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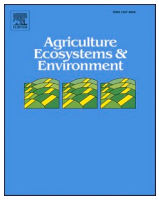

Drainage alters bacterial co-occurrence networks and net nitrogen mineralization rate in peatlands under different forest management regimes

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ABSTRACT

Peatlands are crucial for maintaining ecological balance, supporting biodiversity, and regulating hydrological and biogeochemical cycles. However, extensive drainage for forestry and forest management practices has severely altered their carbon and nitrogen dynamics and microbial communities. This study evaluated the effects of peatland drainage and three forest management practices—clear-cutting, even-aged forest, and continuous cover forestry—on microbial biomass, soil nutrients and bacterial community structure. The results showed that soil microbial biomass carbon was unaffected by forest management or water table depth. However, in pristine peatland, soil microbial biomass nitrogen was influenced by water table depth. Compared with a low water table (-30 cm below the soil surface), the net nitrogen mineralization rate was significantly higher under a high water table (-10 cm below the soil surface). Bacterial diversity was influenced by forest management practices but unaffected by water table depth, with the highest diversity observed in pristine peatland. High water table enhanced the connectivity and complexity of bacterial co-occurrence networks. Soil characteristics (NH_4^+–N, DOC, MBN, net N mineralization rate, and MBC) collectively explained 56.9% of the observed variation in bacterial community structure. Furthermore, bacterial community assembly processes shifted from stochastic processes in high-water-table peatland to deterministic processes in drained sites. This indicates that environmental filtering is intensified, potentially reducing ecosystem stability. These findings highlight the effects of forest management and hydrology on microbial biodiversity and function, providing a key scientific basis for the ecological restoration of degraded peatlands and sustainable forest management.

1. Introduction

Peatlands are carbon-rich ecosystems formed under water-saturated conditions that slow decomposition and enable the accumulation of partially decayed organic matter, or peat (Gong et al., 2026; Günther et al., 2020). Despite covering only 2.84% of the Earth's land surface, peatlands store over one-third of global soil carbon, making them critical natural carbon sinks and regulators of climate change (Evans et al., 2021; Karpińska-Kołaczek et al., 2024). Peatlands host diverse microbial communities that drive essential ecosystem processes, including nutrient cycling and organic matter turnover (Parvin et al., 2018; Sokol et al., 2022). Since the mid−20th century, large areas of boreal peatland have been drained to facilitate tree growth, fundamentally altering hydrological regimes, vegetation composition, and belowground biogeochemical cycles (Laine et al., 2021). Peatland drainage is defined as the anthropogenic modification of hydrological conditions through engineered measures to lower the groundwater table. Following such drainage, one of the predominant land-use practices is so-called

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drainage-based afforestation (Harpenslager et al., 2024). Lowering the water table through drainage enhances soil aeration, which accelerates organic matter decomposition and leads to CO_2 emissions, and export of nutrients and dissolved organic carbon (DOC) to aquatic systems (Juottonen, 2020; Wu et al., 2024).

Forest management refers to the process of achieving sustainable production of timber and other forest products through scientific planning and human intervention, while also protecting and restoring the forest ecosystem (Quartucci et al., 2026). Its core objective is to balance economic benefits with ecological benefits, and to maintain the biodiversity, water and soil conservation capabilities, and carbon sink functions of the forest (Ibrahim et al., 2024). Currently, forest management practices on drained peatlands generally adopt either the even-aged forestry (EAF) model or the continuous cover forestry (CCF) management model. Even-aged forestry refers to a forest stand in which the trees have a similar origin and are generally of the same age. However, due to the uniformity of tree age and growth, this may lead to a more homogeneous and less stable microbial community composition (An et al., 2008). Continuous cover forestry, which maintains continuous tree cover of mixed ages may promote biodiversity, and potentially more stable soil microbial communities (Kim et al., 2021). However, long-term effects of forest management practices on peatland microbial networks and soil quality indicators remain poorly quantified (Juutinen et al., 2021).

Microorganisms in peatlands play an important role in decomposing organic matter, regulating nitrogen (N) mineralization, and sustaining ecosystem productivity (Santoro and Casciotti, 2011; Yu et al., 2025). Under natural, waterlogged conditions, anaerobic bacteria dominate over aerobic bacteria and contribute to slow decomposition and carbon retention (Pavia et al., 2024). Drainage and forest management not only change oxygen availability but also modify microbial species composition, and the complexity of microbial co-occurrence networks (Luo et al., 2022). The microbial co-occurrence network can identify the coexistence patterns of different microbial groups in terms of their spatio-temporal distribution through statistical methods, and infer potential ecological relationships (such as mutualism, competition, or symbiosis) (Wang et al., 2025). In peatland ecosystems, the microbial interaction network can reveal the assembly rules of microbial communities and their response mechanisms to environmental changes. For instance, highly complex network structures usually indicate a more stable ecosystem function and a more diverse material cycling pathway (Li et al., 2023). Meanwhile, these changes can directly influence microbial biomass and nutrient mineralization rates (Briones et al., 2020).

There is limited empirical evidence on how different forest management regimes and altered hydrological conditions to shape bacterial diversity, ecological networks and nitrogen cycling in boreal peatlands (Rowan, 2025). In this study, we investigated the effects of forest management and water table on nitrogen mineralization and bacterial communities in boreal peatlands in Finland. Soil sample cores were taken from pristine undrained peatland forest, and drained forested peatlands that were either uncut, clear-cut, or selectively harvested. The soil cores were incubated at two water table treatments (high and low). We measured net nitrogen mineralization rate, microbial biomass and bacterial communities and co-occurrence networks from the cores after the seven month incubation. We hypothesized that: (1) Pristine peatlands and continuous cover forestry exhibit higher bacterial diversity compared to even-aged forest management and clear-cutting; however, different water level treatment conditions may alter this pattern. (2) The net nitrogen mineralization rate at high water tables is higher than that at low water tables.

