



Characterization of microbial communities in the rhizosphere and water of a field-scale artificial floating island system for nutrient removal[☆]

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ABSTRACT

Eutrophication, caused by excessive nutrient inputs, threatens water quality and aquatic ecosystems worldwide. Artificial Floating Islands (AFIs) offer a promising phytoremediation solution, leveraging aquatic plants and their associated microbes for nutrient removal. However, the microbial communities within AFI systems, particularly under natural conditions, remain poorly understood. In this study, microbial communities were characterized in a field-scale AFI system treating residential raw sewage, with a focus on the rhizosphere of *Carex comosa* (bristly sedge), *Eleocharis obtusa* (blunt spike-rush), and their polyculture. Microbial communities in both rhizosphere and wastewater were analyzed using 16S rRNA gene sequencing, and water physicochemical parameters and plant nutrient assimilation were monitored throughout the study. Results showed significantly higher microbial diversity in the rhizosphere compared to the water. Proteobacteria dominated the rhizosphere (47%–52%) and Cyanobacteria dominated the water (30%). Polyculture system was associated with greater abundance of beneficial microbial taxa and metabolic pathways, which likely supported plant growth and enhanced nutrient assimilation. These effects were attributed in part to species-specific microbial contributions, particularly by *E. obtusa*, which introduced functionally relevant taxa despite limited plant nutrient uptake. Plant nutrient assimilation, rhizosphere microbial communities, and environmental factors such as pH, dissolved oxygen, and temperature were found to be closely interconnected. These findings suggest that polyculture is an effective strategy for enhancing nutrient removal in field-scale AFI systems by promoting microbial diversity and functional potential.

1. Introduction

Eutrophication, primarily driven by the excessive nitrogen (N) and phosphorus (P) inputs, poses a significant global environmental challenge (Lintern et al., 2020; Maúre et al., 2021; Sinha et al., 2017). These nutrient overloads disrupt the nutrient dynamics of freshwater and saltwater ecosystems, triggering a cascade of biogeochemical reactions that can lead to adverse effects, including Harmful Algal Blooms (HABs), hypoxia, water quality degradation, ocean acidification, habitat destruction, risks to human health, diminished recreational opportunities, and reduced economic productivity in watersheds (Maúre et al.,

2021; Nsenga Kumwimba et al., 2023; Sinha et al., 2017). Climate change further exacerbates these issues through rising temperatures, altered precipitation patterns, and shifts in hydrological regimes, along with population growth and changes in land management practices, which increase both the frequency and severity of eutrophication events (Nazari Sharabian et al., 2018; Paerl and Huisman, 2009; Rabalais et al., 2010; Scavia et al., 2002; Sinha et al., 2017). Addressing eutrophication therefore aligns with multiple United Nation Sustainable Development Goals and remains a priority for governments worldwide (Lintern et al., 2020; Nsenga Kumwimba et al., 2023; Rasul, 2016; Stokral et al., 2016).

In response to the urgent need for effective eutrophication

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management strategies, artificial floating islands (AFIs) emerge as a sustainable natural-based solution for addressing nutrient pollution (Chang et al., 2017; Samal et al., 2019). As a phytoremediation technology, AFIs integrate naturally occurring aquatic plants into floating platforms, facilitating nutrient removal through multiple synergistic mechanisms (Chen et al., 2025b; Pavlineri et al., 2017; Samal et al., 2019). The aquatic plants assimilate bioavailable nutrients into their tissues, while their submerged roots provide physical filtration of pollutants such as particulate N and P, creating large bioactive surfaces for microbial attachment and biochemical reactions (Chen and Costa, 2023; Samal et al., 2019). AFIs offer several advantages over traditional best management practices (BMPs), such as detention ponds, manure storage, rain barrels, and underground filters (Pavlineri et al., 2017). They can cover extensive areas of water bodies without the need for permanent infrastructure, making them particularly effective for treating non-point nutrient sources. Additionally, AFIs require no land, allowing for seamless integration into existing water bodies or treatment systems. Their design accommodates water level fluctuations, making them suitable for coastal regions where such changes are expected. Lastly, AFIs are cost-effective to construct and manage, as they can be built with inexpensive or recycled materials like bamboo, plastic bottles, PVC pipes, and plastic buckets, and demand minimal maintenance, mainly involving plant harvesting (Chang et al., 2017; Pavlineri et al., 2017; Samal et al., 2019).

While AFIs have demonstrated numerous advantages, their real-world applicability remains uncertainty due to a lack of field-scale studies. Complex environmental conditions, such as fluctuating temperature, flow rate, and nutrient loads, substantially affect AFI performance, which can only be robustly assessed under field conditions and long-term monitoring. However, most previous studies have been conducted in lab-based mesocosms or macrocosms, which do not fully capture the dynamics and complex nature of the environments (Afzal et al., 2019a, 2019b; Chen et al., 2025a; Garcia Chance et al., 2019; Samal et al., 2019). Research indicates that BMPs can produce different or even opposing effects in field applications compared to lab-scale studies, emphasizing the need for long-term field evaluations to accurately assess AFI effectiveness in real-world conditions (Lintern et al., 2020). Additionally, while AFI performance has been extensively studied, limited research has focused on the microbial communities associated with these systems (Urakawa et al., 2017). Furthermore, existing studies on AFI-associated microbes are primarily lab-based, often investigating microbial inoculation to enhance performance or the impact of a single variable on AFI function (Chen et al., 2019; Cui et al., 2019; Hussain et al., 2019, 2018a; 2018b; Li et al., 2021a; Meng et al., 2023; Rehman et al., 2018; Yasin et al., 2021; Zhang et al., 2024; Zhao et al., 2013). As a result, the interactions between microbial communities, AFI performance, and environmental conditions remain insufficiently explored. Additionally, the microbial communities associated with different plant species and the potential benefits of polyculture over monoculture, have not been fully investigated.

To address the identified research gaps, a field-scale AFI system was constructed at the equalization basin of a wastewater treatment plant (WWTP) in Ohio, featuring two native aquatic plant species: *Carex comosa* (bristly sedge) and *Eleocharis obtusa* (blunt spike-rush). During the warm seasons, microbial communities, environmental conditions, and AFI performance were monitored. Particular attention was given to the design factors, monoculture vs. polyculture configuration, as different plants are expected to host distinct rhizosphere microbes, and polyculture may enhance microbial diversity and function (Das et al., 2022; Haichar et al., 2008; O'Brien et al., 2020; Semchenko et al., 2022; Yoneda et al., 2021). The main objectives of this study are: (1) to characterize the microbial communities associated with field-scale AFI systems in natural environments, (2) to evaluate the effects of plant species and polyculture on microbial compositions, (3) to assess the potential benefits of polyculture on AFI performance.

2. Material and methods

2.1. Study site description and characteristics

The AFI system was installed in the equalization basin of the Plymouth Wastewater Treatment Plant (WWTP) in Ohio, U.S., which receives approximately 950 m³ of residential raw sewage daily via a supply line (inlet). The treated water is subsequently directed to the WWTP facilities through a return line (outlet) for further biological, chemical, and physical treatment. The basin maintains a permanent pool of water with an average depth of 1 m and a minimum depth of 0.6 m (Chen et al., 2025a).

