutrophication control and water quality management.

Reducing phosphorus and nitrogen load is widely accepted as the most critical strategy for cyanobacterial bloom control, like sediment dredging [30]. In addition, other alternatives like artificial salvage are also used to directly reduce the biomass of harmful algae in the eutrophication period [31]. However, these strategies do not always work [15, 25, 32]. Recently, ecological restoration has attracted wide attentions for its strong ecological compatibility and low cost [33]. In a typical ecological restoration project, the key task is to reconstruct the community structure and food web, which aims at controlling the primary productivity of cyanobacteria. For example, by using the principle of competitive exclusion, cyanobacterial biomass in Swarzędzkie Lake was significantly decreased by catching *Cyprinids* and stocking *Pike fry*, and *Chlorophytes*, *Chrysophytes* and *Cryptophytes* flourished [34]. Some other microorganisms [35, 36] or algicidal compounds [37] are also amended as an assistance to the proliferation of harmful cyanobacteria. All these actions benefit other phytoplanktonic species to obtain more illumination and nutrients, and promote the ecological recovery process. Till now, many researchers studying cyanobacterial bloom control reach a consensus that the combination of nutrient reduction and ecological restoration is one of the promising approaches, although the underlying mechanisms remain unclear.

Dianchi Lake is the largest freshwater lake in Yunnan-Guizhou Plateau, China. It is a famous eutrophic lake with frequent cyanobacterial blooms in China for nearly 40 years. Dianchi is hydrologically separated into two parts, Caohai (north) and Waihai (south). Since 2007, several restoration projects were conducted in Caohai, *e.g.*, wetland construction and large-scale aquatic plant community restoration, and achieved some gratifying results [38–40]. Around 3.3 km<sup>2</sup> of hydrological basin has been recovered with 20 species of aquatic plants, including *Eichhornia crassipes*, *Phragmites communis*, *Trin-Nelumbo nucifera* and *Gaertn-Potamogeton pectinatus* Linn [38, 41, 42]. In contrast, ecological restoration is seldom conducted in Waihai except for limited wetlands constructed along the lakeside. In this work, we collected 249 water samples at 23 sites from Dianchi Lake at different time and depths to explore the water physiochemical variables and communities of bacteria or photoautotrophs in both Caohai and Waihai. We aimed to: 1) identify the relationships between water physiochemical variables and communities of bacteria or photoautotrophs, 2) compare the different links of physiochemical variables and microbial communities between aquatic ecosystems with and without ecological restoration, and 3) evaluate the assembly processes of aquatic microbial communities between aquatic ecosystems with

and without ecological restoration. Our findings can offer suggestions for the effective prevention, control and ecological restoration of cyanobacterial blooms in other eutrophic lakes.

## 2. Materials And Methods

### 2.1 Study area and sample collection

Dianchi Lake (24°40′-25°02′ N, 102°36′-102°40′ E) is located in Kunming, Yunnan Province, China. It is a typical shallow plateau lake with an average area of 310 km<sup>2</sup>, an average depth of 4.7 m, and a basin area of 2920 km<sup>2</sup> [41]. It is in the subtropical monsoon climate region with an annual average temperature of 15 °C, and algae growth and reproduction are active in summer and autumn. Haigeng Dam was built in 1996, separating Dianchi into two parts, Caohai (north, 10 km<sup>2</sup>) and Waihai (south, 300 km<sup>2</sup>). Comparing to Waihai, Caohai is not only smaller in area, but also shallower in depth (deepest 2 m in Caohai and 6 m in Waihai). Cyanobacterial blooms are therefore severe in Caohai and the northern part of Waihai as waters are driven by the prevailing southwest wind [43]. The ecosystems in Dianchi Lake are simple and fragile [44].

Since 2007, systematic ecological restoration projects have been listed as the “Six Key Programs” in Dianchi Lake [18], mainly including wetland demonstration, plant floating island, ecological forest and steep shore ecological belt [38–40]. Particularly, in 2015, an ecological restoration demonstration project was launched in an area of about 0.52 km<sup>2</sup> in south Caohai. Indigenous plants such as *Eichhornia crassipes*, *Myriophyllum verticillatum* L., *Vallisneria natans* and *Potamogeton wrightii* Morong, as well as some animals including fishes and snails, were introduced into this experimental area. With gratifying restoration effects, more ecological restoration projects were proposed in 2018 for 1.56 km<sup>2</sup> in Caohai. Nowadays, totally 3.3 km<sup>2</sup> of lakeside wetland have been constructed in Caohai with approximately 20 species of aquatic plants [38, 41, 45]. As for Waihai, only limited wetlands were constructed along the lakeside, only occupying a small area of Waihai (around 12.6 km<sup>2</sup> out of 300 km<sup>2</sup>). Currently, Waihai still suffers from serious eutrophication and cyanobacterial blooms [18, 41, 46, 47], whereas there are relatively mitigatory cyanobacterial blooms in Caohai in the last few years.

As algae are more active in warmer environment, we collected water samples in summer (from July to September, 2020) to study the differences in water physiochemical properties and aquatic microbial communities between Caohai (area with complete ecological restoration) and Waihai (area without any ecological restoration projects). More precisely, water samples were collected at 23 sites in Dianchi Lake (Figure S1) at three different time (T1: 30th July; T2: 20th August; T3: 3rd September in 2019) and depths (0.0-0.2 m, surface; 1.0–3.0 m, middle; 3.0–5.0 m, bottom). Particularly, cyanobacterial bloom seriously occurred on 30th July in Waihai, whereas no cyanobacterial bloom was observed during the sampling period in Caohai. Water samples were split and stored in brown and white polyethylene plastic bottles for the measurement of chlorophyll a and other physiochemical variables, respectively. All samples were transported immediately to the laboratory after sampling.