2. Materials and methods

2.1. Study sites

The experimental sites were established at a drained peatland forest in Paroninkorpi (61°01'20" N, 25°14'32" E) and a pristine peatland site (PP) in Sudenpesänkangas in Southern Finland. Sudenpesänkangas is located 5 km from the Paroninkorpi experiment. The long-term (1990–2019) mean annual temperature in the area is + 4.7°C and the amount of precipitation is 638 mm (Palviainen et al., 2022). The effective temperature sum is 1460 °-days (sum of daily mean temperature exceeding +5°C), and the length of the growing season is 175–185 days. The forest site with *Picea abies* Karst. (L.) as the dominant tree species was formed on drained peatland (Table S1), the main ditches were excavated around the 1940s and the ditching was complemented in the 1960s. The distance between ditches is 65–70 m, and they are 0.6–0.7 m deep. Following drainage, the typical summer groundwater depth in the plot is about 41 cm, and this water table depth is sustained over multiple years. The peat layer is about 1.5 m thick and consists mainly of *Carex* remains, reed (*Phragmites australis*), cattail (*Typha* spp.), and wood residues. Part of the area was clear-cut (CC) in 2017, and adjacent to the clear-cut area, experimental plots were established to study the effect of different forest management practices on soil carbon and nitrogen dynamics. We had three treatments: 1) uncut forest (continuous cover forest), 2) selective harvesting (even-aged forest), and 3) clear-cutting (clear-cut forest). Continuous cover forest is a form of selective logging, referring to a management system in which the forest canopy remains continuously closed throughout the rotation period, and its stands are typically characterized by an uneven-aged structure. The basal area of the stand was 25 m^2 ha^{-1}. Even-aged forest refers to a forest stand in which the trees have a similar origin and are generally of the same age, with the basal area of the stand was 12 m^2 ha^{-1}. Clear-cut forest refers to the complete removal of all trees in the operation area in a single cut, resulting in a bare exposed site.

2.2. Sample collection

Peat columns were collected from the experimental plots using polyvinyl chloride (PVC) pipes (15 cm diameter and 50 cm height). Sixteen peat columns per treatment (PP, CC, CCF, and EAF) were collected. In order to reduce the disturbance to the soil, sampling was done in the coldest month of the year (January 2020) when soil processes are slow. In the peat core sampling method, a PVC tube is driven into the peat and the core is extracted by excavating around the tube, with care taken to keep both ends of the core flat. Throughout the entire coring process, excessive force was avoided on both the PVC tube and the peat core to minimize disturbance and prevent alteration of the physical properties of the peat core. The ground vegetation was kept intact in the peat columns, and the columns were transported and stored at + 4°C dark and cold room. The peat column experiment was conducted from March to October 2020 in the greenhouse of the Natura Building at the University of Eastern Finland, Joensuu, for a total of 7 months. The columns from the four management treatments (CC, CCF, EAF and PP) were placed in 12 L plastic buckets, and the four management treatments were randomly divided into two water table treatments: low-water table (−30 cm from the soil surface) and high-water table (−10 cm from the soil surface). There were 8 replicates per water table treatment in CC, CCF, EAF, and PP. The soil columns were kept at 20–25°C in a greenhouse, and the water table was maintained weekly with deionized water (pH adjusted to 5.5, corresponding to the pH of rainwater). At the end of the experiment, the top 0 to −10 cm of the soil layer was collected for analysis. Soil samples used for measuring soil property (microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), DOC, ammonium nitrogen (NH_4^+–N), and net nitrogen mineralization rate) indicators should be stored in a refrigerator at 4°C and tested as soon as possible, preferably within one week after sampling. Soil samples for bacterial community analysis should be flash-frozen in liquid nitrogen and subsequently stored in a freezer at –80°C.

2.3. Soil properties

Microbial biomass carbon and nitrogen were determined by the chloroform fumigation extraction method (Wu et al., 1990). Two 5 g sub-samples were weighed for each soil core. One of the samples was fumigated with chloroform for 24 h. Then placed into a 50 mL centrifuge tube with 20 mL of 0.5 M K_2SO_4 and 0.5 mL of ethanol-free chloroform was added, and the suspension was shaken at 175 rpm for 1 h. The suspension was left to settle for 10 min and thereafter centrifuged at 4000 rpm for 8 min. The supernatant was 10 mL, and the residual chloroform in the filtrate was removed by bubbling with nitrogen gas for 30 min, and 1 mL of supernatant was taken and diluted 20 times. DOC and total nitrogen (TN) were analyzed using TOC analyzer (TOC-L CSH/CSN, Shimadzu, Japan). Microbial biomass carbon (MBC) and nitrogen (MBN) were calculated as the difference in DOC and TN concentrations, respectively, between fumigated and non-fumigated samples. The specific calculation formula is as follows:

$$DOC_m = TOC_E \times (V_E + (FW\text{-}DW))/1000 \quad (1)$$

V_E is the volume of extract, FW is the fresh weight (g) of soil, DW is the dry weight (g) of soil.

$$DOCc = DOCm / DW \times 1000 \quad (2)$$

DOCc is the DOC concentration (μg g^{-1} DW) in soil, DOCm is DOC (mg) in extract.

$$MBC = DOC_c\ (Chl) - DOC_c\ (Chl^-) \quad (3)$$

DOC_c (Chl) is the DOC concentration (μg g^{-1} DW) in soil sample of chloroform samples, DOC_c (Chl^-) is DOC concentration (μg g^{-1} DW) in soil of non-chloroform samples.

$$MBN = DN_c\ (Chl) - DN_c\ (Chl^-) \quad (4)$$

DN_c (Chl) is dissolved N concentration (μg g^{-1} DW) in chloroform samples, DNc (Chl^-) is dissolved N concentration (μg g^{-1} DW) in non-chloroform samples.

Net nitrogen mineralization rate was determined by laboratory culture method (Grigatti et al., 2007). Two peat subsamples (10 g fresh weight each) were taken; one was immediately extracted with 100 mL of 2 M KCl, and the other was placed in an incubator for 28 days before the extraction. The concentrations of ammonium (NH_4^+), nitrate (NO_3^-), and nitrite (NO_2^-) in samples before and after the incubation were determined spectrophotometrically with a plate reader (Victor 1420) using Griess reagent and vanadium chloride (Miranda et al., 2001; Fawcett et al., 1960). Net nitrogen mineralization rate was calculated from the difference in the NH_4^+, NO_3^- and NO_2^- before and after the extraction. For the specific calculation method, please refer to Grigatti et al. (2007). During the measurement, certain samples yielded values below the lower limit of quantification (LLOQ) of the respective analytical instruments. Specifically, the proportions of samples with undetectable data were as follows: MBC (23.44%), MBN (40.63%), DOC (4.69%), NH_4^+-N (15.63%) and net nitrogen mineralization rate (18.75%). In peatland soils, the extremely high organic matter content often leads to MBC and MBN levels exceeding the upper detection limit, leading to undetectable values. For all treatments, the number of biological replicates with valid data remained ≥ 3, which satisfies the requirements for subsequent statistical analysis. Missing values were excluded from the dataset, and no imputation was performed.

2.4. DNA extraction, Illumina MiSeqsequencing, and data processing

DNA extraction of soil samples was performed using the E.Z.N.A.® Soil DNA Kit (Omega Bio-tek, USA). DNA concentration and purity were determined using NanoDrop2000 (Thermo Scientific, USA). Then, the variable region of 16S rRNA gene was amplified by PCR using upstream primer 338 F (5'-ACTCCTACGGGAGGCAGCAG−3') and downstream primer 806 R (5'-GGACTACHVGGGTWTCTAAT−3') (Fierer et al., 2005). The amplification procedure was as follows: pre-denaturation at 95°C for 3 min, 27 cycles (denaturation at 95°C for 30 s, annealing at 55°C for 30 s, extension at 72°C for 30 s), then stable extension at 72°C for 10 min, and finally preservation at 4°C. The purified PCR products were constructed using the NEXTFLEX Rapid DNA-Seq Kit (Bioo Scientific, USA) and sequenced using Illumina Miseq PE300 (Illumina, USA) platform. Raw data was uploaded to NCBI database (serial number: PRJNA1286112).

