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Dominance of forest structural traits in shaping soil bacterial community assembly in Beijing's urban forests

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Urban forests constitute vital ecological interfaces between built environments and natural systems, yet the mechanisms driving soil microbial community assembly in these ecosystems remain poorly understood. Through an integrated analysis of five dominant forest types (*Populus tomentosa*, *Salix matsudana*, *Robinia pseudoacacia*, *Eucommia ulmoides*, and *Ailanthus altissima*) in Beijing's plain ecological forests, we reveal hierarchical environmental controls over bacterial diversity and network structure. High-throughput sequencing and co-occurrence network analyses demonstrated that *Salix matsudana* forest harbored the highest microbial diversity (Shannon index = 5.82 ± 0.14), with *Proteobacteria* abundance significantly elevated compared to other forest types ($P < 0.01$). Structural equation modeling (SEM) identified soil total nitrogen (TN) as the principal direct suppressor of bacterial diversity (path coefficient = -0.33 , $P < 0.001$), while forest structural traits—particularly diameter at breast height—emerged as critical mediators of community composition through nutrient modulation ($R^2 = 0.502$). Notably, microbial networks exhibited forest-type-specific topologies: *Populus tomentosa* forest stands showed exceptional connectivity (edge density = 0.29), whereas *Robinia pseudoacacia* forest developed modular architectures (modularity = 2.30) enhancing ecological resilience. These findings establish a mechanistic framework linking forest management practices to microbial-mediated ecosystem functions, with direct implications for urban green space optimization under accelerating anthropogenic pressures.

KEYWORDS

soil microbial community, plain ecological forests, co-occurrence networks, forest structural traits, forest management practices

1 Introduction

In the context of accelerating global urbanization, urban forests have emerged as a crucial bridge between urban and natural ecosystems, with their ecological functions becoming increasingly significant (1, 2). Soil microorganisms, as fundamental components of these urban forest ecosystems, play a vital role in the regeneration of understory forest and the processes of ecological restoration (3, 4). They contribute to sustaining ecosystem stability through their involvement in key ecological processes, including the soil fertility enhancement, organic matter decomposition, and carbon sequestration (5–7). However, soil microbial communities are highly sensitive to environmental changes, especially those associated with variations in forest types and soil physicochemical properties, further emphasizing the importance of exploring their response mechanisms. Recent studies have revealed the complex effects of shifts in forest types on the diversity and composition of soil microbial communities (8, 9). Therefore, investigating how soil microbial communities respond to environmental changes driven by different forest types in urban plain forests is of profound significance for guiding the scientific management of these forests.

The assembly of soil microbial communities is influenced by a multitude of environmental factors, rendering it a highly intricate process (10, 11). Variations in forest types and soil physicochemical properties, such as bulk density, pH, nutrient content, and enzyme activity, can significantly affect the structure of microbial community and further regulate soil nutrient cycling and forest growth conditions (8). For example, soil nutrients, particularly soil carbon content, constitute the principal energy source for microbial growth and metabolic processes. Nitrogen is an essential element for constituting microbial cellular biomacromolecules, including proteins and nucleic acids, thereby affecting the structure of microbial communities (12). Meanwhile, soil enzymes are also key factors affecting microbial community structure. For example, cellulase facilitates the decomposition of cellulose in soil, thereby providing carbon sources for microorganisms. The activity level of cellulase is directly associated with the rates of soil carbon cycling and the composition of microbial communities (13, 14). Similarly, β -glucosidase, a crucial enzyme in soil carbon cycling, exerts a significant influence on the structure and function of microbial communities (15). Moreover, appropriate soil moisture content creates a favorable metabolic environment for microorganisms, thereby enhancing their activity and facilitating the decomposition and transformation of soil nutrients (16). However, in the practice of urban plain afforestation, there is still a lack of deep understanding of the specific mechanisms by which established forest types and soil physicochemical properties synergistically drive the construction of soil microbial communities.

Soil microorganisms do not respond to environmental conditions in isolation, but interact as integral components of complex microbial communities. These communities constitute cohesive ecological assemblages, with microorganisms sharing similar environmental adaptability and resource utilization preferences. The interrelationships among these microorganisms can be examined through co-occurrence ecological networks, where microbial taxa are considered as network

nodes and their relationships as network connections (17). Ecological networks provide a powerful supplement to traditional soil microbial community quantification methods, such as alpha and beta diversity (18). In recent years, ecological network analysis has emerged as a crucial tool for analyzing the structural characteristics of soil microbial communities and microbial co-abundance patterns (19, 20). Empirical studies indicate that the conversion of *Populus tomentosa* forests to *Robinia pseudoacacia* forests may strengthen symbiotic relationships within soil microbial networks (21). The nitrogen fixation capability of *R. pseudoacacia* can provide nitrogen sources for other microorganisms, promoting their growth and reproduction (22). Simultaneously, new competitive relationships may also emerge, as increased nitrogen may trigger intense competition among different microorganisms for nitrogen sources. However, how forest type shifts specifically affect inter-microbial interactions remains insufficient understanding.