## 2.2 Chemical analysis

Ten water physiochemical variables were measured, including pH, temperature, conductivity, dissolved oxygen (DO), chlorophyll a, total phosphorus (TP), orthophosphate (PO<sub>4</sub>-P), total nitrogen, ammonia-nitrogen (NH<sub>3</sub>-N) and nitrate (NO<sub>3</sub>-N). Temperature, pH, conductivity and DO were measured on-site by a multi-parameter analyzer (D-74, HORIBA, Japan), and a portable dissolved oxygen device (OM-71, HORIBA, Japan), respectively. According to the standard methods suggested by the Ministry of Ecology and Environment of China, chlorophyll a, TN, NH<sub>3</sub>-N, NO<sub>3</sub>-N, TP and PO<sub>4</sub>-P were all determined using spectrophotometric methods with a UV-VIS spectrometer (TU-1810, Beijing Purkinje General Instrument Co., Ltd., China). Chlorophyll a was analyzed by using ethanol extraction (HJ897-2017), and TN was measured by the potassium persulfate digestion method (HJ636-2012). NH<sub>3</sub>-N and NO<sub>3</sub>-N were determined by the Nessler's reagent colorimetric method (HJ535-2009) and alkaline phenol disulfonic acid colorimetric method (GB7480-87), respectively. TP was determined by ammonium molybdate method (0.13 M, pH = 7) after potassium persulfate digestion (GB11893-89). PO<sub>4</sub>-P was analyzed by the molybdenum blue method (pH = 1, GB/T 5750.5–2006).

## 2.3 DNA extraction and sequencing

Approximately 500 mL of water samples were filtered through a 0.22 µm microporous membrane using a sand core filter unit. The membrane was then cut into small pieces by sterile scissors for DNA extraction with the FastDNA Spin Kit (MP Biomedical, LLC). The duplicated DNA extracts were incorporated and normalized to 25 ng/µL prior to amplicon sequencing analysis. The V4-V5 region of bacterial 16S rRNA gene and plasmid 23S rRNA gene were amplified using a standard thermocycling with specific annealing temperature in triplicates to assess the community composition of bacteria and photoautotrophs according to previous studies (detailed primer sets see Table S1) [48–50]. The amplicon sequencing analysis was performed using an Illumina Miseq PE 300 at Guangdong Magigene Biotechnology Co., Ltd. Sequence assembly and filtering were performed by using FLASH (v1.2.11) [51] and UCHIME (v.4.2.4) [52].

## 2.4 Data processing and statistical analysis

Operational taxonomic units (OTUs) were counted and summarized by using USEARCH GLOBAL [53]. Taxonomical classification was performed using Ribosomal Database Project (RDP) Classifier (v.2.2) [54] trained with 80% confidence cutoff on the Greengenes database [55] for bacterial 16S rRNA gene and self-constructed database originated from NCBI for plastid 23S rRNA gene, respectively. The indices of α-diversity were calculated to evaluate the species richness and evenness for each sample using Mothur software (v.1.32.2). β-diversity analyses were performed to assess the variation of species complexity across samples using QIIME software (v.1.80).

The correlations between different physiochemical variables and dominant microflora were calculated by Pearson correlation coefficient in PAST (v.3.20). The statistical significance was calculated using double total t-test. Principal coordinates analysis (PCoA) was used to explore the differences in bacterial and photoautotrophic communities in different time, depths and areas. Redundancy analysis (RDA) was used

to examine the relationship between environmental variables and microbial community. The spatial distribution of environmental variables is expressed by Kriging method in ArcMap (v.10.4.1). For distance-decay patterns, geographic distances between pairwise samples were calculated according to their geographical coordinates. All the statistical data analyses were performed by SPSS (v.22.0), and graphs were generated by Excel 2010 or Origin 8.0.

Molecular ecological networks for bacteria and photoautotrophs were constructed using Pearson Correlation Coefficient by online Molecular Ecological Network Analyses (MENA, <http://ieg2.ou.edu/MENA>) pipeline with default parameters [56]. The Mantel test was performed to assess the correlation between environmental variables and modules generated from MENA [57].

To test phylogenetic signals, Mantel correlograms were used to measure the correlation coefficients between differences in environmental optima and phylogenetic distances [58, 59]. The phylogenetic signals were detected with significant Mantel correlograms coefficients in short phylogenetic distances, giving a premise of using the null model.

To infer aquatic community assembly processes, the  $\beta$ -nearest taxon index ( $\beta$ NTI) was calculated, representing the difference between observed  $\beta$ MNTD and mean of the null distribution of  $\beta$ MNTD normalized by its standard deviation [60].  $\beta$ NTI < -2 indicates the dominance of deterministic processes induced by environmental homogeneous selection (Dini-Andreote et al., 2015), whereas  $\beta$ NTI > 2 indicates the dominance of deterministic processes, induced by environmental heterogeneity. If the absolute values of  $|\beta$ NTI| < 2 indicates that aquatic community assembly is dominated by stochastic processes [61–63].

## 3. Results

### 3.1 Water physiochemical variables

The spatial distribution of water physiochemical variables in Dianchi Lake is illustrated in Fig. 1. The concentration of chlorophyll *a*, TP, TN, NO<sub>3</sub>-N, and DO gradually increased from south to north, while PO<sub>4</sub>-P and conductivity were opposite. The highest concentration of TP in Caohai (0.46 mg/L) was much higher than that in Waihai (0.21 mg/L), and TN was similar between Caohai (3.68 mg/L) and Waihai (3.94 mg/L). In both areas, TN and TP exceeded the Class V limits (0.2 mg/L for TP and 2 mg/L for TN) according to the Environmental Quality Standards for Surface Water (GB3838-2002). Except for temperature, NH<sub>3</sub>-N, PO<sub>4</sub>-P and DO, all the other variables were significantly different between Caohai and Waihai ( $p < 0.05$ ). In addition, pH, NH<sub>3</sub>-N and temperature were at relatively high levels in the northern part of Waihai, where cyanobacterial blooms were frequent.

Water physiochemical variables did not show significant difference across depths (Figure S2), but fluctuated with time (Figure S3). Chlorophyll *a* and most of the nutrients (TN, NO<sub>3</sub>-N and PO<sub>4</sub>-P) in Waihai were the highest on 30th July, when cyanobacterial bloom occurred ( $p < 0.05$ ). As for Caohai, TP, PO<sub>4</sub>-P

and  $\text{NH}_3\text{-N}$  were the highest on 30th July ( $p < 0.05$ ), whereas chlorophyll *a* and other nutrients remained at stable levels (Figure S3).