2.2. AFI construction and design

The AFI units were constructed using polyvinyl chloride (PVC) pipe frames (5 cm in diameter, 60 × 60 cm in size) and ethylene-vinyl acetate (EVA) foam mats with a thickness of 1.3 cm. Each EVA foam mat contained eight pre-cut holes into which luffa sponges were inserted. The sponges served to retain moisture, support macrophyte seedlings, and provide surface area for microbial attachment. Two native aquatic plant species, *C. comosa* and *E. obtusa*, were selected based on prior pilot testing (Chen et al., 2025a, 2025b; 2024; Chen and Costa, 2023). To evaluate the potential of polyculture in enhancing AFI performance, two culture treatments were implemented: monoculture and polyculture. In the monoculture systems, only one plant species was installed per unit, while the polyculture systems contained an equal ratio of both species. A total of twelve AFI units were deployed: three units each for *C. comosa* monoculture, *E. obtusa* monoculture, polyculture, and unplanted controls (Fig. S1).

2.3. Sampling procedures

Weekly in-situ monitoring of water physicochemical parameters was conducted at six designated sites within the equalization basin from late-April to mid-November 2022 (Fig. S1). Measurement of water temperature, pH, oxidation-reduction potential (ORP), and dissolved oxygen (DO) were obtained 10 cm below the water surface using handheld field meters (YSI® ODO/BDO meter kit, YSI Inc, Yellow Springs, Ohio, U.S.; Oakton® multiparameter kit, Oakton Instrument, Vernon Hills, IL, U.S.). Water samples for nutrient analysis were collected at the same depth and locations, following preprocessing methods adapted from (Chen et al., 2025a). To capture the overall environmental conditions at a field-relevant scale, data from all six sites were spatially averaged.

Plant tissue samples were collected every six weeks to assess biomass accumulation and nutrient storage. The dry biomass of plant shoots and roots was measured separately after drying the plant tissues in an oven at 80 °C for 48 h, following established methods (Chen et al., 2025b). Nutrient concentrations in plant tissues were determined using acetic acid extraction methods outlined by Robert O. Miller (1998).

Nutrient concentrations for water and plant samples were analyzed at the Water Isotope and Nutrient Laboratory (WINL) in Columbus, Ohio, U.S. Concentrations of NO_x (NO₂⁻ + NO₃⁻), PO₄³⁻, and NH₄⁺ were determined using a Skalar® SAN⁺⁺ Flow Injection Analysis (FIA) system (Skalar Analytical B.V., Breda, Netherlands), and data were calibrated using FlowAccess (v2.0.25) (Skalar, 2006).

Water and plant root samples for microbial analysis were collected every four weeks. Composite samples (100 mL) of raw wastewater were obtained from Site 1, 2, 3, and 4 during each sampling event (Fig. S1). Root samples were collected as composites from monoculture AFIs and from each plant species within polyculture AFIs. Rhizosphere microbial sampling protocols were adapted from terrestrial plant root sampling methods (Calheiros et al., 2020; Simmons et al., 2018). Approximate 2g of root tissue was cut in the field using scissors sterilized using 70 % ethanol. All samples were immediately stored on ice after collection and transported to the laboratory for further processing.

2.4. DNA extraction

Before DNA extraction, 1 g of root samples was collected and transferred to a 50 mL conical vial containing 25 mL of phosphate-buffered saline (PBS). The mixture was vortexed to obtain rhizosphere microbes. The supernatant was then filtered through an Isopore Membrane filter (0.22 μm pore size, EMD Millipore, Burlington, Massachusetts, U.S.) to recover microbes attached to the plant root hairs. The same filtration procedure was applied to the wastewater samples. After filtration, the filters were collected for DNA extraction, which followed the standard protocol using the DNeasy PowerSoil Pro Kit (Cat. No. 47016-250, Qiagen, Hilden, Germany). DNA concentration and quality were then measured using a NanoDrop™ 2000 Spectrophotometer (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.) (Lancaster et al., 2024; Mills et al., 2022). Samples with a DNA concentration below 5 ng/ μL were excluded from gene quantification, resulting in the exclusion of one water sample collected on July 13. In total, microbial DNA was successfully extracted from 84 rhizosphere samples and 27 water samples.

2.5. Microbial community analysis

Paired-end 16S rRNA gene sequencing was performed for all 111 water and rhizosphere samples. The V4-V5 region of the 16S rRNA gene was sequenced at the Molecular and Cellular Imaging Center (Wooster, Ohio, U.S.) on the Illumina MiSeq platform using primers 515F (5'-GAGTCCAGCMGCCGCGTAA-3') and 806R (5'-ACGGAC-TACHVGGGTWCTAAT-3'). Raw reads were analyzed using the comprehensive QIIME2 pipeline (Bolyen et al., 2019; Lancaster et al., 2024; Mills et al., 2022), with DADA2 employed for quality control (Callahan et al., 2016). Both forward and reverse reads had a base cutoff of 210. To normalize for alpha and beta diversity analyses, data were rarefied and sampled at a depth of 13,867, which resulted in the exclusion of four water samples collected on October 7. The sequencing depth for the remaining 107 samples is detailed in Table S1, which includes the total number of amplicon sequence variants (ASVs) per sample and the average ASVs by sample type.

Alpha diversity metrics, including Shannon diversity index, Faith's phylogenetic diversity, observed features, and Pielou's evenness, were calculated using the QIIME2 q2-diversity plugin (Bolyen et al., 2019). Significant differences among sample types were assessed using Kruskal-Wallis tests. For subsequent pairwise comparisons, Wilcoxon Rank Sum tests were conducted with Bonferroni adjusted *p*-values if the initial test indicated significance (*p*-value < 0.05). Beta diversity was evaluated using Jaccard distance, weighted and unweighted Unifrac distance, and Bray-Curtis distance. Significant differences in beta diversity were assessed using Permutational Multivariate Analysis of Variance (PERMANOVA). Taxonomy was classified using a Naive Bayes classifier trained on the 99% SILVA 138 database (Bokulich et al., 2018; Robeson et al., 2021). Additionally, predictive functions were analyzed with PICRUSt2 from amplicon sequencing profiles (Douglas et al., 2020). Significant differences in taxonomy and MetaCyc pathways by culture type and plant species were determined using linear discriminant analysis effect size (LefSe), with an LDA >3 (Lancaster et al., 2024; Mills et al., 2022).

2.6. Plant variable quantification and statistical analysis

Nutrient storage (*S* [mg]) of NO_x , PO_4^{3-} , or NH_4^+ in plant tissues for shoots (S_{shoot}) and roots (S_{root}) was calculated separately as:

$$S_{\text{shoot or root}} = C_{\text{shoot or root}} \times DB_{\text{shoot or root}} \quad (1)$$

where *C* [mg/g] is nutrient concentration (for NO_x , PO_4^{3-} , or NH_4^+) in the plant shoots or roots, and *DB* [g] is the dry biomass of the respective plant parts.