In this study, we selected five representative forest types within the plain ecological forests of Beijing: *Populus tomentosa* Carrière (PT), *Salix matsudana* Koidz (SM), *Robinia pseudoacacia* (RP), *Eucommia ulmoides* Oliver (EU), and *Ailanthus altissima* (Mill.) Swingle (AA). The species chosen for this study exhibit contrasting ecological strategies: PT and SM, fast-growing riparian species; RP, an N-fixing pioneer; EU, a medicinal tree with deep roots; and AA, a pollution-tolerant invasive species. Collectively, these species account for the main part of the tree biomass in Beijing's plain afforestation project, enabling an evaluation of how dominant management choices influence soil microbial communities. We conducted an analysis of the soil physicochemical properties and microbial community structures, as well as their interrelationships, across these five forest types. The objective of this study was to reveal the mechanisms through which different forest types influence soil microbial community structures. We hope that this study will provide scientific guidance for ecological management and biodiversity conservation.

2 Materials and methods

2.1 Study site and soil sampling

The study area is located in the Lucheng Collective Forest Farm, Tongzhou District, Beijing (39.84°N, 116.81°E) (Supplementary Figure S1). The terrain of the study area is flat, with loam soil predominant. The climate is warm temperate, featuring a semi-humid and semi-arid continental monsoon pattern, with hot rainy summers and cold, dry winters. Annual precipitation averages 400–600 mm, concentrated mainly from June and August. The soil is neutral in pH. The study area is part of the million-acre afforestation and greening project implemented in the plain areas of Beijing in 2013, with forest stands established as part of the project, each approximately 11 years old. Over the past decade, more than 3 to 5 million trees of species such as *Populus tomentosa* Carrière (PT), *Salix matsudana* Koidz (SM), *Robinia pseudoacacia* (RP), *Eucommia ulmoides* Oliver (EU), and *Ailanthus altissima* (Mill.) Swingle (AA) have been planted and were selected for our study. Currently, the forest stands are single-layered, differing

significantly from the ideal state of mixed, multi-layered, multi-aged, and multifunctional forest communities. Three spatially independent sampling sites were established for each forest type within an area exceeding 1 hectare. At each site, we randomly established three 20 m × 20 m plots. We recorded geographical coordinates, elevation slope, and aspect using GPS and a compass (23). Tree density (TD) was obtained by counting all trees within each plot, diameter at breast height (DBH) was measured with a vernier caliper, and tree height (TH) was measured with a Blume-Leiss height meter. Crown width in both east-west and north-south directions were also measured to assess tree canopy (TC) size. Understory vegetation (herbs and shrubs < 2 m in height) was surveyed by recording species composition, coverage, and average height within five 2 m × 2 m randomly placed subplots inside each 20 m × 20 m plot. The 0–10 cm soil depth was selected due to its high density of fine roots, microbial biomass, and enzymatic activity in urban forests (24). This layer serves as the primary zone for litter decomposition and nutrient cycling, thus playing a critical role in assessing forest-microbe linkages. Six to nine soil cores (5 cm diameter, 0–10 cm depth) were randomly collected from each site and pooled to form a composited sample. For each site, three composite samples were obtained. Each composite sample was then homogenized and subdivided into four subsamples for different analyses: (1) (1) determination of soil water content (SWC) and bulk density (BD), with soil packed in a ring knife; (2) analysis of soil physicochemical properties, after air-drying and sieving through a 2 mm mesh using a ball mill; (3) molecular analysis, with fresh soil transported in a portable refrigerator at –20 °C and stored at –80 °C until DNA extraction (25, 26); and (4) measurement of soil ammonium nitrogen (NH₄⁺-N), nitrate nitrogen (NO₃⁻-N), cellulase (CEL) and β-glucosidase (BGL) activities with fresh soil kept at 4°C.