The relationships between environmental variables were different between Caohai and Waihai (Fig. 2). Chlorophyll *a* was only positively correlated with nutrients in Waihai ( $p < 0.05$ ), but not in Caohai. All nutrients exhibited positive pairwise correlations in Waihai ( $p < 0.05$ ), whereas only two pairs of nutrient parameters, i.e.,  $\text{TN}/\text{NO}_3\text{-N}$  and  $\text{TP}/\text{PO}_4\text{-P}$ , were positively correlated in Caohai ( $p < 0.05$ ). pH exhibited consistent negative correlations with TP,  $\text{NH}_3\text{-N}$ ,  $\text{PO}_4\text{-P}$  and conductivity in both Caohai and Waihai ( $p < 0.05$ ), but inconsistent correlations with chlorophyll *a* between two areas (negative in Waihai and positive in Caohai).

### 3.2 Bacterial and photoautotrophic community structure

In total, across 249 water samples, bacterial community was constituted of 34,919 OTUs affiliating to 68 bacterial phyla. Bacterial community structure was similar in Caohai and Waihai (Fig. 3A). The predominant bacterial phyla included *Cyanobacteria* (43.7% in Caohai and 44.5% in Waihai, the same as follows), *Proteobacteria* (20.7% and 16.9%), *Bacteroidetes* (12.6% and 17.1%), *Actinobacteria* (12.5% and 10.7%), *Planctomycetes* (6.0% and 6.2%), *Verrucomicrobia* (2.3% and 1.9%) and *Chloroflexi* (< 1.0% and 1.1%). The relative abundances of *Chloroflexi* and *Bacteroidetes* were significantly higher in Waihai than those in Caohai ( $p < 0.01$ ), whereas *Proteobacteria* and *Verrucomicrobia* behaved oppositely ( $p < 0.05$ ).

For prokaryotic and eukaryotic photoautotrophs, it was constituted of 6,883 OTUs affiliating to 39 classes, 17 phyla, and 5 kingdoms. Photoautotrophs were significantly different between Caohai and Waihai (Fig. 3B). Prokaryotic *Cyanophyceae* was the most dominant class in both areas, showing much higher abundance in Waihai (89.9%) than Caohai (42.7%). Eukaryotic *Mediophyceae* (20.9% in Caohai and 4.8% in Waihai) and *Cryptophyceae* (7.1% in Caohai and 2.1% in Waihai) were the second and third predominant classes. There was no other photoautotroph with abundance > 1% in Waihai, whereas more eukaryotic photoautotrophs found in Caohai included *Bacillariophyta* (12.0%, unclassified), *Chlorodendrophyceae* (4.5%), *Chromista* (3.4%, unclassified), *Chlorophyceae* (3.3%), *Dinophyceae* (2.0%), *Trebouxioephyceae* (1.3%) and *Eustigmatophyceae* (1.1%). It indicated a remarkably higher diversity of photoautotrophs in Caohai (Shannon index of 5.3) than Waihai (Shannon index of 4.4). To be more precise, predominant *Cyanophyceae* were further classified into 9 orders, primary including *Chroococcales* (29.8% in Caohai and 58.4% in Waihai), *Synechococcales* (5.8% in Caohai and 23.4% in Waihai), *Nostocales* (5.6% in Caohai and 6.8% in Waihai) and *Oscillatoriales* (1.1% in Caohai and < 1.0% in Waihai).

PCoA score plots illustrated a complete separation of both bacterial and photoautotrophic community structures in Caohai and Waihai (Fig. 4A and 4B), further evidenced the change of aquatic microbial communities after ecological restoration. As for different time, both bacterial and photoautotrophic communities in Caohai were grouped together (Fig. 4C and 4D). In contrast, the group of microbial communities on 30th July (T1) in Waihai was clearly separated from those on 20th August (T2) and 3rd

September (T3), and the latter two groups were clustered together (Fig. 4E and 4F). These results suggested that aquatic microbial communities were different in the period of cyanobacterial bloom, and successful ecological engineering projects in Caohai has stabilized microbial communities. There was no significant difference in microbial community compositions between different depths in either Waihai or Caohai (Figure S4).

### 3.3 Relationship between physiochemical variables, bacterial and photoautotrophic lineages

Pearson correlation analyses illustrated the key relationships between water physiochemical variables and microbial lineages (Fig. 5). In Waihai, many bacterial and photoautotrophic populations were strongly associated with physiochemical variables, *e.g.*, chlorophyll a, TN and pH. Particularly, the relative abundance of *Cyanobacteria* exhibited positive correlations with chlorophyll a and TN. To be more precise, four dominant orders in *Cyanophyceae* (*Chroococcales*, *Nostocales*, *Oscillatoriales* and *Synechococcales*) were positively correlated with nutrients (TN, NO<sub>3</sub>-N or PO<sub>4</sub>-P,  $p < 0.05$ ). In Caohai, no such correlation was observed.

RDA score plot further visualized the impacts of water physiochemical variables on bacterial and photoautotrophic community structure. In Caohai, the first two components together explained 32.27% and 50.25% of the total variance of bacterial and photoautotrophic communities, respectively (Fig. 6A and 6B). Among all variables, NO<sub>3</sub>-N, DO, TP and temperature were significant ( $p < 0.05$ ) and together explained 45.5% of bacterial community, where photoautotrophs were mainly explained by temperature, TP, pH, NO<sub>3</sub>-N, TN and conductivity (together 67.0%). In Waihai (Fig. 6C and 6D), a fewer variance was explained by water physiochemical variables and the significant variables ( $p < 0.05$ ) were pH, DO, TN, conductivity, TP, PO<sub>4</sub>-P and temperature for bacterial community (together 19.1%), and pH, temperature, TN, conductivity, TP, NO<sub>3</sub>-N and NH<sub>3</sub>-N for photoautotrophs (together 28.7%).

### 3.4 Microbial ecological network

The molecular ecological networks described the inner-relationships of bacteria and photoautotrophs in Caohai and Waihai (Fig. 7). Bacterial networks of Caohai and Waihai consisted of 6 and 5 major modules, respectively, and the core nodes were *Proteobacteria*, *Bacteroidetes*, *Cyanobacteria* and *Actinobacteria* (Fig. 7A and 7C). Photoautotrophic network had 5 major modules for Caohai with *Cyanobacteria*, *Chlorophyta* and *Bacillariophyta* as the core nodes (Fig. 7B), and 3 major modules for Waihai in which *Cyanobacteria* accounted for 65.25% of the core nodes (Fig. 7D).