The fastp (https://github.com/OpenGene/fastp, version 0.19.6) software was used for data quality control, and FLASH (http://www.cbcb.umd.edu/software/flash, version 1.2.11) was used for sequence splicing. Noise reduction was performed using the DADA2 plug-in in the QIIME2 process (Callahan et al., 2016). The average sequence coverage of each sample could still reach 99.09% after the number of all sample sequences was flattened to 126,001. Based on the Silva 16S rRNA gene database (v.138), the Naive Bayes classifier in QIIME2 was used for species classification of Amplicon Sequence Variants (ASVs).

2.5. Statistical analysis

To evaluate the respective contributions of deterministic processes versus stochastic factors in microbiome assembly, we computed the beta nearest taxon index (βNTI) through null model simulations (999 iterations). The βNTI metric represents the standardized effect size derived from comparisons between observed beta mean nearest taxon distance and phylogenetically informed null expectations. Using 50% as the boundary point between certainty (< 50%) and randomness (> 50%) assembly, a normalized random ratio (NST) index was established. Nm, which is the product of the community size (N) and the migration rate (m) (Nm = N × m), quantifies the diffusion estimation between communities and determines the correlation between the occurrence frequency and the relative abundance in the area. To construct the microbial single-factor co-occurrence network, the association strength between ASVs was calculated. To construct the dual-factor co-occurrence network, the association strength between ASVs and environmental factors was calculated, and the network diagram was constructed based on the association matrix. The network graph was visualized using Gephi, and the overall structure and key nodes were calculated. The nodes represent the basic units that have been selected and retained in the microbial community. The average path length was calculated as the average shortest path length between all node pairs in the network, serves as a key metric for the overall integration, efficiency, and "small-world" character of the microbial community.

One-way analysis of variance (ANOVA) was used to evaluate the differences in soil MBC, MBN, DOC, NH_4^+–N and net nitrogen mineralization rate. Post hoc comparisons were then conducted using Tukey's HSD multiple-range test, with statistical significance set at $P < 0.05$. Co-occurrence network analysis uses the R software "*igraph*" package to calculate the topological properties of each network, and network visualization was done using the Gephi (version 0.9.1) software. Alpha diversity analysis of bacterial communities, Venn diagram, variance partitioning analysis, non-metric multidimensional scale (NMDS), and correlation heat maps, were done using the "*vegan*" package in R. The "*ggplot2*" package in R was used for creating neutral community model and partial least squares-path modeling.

3. Results

3.1. Soil biological characteristics

The soil MBC, DOC and NH_4^+–N concentrations showed no significant differences ($P > 0.05$) between high and low water tables across most forest management treatments (Fig. 1). The MBN in PP was significantly higher at low water table than at high water table treatment (Fig. 1b). DOC concentration in CC and CCF sites was significantly

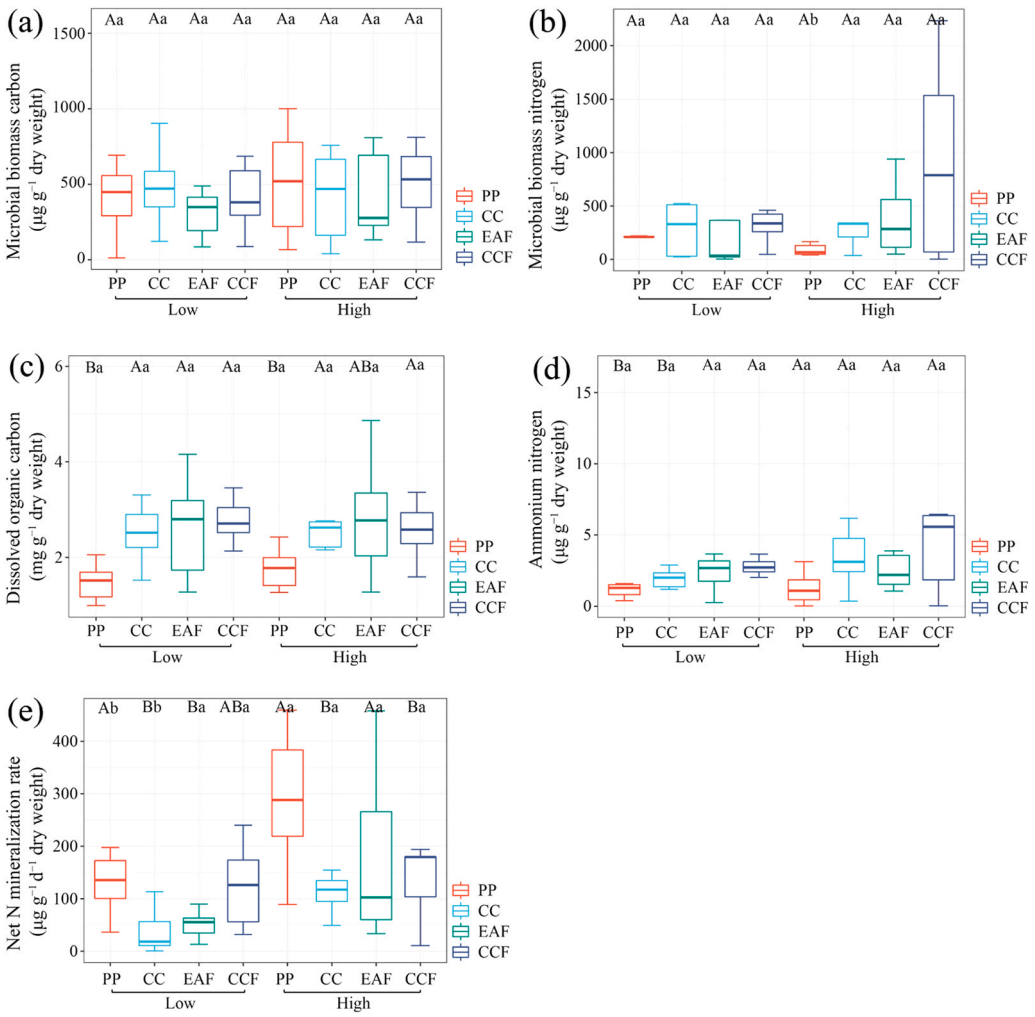

Fig. 1. Soil biological properties in different forest types with low and high water tables. (a) Microbial biomass carbon, (b) Microbial biomass nitrogen, (c) Dissolved organic carbon, (d) Ammonium nitrogen, and (e) Net nitrogen mineralization rate. Upper-case letters indicate significant differences among forest types ($P < 0.05$). Lower-case letters indicate significant differences between water tables within the same forest type ($P < 0.05$). Abbreviation: Low = low water table treatment, High = high water table treatment, PP = Pristine Peatland, CC = Clear-cut Forest, EAF = Even-Aged Forest, CCF = Continuous Cover Forest.

higher than that in PP at both water table treatments (Fig. 1c). At low water table, EAF and CCF sites exhibited elevated NH_4^+–N compared to PP and CC, whereas no significant differences ($P > 0.05$) in NH_4^+–N were observed across forest management treatments under high water table (Fig. 1d). Net nitrogen mineralization rate was significantly higher at high water table than at low water table in both PP and CC sites (Fig. 1e). Among all management treatments, PP consistently exhibited the highest ($P < 0.05$) net nitrogen mineralization rates at both water tables.

