

Nutrients dynamic and temperature sensitivity of emergent plant litter decomposition in an inland freshwater wetland: perspective of microbial community structure and function

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Abstract

Among the most crucial biogeochemical processes in wetlands, the decomposition of emergent plant litter, significantly influences the dynamics of eutrophication, health and integrity of the ecosystem. However, the mechanisms that govern wetland nutrient and litter decomposition interactions are still not well understood. Here we carried out four different treatments to investigate the effect of different temperature (20 and 35 °C), ammonia nitrogen (NH₃-N) concentration (0.8 and 1.2 mg/L) and sediment on the changes of the water quality, organic matter composition and bacterial community succession in the leaf litter of lotus (*Nelumbo nucifera*). The results revealed that, all four water quality indexes chemical oxygen demand (COD), NH₃-N, total nitrogen (TN), total phosphorus (TP) initially showed an increasing and followed by a subsequent decrease over the 4 days of decomposition, and the concentration at the end of the test were higher than the initial value. More organic matters, nitrogen and phosphorus were obviously released from 35 °C treatments, while the increase of NH₃-N content inhibited the release of nutrients, and there was an adsorption effect of the sediment on nitrogen and phosphorus. Excitation emission matrix parallel factor analysis identified the presence of difficult biodegradable aromatic hydrocarbon structures of humus under the 35 °C treatments, and the litter decomposition at low NH₃-N concentrations and sediment treatments released more dissolved organic matter (DOM), especially the involvement of sediment promotes the production of amides and proteins. At 72 h, the decomposition of plant litters under 35 °C and low NH₃-N content improved the microbial diversity, and the main microorganisms included Proteobacteria (96.82 %), while the 20 °C and sediment were more suitable for the growth of Bacteroidota (25.20 %) and Firmicutes (9.91 %), respectively. Canonical correspondence analysis suggested that differences in bacterial abundance and diversity significantly correlated with COD and NH₃-N, and the relationship between bacterial diversity and environmental parameters was affected by decomposition phases. Moreover, the microbial differences between the early and late stages of decomposition were significant. Thus, we provide evidence that the complex litter decay in wetlands is the result of dynamic effects of nutrients and environmental conditions, accompanied by bacterial diversity succession.

Introduction

Plant litter is a key link in material cycling through organic matter decomposition and nutrient release, affecting the carbon budget of terrestrial ecosystem (Henry et al. 2015). Defoliation is a major source of nutrients in freshwater ecosystems. Unlike terrestrial ecosystems, litter decomposition in aquatic ecosystems is predominantly driven by a combination of environmental factors and the inherent characteristics of aquatic plants. It is estimated that 20–30% of the global soil carbon stocks in wetlands that only account for 5–8% of global land area, with a carbon sink intensity of 830 Tg/year (Mitsch et al. 2013). Litter in the inland freshwater wetland ecosystem can act as both source and sink of carbon due to the process of decomposition and accumulation of organic carbon, as well as the acceleration of microorganism turnover, which leads to the release of greenhouse gases such as carbon dioxide and methane. Large aquatic plants play a crucial role in maintaining ecosystem balance and water quality in grass-type lakes for absorbing and filtering pollutants from the surrounding environment,

particularly during the growing season (Bragato et al. 2006; Pinder et al. 2006). The rhizosphere microorganism associated with plants can also degrade pollutants (Ong et al. 2010), whereas the nutrients are released back into the water after the death and decomposition of plants, due to the limited utilization and consumption of aquatic organisms and microorganisms (Alvarez et al. 2006). Moreover, large aquatic plants primarily consist of refractory substances, such as lignin, which have a low degradation rate, so the accumulation of plant residues contributes to the increase in carbon stocks and sediment layers, which in turn accelerate the process of terrestrialization and carbon conversion (Kuehn et al. 2000) (Song et al. 2015). Plant decomposition is commonly recognized as a process involved in nutrient transport, elements such as C, N, P and some soluble components in plants are greatly lost due to leaching in the initial leaching stage of decomposition, while insoluble substances are more resistant to degradation (Serna et al. 2013). In the later stages of decomposition, these insoluble substances are slowly degraded under the action of microorganisms, which are then typically stored in the soil as residues after humification (Song et al. 2015). In recent years, the decomposition process of wetland plant litter and related microbiome has received increasing attention.

Litter decomposition processes are unique in different ecosystems, most studies on ecosystem processes have focused on forests and grasslands rather than wetland systems (Chen et al. 2023; Zhang et al. 2020b; Zhao et al. 2015). Litter decomposition is a key part of nutrient cycling in forest ecosystems, and the decomposition rates of different tree species vary due to differences in leaf litter qualities. Craig (Craig et al. 2022) discovered that high-quality (rapidly decomposing) litter promotes microbial carbon utilization efficiency, growth, and turnover. Soil microorganisms prioritize the utilization of high-quality litter because the decomposition of low-quality litter consumes more energy (Prescott 2010; Rahman et al. 2013). Additionally, there is also “home field advantage” in forest ecosystems, that litter decomposes more rapidly in its native environment compared to other environments (Wang et al. 2013). Large herbivores can impact litter decomposition by altering the litter quality, and regenerated plants after grazing tend to promote the accumulation of nutritious, thereby creating a positive feedback effect on carbon cycle in grassland (Penner et al. 2019). Aquatic plant types, litter quality, environment conditions and the interaction of these parameters are significant drivers of litter decomposition. Besides the impact of root exudates input on wetland carbon cycling, the dead residues of aquatic plants also accumulated in the water and substrates. The decomposition of plants also emits greenhouse gases into the environment, altering soil respiration and contributing to climate change (Duval et al. 2020), resulting in an important component of the wetland carbon cycle. Previous studies have observed an increased impact on water quality (TOC, TP, $\text{NH}_3\text{-N}$, etc.) with the higher litter quality, serving as an important factor in controlling the pollution generated by the decomposition of litter (Wu et al. 2017). The carbon-to-nitrogen ratio (C/N) of litter has been recognized as a key factor affecting decomposition and remineralization of decaying submerged plants (Yang et al. 2020). To date, few studies investigated both nutrient levels and temperature effect on litter decomposition in a single study, and their relative contributions to the composition of microbial community involved in litter decomposition are not well explored.

Because litter decomposition involves physical, chemical and biological processes, various environmental factors including the level of water dissolved oxygen (Asaeda et al. 2002), pH (Cornut et al. 2012), water temperature (Geraldes et al. 2012; Velthuis et al. 2018) and nutrients in the water environment (Hayes et al. 2017) can have an impact on breakdown, dissolution and substance transformation. Studies have shown that plant decomposition occurs at a slower rate when there are lower levels of dissolved oxygen and pH (Ruppel et al. 2004). Temperature strongly influences plant decomposition (Tao et al. 2019), and generally an increasing temperature promotes the release of substances during aquatic plants decomposition (Geraldes et al. 2012; Velthuis et al. 2018). The concentration of nutrients in the water environment affects the material leaching process of aquatic plants, which is mainly achieved by providing nutrients for the growth of microorganisms, affecting the microbial types and quantities, as well as the decomposition rate of litter. Typically, aquatic plants are more difficult to decompose in nutrient-poor environments than in eutrophic environments, potentially due to lower microbial load in nutrient-poor wetlands (Zhang et al. 2020a). Previous studies have predominantly examined the factors influencing the decomposition process of aquatic plants, including environmental conditions and the composition of the plants themselves, however, the underlying mechanisms driving these influences have not been thoroughly investigated.

Microorganism is one of the main factors influencing the rate of litter decomposition, and the alterations in litter composition also impact the structure and function of the microbial community. Fungi play an important role in the decomposition of litter and possess the capability to secrete diverse enzymes that facilitate the breakdown of recalcitrant organic matter (Purahong et al. 2014). The early stages of litter decomposition are primarily controlled by the concentration of different nutrients and the availability of carbon sources. In contrast, the later stages of decomposition are predominantly influenced by lignin (Berg 2000), and it has been observed that the fungal communities of the two decomposition stages could be categorized into four modules, each exhibiting a distinct relationship with the litter physicochemical properties (Purahong et al. 2016). In addition, bacteria mainly regulate the rate of decomposition of aquatic plants, with the decomposition accounting for approximately 90% of the total plants mass (Barik et al. 2000). The phylum *Proteobacteria* exhibits a high relative abundance of nitrogen-fixing bacteria (Hernes et al. 2001), and *Proteobacteria* and *Bacteroidota* mainly utilize easily degradable carbon as a carbon source in the early stages of decomposition (Golebiewski et al. 2019). Furthermore, research has demonstrated that certain colonies of Actinomycetes produce enzymes capable of breaking down lignin and cellulose, thereby functioning as decomposers of plant organic residues (Crawford 1978). It has been suggested that bacteria promote fungal degradation by providing electrons or essential micronutrients, thus are indispensable decomposers in the litter decomposition process (Osono et al. 2014). The coordination between microbial decomposability and environmental factors can be achieved through combined regulatory strategies, which implies that a feedback mechanism between microorganisms and environmental nutrient conditions could sustain the litter mineralization requirement.