The relationships between major modules and environmental variables were calculated using Mantel test (Table S2). There was no variable associating with all modules in the bacterial network of Caohai, and the key variables were TP (Module 1, 2, 5 and 6), NO<sub>3</sub>-N (Module 1, 2, 3, 5 and 6), pH (Module 1, 2, 3 and 4) and DO (Module 1, 2, 3, 4 and 6). In contrast, pH, conductivity and nutrients (NH<sub>3</sub>-N, NO<sub>3</sub>-N, PO<sub>4</sub>-P) were linked with all modules in the bacterial network of Waihai. Similarly, no variable was linked with all modules in the photoautotrophic network of Caohai and the key ones included NO<sub>3</sub>-N, PO<sub>4</sub>-P, pH, DO,

temperature and conductivity (Table S2), whereas chlorophyll a,  $\text{NH}_3\text{-N}$ ,  $\text{NO}_3\text{-N}$  and conductivity were associated with all photoautotrophic networks of Waihai (Table S2). These results hinted that both bacterial and photoautotrophic communities in Waihai were more sensitive to environmental variables than those in Caohai.

### 3.5 Community assembly processes and distance decay pattern of bacterial and photoautotrophic communities

Phylogenetic turnover of microbial communities in both Caohai and Waihai at each sampling time across the geographic distance was quantified using the null model (Fig. 8A-8D). In either area, both deterministic (50–80%,  $\beta\text{NTI} > 2$  or  $\beta\text{NTI} < -2$ ) and stochastic (20–50%,  $-2 < \beta\text{NTI} < 2$ ) processes contributed to the difference in bacterial assemblages, and deterministic process (> 90%) dominated the assembly of photoautotrophs.  $\beta\text{NTI}$  of bacterial communities decreased with geographic distances in both Caohai and Waihai, hinting that the assembly process headed from neutral selection to homogenizing selection and bacterial communities were more deterministically assembled in a larger geographic distance. On the contrary,  $\beta\text{NTI}$  of photoautotrophic communities increased with geographic distance, and the assembly of photoautotrophs tended to follow stochastic processes at a larger geographic distance. Comparing to Waihai, the proportions of stochastic processes for both bacterial and photoautotrophic communities decreased after ecological restoration in Caohai, hinting that ecological restoration projects seemed to stabilize microbial communities in Caohai, which were more controlled by the deterministic processes, *e.g.*, homogenizing selection.

Distance-decay patterns were observed between the taxonomic dissimilarity based on  $\beta$ -diversity of bacterial (Fig. 8E) and photoautotrophic (Fig. 8F) communities from 20 sites in Waihai. The dissimilarities of bacterial and photoautotrophic communities significantly increased with the geographic distances ( $p < 0.05$ ). It is worth noting that the distance-decay rate was much smaller on 30th July (T1, cyanobacterial bloom) than the other two periods, suggesting fewer microbial spatial heterogeneity during cyanobacterial blooms.

## 4. Discussions

Cyanobacterial bloom is a natural phenomenon by an aging process of nutrient enrichment, and eutrophication is one of the most critical drivers [2, 22, 27, 64], whereas human activities have intensified its level. Recently, numerous lakes and rivers around the world are suffering from serious cyanobacterial blooms, such as Erie Lake [65], Loch Logan [66], Taihu Lake [27], and some rivers [67, 68]. Among these cases, phosphorus and nitrogen are of the most concern, as they are the limiting nutrients for cyanobacterial growth and reproduction [69]. Dianchi Lake has suffered high nutrient levels since 1988 (TP:  $\sim 0.57$  mg/L in 1998 and  $\sim 1.43$  mg/L in 2009; TN:  $\sim 8.21$  mg/L in 1988 and  $\sim 15.34$  mg/L in 2009) [70], which far above the Class V limits of surface water in China. In the present study, the nutrient level is still higher in Caohai (TP of 0.46 mg/L and TN of 3.68 mg/L) than Waihai (TP of 0.21 mg/L and TN of 3.94 mg/L), attributing to the fact that Caohai receives wastewater discharge from Kunming city which contains relatively higher level of nutrients than other rivers flowing into Waihai [38]. Nevertheless,

cyanobacterial blooms in Waihai were more frequent than Caohai, and the water physiochemical variables fluctuated significantly along time in Waihai (Figure S3), revealing an eutrophic and unstable aquatic environment. In addition, chlorophyll *a*, which reflects the degree of cyanobacterial bloom to some extent [71], significantly and positively correlated with nutrients of TP, TN, NH<sub>3</sub>-N and NO<sub>3</sub>-N (Fig. 2A). This finding is consistent with previous studies that, the nutrient level is an important driving force for the occurrence of cyanobacterial blooms in this area [25, 72, 73].

Notwithstanding the similar levels of nutrients and chlorophyll *a* as Waihai (Fig. 1), cyanobacterial bloom did not occur in Caohai during the study period and chlorophyll *a* concentration had no significant correlation with nutrients (Fig. 2B). It might be attributed to the change of bacterial and photoautotrophic communities in Caohai after 15-year of ecological restoration projects [38, 41]. We found that the bacterial communities were similar in Caohai and Waihai, both dominated by *Proteobacteria*, *Bacteroidetes*, and *Cyanobacteria* (Fig. 3A), consistent with a previous study in Dianchi lake [74]. However, Caohai had a lower abundance of *Cyanophyceae* and more abundance of other photoautotrophs (Fig. 3B), possessing a more diverse community of photoautotrophs than Waihai. Cyanobacteria have physiological adaptations to successfully compete for limited resources, including luxury N and P uptake, buoyancy regulation using gas vesicles, and sustained growth at elevated temperatures [75]. In addition, they have grazer avoidance mechanisms, such as cyanobacterial toxicity and unpalatable [76]. Accordingly, cyanobacteria can occupy the niche of other primary producers and overwhelm the food web of the water ecosystem along with eutrophication. Consequently, the ecosystem becomes fragile and cyanobacterial bloom occurs frequently. To turn this situation around, ecological restoration projects change the microbial community by introducing other primary producers and reconstructing the food web. In this study, the significant change and higher diversity of photoautotrophic communities in Caohai with ecological restoration projects demonstrated a positive trend in the aquatic ecosystem. Together with sediment dredging and outer watershed replenishment activities, the pressure of cyanobacteria bloom was alleviated in Caohai, showing the critical roles and feasibility of ecological restoration projects in stabilizing aquatic microbial community structures. In addition, fewer photoautotrophic cyanobacteria and more complexity of communities in Caohai represented a stronger tolerance to eutrophication shock and improved food web [38, 41], consistent with another cyanobacterial bloom control project based on interspecies interaction [77].