3.2. Bacterial community composition and diversity

Non-metric multidimensional scaling (NMDS) indicated distinct bacterial community structures at both high and low water tables (Fig. 2a and Table S2). There were significant differences in microbial community structure between water tables and management types. Under both low water table and high water table conditions, the bacterial community structure treated by PP shows significant differences ($P < 0.05$) compared with that of CC, EAF and CCF. Under low water table conditions, the bacterial community structures of the CC treatment are significantly different from those of the EAF and CCF treatments. Partitioning of variance indicated that environmental factors—including NH_4^+–N, DOC, MBN, net nitrogen mineralization rate, and MBC—collectively explained 56.9% of the observed variation in bacterial community structure. Among these, NH_4^+–N and DOC were the most influential (Table S3). Venn diagram analysis showed that 14 ASVs were shared across all treatments, with PP hosting the highest number of unique ASVs under both water tables (Fig. 2b). Although no significant differences in Ace and Shannon diversity indices were observed between water tables within the same treatment (Fig. 2c, d), PP consistently exhibited higher bacterial richness and diversity than EAF and CC.

The bacterial community composition was dominated by Acidobacteriota, Proteobacteria, Actinobacteriota, Verrucomicrobiota and Chloroflexi (Fig. 2e). The water table had no significant effect on the relative abundance of most phyla, including Acidobacteriota, Actinobacteriota, Verrucomicrobiota, WPS−2 or Bacteroidota (Fig. S1). However, there were significant interactions of forest treatment and water table. At low water table, PP treatment exhibited lower relative abundance of Acidobacteriota and Proteobacteria but higher abundance of Verrucomicrobiota, Chloroflexi and Desulfobacterota than the other managed forest types (CC, EAF and CCF). Conversely, at high water table, PP treatment had higher abundance of Proteobacteria, Bacteroidota and Desulfobacterota, but lower relative abundance of Acidobacteriota and Desulfobacterota compared to managed forest types.

3.3. Bacterial community assembly processes

To assess the ecological deterministic and stochastic processes in

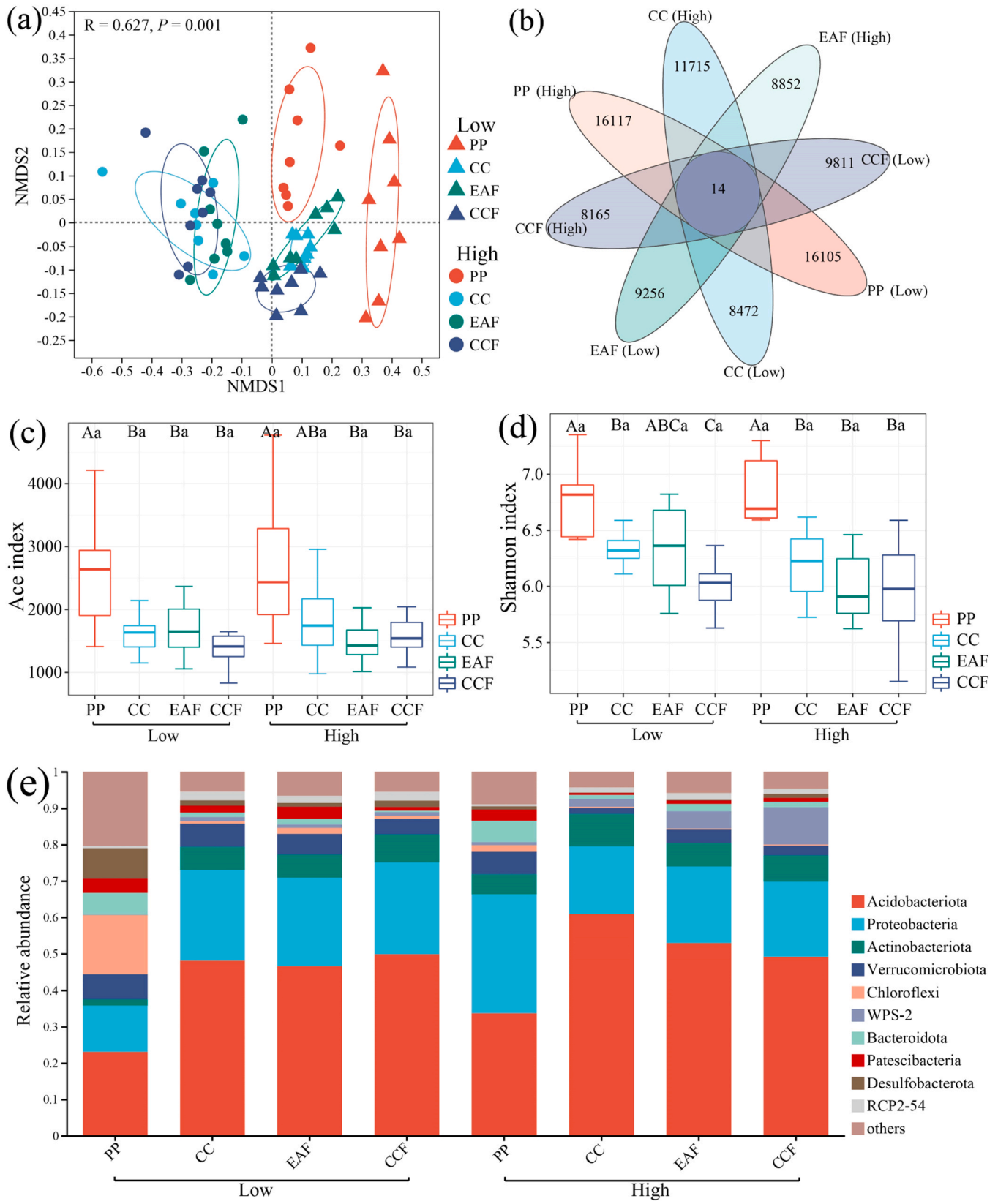

Fig. 2. Bacterial community diversity and structure in different forest types with low and high water tables. (a) Non-metric multidimensional scaling (NMDS) displaying differences in bacterial community structure, (b)Venn diagram of unique and shared ASVs, (c) Community species richness index (Ace index), (d) Community diversity index (Shannon index) and (e) Relative abundance of major taxa at the phylum level. Upper-case letters indicate significant differences among forest types ($P < 0.05$). Lower-case letters indicate significant differences between water tables within the same forest type ($P < 0.05$). Abbreviation: Low = low water table treatment, High = high water table treatment, PP = Pristine Peatland, CC = Clear-cut Forest, EAF = Even-Aged Forest, CCF = Continuous Cover Forest.