Baiyangdian wetland is a typical inland freshwater wetland in North China, there has been little previous research about the interactive effects of different nutrient and temperature levels on litter decomposition

mechanism. Thusly, we took the main emerged plant of the Baiyangdian lotus as the object of study, and explored three main inquiries: (1) effects and synergies of different nutrient and temperature conditions on organic matter composition, water quality and decomposition rate during litter decomposition; (2) variation in microbial community succession during litter decomposition and keystone species different between bacteria; (3) the driving mechanism of nutrient-temperature factors on microbial community succession and the co-occurrence network patterns.

Materials and methods

Study area

This study was conducted in Baiyangdian wetland, located in the Xiongan New Area, a core area of the Beijing-Tianjin-Hebei region, China (38°43'~39°2'N, 115°38'~116°7'E). The wetland is the most representative shallow lake and herbaceous marsh wetland in northern China (Yuan et al. 2021a). The geographical scope belongs to the Daqing River system, which mainly consists of many deposits of varying sizes, with a total area of 366 km². The basin has a temperate monsoon climate with an average annual temperature of 7.3–12.7 °C and annual average precipitation of 563.9 mm. The elevation is high in the western part of the basin and low in the east, including mountains, plains and other types of landforms (Li et al. 2022). The main dominant groups of aquatic plants in Baiyangdian are submerged and emergent plants such as *Potamogeton crispus* L., *Potamogeton pectinatus* L. and *Nymphaeaceae* (Zhang et al. 2019). Baiyangdian wetland provides essential ecosystem services for the Beijing-Tianjin-Hebei region, including water supply and purification, hydrological control, biodiversity conservation, and climate regulation, and serves as an important tourist area (Ge et al. 2022). However, since the mid-20th century, the ecosystem function of this wetland has progressively deteriorated due to the escalating anthropogenic impacts such as hydrological changes and environmental pollution (Li et al. 2021).

Experimental design

In August 2020, fresh lotus (*Nelumbo nucifera*) leaves were collected from Shaochedian (38°54'52.56"N, 115°59'48.12"E), the lotus dominant community areas in the central wetland, and brought back to the laboratory according to the method described in Zhai et al. (Zhai et al. 2020). The litter bag method was used for litter decomposition experiment, and freshly collected lotus leaves were thoroughly washed and air-dried under natural conditions for 72 h, then the plant samples were subjected at 105 °C for 15 min to terminate any biological activity and dried at 80 °C to a constant weight. The treated lotus leaves were cut into 10 cm pieces and packed into 300 mesh nylon mesh bags with the dimension of 15×20 cm. An acrylic tube was used as the experimental container, filled with 1.2 L of water and placed inside a nylon mesh bag contained aforementioned plant pieces (Fig. S1). Four experimental treatment groups were set up, incorporating two influencing factors, among which the temperature factor included group A (20°C) and group B (35°C), the nutrient factor include NH₃-N concentration (0.8 and 1.2 mg/L) and sediment. Experimental water was synthetic, and the NH₃-N, COD, and TP concentrations in the initial were 0.72 (group A) and 1.27 (group B) mg/L, 0, and 0.43 ~ 0.6 mg/L, respectively. Sediment samples

(upper 5 cm) were obtained from three sediment cores from Shaochedian. The evenly mixed sediment was added to the bottom of the experimental container for 3 cm thick, the experimental water prepared above was added, and then put into the litter bag after the standing container for about 24h. The specific treatment groups were shown in Table 1. The experiment was conducted over a period of 3 d, and the biomass density of litter bag was set at 0.9 g/L. The water quality indicators (COD, NH₃-N, TN, TP) were measured at specific time intervals (0 h, 2 h, 4 h, 8 h, 16 h, 24 h, 72 h, 168 h, 408 h, 648 h) for each experimental group. Litterbags were periodically retrieved at 72 h and 648 h for component analysis and bioanalysis, including the Fourier infrared spectroscopy (FTIR), three-dimensional fluorescence, and UV-visible near-infrared diffuse reflectance.

Table.1 Standard table of experimental

Treatment	Temperature (°C)	NH ₃ -N (mg/L)	sediment
A2	20	0.8	3cm thick into the bottom of the experimental container
A3	20	0.8	--
B1	35	1.2	--
B3	35	0.8	--

Measurements of physical and chemical properties

Water samples were collected at each sampling stage in each experimental group and measured in the laboratory. TN was determined by alkaline potassium persulfate digestion-UV spectrophotometric method (7230G Uv-visible spectrophotometer; INESA INSTRUMENT). TP was determined by ammonium molybdate spectrophotometric method (7230G Uv-visible spectrophotometer; INESA INSTRUMENT). The ammonia nitrogen (NH₃-N), chemical oxygen demand (COD), of water were measured by a UV-visible water quality tester (LH-3BA, Beijing Lianhua Technology Co., LTD, China). All measurements were performed in triplicate.

Spectroscopic metrics characterization

Spectral characterization was carried out by taking 72 h (Sample-72 h) and 648 h (Sample-648 h) water samples. The water samples were passed through a 0.45 filter membrane, UV-vis absorption spectra were recorded from samples in within 1-cm quartz cuvettes by a spectrophotometer in a wavelength range of 200–800 nm at intervals of 1 nm. Absorbances (A) at each wavelength were baseline corrected by subtracting the measured absorbance at 680–700 nm (Pirie et al. 2005). To assess the relative aromaticity of DOM, the sample’s decadic absorption coefficient at 254 nm (m⁻¹) was divided by DOC concentration (mg⁻¹) to calculate the specific UV absorbance (SUVA254) metric (Helms et al. 2009).

The water samples were passed through a 0.45 filter membrane, EEMS (HitachiF7000, Japan) was measured using a spectrofluorometer (excitation: 200–500 nm with 3 nm interval and integration time at 10s; emission: 250–500 nm with approximately 1 nm interval). The fluorescence index FI, HIX and BIX were computed from the EEMS, giving ecologically relevant estimates of the relative proportion of microbial FDOM sources and the degree of humification, respectively.

FTIR is mainly based on the different absorption frequencies of the chemical bond to the infrared light in order to obtain the information of the chemical bond. Through the infrared data, combined with the spectral library can perform qualitative and quantitative analysis. In our study, we used KBr pellet technique (Haberhauer et al. 1998), the samples were prepared as follows: 50 ml of the overlying water was taken and freeze dried, then ground and pulverize it in an agate mortar. 1mg of homogenized ground sample was mixed and ground with 100mg of KBr, rolled into thin slices with a tablet press. The flakes were placed on a sample holder, corrected for environmental air as the background spectrum, and FTIR spectra were scanned at 500 nm–4000 nm (Thermo Scientific Nicolet iS20, USA).

DNA extraction and high-throughput sequencing

The samples for microbial high-throughput sequencing analyses labelled as A2/A3/B1/B3-1, A2/A3/B1/B3-2, representing the 72 h and 648 h, respectively. A 200 mL water sample was filtered onto a polycarbonate membrane with a pore size of 0.2 µm (Millipore). PCR amplification was performed using an ABI GeneAmp® Model 9700 PCR instrument. The V3-V4 region of bacterial 16S rRNA genes was amplified by the primer 338F(5'-ACTCCTACGGGAGGCAGCAG-3') and primer 806R(5'-GGACTACHVGGGTWTCTAAT-3') as previously described (Shen, 2016). The PCR reaction system was TransGen AP221-02: TransStart Fastpfu DNA Polymerase, 20 µl PCR reaction system. The program was as following: 95 °C for 3min; 95 °C for 30s, annealing temperature for 30s, and 15 cycles of 72 °C; 10 minutes at 72°C, and 10°C until halted by user. The resulting PCR products were detected using 2% agarose gel electrophoresis and then were subjected to Illumina MiSeq sequencing.

Data analyses and statistics

SPSS and Origin 9.0 software were used for statistical calculation and illustration. Redundancy Analysis (RDA) was used to analyse the relationship between bacteria community composition and environmental factors. Co-occurrence network analysis of nutrient cycling functional communities was performed using Gephi software (version 0.9.2) based on the Spearman correlation index ($p < 0.05$) to explore the relationship between dominant species and water quality indexes and plant components at the genus level.

Results and discussion

Impact of different microenvironment on water quality during the litter decomposition

The variation trend of COD concentration was similar among the different treatment groups, Fig. 1-a showed the COD concentration at 35°C was higher than that at 25°C by comparing the A3 and B3 groups ($p > 0.05$). Initially, the COD in both temperature groups increased to 135.9 ± 0.00 mg/L and 135.53 ± 0.55 mg/L within the first 4 h due to the release of organic matter by the litter decomposition, and then gradually decreased to 13.17 ± 0.29 mg/L and 15.06 ± 0.12 mg/L with the microbial degradation. Higher temperature promotes the growth of aerobic cellulose-decomposing bacteria, thereby accelerating the rate of microbial decomposition of plant residues (Bornette et al. 2011). The concentration of $\text{NH}_3\text{-N}$ and TP at A3 increased to approximately 3.185 ± 0.01 mg/L and 1.053 ± 0.01 mg/L, respectively. There were no significant differences between A3 and B3 ($p < 0.05$). Similarly, TN in the overlying water at A3 reached the maximum value of 6.81 ± 0.01 mg/L at 4 h and then fluctuated downward. The unit cumulative release of COD was highly significant greater in group B3 than in group A3 during the experiment, with 4.55 ± 0.00 mg/g/d ($p < 0.001$) (Table 2). The inhibition of microbial activities under low temperature conditions resulted in a reduce rate of nitrogen cycling and transport, leading to a high nitrogen content. Apoplasts, which contain organic nitrogen, decompose at a relatively slow rate. Additionally, nitrogen-fixing bacteria exist on the surface of apoplasts and immobilizes nitrogen in the surrounding medium through nitrogen fixation (Hernes et al. 2001), leading to the accumulation of nitrogen residues. The processes of nitrogen release, ammonification, nitrification, denitrification and nitrogen fixation by nitrogen-fixing bacteria exist simultaneously in the water body, contributing to fluctuation and changes observed in TN.