Bioconcentration factor (BCF) was used to assess the accumulation of nutrients in plant tissues relative to their concentration in the surrounding aquatic environment (Abbas et al., 2019). BCFs [L/g] for NO_x , PO_4^{3-} , or NH_4^+ were calculated as:

$$BCF = \frac{C_{\text{shoot}} \times DB_{\text{shoot}} + C_{\text{root}} \times DB_{\text{root}}}{(DB_{\text{shoot}} + DB_{\text{root}}) \times C_{\text{water}}} \quad (2)$$

where C_{water} [mg/L] is the concentration of NO_x , PO_4^{3-} , or NH_4^+ in the water.

For correlation analysis, three categories of variables were considered: (1) plant nutrient assimilation variables, including BCFs and nutrient storage for NO_x , PO_4^{3-} , or NH_4^+ in plant shoots and roots; (2) water physicochemical parameters, including DO, water temperature, ORP, pH, and concentrations of NO_x , PO_4^{3-} , or NH_4^+ ; and (3) microbial variables, including alpha diversity of rhizosphere microbial communities and the relative abundance of key genera.

Pearson coefficients were calculated to assess bivariate correlations. Shapiro tests were performed to evaluate the normality of the variables. All statistics were conducted using R Statistical Software (R Core Team, 2023). LefSe analysis was conducted with the microeco R package (Liu et al., 2021). Figures were created using the ggplot2 R package (Wickham, 2016).

3. Results

3.1. Microbial community differences by sample type and sampling date

Sample type (rhizosphere or water) and sampling date were the most significant factors influencing microbial community composition. All four measured alpha diversity indices – Shannon diversity index, Faith's phylogenetic diversity, observed features, and Pielou's evenness – showed significant differences by sample type and sampling date (Kruskal-Wallis test *p*-value < 0.001 for both factors). The Shannon diversity index was used to describe community diversity, and significantly lower diversity was observed in water samples compared to all rhizosphere samples (pairwise Wilcoxon Rank Sum tests, *p*-value < 0.001). Notably, there was no significant difference in diversity among rhizosphere samples across plant species or culture types (*p*-value > 0.05) (Fig. 1a). Although no significant differences in temporally averaged rhizosphere microbial diversity were detected across culture types, notable differences were observed on specific sample dates. In particular, polyculture systems exhibited higher diversity than monoculture systems on July 13 and August 10 for both plant species (Fig. 1b).

All calculated beta diversity indices, including weighted and unweighted Unifrac distance, Bray-Curtis distance, and Jaccard distance, differed significantly by sample types (rhizosphere vs. water), as confirmed by PERMANOVA testing (*p*-value = 0.001) (Fig. 1c). Based on the weighted Unifrac distance, water samples were found to differ significantly from all rhizosphere samples (*p*-value = 0.001), while no significant differences were detected between plant species (*p*-value > 0.05) or between culture types (*p*-value > 0.05).

In all samples, Proteobacteria, Bacteroidota, Cyanobacteria, Verrucomicrobiota, Planctomycetota, Actinobacteriota, and Acidobacteriota presented in the top ten phyla at varying relative abundances. Proteobacteria dominated the rhizosphere samples, comprising 47% to 52% of the community, while Cyanobacteria prevailed in the water samples, accounting for 30%. (Fig. 1d and Table S2). The four rhizosphere samples shared the same top ten phyla, although their relative abundances led to slight differences in their ranks (Table S2).

Microbial compositions also varied over time. In water samples, Proteobacteria was the dominant phylum on the initial sampling date, but was subsequently overtaken by Cyanobacteria, which maintained dominance during summer (Fig. S3 and Table S3). Cyanobacteria reached its peak abundance of 62.1% on August 10, coinciding with the highest water temperature recorded during the study period (Fig. S2a,

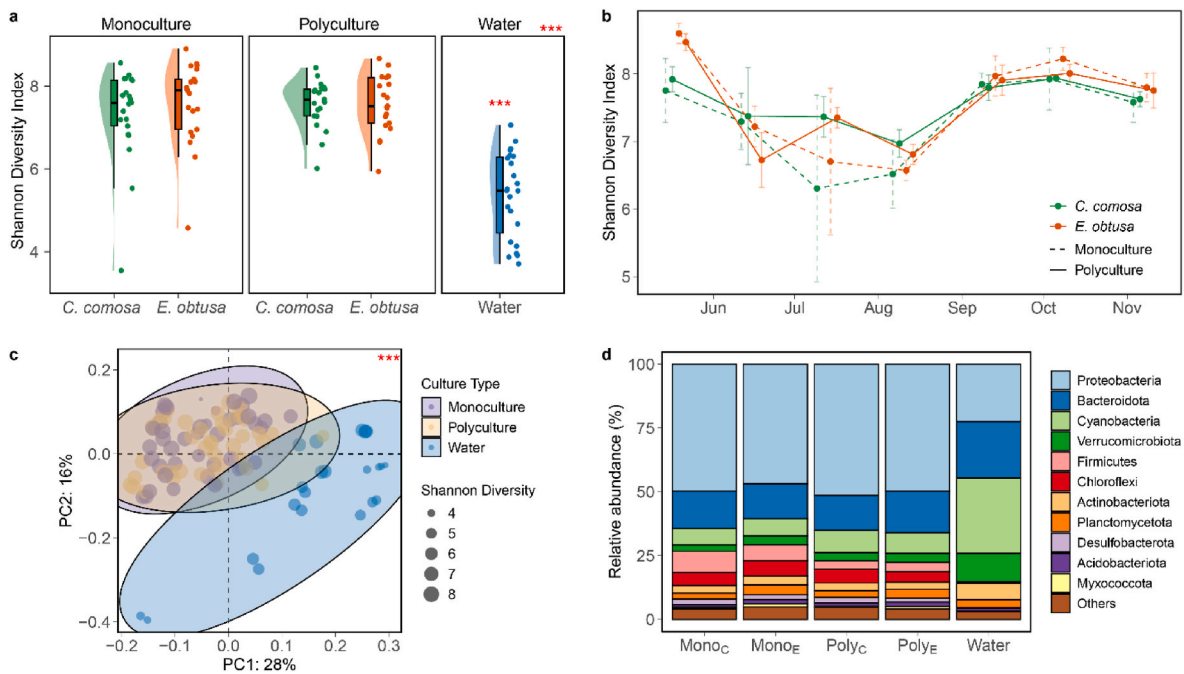


Fig. 1. Summary of microbial community analyses. (a) Shannon diversity index for microbial communities, showing significant differences by sample type (Kruskal-Wallis test p -value < 0.001). (b) Temporal variations of the Shannon diversity index for microbial communities from plant rhizosphere. (c) Beta diversity shown as a principal coordinate analysis (PCoA) plot of weighted Unifrac distance, showing significant differences by sample type (PERMANOVA p -value = 0.001). (d) Relative abundance of microbial communities averaged by sample type at the phylum level. MonoC represents monocultural *C. comosa*, MonoE represents monocultural *E. obtusa*, PolyC represents polycultural *C. comosa*, and PolyE represents polycultural *E. obtusa*. Three asterisks indicate p -value < 0.001.

Fig. S3 and Table S3). In contrast, Proteobacteria consistently dominated rhizosphere samples throughout the study, ranging from 43 % to 58 %, followed by different phyla, including Actinobacteriota, Cyanobacteria, Firmicutes, Chloroflexi, and Bacteroidota on various sampling dates (Fig. S3 and Table S3). The top ten families within Proteobacteria were further examined across the four rhizosphere sample types (monocultural *C. comosa*, monocultural *E. obtusa*, polycultural *C. comosa*, and polycultural *E. obtusa*). *Comamonadaceae* was identified as the most prevalent family in all rhizosphere samples, comprising 8 % to 10 % of the community (Table S4).