bacterial community assembly, beta nearest taxon index (βNTI) and the Bray-Curtis dissimilarity index (RC_Bray) were employed. In PP, community assembly was primarily driven by dispersal limitation ($|\beta NTI| < 2$, RC_Bray > 0.95) under both water tables, with a stronger signal of dispersal limitation compared to managed forest types (CC, EAF and CCF) (Fig. 3a). In contrast, CC, EAF, and CCF communities were governed more by stochastic processes and homogeneous dispersal ($|\beta NTI| < 2$, $|RC\_Bray| < 0.95$). Niche similarity test (NST) showed that stochastic processes predominated in PP, while deterministic processes had a greater influence in CC, EAF, and CCF sites (Fig. 3b). Neutral community model (NCM) fitting showed strong explanatory power ($R^2 > 0.7$), supporting the role of neutral processes in shaping community composition (Fig. 3c). Diffusion limitation, as indicated by lower Nm values (Nm is the product of the population size (N) and the migration

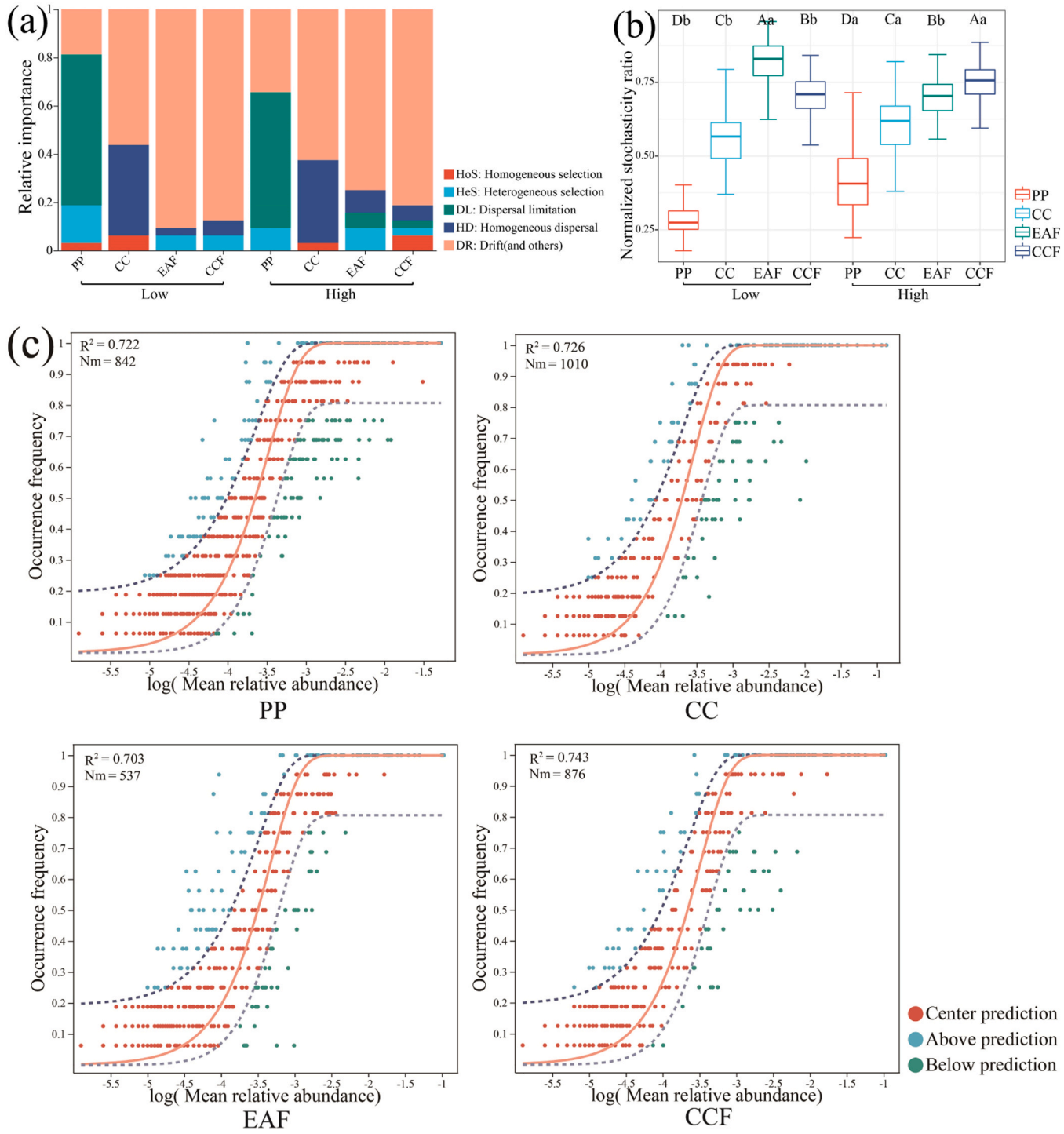

Fig. 3. Bacterial community assembly process in different forest types. (a) Relative contribution of microbial deterministic and stochastic processes, (b) Null model assessing species turnover, and (c) Neutral community model distinguishing the role of random processes in microbial community aggregation in each forest. Uppercase letters indicate significant differences among forest types ($P < 0.05$). Lower-case letters indicate significant differences between water tables within the same forest type ($P < 0.05$). Abbreviation: Low = low water table treatment, High = high water table treatment, PP = Pristine Peatland, CC = Clear-cut Forest, EAF = Even-Aged Forest, CCF = Continuous Cover Forest.

rate (m) of the community), was lower in PP than in CC and CCF, but greater than in EAF.

3.4. Bacterial co-occurrence network

Network complexity, as indicated by the number of links and average degree, was higher under high water table in PP, CC, and CCF compared to low water table (Fig. 4 and Table 1). At low water table, the diameter of the network for PP treatment is smaller compared to the other three treatments, but its modularity, average path length and clustering coefficient are higher (Table 1). Under high water table, CCF treatment exhibited the most complex network, with the highest number of links and average degree, and the shortest average path length. Overall, positive correlations dominated the bacterial co-occurrence networks, accounting for more than 69.3% of all correlations (Fig. S2). At high water table, CC, EAF, and CCF treatment networks had a higher proportion of positive correlations compared to low water table conditions. In contrast, PP treatment had more positive interactions at low water table than at high water table.