The decomposition of lotus leaves was impeded by high N concentration. In condition with $\text{NH}_3\text{-N}$ concentration of 0.8 mg/L (B1) and 1.2 mg/L (B3), the water TN showed no significantly difference with the measured concentration at 4.31 ± 0.01 mg/L and 4.14 ± 0.01 mg/L at the 648 h, respectively ($p < 0.05$). Previous research has indicated that increased concentration of $\text{NH}_3\text{-N}$ can influence the community structure of filamentous bacteria, resulting in the decrease in the rate of plant decomposition (Cornut et al. 2012). Moreover, the nitrogen application has been found to inhibit release of nutrients from leave litters under various nitrogen application conditions (Zhang et al. 2020a). However, a study by Menendze on the decomposition of *Ruppia cirrhosa* Petagna (Grande) suggested that the nitrogen application actually enhanced litter decomposition, possibly due to the presence of different microbial species in the experiment (Menéndez et al. 2003). In this study, it was observed that the rate of litter decomposition was higher under low nitrogen concentrations, suggesting that the microorganisms in the system might be better adapted to survive under such conditions.

The addition of sediment treatments (A2) enhanced litter decomposition rate compared with A3 treatment. The concentrations of water TN, TP and COD with sediment addition increased to the maximum value of 7.79 ± 0.01 mg/L, 1.12 ± 0.00 mg/L and 145.73 ± 0.64 mg/L earlier compared to the A3 treatment. The sediment serves as a habitat for abundant microorganisms that contribute to the consumption of organic matter, thereby facilitating plant decomposition. And the unit cumulative release of nutrient was significantly greater in the group A2 than in the group A3 ($p < 0.05$). As microorganisms decompose plant residues, nitrogen-fixing bacteria also thrive on the surface of the litter, giving rise to a

variety of microbial symbiotic networks and lead to fluctuating changes in $\text{NH}_3\text{-N}$ levels. Furthermore, sediment demonstrate an adsorption effect on nitrogen and phosphorus, which leads to a decrease in TN and TP contents in water, as the adsorption effect surpasses the decomposition effect. The sediment contains enzymes such as β -glucosidase, cellulose hydrolase, and acetylglucosaminidase, which play a dominant role in litter decomposition by supplying sugars and nutrients for microorganisms, in turn, accelerates the rate of decomposition (Zhang et al. 2007). Moreover, sediment-associated functional microorganisms actively participated in initial microbial decomposition of insoluble components, facilitating the breakdown process and reducing its duration (Hui et al. 2019).

Table.2 The unit cumulative release of nutrients

mg/(g·d)	A2	A3	B1	B3
COD	168.42 ± 0.52 ^a	110.59 ± 0.06 ^c	147.44 ± 0.18 ^b	110.37 ± 0.03 ^c
NH ₃ -N	2.40 ± 0.01 ^b	1.35 ± 0.01 ^c	2.85 ± 0.03 ^a	1.14 ± 0.00 ^d
TN	6.87 ± 0.01 ^a	3.68 ± 0.00 ^d	6.16 ± 0.01 ^b	4.55 ± 0.00 ^c
TP	1.25 ± 0.016 ^a	0.72 ± 0.021 ^d	1.02 ± 0.039 ^b	0.84 ± 0.028 ^c

Changes in dissolved organic matter during decomposition of litter

The UV-Vis spectra of the dissolved organic matter at 72 h and 648 h were analyzed (Fig. 2), and the spectral curves consistently demonstrated a reduction in absorbance with increasing wavelength. The samples exhibited absorption peaks ranging from 220 to 300 nm, corresponding to the B absorption band caused by the π - π^* jump of the benzene ring (Nishijima et al. 2004).This indicates the presence of aromatic ring structure, as well as the presence of lignin, phenols and other recalcitrant substances. The absorption peak at around 280 nm at 72 h was used to evaluated the extent of aromatic conformation (Chin et al. 1994), and the higher value correspond to a greater degree of aromatic conformation (Fan et al. 2006), which can further provide insight into the molecular weight of the organic matter. Figure 2 showed that the absorbance of B3 was higher than that of B1. It is worth noting that the magnitude of the absorbance is positively correlated with molecular weight of the organic matter (Wang et al. 2009). This suggested that organic matter exhibits a greater molecular weight under a concentration of 0.8 mg/L $\text{NH}_3\text{-N}$, which in turn promotes litter decomposition.

SUVA254 provides an indication of the percentage of DOM that is in the form of highly photoreactive, relatively biologically stable aromatic carbon (Stubbins et al. 2008). The SUVA254 value indicates the extent of humification, with higher values suggesting a greater degree humification. The absorption peaks at 254 nm are associated with samples that contain compounds with unsaturated carbon-carbon bonds (Fig. 3-a), such as aromatic compounds (Schnitzler et al. 2007). This observation aligns with the explanation, which primarily attributes the presence of these compounds to the oxidation and

fragmentation of lignin-derived compounds (Chefetz et al. 1998). Additionally, Boissier found a significant correlation between phenols, polyphenols, and the degree of organic matter decomposition (Boissier et al. 1993). The SUVA₂₅₄ values of all experimental groups showed a slight increase during the decomposition process, suggesting an increase in unsaturated bonds within the organic matter, this also indicates the removal of non-aromatic compounds or the production of small amounts of aromatic compounds as the decomposition time advanced (Zhou et al. 2022b). At 648 h, the SUVA₂₅₄ value was higher at 35 °C compared to 20 °C, indicating a higher concentration of aromatic substances in the samples. The elevated temperature enhances microbial activity, leading to an accelerated decomposition rate of litter and a facilitated microbial-dominated humification process, ultimately increasing the degree of humification (Cotrufo et al. 2013; Zhou et al. 2022a). Throughout the experimental cycle, group B3 exhibited the maximum SUVA₂₅₄ value of 1.231 at 648 h, suggesting the highest level of humification. A comparison of A₂₅₀/365 (Peuravuori et al. 1997) revealed that the experimental group was less humified at 72 h, corresponding to the presence of humin in samples, which is known to be resistant to decomposition (Fig. 3-b). As the experiment progressed, the samples underwent a shift towards predominantly fulvic acid at 648 h, influenced by microbial activity (Minero et al., 2007). The values of A₂₅₃/203 indicated a higher presence of unsubstituted aromatic ring structures in all treatment groups at 72 h (Fig. 3-c). In contrast, the substituents exhibited more carboxyl, carbonyl, hydroxyl, and esters at 648 h (Korshin et al. 1997), except in the experimental group with sediment, and the difference could be attributed to the influence of microorganisms.

Fourier infrared spectroscopy (FTIR) was employed to identify the functional groups and vibrational spectra of vibrational polar bonds (Dean et al. 2010), enabling the determination of the chemical components of the samples (Fig. 4). The curve trends in treatment groups were approximately similar, with variations primarily observed in transmittance magnitude. The presence of a broad absorption peak at 3750–3200 cm⁻¹ indicated a significant amount of O-H in the sample, originating from carbohydrates in the apoplast, including polysaccharides and proteins, thus indicating the presence of substances like cellulose (Dean et al. 2010; Olk et al. 2000). A minor absorption peak at 3000–2700 cm⁻¹ suggested the presence of an aliphatic alkane structure, further indicating that the sample contains sugars (glycosides) or vitamins (Filip et al. 1988; Her et al. 2008). The peak observed at 2500–2000 cm⁻¹ in the infrared spectrum is typically associated with C ≡ C stretching vibrations, indicating the presence of heptyne. Furthermore, the absorption peak at 1900–1630 cm⁻¹ confirms the presence of heptyne in the sample. However, variations in the intensity of the absorption peaks were observed, the absorption peaks at 1628–1411 cm⁻¹ indicated the presence of amides and possibly proteins, and most of the absorption peaks in B1 were higher compared to A3, indicating that rising temperature promoted litter decomposition and resulted in a higher concentration of organic matter. Moreover, there were fewer absorption peaks observed at 648 h compared to 72 h, which could be attributed to the secretion of extracellular enzymes by microorganisms during litter decomposition, and break down polymers such as cellulose and proteins into the soluble monomer materials. The narrower absorption peaks in group B1, as depicted in Fig. 3-a, suggested that the NH₃-N concentration at 1.2 mg/L was unfavorable for the synthesis of amide or protein compared to B3. This finding was consistent with the research conducted

by Brock et al on the *Nymphaea alba* L., which revealed that N supplementation promotes lignin content in white water lily residues, thus impeding the decay process (Brock et al. 1985). Based on the analysis of the graph comparing the A2 and A3 groups, it was evident that all three curves exhibit an absorption peak except for A3–72 h, which lacked an absorption peak at $1628\text{--}1411\text{ cm}^{-1}$, could be assigned of the involvement of the substrate was advantageous for the synthesis of amide or protein compounds. Overall, the comparison result highlights the positive impact of substrate involvement on the production of amide or protein compounds, as well as the subsequent nutrient release and microbial activity enhancement in the water. The participation of microorganisms in plant decomposition further reinforces the significance of the substrate in ecological processes.