2.2 Environmental variable selection

We selected environmental variables known to influence the soil microbial community in Beijing's plain forests, grouping them into forest structure and soil factors (23, 27). Forest structure variables included TD, DBH, TH, and TC. Soil properties included pH, SWC, BD, soil organic carbon (SOC), total nitrogen (TN), carbon-to-nitrogen ratio (C/N), total phosphorus and (TP), and dissolved organic carbon (DOC). Soil pH was measured using a METTLER TOLEDO pH electrode with a 1:2.5 soil/water ratio. BD and SWC were determined using the ring knife method: fresh soil samples were oven-dried at 105 °C ± 2 °C for 12–24 hours to obtain dry weight. SOC was determined using the Potassium dichromate external heating method, while TN was quantified with an elemental analyzer (2400 Series II, Perkin Elmer, Boston, MA, USA). TP was measured by the molybdenum antimony anti-colorimetric method, and DOC was extracted with water, filtered through a 0.45 μm membrane, and analyzed using the potassium permanganate-sulfuric acid heating method. NH₄⁺-N and NO₃⁻-N were determined by the indophenol blue colorimetric method and salicylic acid colorimetric method, respectively, following extraction

with 2 M KCl. CEL and BGL activities were assayed using 3,5-dinitrosalicylic acid and p-nitrophenol methods, respectively (28, 29).

2.3 DNA extraction sequencing and bioinformation analysis

We extracted genomic DNA from 0.25 g soil samples using kits from Guangdong Magigene Biotechnology Co., Ltd. (Guangzhou, China). The integrity and purity of the extracted DNA were initially verified by 1% agarose gel electrophoresis, Quantus Fluorometer, and NanoDrop2000. Subsequently, DNA concentration and purity were further assessed using Qubit 4.0 and NanoDrop One instruments (Thermo Fisher Scientific, Waltham, USA). Qualified DNA samples underwent library preparation using the ALFA-SEQ DNA Library Prep Kit. This process included DNA fragmentation, end repair, 3' adenylate addition, adapter ligation, fragment selection and purification, PCR amplification, and a final purification step. This size distribution of prepared libraries was evaluated using the Qsep400 High-Throughput Nucleic Acid-Protein Analysis System (Hangzhou Houze Biological Technology Co., Ltd., China), and their concentrations were measured with the Qubit 4.0. Finally, sequencing was performed on either the Illumina or MGI platform using PE150 sequencing (Guangdong Magigene Biotechnology Co., Ltd.).

Raw data were processed using Fastp software (parameters: -5 -W -5 -M 20 -q 15 -u 40 -l 50 -dedup) to obtain clean data (30). The MEGAHIT assembler (V1.2.9) was used for sequence assembly (<https://github.com/voutcn/megahit>), and Diamond software (<https://github.com/bbuchfink/diamond/>) was employed for alignments against the NCBI NR database (31). The LCA algorithm in the MEGAN software system was used for classification, and species annotation was determined based on an E value threshold of 1e-10 (32). A table containing gene average depth (AVG depth) and abundance information at various classification levels (kingdom to species) was generated based on LCA annotation and gene AVG depth or abundance tables (33). Species abundance within a sample was calculated as the sum of annotated gene abundances, while gene AVG depth for a species was the sum of non-zero abundance gene AVG depths.

2.4 Microbial network analysis

We constructed ecological association networks for each sampling site based on plot-level estimated bacterial OTUs (34). To ensure the reliability of our correlations, we adopted a rigorous filtering approach (35, 36), retaining only OTUs present in more than 25% of soil samples and with relative abundances exceeding >0.001%. For robust network construction, we utilized Random Matrix Theory (RMT)-based correlations (34), which involved four key steps: majority selection, similarity matrix calculation, RMT-based cutoff determination, and network generation. The network construction and analysis were performed using the integrated

Network Analysis Pipeline (iNAP) (accessible at: <https://inap.denglab.org.cn/>). Visualization of the networks was achieved with the Gephi interactive platform (available at: <http://gephi.github.io/>) (37).

2.5 Statistical analysis

We evaluated differences in environmental properties (forest structure and soil factors), alpha diversity of the microbial community, and network properties using one-way ANOVA with Tukey HSD tests at $p < 0.05$. Nonmetric Multidimensional Scaling (NMDS) ordination, based on taxonomic abundance tables, quantified differences in soil microbial community structures, with inter-group differences tested using Adonis and Anosim analyses. To ensure comparability, all predictors and response variables were standardized using Z-scores before conducting Mantel Test (MT), Random Forest (RF), and Generalized Linear Models (GLMs). When necessary, predictors were log-transformed (38). To address potential multicollinearity among soil physiochemical properties, Spearman's correlation was used, confirming no issue of collinearity (Supplementary Table S1). In ecological prioritization, correlated variables with comparable Variance Inflation Factors (VIFs) were considered, such as the preference for retaining DOC over SOC due to its direct microbial bioavailability. We employed Principle-Component Analysis (PCA) to create a composite variable describing network complexity, encompassing total links, edge density, avgK, APL, avgCC, degree centrality, and closeness centrality. The first component captured 65.21% of the variation (Supplementary Table S2). MT was used to analyze relationships between forest types, climate factors, forest structure, soil characteristics, and microbial diversity (community structure). RF analysis determined the influence of these environmental factors on microbial community assembly. We constructed a Structural Equation Model (SEM) to examine the pathways through which environmental factors affect the microbial diversity. To assess the model's adequacy, we utilized several