At the genus level, the most pronounced differences in microbial communities were observed between sample types. Water samples were dominated by the genera *Microcystis* PCC-7914 and *Cyanobium* PCC-6307, both exceeding 10 % relative abundance. Conversely, rhizosphere samples showed no dominant genera, regardless of culture type or plant species, indicating greater taxonomic richness without any single genus constituting a significant portion of the community (Table 1 and Fig. S4). Both polyculture samples and water samples shared *Microcystis* PCC-7914 as the most abundant genus (Table 1).

Table 1

Top five taxonomic genera by sample type. The average relative abundance of the top five genera for each sample type, along with their corresponding phylum. MonoC represents monocultural *C. comosa*, MonoE represents monocultural *E. obtusa*, PolyC represents polycultural *C. comosa*, and PolyE represents polycultural *E. obtusa*.

| MonoC | | MonoE | | PolyC | | PolyE | | Water | |
|-----------------------------|--------|-----------------------------|--------|-----------------------------|--------|-----------------------------|--------|-----------------------------|--------|
| Genus | RA (%) | Genus | RA (%) | Genus | RA (%) | Genus | RA (%) | Genus | RA (%) |
| <i>Exiguobacterium</i> | 4.0 | <i>Flavobacterium</i> | 3.4 | <i>Microcystis</i> PCC-7914 | 3.6 | <i>Microcystis</i> PCC-7914 | 4.4 | <i>Microcystis</i> PCC-7914 | 16.3 |
| Firmicutes | | Bacteroidota | | Cyanobacteria | | Cyanobacteria | | Cyanobacteria | |
| <i>Acinetobacter</i> | 3.6 | <i>Acinetobacter</i> | 2.9 | <i>Cyanobium</i> PCC-6307 | 3.2 | <i>Flavobacterium</i> | 3.7 | <i>Cyanobium</i> PCC-6307 | 10.7 |
| Proteobacteria | | Proteobacteria | | Cyanobacteria | | Bacteroidota | | Cyanobacteria | |
| <i>Microcystis</i> PCC-7914 | 3.5 | <i>Cyanobium</i> PCC-6307 | 2.9 | <i>Flavobacterium</i> | 3.0 | <i>Cyanobium</i> PCC-6307 | 2.7 | <i>LD29</i> | 8.9 |
| Cyanobacteria | | Cyanobacteria | | Bacteroidota | | Cyanobacteria | | Verrucomicrobiota | |
| <i>Flavobacterium</i> | 3.3 | <i>Exiguobacterium</i> | 2.9 | <i>Methyloparacoccus</i> | 2.2 | <i>Methyloparacoccus</i> | 2.0 | <i>Flavobacterium</i> | 7.8 |
| Bacteroidota | | Firmicutes | | Proteobacteria | | Proteobacteria | | Bacteroidota | |
| <i>Pseudomonas</i> | 2.7 | <i>Microcystis</i> PCC-7914 | 2.8 | <i>Pseudomonas</i> | 2.1 | <i>Methylomonas</i> | 1.8 | <i>PeM15</i> | 3.0 |
| Proteobacteria | | Cyanobacteria | | Proteobacteria | | Proteobacteria | | Actinobacteriota | |

3.2. Differentially abundant taxa and metabolic pathways

Distinct microbial community patterns were identified across sample types. At the phylum level, broad compositional differences were detected, including significantly higher relative abundance of Cyanobacteria in water samples, Proteobacteria in polycultural systems, and Firmicutes in monocultural rhizospheres. At the genus level, 45 differentially abundant genera were detected among water, polycultural, and monocultural rhizosphere samples (Fig. 2). To evaluate the contribution of specific plant species to the composition of these genera, LefSe analysis was conducted by grouping samples according to plant species (water, *C. comosa*, and *E. obtusa*) and culture type (water, monoculture, polyculture). Among the 22 genera that were enriched in polyculture systems, 14 were also more abundant in *C. comosa*, while 8 were more abundant in *E. obtusa* (Fig. 2). These results suggest species-specific influences on microbial community composition within polyculture systems.

Significant differences were identified in 12 MetaCyc pathways among water, monocultural, and polycultural rhizosphere (Fig. 3).

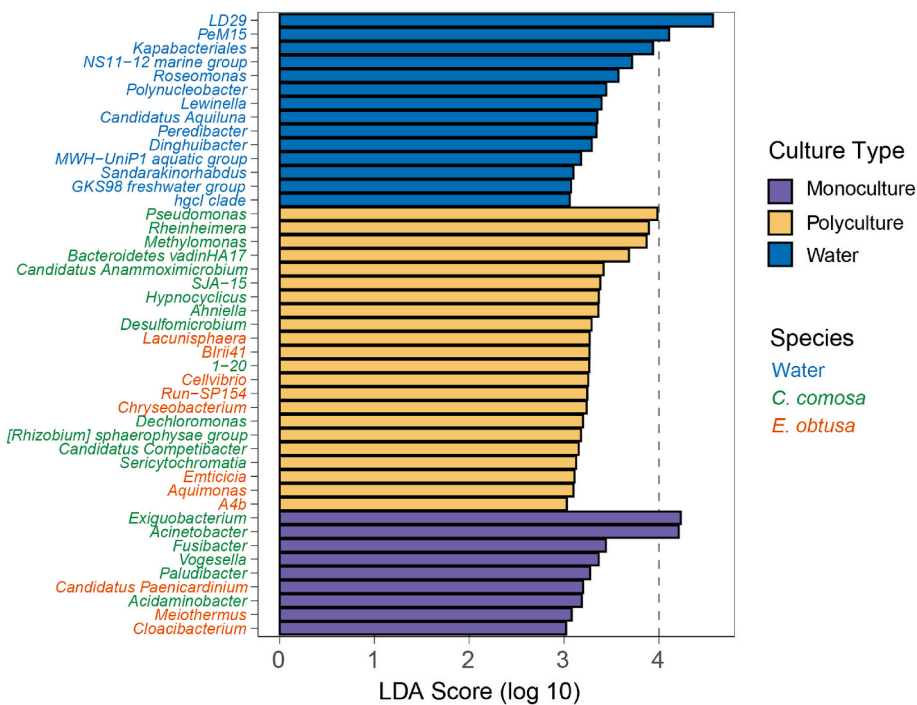


Fig. 2. Differentially abundant genera by sample type. Differentially abundant genera were identified via LefSe (LDA >3.0, *p-value* < 0.01) among water, monocultural, and polycultural rhizosphere samples. The texts of genera on the y axis are color coded by plant species, showing differentially abundant genera in each species. Genera are ranked according to their LDA scores. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