3.5. Relationship between soil nutrient contents and microbial communities

Correlation network analysis showed that PP treatment harbored the highest number of ASVs correlated with soil nutrient parameters (DOC, MBC, NH_4^+–N, MBN, net nitrogen mineralization rate) (130 ASVs), followed by CCF (115 ASVs), EAF (99 ASVs), and CC (59 ASVs) (Fig. 5a, b). PP also had the greatest number of ASVs associated with net nitrogen mineralization rate and MBC. Among environmental variables, DOC was negatively correlated with Ace and Shannon indices but positively correlated with the relative abundances of Acidobacteriota and Actinobacteriota (Fig. 5c). NH_4^+–N was significantly negatively correlated with bacterial diversity (Shannon index). Partial least squares path modeling (PLS-PM) indicated that higher water tables have a significant positive impact on the microbial nutrients (MBC, MBN), but the available nutrients in the soil have a significant negative correlation with bacterial diversity (Fig. 5d). The water table and net nitrogen mineralization rate have a positive correlation with microbial diversity, whereas soil nutrient availability was negatively correlated with microbial diversity (Fig. 5e).

4. Discussion

4.1. Soil characteristics

Our study demonstrated that soil MBC contents were not significantly affected by forest management, indicating that MBC in peatland forest soil is relatively stable across forest management regimes. This result may be due to the microorganisms are very sensitive to soil properties such as temperature and pH, and the complex interaction of these properties determines the MBC in the soil (Khan et al., 2024). Forest management significantly influenced bacterial community composition and diversity, it did not affect MBN, suggesting that changes in microbial community structure did not translate into altered MBN pools. The absence of significant differences in MBN across forest management gradients could be partly attributed to the negligible variation in NH_4^+–N concentrations observed in this study. It is well established that NH_4^+–N serves as a pivotal nutrient modulating microbial proliferation (Bell et al., 2008; Han et al., 2025). Accordingly, the limited fluctuation in NH_4^+–N availability would impose a constraining effect on microbial biomass turnover, thereby yielding statistically indistinguishable MBN values among treatments. This study show that the nitrogen mineralization rate of at high water level peatlands in PP and CC is higher than that of at low water level peatlands. Some studies indicate that high water level is more conducive to microbial growth and metabolic activities in peatland, promotes microbial degradation of organic matter, and thus increases the rate of nitrogen mineralization (Solly et al., 2023). Interestingly, this increase occurred despite stable microbial biomass and diversity, suggesting that microbial functional activity may be more sensitive to hydrological conditions than community size or diversity (Xiao et al., 2024). The elevated relative abundance of Proteobacteria under high water table—known for roles in ammonification and nitrification—supports this interpretation (Tang et al., 2025). Furthermore, the observed increase in the nitrogen mineralization rate may also be attributed to the substantially higher temperature in the greenhouse incubation compared to the average soil temperature of typical boreal peatlands. This temperature elevation could have amplified the actual decomposition and mineralization rates that would occur under field conditions, thereby leading to discrepancies. Furthermore, the pristine peatland and other forest types are located in close proximity, thereby reducing the likelihood of soil heterogeneity. However, sampling was conducted only over a short

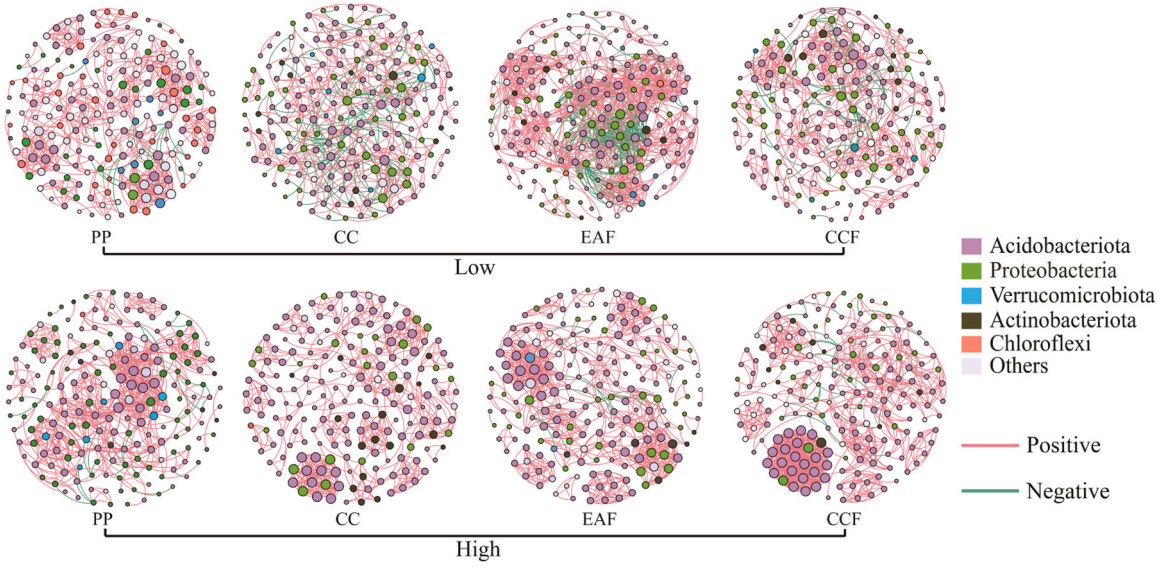

Fig. 4. Bacterial co-occurrence networks among taxa in different forest types with low and high water tables. "Positive" indicates a positive correlation among ASVs, while "negative" indicates a negative correlation ($R > 0.8$, $P < 0.05$). Abbreviation: Low = low water table treatment, High = high water table treatment, PP = Pristine Peatland, CC = Clear-cut Forest, EAF = Even-Aged Forest, CCF = Continuous Cover Forest.

Table 1
Topological characteristics of soil bacterial community network in different forest types.

Water table	Forest type	Network Parameters					
		Links	Average degree	Network diameter	Modularity	Average path length	Average clustering coefficient
Low	PP	658	6.82	12	0.82	4.87	0.70
	CC	508	5.18	13	0.71	4.74	0.46
	EAF	1017	10.22	13	0.61	3.74	0.61
	CCF	593	6.28	14	0.74	4.86	0.65
High	PP	690	7.11	13	0.74	4.97	0.67
	CC	575	5.99	15	0.87	6.22	0.76
	EAF	695	7.13	13	0.79	5.01	0.72
	CCF	822	8.47	13	0.77	4.54	0.71

Abbreviation: Low = low water table treatment, High = high water table treatment, PP = Pristine Peatland, CC = Clear-cut Forest, EAF = Even-Aged Forest, CCF = Continuous Cover Forest.