Community stability is an important indicator of aquatic ecosystems [78]. Extensive industrialization and agricultural practices increase environmental pressure and ecological risks to lakes, thereby how to reconstruct a strong and robust aquatic ecosystem is crucial for managers and policy makers [79, 80]. In the present study, individual bacterial or photoautotrophic taxa in Waihai were strongly correlated with water physiochemical variables, where such correlations were seldomly found in Caohai (Fig. 5). Compared with other time points, the different community structure was only found on 30th July (T1) in Waihai, but not in Caohai (Fig. 4). In addition, results from RDA and ecological networks suggested that environmental variables that have close relationships with cyanobacterial bloom have a higher impact on bacterial or photoautotrophic communities in Waihai than those in Caohai (Fig. 6), and their total

explanation was also weaker in Caohai (Table S2). Thus, although the environmental conditions varied across different spatial-temporal scales in both Waihai and Caohai, the aquatic ecosystem of the microbial community in Caohai was more stable and not prone to disturbance. It might be attributed to the higher diversity of photoautotrophs in Caohai. According to the complexity-stability theory, ecosystem diversity is normally positively correlated with its stability, owing to the complex communities, made up of many predators and parasites, which can prevent populations from undergoing explosive growth [81]. In this study, the increased diversity of photoautotrophs improved the interspecific competition with the inedible cyanobacteria [82], consequently raising the complexity of food web and reconstructing the energy and element cycles [83–85]. As a result, Caohai after ecological restoration projects might have an accelerated energy and element flow, which can neutralize the exceeded nutrient load or other environmental changes and inhibit the cyanobacterial bloom to some extent and then increase the microbial diversity.

The dissimilarity of microbial community is generally reported to increase along with geographical distance [86–88], consistent with the increasing dissimilarities of both bacterial and photoautotrophic communities in Waihai with geographic distance in this study (Fig. 8E and 8F). Nevertheless, such pattern was weakened on 30th July (T1, Fig. 8E and 8F) with altered microbial community structures (Fig. 4E and 4F) when cyanobacterial bloom occurred, which might be explained by the homogenization of aquatic microbial community driven by cyanobacterial blooms. Different aquatic microbial communities were reported between algal bloom and non-algal bloom in a lake [89], and bacterioplanktonic communities gradually lose dissimilarities when algal bloom expanded in Amundsen Sea Polynya [90]. Furthermore, the higher stochastic microbial assembly of both bacterial and photoautotrophic communities in Waihai than in Caohai (Fig. 8A-8D) indicated that cyanobacterial bloom could result in more stochastic assembly. Previous studies have confirmed that stochastic processes play an important role in microbial assembly during cyanobacterial bloom [61, 91, 92], possibly enhanced by the lower microbial diversities, fewer competitions between different microbial taxa, and/or other stochastic processes [61]. Such increased stochastic processes, *e.g.*, probabilistic dispersal, weak selection, weak dispersal, diversification, and drift [93], can destabilize the aquatic ecosystem. For example, microbial taxa with a low abundance more likely to undergo inherent stochastic processes of birth, death, and reproduction due to the ecological drift (*e.g.*, random changes in organism abundance) [94, 95]. Accordingly, when cyanobacterial bloom occurred, more stochastic processes and less evident distance-decay patterns together aggravated the instability of aquatic ecosystem in Waihai. In contrast, ecological restoration projects seemed to stabilize microbial communities in Caohai, which were more controlled by the deterministic processes such as selections under homogeneous abiotic and biotic environmental conditions.

Decreasing nutrient levels by non-point source management and engineering measures is often viewed as the most common approach for cyanobacterial bloom control, which has been well practiced in several lakes [15, 92, 96]. Nevertheless, there are still some cases showing that the frequencies of cyanobacterial blooms do not decrease as expected after adopting nutrition control strategies. Taihu Lake and Okeechobee Lake are typical examples that well-designed nutrient control measures suffer from

nutrient input from tributaries [32, 97] and endogenous sources [98], respectively. Besides, as cyanobacterial bloom is the result of a combination of multiple environmental factors, nutrient control measures may be necessary but insufficient. In this study, the ecological restoration projects in Caohai hinted more focus on the stability of aquatic ecosystem for microbial communities. In a more stable ecosystem in Caohai, which had a similar nutrient level but higher biodiversity comparing to that in Waihai, microbial community displayed higher resistance in response to the environmental perturbation closely related to cyanobacterial bloom. Thus, compared with Waihai, microbial community composition in Caohai is relatively less affected by environmental variables to form cyanobacterial bloom. Additionally, from the lake morphological perspective, Caohai has a much smaller size and shallower depth, exhibiting faster and easier response to ecological restoration [99]. The larger area and deeper water of Waihai might challenge the performance of ecological restoration and require further study or engineering exploration. Nevertheless, there is no denying that a healthy aquatic ecosystem with high biodiversity and stability faces fewer risks of cyanobacterial blooms, and both nutrient control and ecological restoration are important boosts to ameliorate aquatic ecological health for algal bloom control.

## 5. Conclusion

In this study, we explored water physiochemical variables, bacterial communities and photosynthetic communities in Dianchi Lake. Although both Caohai and Waihai had a similar nutrient level and bacterial community structure, photosynthetic communities were significantly different and cyanobacterial bloom frequently occurred in Waihai in the period of the present work. It was explained by a lower diversity of photosynthetic community (Shannon index: 4.4 in Waihai; 5.3 in Caohai) with higher abundance of *Cyanophyceae* (89.9% in Waihai; 42.7% in Caohai), more correlations between environmental variables and microbial taxa, and stronger impacts of environmental variables on microbial assembly in Waihai. The nearly 15-year ecological restoration engineering created a relatively stable aquatic ecosystem in Caohai, which is less vulnerable to environmental change compared to Waihai. Nutrient levels are therefore the key driving force of cyanobacterial blooms in Waihai, not in Caohai. Our results proved that, besides nutrient load control, aquatic microbial community recovery by ecological restoration is also effective and feasible for cyanobacterial bloom control. Ecological restoration is a promising approach to recover aquatic community structure and diversity, particularly those of photoautotrophs, and the successful case of Caohai brings experience and reference for Waihai and other eutrophic lakes.