Fluorescence EEMS have proven critical to the description of DOM bioavailability, and therefore, its role in terrestrial and aquatic ecosystem nutrient cycling (Zhao et al. 2013). The decomposition of aquatic plant apoplast results in release of soluble organic matter into the overlying water (Abril et al. 2016), and three-dimensional fluorescence spectra are capable of representing organic matter such as humus and protein-like compounds (Cuss et al. 2015; Zhao et al. 2015). Figure 5 illustrated that all the water samples contain tryptophan-like, aromatic proteins, tyrosine, humus, humic acid and fulvic acid substances. Humus-like substances are typically derived from decay and decomposition products of plants. Tryptophan production, apart from being influenced by microbial activity, mainly originates from polycyclic aromatic hydrocarbons or related substances and by-products, which affect the ratio of amine to protein-like substances. In the pre-decomposition stage, soluble components such as sugars, proteins, organic acids, phenols, etc., were rapidly released with high intensity fluorescence. Subsequently, the release rate of tyrosine and acid-like humic acids occurred at a slower pace, so that the concentration of dissolved substances decreased towards the end of the experiment, and the fluorescence peaks at 648 h exhibited a significant reduction compared with that at 72 h. The fluorescence intensity of the samples at 35°C (A groups) was greater than that at 20°C (B groups), this difference could be attributed to the fact that elevated temperatures promote the metabolic and growth rate of microorganisms, resulting in faster cycling of organic matter (Zhou et al. 2016). Moreover, elevated temperatures stimulate species interactions, leading to increased metabolism activity of individual microorganisms, higher abundance of degradation-dominant bacteria, and accelerated litter decomposition. Samples in B3 groups with $\text{NH}_3\text{-N}$ concentrations of 0.8 mg/L , as well as sediment involvement groups (A2), exhibited higher fluorescence intensity, contributing to the litter decomposition released greater amount of soluble organic matter at a faster rate.

The fluorescence index FI is commonly used to differentiate DOM originating from various sources (McKnight et al. 2001), the aquatic and microbial sources typically exhibit an FI value of 1.9, whereas terrestrial and soil sources tend to have an value of 1.3. As data presented in Table 3, the FI values of each treatment group surpassed 1.9, indicating that the DOM was a result of microbial action (Cui et al. 2022). The humification index (HIX) value at 72 h lower than that at 648 h and negatively correlated with TP but positively correlated with TN ($p > 0.05$) (Fig. 5-b), indicating an increase in complex molecules, such as aromatics, and suggested that humification intensified as the experiment progressed. The

humification was higher in the groups exposed to 35 °C, as indicated by the greater HIX value of B3, which indicated a promotion of litter decomposition at 35 °C. On the other hand, the BIX representing the dissolved organic matter produced by microbial activities. The BIX values at 72 h for the A2 and B3 groups were smaller than that at 648 h and positively correlated with COD ($p > 0.05$), which was corresponding to a significant change in the source of organic matter, and primarily relied mainly on exogenous inputs released by litter decomposition in the early stage. At 648 h, the BIX value exceeded 1, which was predominantly related to the dissolved organic matter produced by bacteria (Huguet et al. 2008). Initially, microbial activity was limited due to leaching being the primary process, while towards the end of the experiment, microbial activity became more prominent. Dissolved organic matter showed strong primary characteristics, as indicated by the BIX value for A2-72 h ranging from 0.6 to 1, that likely originating from the sediment. Based on the significant increase of BIX value at 648 h, the presence of sediment facilitated the decomposition of apoptotic matter. According to previous research, which also demonstrated the presence of robust biogenic properties in wetland soils in the riparian zone of Chongming Island (Wang et al. 2015).

Table.3 Spectral parameters of dissolved organic matter under different conditions

Sample	FI	HIX	BIX
A2-72 h	2.41	1.67	0.66
A2-648 h	2.64	3.30	2.82
A3-72 h	2.59	1.58	0.55
A3-648 h	2.53	1.251	0.50
B1-72 h	2.87	1.28	0.48
B1-648 h	2.35	1.88	0.55
B3-72 h	2.83	2.51	0.33
B3-648 h	2.63	2.58	1.20

Changes in bacterial community composition and diversity

The sequence detection data of all the samples in the 72 h and 648 h of the whole experimental cycle were statistically analyzed (Table S1), and the results after sequencing showed that the range of the number of sequences of all the valid sequenced genes was 39310 ~ 74772. Microbial abundance increased as decomposition time progressed, and the Chao and Shannon indexes ranged from 100.5 to 351.12 and from 2.31 to 4.00, respectively. The dilution curve of Shannon diversity index (Fig. S2) tended to flatten, and were always smooth state, representing that the change of the number of sequences can be enough to respond to the information of the diversity of bacteria within the sample. Chao index and Shannon of bacterial community diversity in the overlying water at 20°C at 648 h (Table 4) were significantly lower than that at 35°C ($p < 0.05$), which was consistent with previously study by Yuan that

the increase in temperature favors microbial growth (Yuan et al. 2021a). The bacterial richness of the added sediment was higher, but there was no significant difference ($p > 0.05$) in Chao index with the unadded groups, whereas the Shannon's index was significant different ($p < 0.05$). In this regard, that the addition of sediment has been found to increase the microbial abundance and diversity in the water due to the presence of *Chloroflexi*, *Proteobacteria*, and *Acidobacteria* (Wang et al. 2018), which are released from the sediment. Increasing the concentration of $\text{NH}_3\text{-N}$ resulted in the Chao index, and a significant difference was observed between the two experimental groups ($p < 0.05$). In our study, higher $\text{NH}_3\text{-N}$ concentrations were found to reduce microbial abundance compared to lower $\text{NH}_3\text{-N}$ concentrations. While increased nitrogen availability provides nutrients to microorganisms, the pH reduction caused by added nitrogen has a detrimental effect on microorganisms (Sun et al. 2018).

As the decomposition time progressed, microbial abundance and diversity were higher at 648 h compared to 72 h in all experimental groups. The water quality indicators exhibited changes during the experiment, resulting in the suppression of certain microorganism activities and alterations in dominant microbial populations. In the later stages of litter decomposition, the insoluble material that remains undergoes humification in the water, leading to an increase trend in the Shannon index. Aneja investigated the variation of microbial communities during litter decomposition by using litterbags in streams, revealed that the litter quality played a crucial role in microbial succession (Aneja et al. 2006). During the process of decomposition, the levels of easily accessible carbon in the form of sugar and starch decrease, while the recalcitrant carbon such as lignin and phenol increase, with the change in the litter quality also result in the change of microorganism community composition (Xu et al. 2013).

Table.4 Microbial Alpha Diversity Index

Group	Sample	Chao	Shannon	Coverage
A2	A2-72 h	208.15	3.01	99.88%
	A2-648 h	351.12	3.29	99.93%
A3	A3-72 h	135.88	2.43	99.93%
	A3-648 h	246.71	3.14	99.94%
B1	B1-72 h	128.00	2.31	99.95%
	B1-648 h	314.24	4.00	99.96%
B3	B3-72 h	100.50	2.84	99.95%
	B3-648 h	237.60	3.30	99.96%