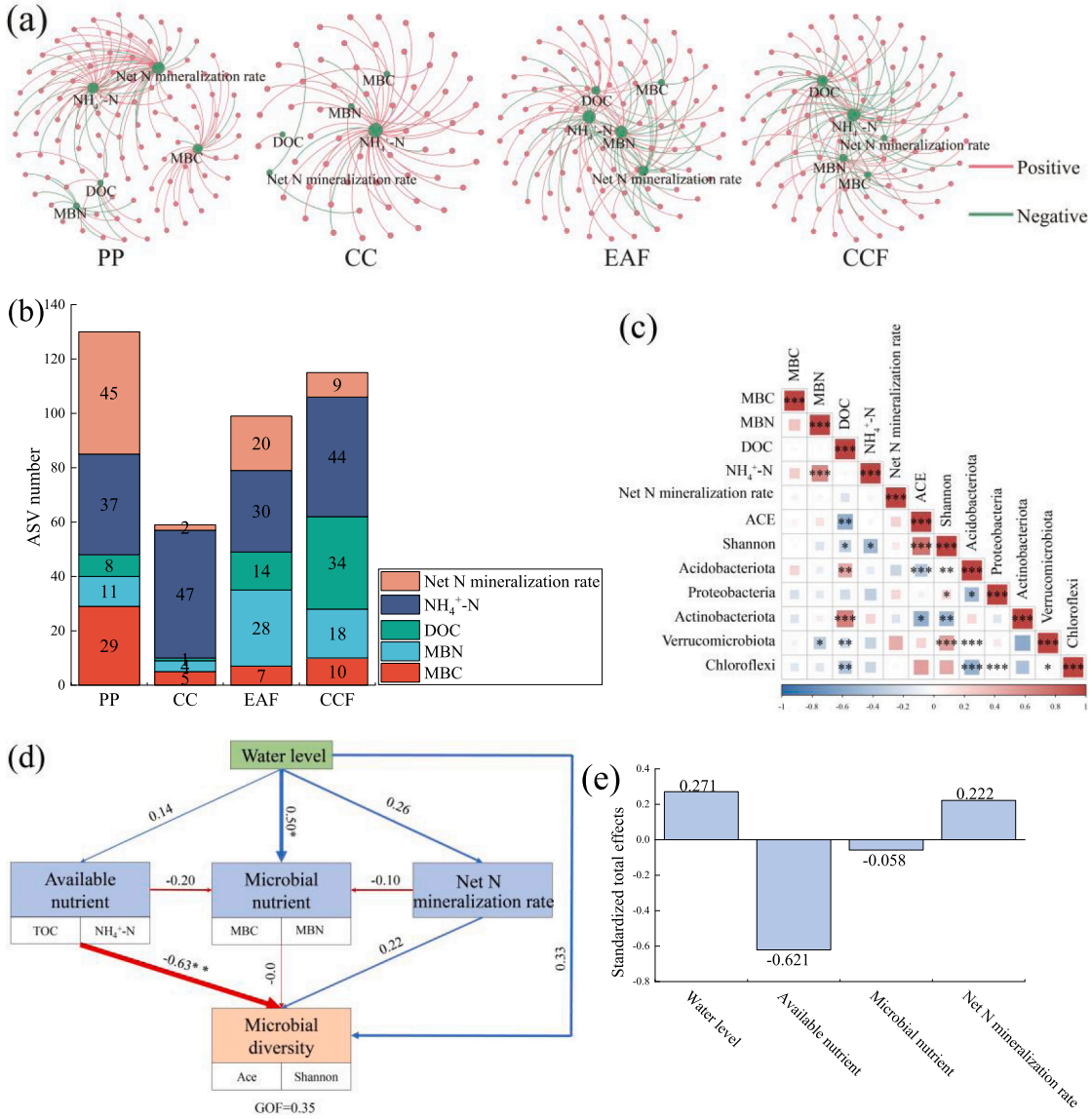

Fig. 5. Correlation between soil biological properties and bacterial communities. (a) Co-occurrence network of bacterial ASVs and soil biological properties ($R > 0.7$, $P < 0.05$) in each forest, (b) The number of ASVs associated with soil properties in the co-occurrence network, (c) Correlation heat maps between soil properties and bacterial diversity, where correlation coefficients range from + 1 (red) to −1 (blue) with square size reflecting strength of the correlation, (d) Partial least squares path model analysis showing the effects of forest type and water table on bacterial community diversity, and (e) Normalized influence of environmental factors on bacterial community diversity, with values next to the columns representing the normalized coefficients from the partial least squares path model. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. Abbreviation: Low = low water table treatment, High = high water table treatment, PP = Pristine Peatland, CC = Clear-cut Forest, EAF = Even-Aged Forest, CCF = Continuous Cover Forest.

distance within the pristine peatland and thus failed to capture its internal spatial variation, which constitutes a limitation of this study.

4.2. Bacterial community and assembly process

Water table and forest management significantly shaped bacterial community and alpha diversity. The bacterial diversity in the pristine peatland is higher than that in the artificially managed forest, which highlights the ecological role of the original peatland in maintaining microbial diversity (Andersen et al., 2013; Nurulita et al., 2016). In contrast, management practices such as clear-cutting or afforestation appeared to reduce microbial diversity, potentially due to homogenized plant communities and reduced spatial heterogeneity (Urbanová and Bárta, 2016; Wang et al., 2021). This study found that under low water level conditions, the Ace index differed significantly between PP and CC; however, under high water level conditions, no significant difference was observed between PP and CC. For the Shannon index, there was no significant difference between PP and EAF under low water level conditions, but a significant difference emerged under high water level conditions. These results indicate that the effect of water level changes on bacterial diversity is not consistent across different forest types. This inconsistency arises because water level fluctuations alter soil redox status, carbon and nitrogen availability, and plant root activity, and different forest management types exhibit varying sensitivities and response mechanisms to these changes (Hillgén et al., 2024). NMDS and variation partitioning analyses revealed that NH_4^+–N and DOC were the most influential factors driving community composition, while high water tables likely altered oxygen availability, shifting microbial communities toward anaerobic or facultative taxa (Askaer et al., 2010; Ma et al., 2024). For instance, Chloroflexi—a phylum associated with the decomposition of recalcitrant organic matter—was more abundant under low water conditions, particularly in pristine peatland, likely due to better oxygen availability for aerobic degradation processes (Lee et al., 2011).

Microbial community assembly processes also differed among forest management and water table treatments. In pristine peatland, stochastic processes, particularly dispersal limitation, were dominant, as indicated by βNTI and RCBray metrics, while deterministic processes such as homogeneous selection prevailed in managed forests (clear-cut forest, even-aged forest, and continuous cover forest), likely due to their simplified and more uniform environment (Xun et al., 2019). The neutral community model, where pristine peatland showed intermediate migration rates (Nm), indicates a balance between stochastic dispersal and environmental filtering. The ecological functions of bacteria in peatlands—such as organic matter decomposition, nitrogen fixation, and carbon sequestration—are crucial for ecosystem health (Siljanen et al., 2019; Xu et al., 2022). Finally, while clear-cut forest and continuous cover forest treatments showed high NCM values, indicating high diversity and dispersal potential, they also exhibited reduced microbial interactions and niche differentiation.