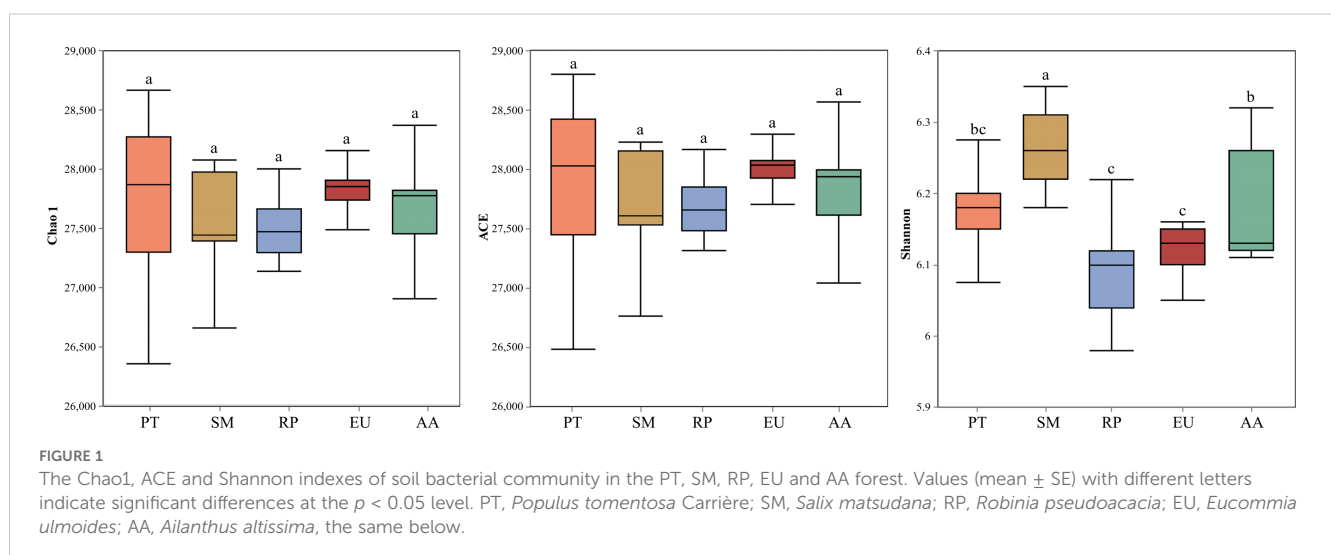
goodness-of-fit indices, including the Chi-square test (χ^2), Root Mean Square Error of Approximation (RMSEA), Standardized Root Mean Square Residual (SRMR), and Comparative Fit Index (CFI). For evaluating model fit in the presence of non-normally distributed variables, we employed the Bollen-Stine bootstrap test, considering bootstrap P-values ranging from 0.10 to 1.00 as indicative of an acceptable fit. All statistical analyses were performed using RStudio (R version 3.6.1).