Research has demonstrated that variations in environmental and nutritional conditions can disrupt the natural ecological balance of water, subsequently leading to alterations in the composition of bacterial communities (Ferreira et al. 2016). Specifically, the microbial community composition at the phylum level displayed structural variations across different decomposition periods and experimental groups (Fig. 6-

a), however, *Proteobacteria* (44.0–96.8%) consistently emerged as the dominant phylum. The other dominant phyla were *Bacteroidota* (1.56–35.2%) and *Firmicutes* (0.24–41.83%). Significant quantities of nitrogen and phosphorus were released into the water during the initial stage of plant decomposition, primarily through the activity of *Proteobacteria*, and specifically, higher temperatures have been found to be associated with an increase in *Proteobacteria* abundance (Tao et al. 2019). *Bacteroidota* was the second most prevalent phylum, with the exception of the sediment supplemented groups with the more prevalent of *Firmicutes* in the initial stages. This was consistent with the previous study that have reported similar high abundant of *Bacteroidota* and *Firmicutes* during litter decomposition (Wang et al. 2020). It is noticeable that the abundance of *Firmicutes* can be markedly involved in the decomposition of various substances and elements, owing to their function of participate in the refractory substances decompose such as cellulose and lignin (Michaud et al. 2009). On the other hand, *Bacteroidota* is indeed associated with the transformation of organic compounds including DNA and proteins (Goffredi et al. 2010). In comparison with 20°C, warming significantly increased the abundance of *Proteobacteria*, decreased the number of *Bacteroidota*, and increased the bacterial species. This result ties well with previous studies wherein Wu, the contrasting temperatures would kill many of the original cold-adapted organisms, enabling the proliferation of organisms that are resistant and resilient to higher temperatures (Wu et al. 2015). Yuan found that warming significantly increases the complexity of microbial networks, including network size and number of key species, as compared to environmental controls (Yuan et al. 2021b). In the later stages of decomposition, there were no significant differences between the two experimental groups (A3-2 and B3-2) ($p > 0.05$). Moreover, γ -*proteobacteria* (20.74–86.42%) was found to be first dominant class (Fig. 6-b), which play a crucial role in metabolizing carbon sources and possess a denitrifying function (Purkhold et al. 2000). The *clostridia* (5.23%~30.30%) and *Bacteroidia* (3.50%~25.18%) were significantly abundant in A2 group due to the introduction of bacteria-containing sediment into the reaction vessel, which leading to a distinct microbial composition and micro-environment (Shen et al. 2016). This finding aligns with the research conducted by Wu, where an evaluation in the abundance of *clostridia* and *Bacteroidia* was observed following the addition of the substrate (Wu et al. 2017). The observed increase in α -*proteobacteria* and their functions, including organic matter consumption, $\text{NH}_3\text{-N}$ decomposition and nitrogen fixation, indicate their important role in maintaining ecosystem health and nutrient cycling (Purahong et al. 2016). Furthermore, the increase in α -*proteobacteria* abundance observed in response to higher temperature and reduced $\text{NH}_3\text{-N}$ concentration, along with the resulting acceleration of litter decomposition, highlights their important role in ecosystem nutrient dynamics.

According to the bacterial genus level data of litter decomposition, the relatively high abundance of *Pseudomonas* (0.34–43.75%), *Curvibacter* (1.95–57.87%) and *Flavobacterium* (0.04–28.74%) might be the result of the nitrogen-fixing abilities consistent with other studies (Zhu et al. 2022). There were 92 genera common to all experimental groups, indicating a highly similar microbial composition (Fig. 7). Among them, *Flavobacterium* showed the significantly higher abundance in A3-72 h ($p < 0.05$), which was classified among bacteriophages that actively contribute to the process of carbon cycling and reduce the COD content in water (Garcia-Pausas et al. 2011; Teeling et al. 2012). Additionally, there were

substantial differences in bacterial community structures at the genus level among the different stages of decomposition. The abundance of *Flavobacterium* in anaphase of litter decomposition was lower compared to initial phase ($p > 0.05$), and the abundance of *Pseudomonas* and *Curvibacter* was higher in initial 72 h ($p > 0.05$) (Fig. S3). Nutrient release during litter decomposition drives the changes in bacterial communities, with certain microorganisms emerging as dominant species due to nutrient utilization. *Pseudomonas*, belongs to *Proteobacteria*, is a Dissimilatory phosphate-accumulating organism (DPAO), which has been involved in the P cycle and transformation, as well as the nitrification in the nitrogen (N) cycle. The genus-level bacterial diversity was higher in A3-2 (Fig. 6-b). *Pseudomonas* exhibited the highest abundance in the non-added sediment group and maintained a relatively high abundance throughout the early and late stages of litter decomposition (A3-1 and A3-2). *Curvibacter* exhibited the highest abundance in the high $\text{NH}_3\text{-N}$ group and played a role of denitrification, converting $\text{NH}_3\text{-N}$ to $\text{NH}_2\text{-N}$, while utilizing $\text{NH}_3\text{-N}$ and organic matter as the nitrogen source. This finding aligns with previous studies that demonstrated an increase in N-related bacterial abundance due to N fertilization (Sun et al. 2018).

Identifying core microorganisms and interspecies relationships in the plant litter decomposition

To investigate the relationship between microbial communities, environmental variables with litter decomposition, bacterial community and environmental parameters were used for redundancy analysis (RDA and CCA). On phylum level, 60.64% of the variance was explained by the RDA1 axis and 14.00% by the RDA2 axis (Fig. 8-a), which collectively explained 74.64% of the variance difference. Among the factors, COD ($p = 0.083$) and TP ($p = 0.117$) exerted a stronger influence on the bacterial community compared to other variables. On genus level, 21.10% of the variance was explained by the CCA1 axis and 16.25% by the CCA2 axis (Fig. 8-b), which collectively explained 37.35% of the variance difference. Among the factors, COD ($p = 0.048$) and $\text{NH}_3\text{-N}$ ($p = 0.049$) exerted a stronger influence on the bacterial community compared to other variables. Previous studies have consistently identified COD as the primary determinant of microbial community changes (Fang et al. 2023). Meanwhile, TP has been recognized as another significant factor influencing the alterations in microbial communities (Zhang et al. 2012). Wang confirmed the significance of P as a key driver of biological metabolism in water (Wang et al. 2018). Despite the high nitrogen concentration, its impact on the microbial community was insignificant, possibly due to the microbial community's resistance to the effects of nutrient enrichment. In addition, N is a crucial element utilized by microorganisms. The TN content in the water showed higher variability during litter decomposition. It may be a result of increased microbial demand for N, which leads to the fixation of N and thus reduction of N release (Gessner 2010). Consequently, the decomposition of N in litter is primarily influenced by biological factors, nitrogen content fluctuates in correlation with the decomposition of organic matter.

The species and environmental factors (TP, TN, COD and $\text{NH}_3\text{-N}$) with the top 20 total abundance at the phylum classification level were analyzed by Heatmap (Fig. 9). The relationship between environmental factors and microorganisms was different at different times. In the pre-experimental period, only COD

and TP were associated with bacterial community composition, *Proteobacteria* showed a significant positive correlation with TP. Actinobacteria showed a significant negative correlation with COD. *Firmicutes* showed a significant negative correlation with TP, but *Bacteroidota* did not show a significant correlation with the environmental factors (Fig. 9-a). The relationship between environmental factors and microorganisms was stronger at the end of the experiment than at the beginning of the experiment, and only $\text{NH}_3\text{-N}$ and TN were related to microbial community composition. Actinobacteria showed a significant positive correlation with TN. *Proteobacteria*, *Firmicutes*, and *Bacteroidota* did not show a significant correlation with environmental factors.

During the process of litter decomposition, microbial community dynamics interact with various environmental factors. The network analysis was employed to identify the core bacteria at the genus level associated with water quality during litter decomposition, where each node was represented as a genus. As shown in Fig. 10-b, the majority of nodes associated with TP at 72 h showed a negative correlation with large proportion of bacteria, with over 60% belonging to Firmicutes genus, but only 5 nodes displayed the correlation at 648 h (Fig. 10-c). At the initial stage, the microorganisms were influenced by the environment and the adapted microorganisms proliferated, decomposing insoluble substances and causing the release of large amounts of phosphorus from plant residues (Ozalp et al. 2007). This process inhibited the growth of certain genus, while promoting proliferation of other adapted genus. The number of nodes involved in COD conversion was not significantly different between 72 h and 648 h ($p > 0.05$). Initially, only a few nodes were involved in the conversion of $\text{NH}_3\text{-N}$ and TN, but most of the nodes exhibited N fixation after 648 h had, which was consistent with Purahong's findings (Purahong et al. 2016). Flavobacterium enhances the nitrogen fixation by nitrogen-fixing bacteria by influencing the secretion flavonoids (Dardanelli et al. 2010). A large number of *Proteobacteria* nodes appeared in both phases, suggesting that it was mainly Proteobacteria that played a role throughout the whole experiment period (Zhang et al. 2020b). In addition, co-occurrence patterns revealed a significant increase in the complexity and connectivity of bacterial interactions in 648 h than during that in 72 h ($p < 0.05$). Previous study states that there are complementarity effects between biotic and abiotic, and that changes in the abiotic environment interact with community composition and the loss diversity, ultimately influencing the efficiency of microbial carbon utilization efficiency within the community (Domeignoz-Horta et al. 2020).

A plethora of microorganisms participate in the decomposition process of aquatic plant litter, each performing distinct functions. Species with high abundance were identified as functional microorganisms decomposing aquatic plants through the utilization of LEfSe multilevel species difference discriminant analysis. It is evident that both the predominant species in 72 h (*Acidovorax*, *Pantoea*, *Pelomonas*, *Herbaspirillum*) and the dominant species in 648 h (*Rhizobiales*, *Azospirillum*, *Pseudacidovorax*, *Xanthobacter*, *Phenylobacterium*) belong to *Proteobacteria*, which is consistent with the results of co-occurrence network analysis (Fig. 10-b; Fig. 10-c). There were subtle variations in microbial abundance trends among different experimental groups (Fig. 10-a), probably attributed to differences in the rate of litter decomposition and nutrient content within the water. Most of the

microorganisms observed in this experiment were nitrogen-fixing bacteria, suggesting that functional microbial taxa have a direct or transient influence on nitrogen cycling processes. Previous study has also highlighted that the abundance of nitrogen-fixing genes changed with vegetation type (de Sosa et al. 2018).