## Declarations

### Ethics declarations

### Ethics approval and consent to participate:

Not applicable

**Consent for publication:**

Not applicable

**Competing interests:**

The authors declare no competing interests.

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**Authors' contributions:**

DZ, SD and GL contributed to the conception and design of the study. YX, DL, FH and JD collected the samples and did the lab work. YX, YS, SD, LJ, CL and DZ did the data analysis. YX and SD performed the statistical analysis. YX, SD and DZ drafted the manuscript. YX and DZ revised the manuscript. All authors approved the submitted version.

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## Figures

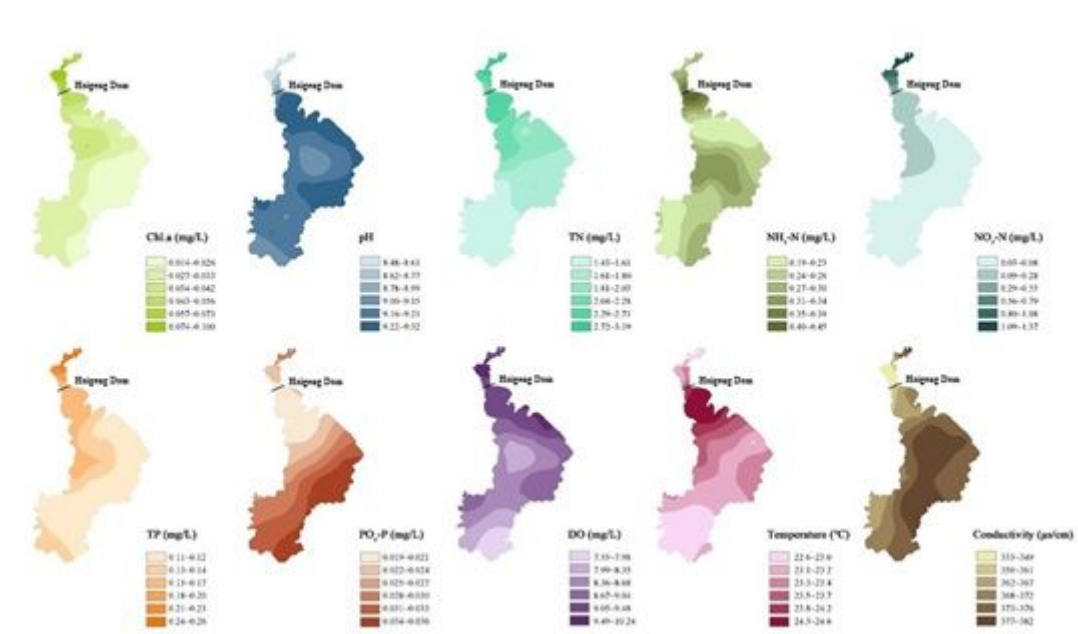


Figure 1

Water physiochemical properties at different sampling sites in Dainchi Lake. The spatial distribution is calculated by Kriging method in ArcMap (v.10.4.1) from the means of data at different time and depth for each sampling site.



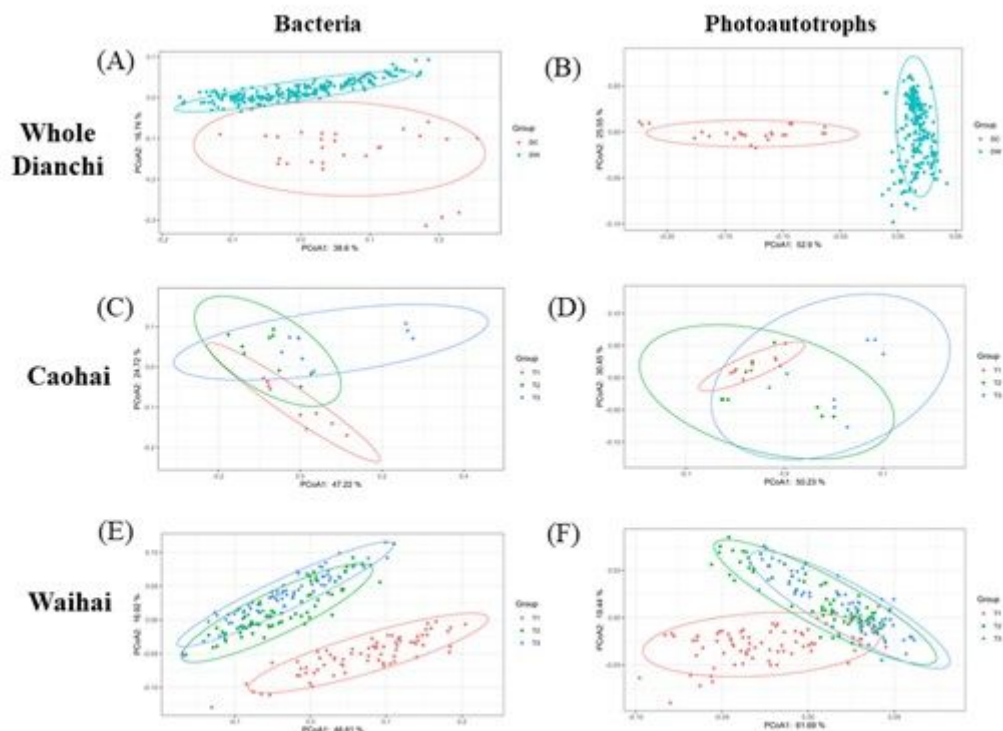
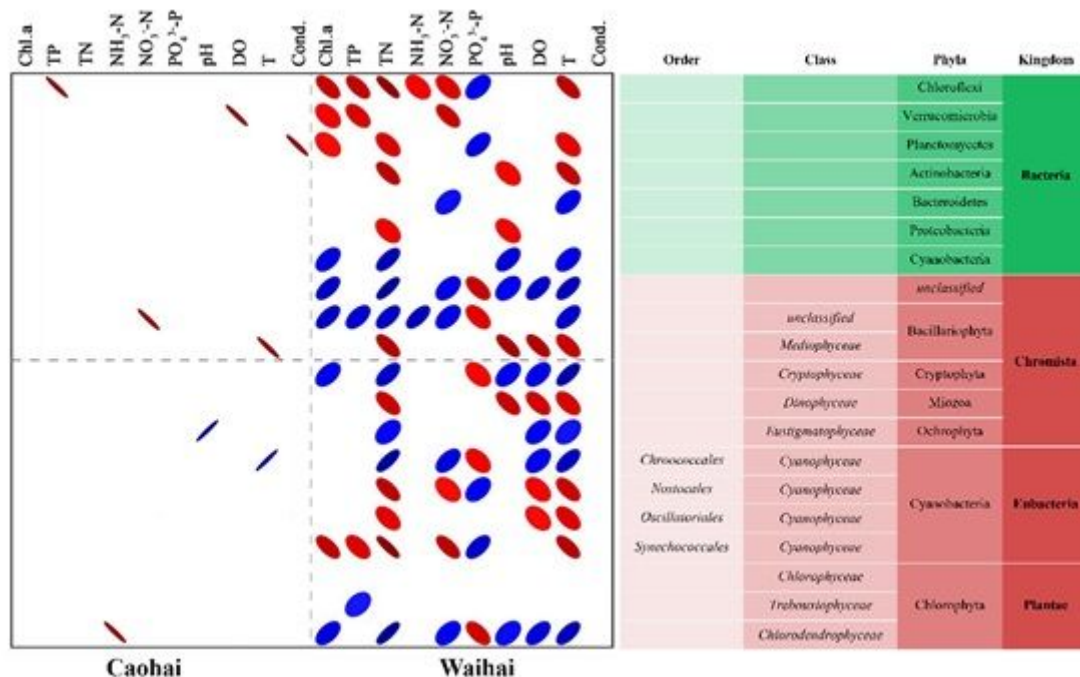