4.3. Bacterial co-occurrence network

The structure of bacterial co-occurrence networks varied significantly with water table and forest management, revealing how environmental conditions shape microbial interactions (Xiao et al., 2024). Under high water table, networks exhibited greater complexity and connectivity, especially in CCF —as shown by increased edge numbers and higher average degree. High water table was also associated with elevated net nitrogen mineralization rates, indicating faster nutrient turnover. Such enriched conditions may promote mutualistic relationships over competition, fostering the development of diverse and interactive microbial communities. These findings are consistent with previous studies showing that nutrient-rich, moist soils support more complex and tightly linked microbial networks (Lindsay et al., 2021). This shift likely facilitates microbial growth and community stability, further reinforcing ecosystem functions such as decomposition and nutrient cycling (Li et al., 2023; Wang et al., 2025). Interestingly, pristine peatland and CCF also maintained relatively high levels of positive bacterial interactions even under low water tables. Moreover, higher modularity observed in pristine peatland suggests the presence of robust sub-community structures, potentially enhancing resistance to environmental disturbances. Modular networks are known to support ecological resilience by localizing disturbances and preserving functional redundancy (Yu, 2025).

4.4. Relationship between soil biological characteristics and microbial communities

Our results showed that the number of ASVs potentially associated with nitrogen mineralization rates varied among forest type treatments, with the highest number observed in the pristine peatland. This suggests that a greater diversity of bacterial taxa may be involved in nitrogen mineralization in the pristine peatland. These findings are consistent with those of Masuda et al. (2022), who reported significant differences in nitrogen mineralization rates among soils under different forest types. The higher number of potentially related ASVs in the pristine peatland may also be attributable to its greatest bacterial diversity, which likely provides a larger pool of taxa that could be associated with nitrogen mineralization. However, it is important to note that our current dataset, derived from 16S rRNA gene amplicon sequencing, provides taxonomic composition but does not directly reveal the functional contributions of individual taxa. Acknowledging this limitation, we refrain from drawing strong causal inferences regarding the role of bacterial communities in driving nitrogen mineralization. In the absence of targeted functional analyses—such as quantification of nitrogen-cycling functional genes (e.g., *amoA*, *nirK*, *nirS*, *nosZ*) or metatranscriptomic profiling—our interpretations remain focused on community-level patterns and their statistical associations with environmental variables (Lee et al., 2011). Future studies employing functional gene approaches or isotope-tracing techniques are needed to elucidate the mechanistic pathways underlying the observed patterns.

The results indicated that elevated water levels exerted significantly positive effects on MBC and MBN. However, the availability of DOC and NH_4^+-N in the soil exhibited a pronounced negative correlation with bacterial diversity. This seemingly counterintuitive finding precisely underscores the decoupling between "resource pool size" and "resource chemical form" in governing soil microbial assemblages in peatlands. High water levels facilitate microbial assimilation and immobilization of carbon and nitrogen, primarily by retarding organic matter mineralization and fostering anoxic microenvironments that confer protective conditions (Solly et al., 2023). Nevertheless, excessive accumulation of DOC and ammonium does not necessarily translate into enhanced resource accessibility. Elevated DOC concentrations are frequently accompanied by substantial proportions of recalcitrant humic substances or low-molecular-weight organic acids, which remain refractory to assimilation by the majority of microbial taxa, thereby driving a decline in community diversity (Lu et al., 2025). These findings highlight that peatland ecological management should prioritize nutrient turnover dynamics over static concentration metrics, and that over-accumulation of soluble carbon may act as an overlooked latent driver of biodiversity loss.

This study provides mechanistic insights from a seven-month greenhouse incubation with controlled water table levels at 20–25 °C. However, extrapolating these results to field conditions has certain limitations. This is because field environments are more complex and exhibit greater spatial heterogeneity, and dynamic changes in temperature, plant root activity, and seasonality may also influence the outcomes. Peat cores were collected in January, when microbial activity is typically at its lowest, and subsequently incubated at a constant temperature of 20–25°C. Such persistently warm conditions likely accelerated microbial metabolism beyond natural rates, thereby amplifying the

treatment effects and shortening the time required to observe responses. Moreover, the absence of seasonal freeze-thaw cycles in the greenhouse represents a major deviation from field conditions, which may contribute to discrepancies between laboratory and field results (Wang et al., 2026). Despite these constraints, we consider the relative differences among water-table treatments—rather than absolute values—to be more robust and informative for predicting field responses, suggesting that the direction of the observed trends is ecologically meaningful. However, caution should be exercised when extrapolating the magnitudes and rates of change to real-world situations. To bridge the gap between controlled experiments and field scenarios, future studies should include long-term monitoring across multiple seasons to validate the trends observed here. Furthermore, this study was only conducted in the research area of Finland. In the future, more attention should be paid to global ecological changes or the use of global data for exploration.

5. Conclusion

This study showed that soil microbial biomass carbon was unaffected by forest management or water table depth. Bacterial community composition was shaped by water table and nutrient availability, whereas bacterial diversity was primarily influenced by forest management, with pristine peatland showing the highest diversity. Under the conditions of pristine peatland and high water tables, the ecological screening effect would be weakened, making the community formation dependent on random events; while human management, by directly altering the environment, strengthened the deterministic screening, resulting in a fundamental transformation of the biodiversity maintenance mechanism. Additionally, high water tables increased bacterial network complexity and positive interactions, suggesting enhanced microbial cooperation. Accordingly, we contend that future management frameworks for peatland forests should incorporate ongoing hydrological surveillance and utilize microbial metrics as sentinel indicators of impending biodiversity loss, rather than relying exclusively on aboveground floristic criteria. Such a strategy would provide substantial practical guidance for refining silvicultural operation decisions in peatland ecosystems.

CRediT authorship contribution statement

Heidi Aaltonen: Investigation. **Qu Zhaolei:** Software, Formal analysis. **Yunuo Hu:** Formal analysis, Data curation. **Jukka Pumpanen:** Writing – review & editing, Funding acquisition, Conceptualization. **Ning Li:** Writing – original draft, Conceptualization. **sun Hui:** Writing – review & editing, Software. **Lin Huang:** Writing – review & editing. **Anne Ojala:** Investigation. **Xudan Zhu:** Investigation. **Frank Berninger:** Investigation, Data curation. **Annamari Laurén:** Writing – review & editing, Investigation, Data curation. **Marjo Palviainen:** Writing – review & editing, Investigation, Data curation.

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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Data availability

Data will be made available on request.

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