Conclusion

This study examined the effects of various environmental factors on the decomposition of emergent plant litter, considering higher temperature, low $\text{NH}_3\text{-N}$, and sediment addition promote litter decomposition, organic matter and other nutrients release. The fluorescence analysis displayed that litter decomposition characterized by low humification, microbial activity and sediment addition increased DOC during the decomposition process. At the end of the experiment, the diversity and richness of microorganisms increased, the first dominant group of bacteria did not change, were Proteobacteria, but the proportion of the total number of bacteria increased. COD and TN explained the bacterial community more than the other factors, and most of the bacteria in the later period of the experiment were associated with TN, mostly nitrogen-fixing bacteria.

Declarations

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Figures

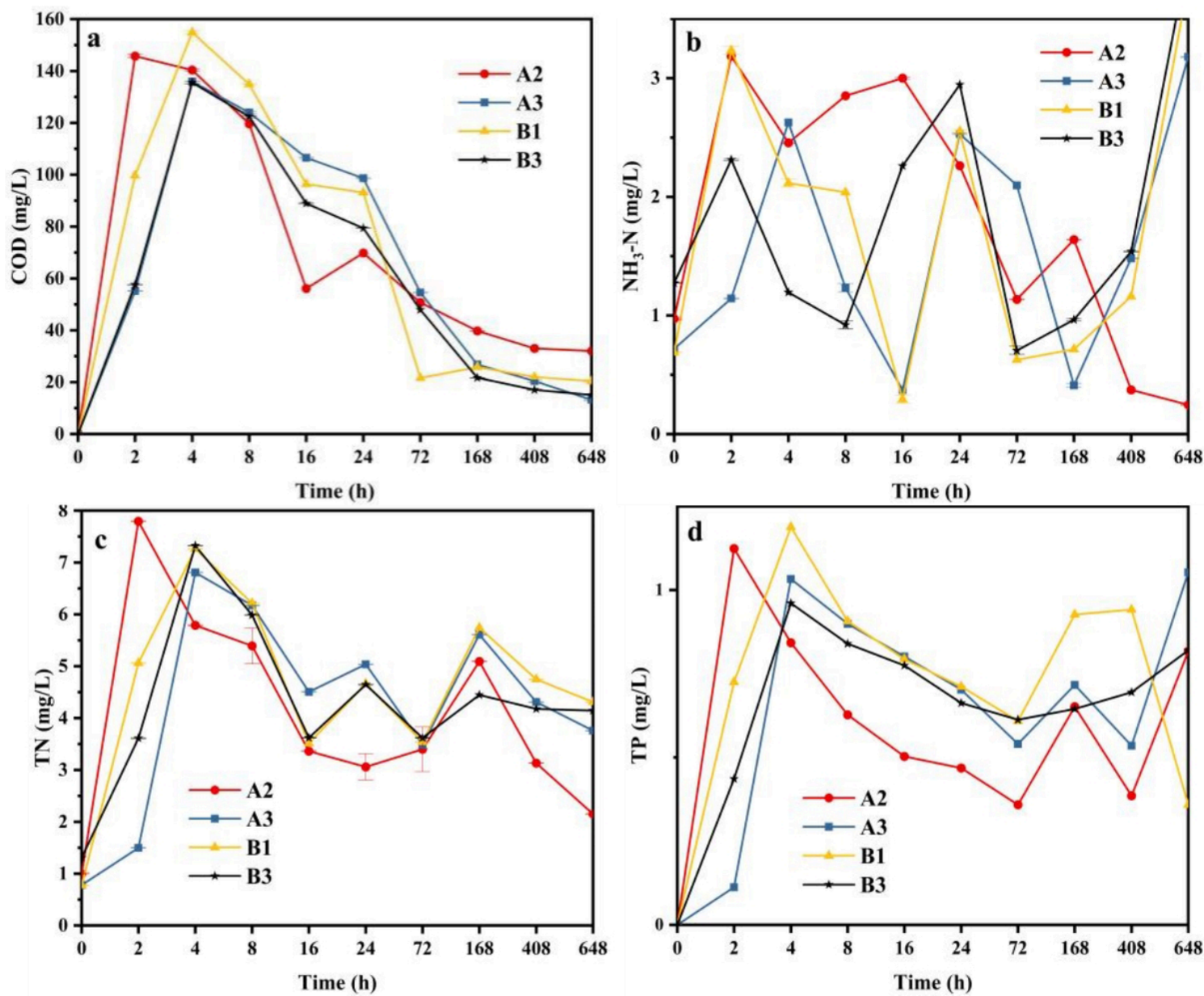


Figure 1

Water quality indicators with temperature change curve: (a) overlying water COD change; (b) overlying water NH₃-N change; (c) overlying water TN change; (d) overlying water TP change.

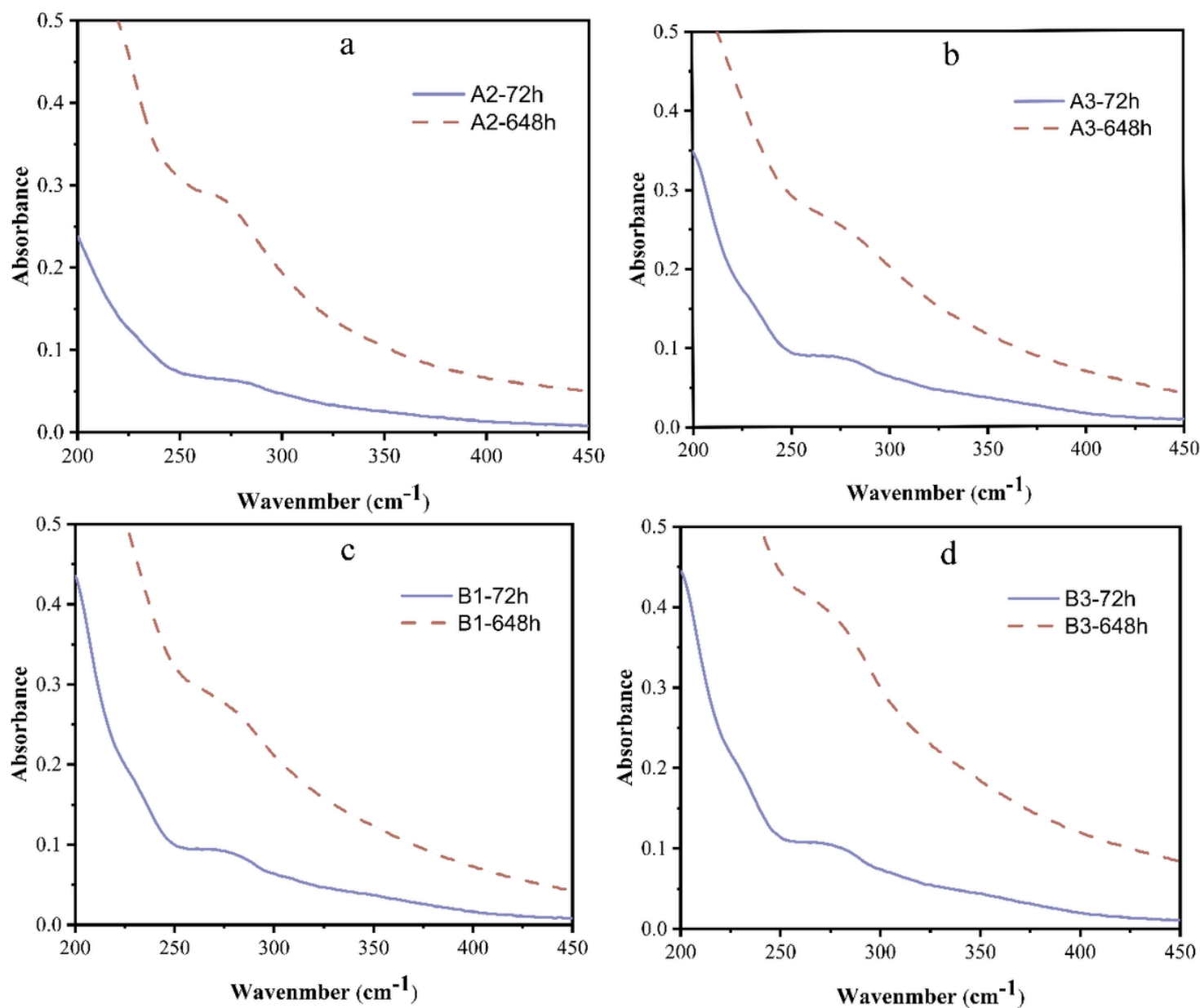


Figure 2

UV-Vis spectra under different conditions: A2(a); A3(b); B1(c); B3(d).