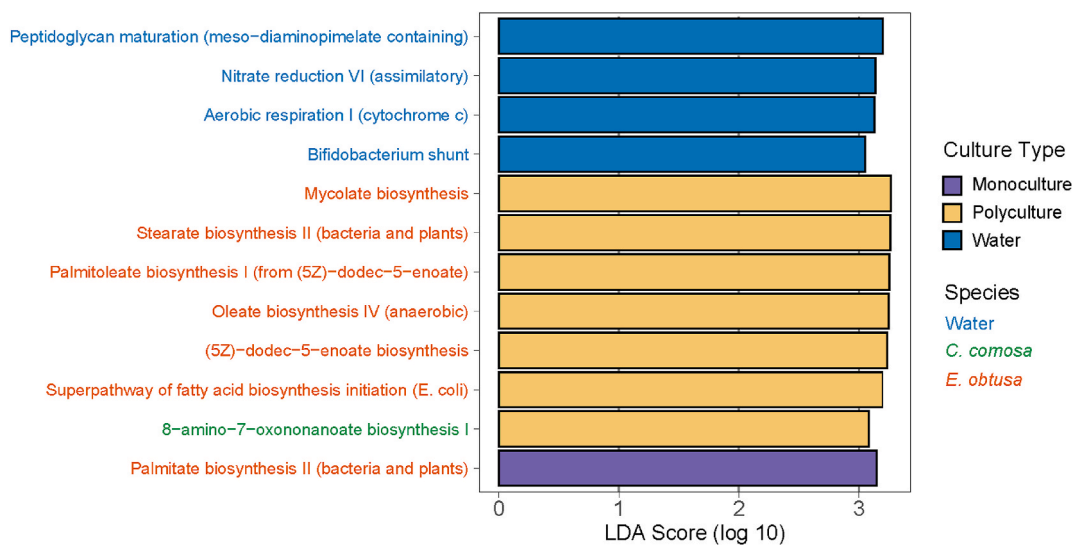


Fig. 3. Differentially abundant MetaCyc pathways. Differentially abundant MetaCyc pathways were identified via LefSe (LDA >3.0, *p-value* < 0.01) among water, monocultural, and polycultural rhizosphere samples. The texts of pathways on the y axis are color coded by plant species, showing differentially abundant MetaCyc pathways in each plant species. Pathways are ranked according to their LDA scores. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Seven pathways, including mycolate biosynthesis, stearate biosynthesis II, palmitoleate biosynthesis I, oleate biosynthesis IV, (5Z)-dodec-5-enoate biosynthesis, superpathway of fatty acid biosynthesis initiation, 8-amino-7-oxononanoate biosynthesis I, were more abundant in polyculture systems. Conversely, only one pathway, palmitate biosynthesis II was more abundant in monoculture systems. Notably, six of the seven pathways enriched in polyculture systems were also more abundant in *E. obtusa*. All three rhizosphere sample types exhibited differentially abundant pathways within the biosynthesis superclass, while

degradation/utilization/assimilation and generation of precursor metabolites and energy superclasses were unique to water samples. Importantly, all differentially abundant pathways in rhizosphere samples belonged to the biosynthesis superclass (Table S5).

3.3. Microbial associations with plant nutrient assimilation and environmental conditions

The subset of 84 plant rhizosphere samples was used to analyze the

associations among plant nutrient assimilation, environmental conditions, and rhizosphere microbial communities. Three types of variables were included: (1) plant nutrient assimilation variables, including BCFs and nutrient storage for NO_x , PO_4^{3-} , and NH_4^+ in plant shoots and roots; (2) water physicochemical parameters, including DO, water temperature, ORP, pH, and concentrations of NO_x , PO_4^{3-} , and NH_4^+ ; and (3) microbial variables, including the alpha diversity of rhizosphere microbial communities and the relative abundance of key genera. For the key genera, the top five most abundant genera in each type of rhizosphere sample were assessed, including *Exiguobacterium*, *Acinetobacter*, *Microcystis* PCC-7914, *Flavobacterium*, *Pseudomonas*, *Cyanobium* PCC-6307, *Methyloparacoccus*, *Methylomonas*, *LD29*, and *PeM15* (Table 1). Additional genera associated with nutrient cycling, such as *Nitrosomonas*, *Nitrospira*, *Nitrosococcus*, *Nitrospira*, *Nitrobacter*, *Nitrospina*, *Nitrococcus*, *Paracoccus*, *Rhizobium*, and *Anabaena* (Urakawa et al., 2017), were also examined. However, these taxa were excluded from further analysis due to their relatively low abundance across samples (<50 %).

A principal component analysis (PCA) was conducted to explore the relationships among all variables. The first two principal components (PCs) accounted for 60 % of the total variance (Fig. 4a). The first axis (PC1), explaining 42.4 % of the variance, was dominated by nutrient storage within plant tissues and water physicochemical parameters, including DO, ORP, pH, and concentrations of PO_4^{3-} and NO_x , as indicated by their loadings. The second axis (PC2), explaining 17.5 % of the variance, was primarily dominated by microbial alpha diversities and NH_4^+ concentration (Fig. 4b). The relative abundance of key genera was not well represented by the first two PCs, as indicated by low cos^2 value ($\text{cos}^2 < 0.5$); only *LD29* and *Cyanobium* PCC-6307 had cos^2 values greater than 0.5 (Fig. 4b). In the resulting PCA space, nutrient assimilation was largely explained by water physicochemical parameters, with higher assimilation of NO_x , PO_4^{3-} , and NH_4^+ positively correlated with DO, ORP, and concentrations of NO_x and PO_4^{3-} , while showing a negative correlation with pH (Fig. 4b). However, microbial diversity had limited influence on nutrient storage within plant tissues. These PCA results emphasize the complexity of natural environments, suggesting that environmental conditions may be the primary factors affecting plant nutrient assimilation.

To further investigate these associations, pairwise correlations among key factors were examined. Rhizosphere microbial diversity exhibited weak correlations with nutrient storage (Fig. 5). However, several key genera showed significant correlations with the assimilation of NO_x , PO_4^{3-} , and NH_4^+ . Specifically, *Methylomonas*, *Microcystis* PCC-7914, and *Flavobacterium* were positively correlated with the

assimilation of all three nutrient species (p -value < 0.05, Fig. 5). In contrast, *Acinetobacter*, *Cyanobium* PCC-6307, *Exiguobacterium*, and *LD29* showed consistently significant negative correlations with these nutrient assimilations (p -value < 0.05, Fig. 5).

Rhizosphere microbial communities showed strong associations with environmental variables. All four alpha diversity indices were significantly positively correlated with NO_x and PO_4^{3-} concentrations, as well as ORP, while they were negatively correlated with DO, water temperature, and pH (p -value < 0.05, Fig. 5). The relative abundance of key genera was closely linked to water physicochemical parameters, with significant associations observed for pH, DO, and ORP (p -value < 0.05, Fig. 5). Additionally, *Microcystis* PCC-7914 and *Acinetobacter* exhibited strong positive correlations with water temperature (p -value < 0.05, Fig. 5).

4. Discussion

4.1. The rhizosphere hosted distinct microbial communities compared to water

Microbial communities in the plant rhizosphere were found to be significantly more diverse than those in the surrounding water, regardless of plant species or culture type. This result is consistent with prior work showing that plant root surfaces provide large bioactive surfaces and favorable microenvironments that promote microbial colonization and diversity. For example, Urakawa et al. (2017) reported greater microbial diversity in the rhizosphere of *Canna flaccida* (golden canna) and *Juncus effusus* (soft rush) compared to treated stormwater. Similarly, Tanaka et al. (2012) observed higher microbial diversity in the roots of *Phragmites australis* (reed) and *Lythrum anceps* (Japanese loosestrife) relative to pond water.