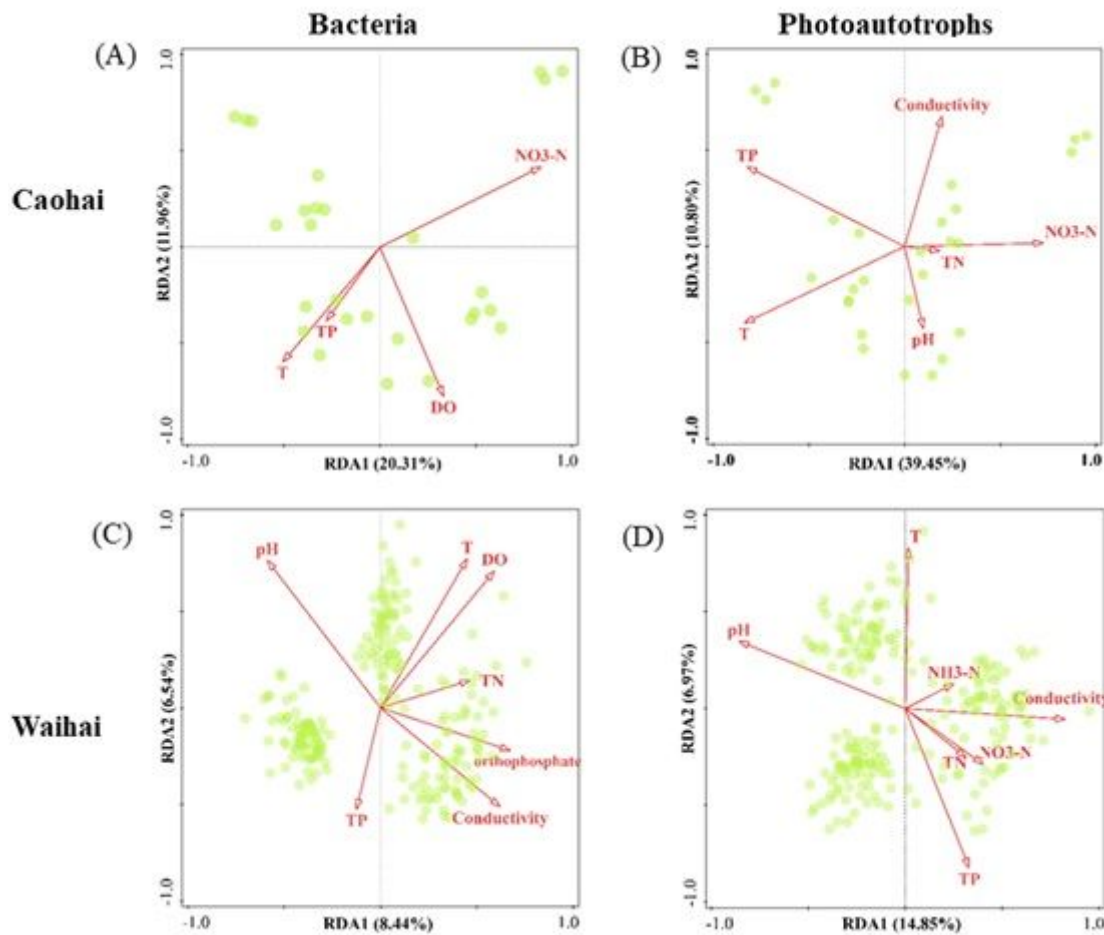
Figure 4

PCoA score plots for bacterial community (A) and photoautotroph community (B) between Caohai and Waihai. PCoA score plots for bacteria community (C) and photoautotrophic community (D) between three sampling time (T1 for 30th July, T2 for 20th August, T3 for 3th September) in Caohai. PCoA score plots for bacteria community (E) and photoautotroph community (F) between three sampling time (T1 for 30th July, T2 for 20th August, T3 for 3th September) in Waihai.