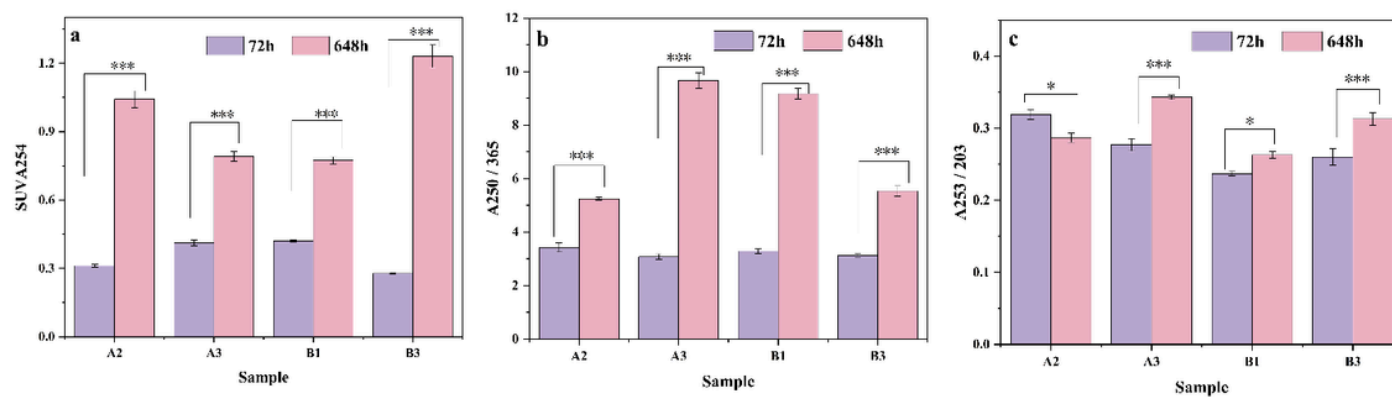


Figure 3

Spectral absorption values under different groups SUVA₂₅₄(a); A_{250/365}(b); A_{253/203}(c)

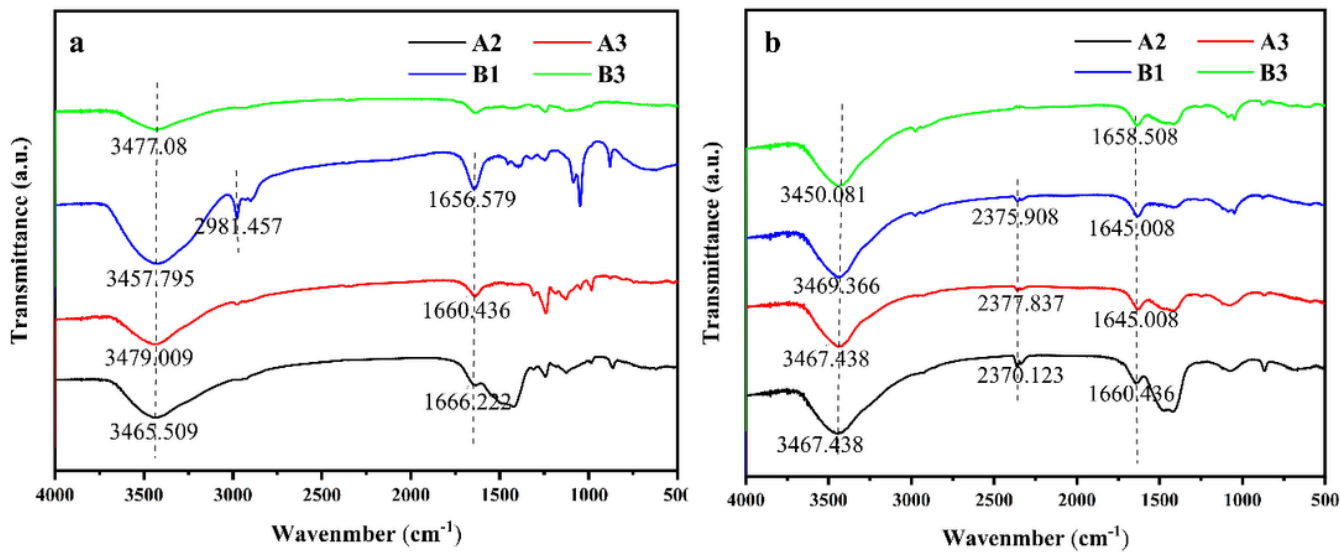


Figure 4

FTIR of samples at 72 h(a) and at 648 h(b)

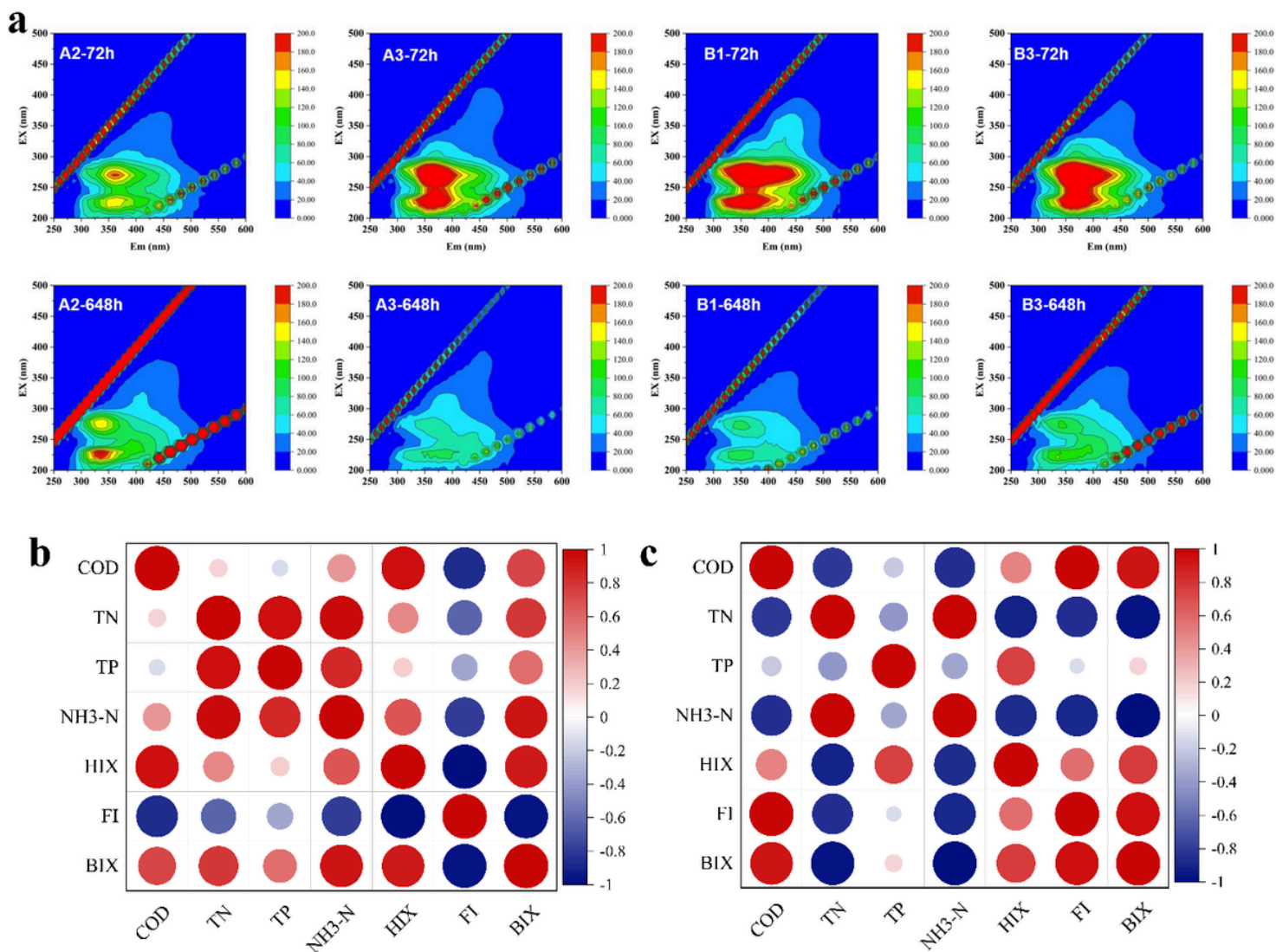


Figure 5

Analysis of three-dimensional fluorescence spectra under different conditions(a); Pearson's correlation between water quality and fluorescence indexes at 72 h (b) and 648 h (c).