Genus-level analysis further supported these findings. In the rhizosphere samples, the top five genera accounted for less than 17 % of the entire community, indicating a lack of dominance by any single genus. In contrast, water samples were dominated by a few genera, with the top five comprising over 50 % of the total population (Table 1). However, greater microbial diversity in the rhizosphere did not correspond to a higher number of unique taxa. The average number of ASVs was greater in water samples (30,217) than in rhizosphere samples (<29,199) (Table S1). A high degree of ASV overlap was observed between rhizosphere and water samples, with *C. comosa* and *E. obtusa* sharing 90 % and 88 % of their ASVs with water, respectively, while only 1.7 % of ASVs were unique to either species. These findings suggest that the majority of rhizosphere-associated microbes were recruited from the

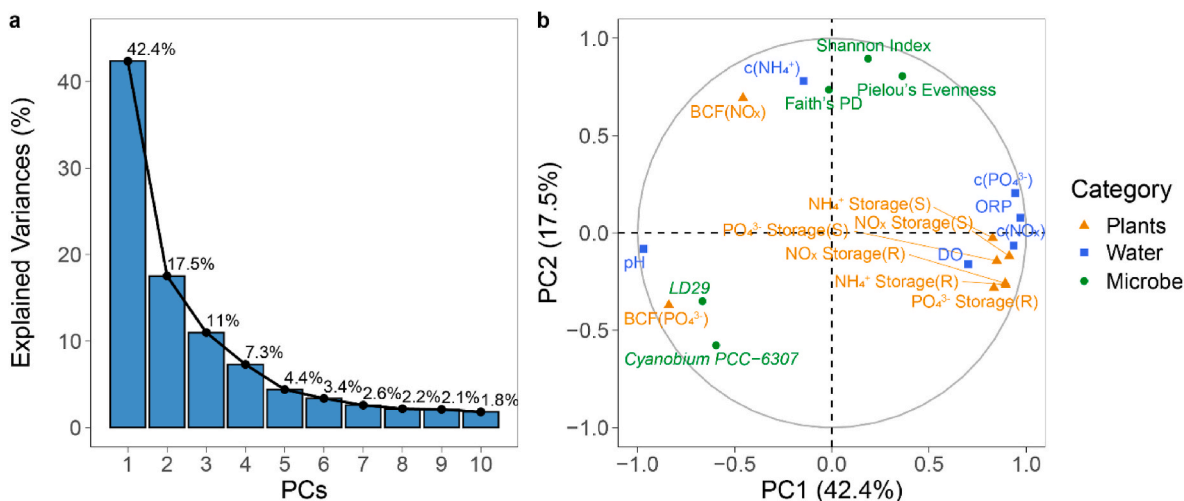


Fig. 4. PCA of plant nutrient assimilation, water physicochemical parameters, and microbial variables. (a) Scree plot showing the variances explained by each PC. (b) PCA correlation circle showing the relationships between variables. For visualization purpose, only variables with $\text{cos}^2 > 0.5$ were shown.

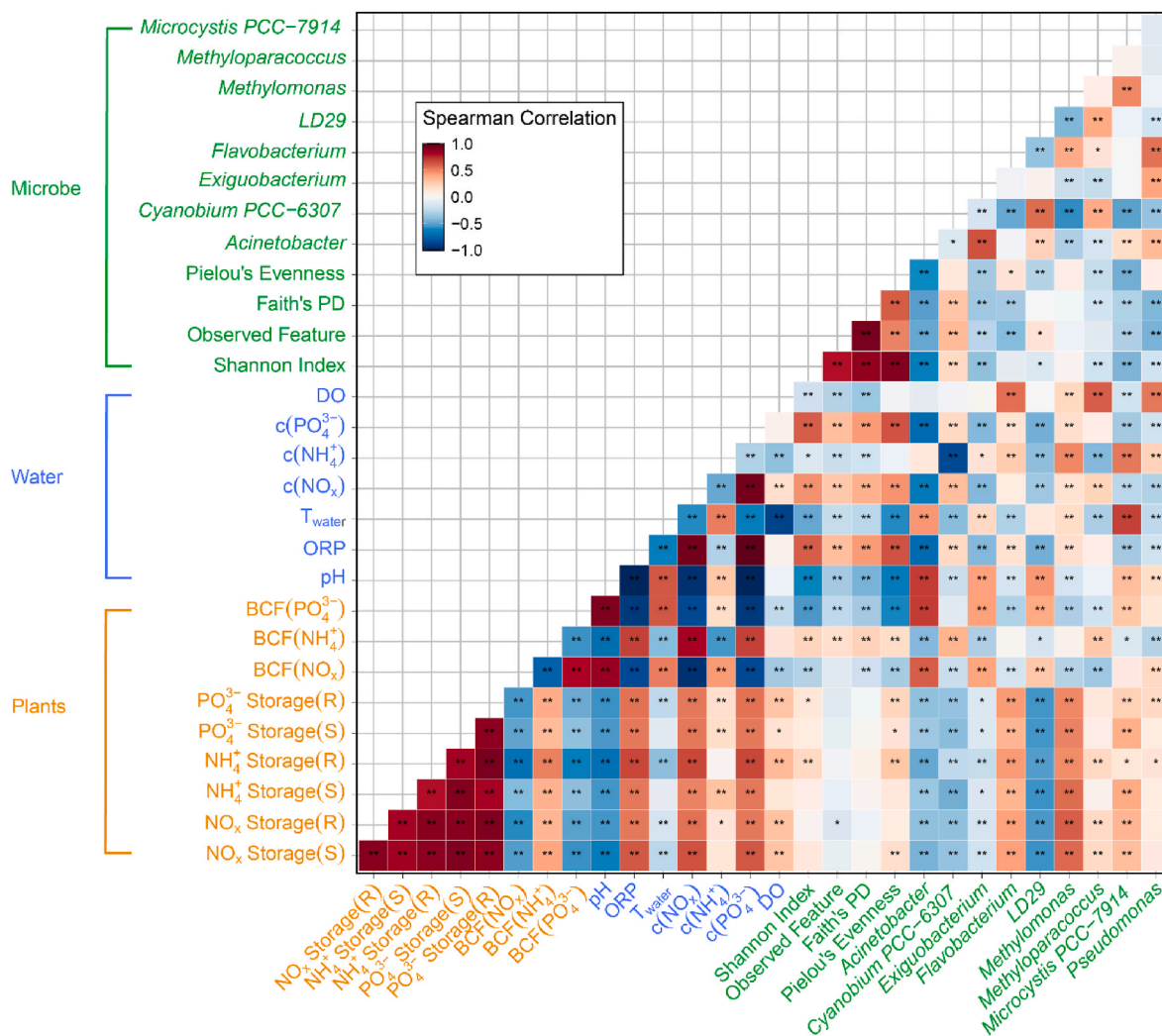


Fig. 5. Heatmap of Spearman's pairwise correlations. Spearman's correlation coefficients among plant variables (nutrient storage and BCFs), water physicochemical parameters (DO, nutrient concentrations, water temperature, ORP, and pH), and microbial variables (alpha diversity indices and relative abundance of key genera). Box colors indicate the direction and strength of the correlations. Asterisks within the boxes denote p-values: one asterisk for p -value < 0.05 and two asterisks for p -value < 0.01 . (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

ambient water, while plant roots selectively shaped distinct rhizosphere communities (Urakawa et al., 2017).