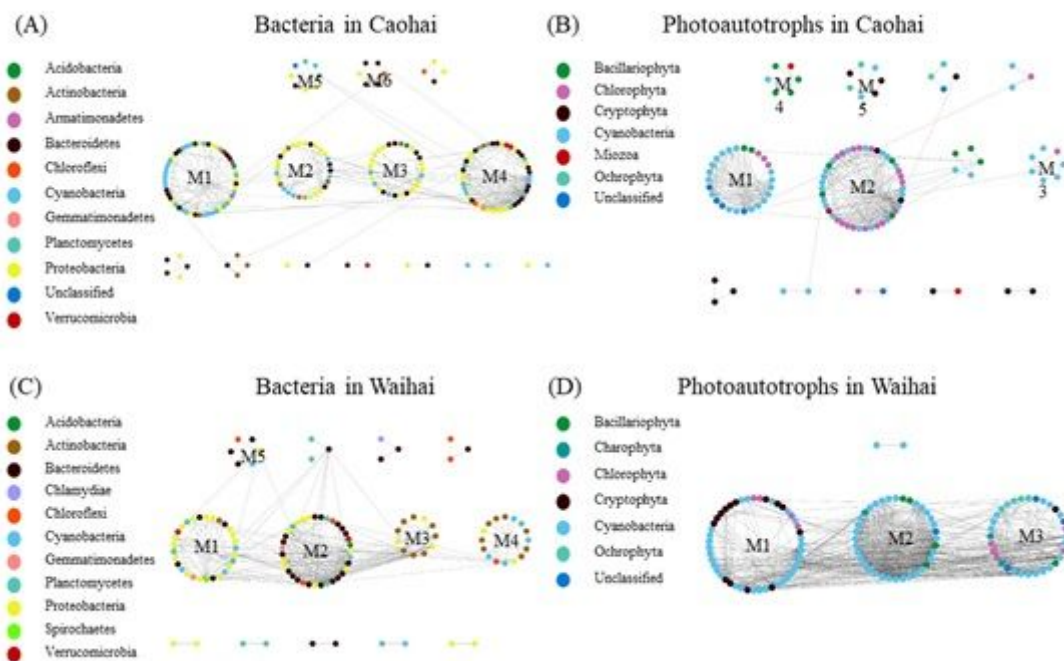
**Figure 5**

Correlation between water physiochemical properties and dominant bacterial lineages or photoautotrophic lineages. Blue and red ellipses represent significant positive and negative correlations, respectively ( $p < 0.05$ ). Darker color and larger ellipse represent stronger correlations.



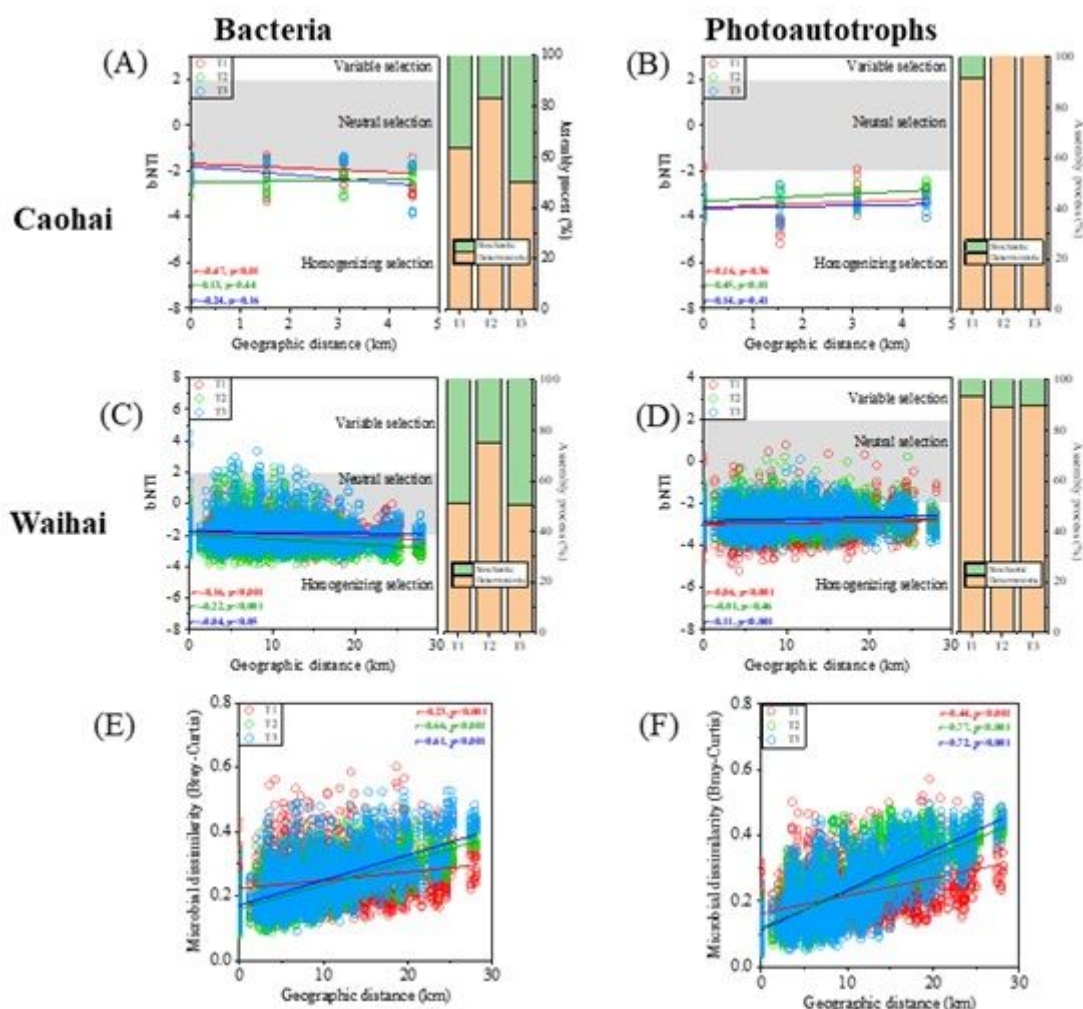
**Figure 6**

RDA score plots of bacteria community (A) and photoautotroph community (B) with key physiochemical variables in Caohai. RDA score plots of bacteria community (C) and photoautotroph community (D) with key physiochemical variables in Waihai.



**Figure 7**

Microbial ecological networks for bacterial communities (A) and photoautotrophic communities (B) in Caohai. Co-occurrence ecological network for bacterial communities (C) and photoautotrophic communities (D) in Waihai.



**Figure 8**

Geographic distance versus  $\beta$ NTI of bacterial communities (A) and photoautotrophic communities (B) in Caohai. Geographic distance versus  $\beta$ NTI of bacterial communities (C) and photoautotrophic communities (D) in Waihai. Pairwise microbial dissimilarity (Bray-Curtis distance) versus geographic distance of bacterial communities (E) and photoautotrophic communities (F) in Waihai.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterials.docx](#)