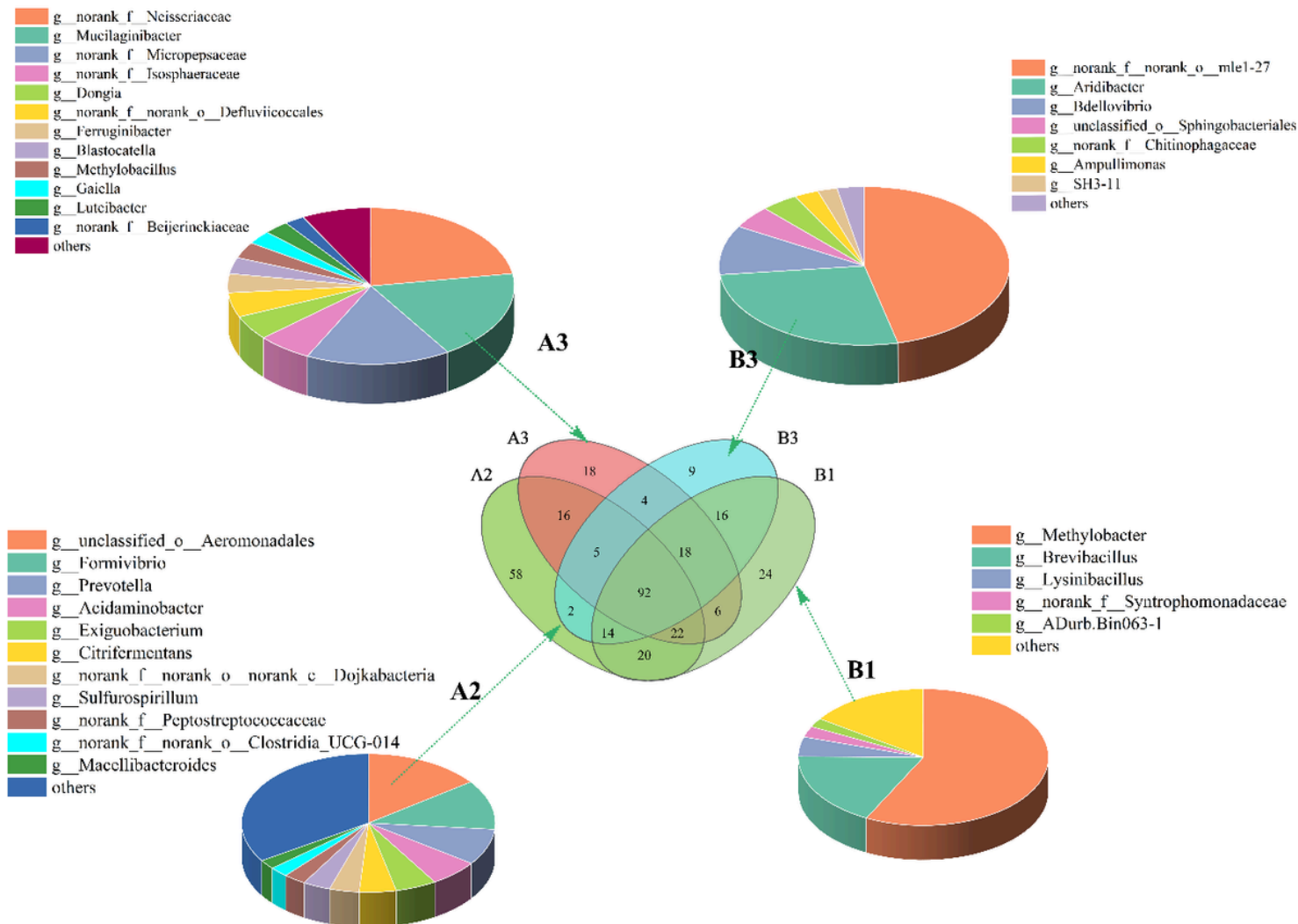


Figure 7

Venn diagram for bacterial diversity showing the unique and shared genus between all groups.

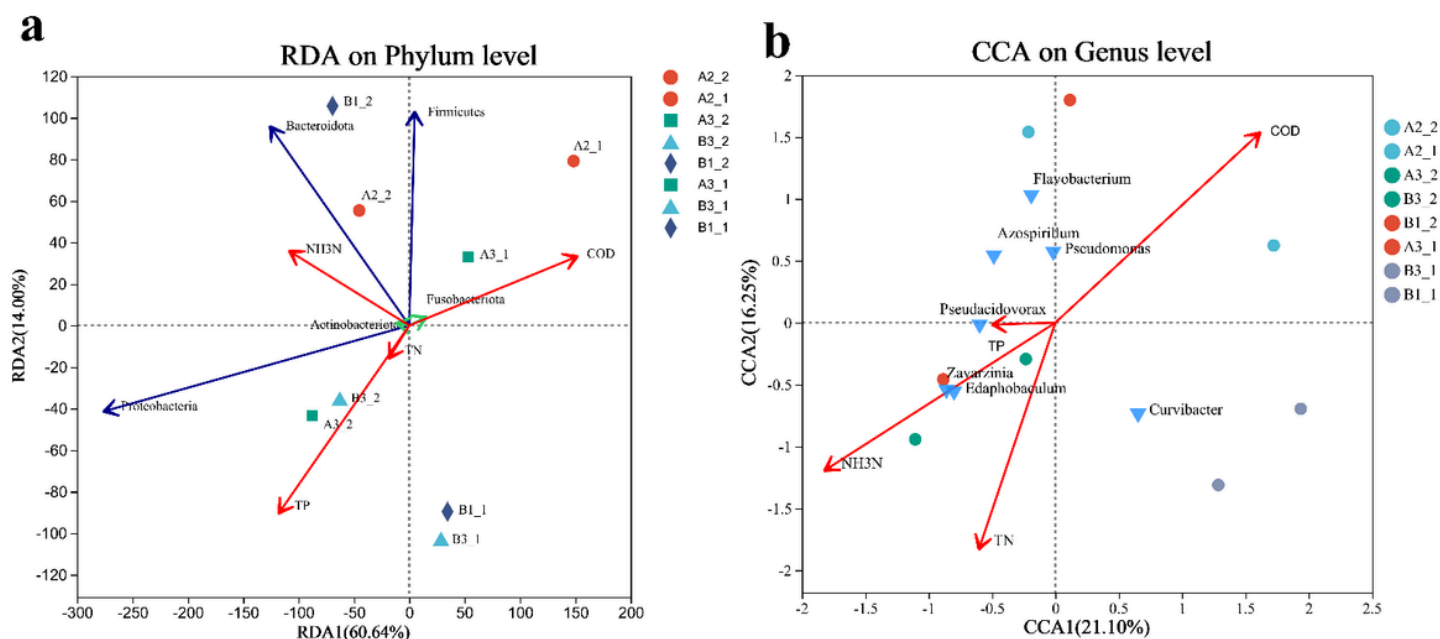


Figure 8

Correlation analysis of bacterial community structure and environmental factors on phylum level(a) and on genes level(b)

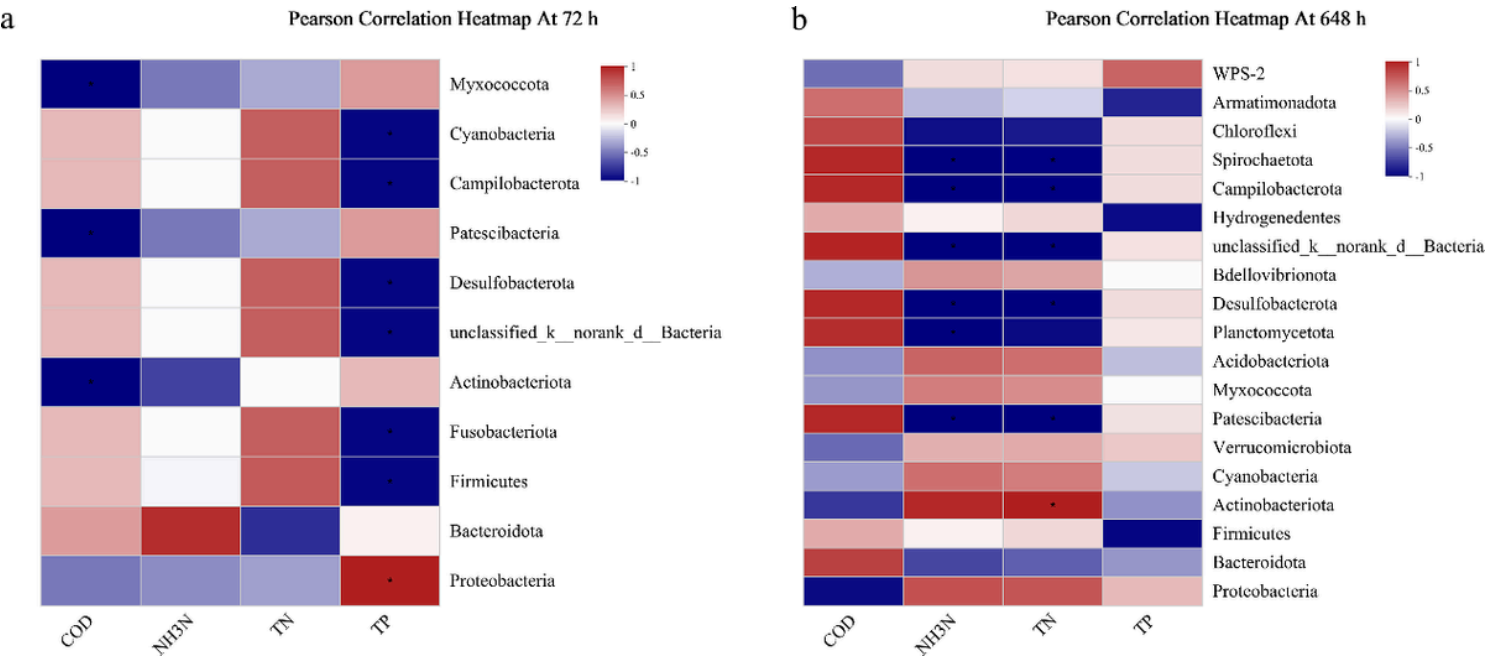


Figure 9

Relationship between bacteria and environmental factors at 72 h(a) and 648 h(b).