Composition analysis confirmed that the rhizosphere and water microbial communities were taxonomically distinct. In all rhizosphere samples, Proteobacteria and Bacteroidota dominated, together accounting for over 60 % of the community (Fig. 1d and Table S2). These phyla are commonly associated with wetland and rhizosphere habitats and are frequently reported in AFI systems (Gao et al., 2017; Han et al., 2018; Lopardo et al., 2019; Shen et al., 2022; Urakawa et al., 2017). Proteobacteria plays a central role in biogeochemical cycling (Ansola et al., 2014; Liu et al., 2016), and Bacteroidota contributes to nitrogen and phosphorus removal (Waller et al., 2018; Zhang et al., 2022). In contrast, Cyanobacteria dominated the water samples and ranked among the top five phyla detected in the rhizosphere. This pattern likely reflects seasonal algal blooms observed in the nutrient-dense equalization basin (Fig. 1d and Table S2). Although Cyanobacteria, including *Microcystis* and *Cyanobium*, were detected in both rhizosphere and water samples, their relative abundance was significantly lower in the rhizosphere (total < 6.8 %) compared to water (27.0 %) (Table 1 and Fig. 2). This reduction may reflect shading effects of the AFIs, which have been shown to suppress cyanobacterial growth (Samal et al., 2019; Urakawa et al., 2017).

Rhizosphere samples also supported functionally diverse microbial

communities associated with biodegradation, nutrient cycling, and plant growth promotion. *Exiguobacterium* has diverse metabolic functions and plays an important role in carbon and nutrient cycling (Vishnivetskaya et al., 2009). Some *Acinetobacter* strains are plant growth promoting rhizobacteria (PGPR), known for their roles in both autotrophic and heterotrophic denitrification (Lee et al., 2013; Soltani et al., 2010; Xia et al., 2020). Certain *Pseudomonas* species enhance plant growth and suppress diseases, demonstrating versatility in biodegradation (Mercado-Blanco and Bakker, 2007; Urakawa et al., 2017). Methanotrophic genera, including *Methylomonas* and *Methyloparacoccus*, use methane or methanol as their sole carbon source and play key roles in the carbon cycle (Iguchi et al., 2015). Additionally, some *Flavobacterium* species promote plant growth by contributing to nitrogen and phosphorus cycling (Soltani et al., 2010).

Notably, the coexistence of anaerobic (e.g., *Exiguobacterium*, *Candidatus Anammoximicrobium*) and aerobic (e.g., *Flavobacterium*, *Acinetobacter*) taxa within the rhizosphere indicates the presence of micro-scale oxygen gradients, despite the roots being exposed to aerobic ambient water (Fig. S4). This pattern suggests an oxic-anoxic gradient formed within the dense plant root systems, a phenomenon also observed in other studies (Urakawa et al., 2017). Such gradients likely facilitate the coexistence of both anaerobic and aerobic reactions to occur within the rhizosphere.

4.2. Microbial communities in the rhizosphere of different plant species

No significant difference in rhizosphere microbial alpha diversity were observed among plant species. Similar results have been reported in other studies. For example, Zhang et al. (2014) found no significant differences in Shannon diversity among five aquatic plant species in AFIs (*Canna generalis*, *Scirpus validus*, *Alternanthera philoxeroides*, *Cyperus alternifolius*, and *Thalia geniculata*). Similarly, Tanaka et al. (2012) reported comparable rhizosphere microbial diversity between *Phragmites australis* and *Lythrum anceps*. These findings may appear counterintuitive, as both aquatic and terrestrial plants are known to release root exudates that shape host-specific microbial communities by attracting beneficial microorganisms involved in development, nutrient acquisition, and stress resistance (Das et al., 2022; Haichar et al., 2008; O'Brien et al., 2020; Semchenko et al., 2022; Yoneda et al., 2021). However, in AFI systems, such host-specific microbial communities appear to be less pronounced in the rhizospheres of aquatic plants.

Several factors may contribute to this reduced host specificity. First, the rooting environment in AFIs differs significantly from that of soil-based systems. Plants in AFIs are often transplanted without soil – either washed to remove native soil (Bissegger et al., 2014; Chen and Costa, 2023), placed in containers with minimal soil (Afzal et al., 2019b; Olguín et al., 2017), or embedded in substrates such as coir fibers (Lopardo et al., 2019; Wang and Sample, 2014). As a result, roots are largely exposed to the water column, creating a dynamic, water-dominated interface that more closely resembles the environment of free-floating plants than rooted terrestrial systems. Second, most studies characterizing microbial communities in AFIs have been conducted over relatively short durations – typically weeks to a few months (Li et al., 2021b; Meng et al., 2023; Peng et al., 2023; Shen et al., 2022; Urakawa et al., 2017; Zhang et al., 2014) – which may not allow sufficient time for the development of stable, species-specific microbial communities. Overall, these findings emphasize the limited differentiation in rhizosphere microbial communities among plant species in AFI systems, and highlight the need for further long-term, mechanistic studies to better understand plant-microbe specificity under such engineered conditions.

4.3. Polyculture offered benefits to plant nutrient assimilation

Polyculture provided potential benefits to AFI systems in terms of plant growth and nutrient assimilation, even though they did not result in increased rhizosphere microbial diversity. A total of 22 genera were found to be more abundant in polyculture systems, compared to only 9 in monoculture (Fig. 2). Many of the genera enriched in polyculture are known to contribute to nutrient cycling or plant growth promotion. For example, *Pseudomonas* and *Methylomonas*, both previously discussed as beneficial taxa, were more abundant in polyculture. Additional beneficial genera that were more abundant in polyculture included *Rheinheimera*, which can inhibit human bacterial pathogens and enhance plant growth (Presta et al., 2017; Zhao et al., 2023), and *Bacteroidetes vadinHA17*, which plays a critical role in the degradation and decomposition of large compounds into smaller, more bioavailable forms (Mei et al., 2020; Qin et al., 2024).

Notably, both plant species, *C. comosa* and *E. obtusa*, contributed to the abundance of these differentially abundant genera (Fig. 2). For example, *Lacunisphaera*, more abundant in *E. obtusa*, promotes plant growth and aids in phytoremediation by providing protection against heavy metals and antibiotics (Jiang et al., 2024). *Cellvibrio*, another genus more abundant in *E. obtusa*, has nitrogen-fixation capacities (Suarez et al., 2014), while *Chryseobacterium* contains species known for their beneficial degradation capabilities (Page et al., 2019).

From a functional perspective, seven differentially abundant pathways were identified in polyculture systems, compared to only one in monoculture (Fig. 3). Six of these seven pathways were associated with fatty acid and lipid biosynthesis, which are crucial metabolic pathways

for plant growth (Table S5). The abundance of these pathways suggests a potential mutualistic relationship between AFI plants and their rhizosphere microbial populations, wherein plants selectively recruit these microbes from the aquatic environment, providing them with surfaces to inhabit, and in return, benefit from microbial contributions to metabolic functions (Urakawa et al., 2017). Six of the seven enriched pathways in polyculture systems were more abundant in *E. obtusa*, suggesting that *E. obtusa* may have enhanced biosynthesis pathways in *C. comosa* when grown together (Fig. 3). This is consistent with the analysis showing that *C. comosa* exhibited greater biomass and nutrient assimilation in polyculture than in monoculture during the growing season (Chen et al., 2025b).

4.4. Interactions between microbial communities, environmental factors, and plant nutrient assimilation

Plant nutrient assimilation was closely related to both microbial communities and water physicochemical parameters. Specifically, concentrations of NO_x , PO_4^{3-} , and NH_4^+ in the water were positively correlated with the corresponding nutrient assimilation in plant tissues (Fig. 5). This pattern aligns with previous studies showing that increased nutrient loads enhance N and P removal performance in AFIs (Chang et al., 2017; Pavlineri et al., 2017; Samal et al., 2019). In addition to nutrient concentrations, plant nutrient assimilation was strongly associated with the abundance of key microbial genera involved in nutrient cycling. For example, *Flavobacterium* and *Methylomonas* showed significant positive correlations with the storage of NO_x , PO_4^{3-} , and NH_4^+ in plant tissues (p -value < 0.05, Fig. 5). Further associations were observed between nutrient assimilation and other water physicochemical parameters, including pH, DO and ORP, all of which were closely related to microbial composition. These findings are consistent with studies showing that water quality in eutrophic environments can influence the structure, composition, and interactions of microbial communities (Manirakiza et al., 2024). Together, the results suggest that environmental factors may influence the composition and structure of rhizosphere microbial communities, which in turn can regulate microbial-mediated nutrient transformations and bioavailability, ultimately impacting plant growth and the overall AFI performance (Chang et al., 2017; Iguchi et al., 2015; Samal et al., 2019; Shen et al., 2022; Soltani et al., 2010).

In contrast, weak correlations were observed between plant assimilation of NO_x , PO_4^{3-} , and NH_4^+ and rhizosphere microbial diversity (Fig. 5). Similar findings have been reported by Zhang et al. (2014), who found no correlation between microbial diversity and the removal of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in AFIs. Several factors may explain these results. First, greater microbial diversity does not necessarily indicate a greater abundance of functional or beneficial taxa. For example, no correlation was found between Shannon diversity and the abundance of *Flavobacterium* or *Methylomonas* (Fig. 5). This is consistent with findings by Urakawa et al. (2017), where low-diversity biofilms exhibited high abundance of *Pseudomonas*. Second, microbial responses to environmental factors may follow nonlinear or threshold-dependent patterns. For instance, *Microcystis aeruginosa* thrives under neutral to weakly alkaline conditions but rapidly declines outside this range (Yang et al., 2018), and cyanobacteria grow actively at temperatures above 20 °C but become dormant below 10 °C (Yang et al., 2020). Thus, a linear relationship between microbial diversity or composition and nutrient assimilation should not be expected.

4.5. Limitations and future directions

One limitation of this study is the exclusive focus on inorganic nutrient forms, specifically NO_x , PO_4^{3-} , and NH_4^+ , without consideration of other nutrient species that may also contribute to nutrient cycling within AFI systems. For P, PO_4^{3-} , a soluble reactive phosphorus (SRP), was selected as the primary focus due to its high bioavailability for

chemical reactions and biological uptake by plants and microorganisms (Macintosh et al., 2018). However, soluble non-reactive phosphorus (SNRP), which can be converted into SRP through enzymatic degradation or photochemical conversion, also represents a bioavailable form of P (Dyhrman et al., 2006; Shen et al., 2022; Zhang et al., 2019). Additionally, particulate P may be removed by AFI through physical filtration by plant root systems (Shen et al., 2022). Similarly, for N, prior studies have demonstrated that AFI systems influence multiple N species. Lopardo et al. (2019) reported the conversion of a significant portion of N into organic forms, while Gao et al. (2017) observed low reduction in NO_x, particularly NO₂-N, but substantial removal of TN. Moreover, different nutrient species respond differently to environmental factors. For example, TN reduction has been shown to be highly temperature-dependent, whereas NO_x reduction is not. Future studies should quantify a broader range of nutrient species to better characterize nutrient transformation dynamics and their relationships with microbial communities within AFI systems.

Another limitation is the exclusive focus on nutrient assimilation and storage within plant tissues, without accounting for nutrients removed through alternative pathways. While many previous studies have estimated the relative contribution of microbial activities and plant assimilation to overall nutrient removal in AFIs (Bu and Xu, 2013; Chang et al., 2017; Duan et al., 2016; Tanner and Headley, 2011), some have attributed a substantial portion of nutrient removal to plant uptake – for example, 49 % of TN and 74 % of TP removal (Keizer-Vlek et al., 2014), and 58.5 % of TN removal (Wang et al., 2019). However, the role of microbes in mediating plant nutrient uptake is often underrepresented in such assessments. Beyond facilitation plant assimilation, microbial communities contribute directly to nutrient degradation, transformation, and incorporation into biofilms (Shen et al., 2022). As a result, the contribution of microbes to total nutrient removal in AFI systems may be underestimated when nutrient storage in plant tissues is credited solely to plant uptake. Given the complex interactions between plants and microbes revealed in this study, a more integrated perspective is needed to evaluate AFI performance. A comprehensive understanding of both microbial and plant-mediated processes, particularly in field-scale applications, will be critical for optimizing system design and management.

5. Conclusions

In this study, microbial communities associated with a field-scale AFI system treating residential raw sewage were characterized. The results revealed that the rhizosphere exhibited significantly higher microbial diversity compared to the raw wastewater, and the community compositions were distant between the two environments. The rhizosphere was predominantly composed of Proteobacteria (~50 %), while Cyanobacteria, especially *Microcystis PCC-7914* and *Cyanobium PCC-6307*, dominated the water samples (~30 %). Although multiple genera were prevalent in the rhizosphere, no single genus was dominant, reflecting a relatively even community structure.

Microbial diversity in the rhizosphere did not differ significantly by plant species or culture types. However, polyculture systems supported a greater number of beneficial microbial taxa and metabolic pathways related to nutrient cycling. Although *E. obtusa* did not contribute significantly to biomass production or nutrient assimilation, its inclusion in polyculture facilitated the presence of several beneficial microbial genera and functional pathways. These findings suggest that polyculture may enhance microbial-mediated processes and contribute to improved nutrient management in AFI systems. This study also demonstrated that plant assimilation of N and P, the diversity and composition of rhizosphere microbial communities, and environmental conditions such as pH, DO, and ORP are closely interconnected. Future studies should explore a broader range of nutrient species to better understand nutrient cycling within AFI systems. Additionally, testing a wider diversity of plant species will be essential for identifying robust plant-microbe

associations that can inform the design and scaling of high-performance AFI systems.

CRedit authorship contribution statement

Zhaozhe Chen: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Liangwei Li:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Min-seung Kim:** Writing – review & editing, Resources, Methodology. **Emma Lancaster:** Writing – review & editing, Resources, Methodology. **Jiyoung Lee:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Ozeas S. Costa:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envpol.2025.126992>.

Data availability

Data will be made available on request.

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