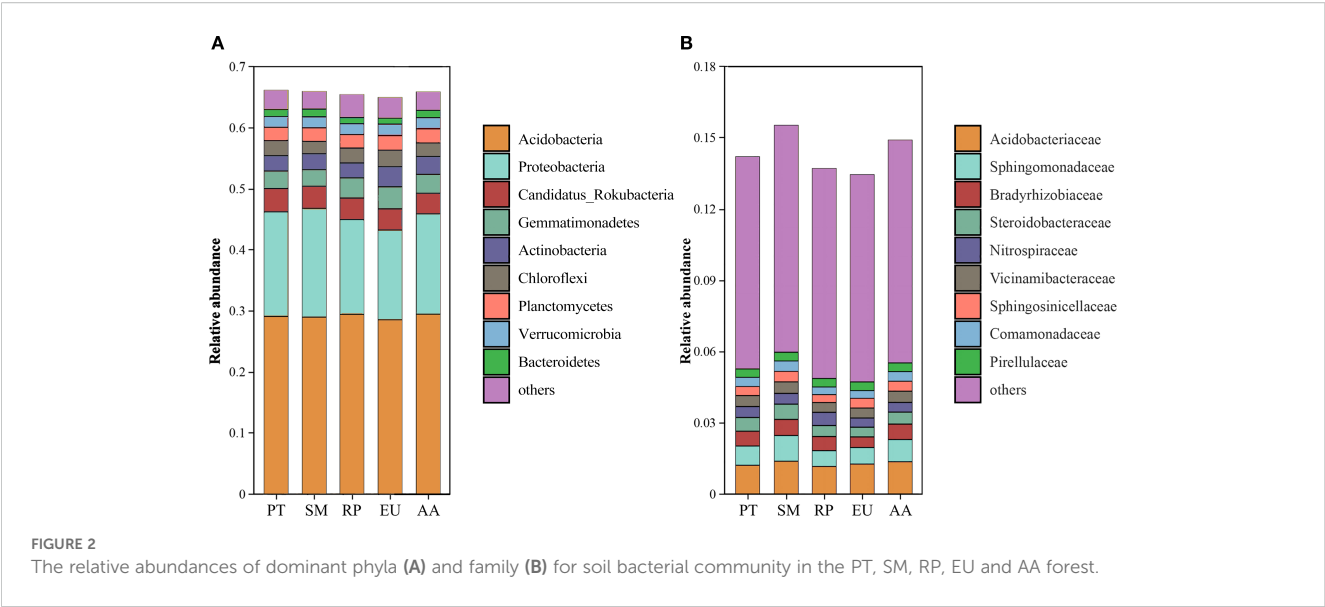
3 Results

3.1 Microbial diversity and composition under different forest types

The Shannon diversity index of soil bacteria exhibited significant differences across all study sites (Figure 1). Specifically, the Shannon index was highest in the SM forest, where it was significantly ($P < 0.05$) higher than in the other four forest sites. The AA forest site followed closely, with a Shannon index that was significantly ($P < 0.05$) higher than those in the RP and EU forest sites. Conversely, no significant ($P > 0.05$) differences were observed in the Chao1 and ACE indices across the PT, SM, RP, EU, and AA forest sites. NMDS analysis based on Bray-Curtis distances showed an acceptable model fit (stress = 0.126) and effectively captured the distance relationships within the microbial community data (Supplementary Figure S3). Adonis and Anosim analysis showed that P values for comparisons such as RP versus EU, RP versus SM, EU versus SM, EU versus AA, and EU versus PT were 0.003, 0.001, 0.001, 0.013, and 0.001, respectively, with statistically significant differences in microbial community structures between the compared forest sites.

The dominant bacterial phyla across were *Acidobacteria* (28.52–29.46%) and *Proteobacteria* (14.69–17.80%), followed by *Candidatus_Rokubacteria* (3.37–3.83%), *Gemmatimonadetes* (2.72–3.62%), *Actinobacteria* (2.43–3.28%), and *Chloroflexi* (2.01–2.71%) (Figure 2). The relative abundance of *Proteobacteria* in the SM site





was significantly higher than that in the RP, EU, and AA forests, while the relative abundance of *Acidobacteria* remained consistent across the PT, SM, RP, EU, and AA forest sites. At the family level, *Acidobacteriaceae* (1.16-1.38%) and *Sphingomonadaceae* (0.66-1.08%) were the most abundant, followed by *Bradyrhizobiaceae* (0.45-0.68%) and *Steroidobacteraceae* (0.41-0.64%). Notably, the relative abundances of *Acidobacteriaceae* and *Sphingomonadaceae* in the SM and AA forests were significantly ($P<0.05$) higher than those in the PT and RP forests.

TABLE 1 Topological properties of the co-occurrence networks in the PT, SM, RP, EU and AA forest.

Network indexes	Site				
	PT	SM	RP	EU	AA
Total Links	5700	4744	3557	4562	5604
Positive links	3122	2622	2400	2712	3339
Negative links	2578	2122	1157	1850	2265
Edge density	0.29	0.24	0.18	0.23	0.28
Average degree (avgK)	57.29	47.44	35.57	45.62	56.04
Average path length (APL)	1.35	1.47	1.53	1.49	1.39
Diameter	2.83	3.55	2.90	4.47	3.37
Average clustering coefficient (avgCC)	0.66	0.64	0.56	0.63	0.66
Degree centrality	0.27	0.24	0.23	0.25	0.30
Betweenness centrality	0.02	0.02	0.01	0.02	0.01
Closeness centrality	0.25	0.22	0.18	0.25	0.31
Relative modularity (RM)	1.46	1.97	2.30	1.39	2.11

3.2 Co-occurrence patterns of soil bacterial community

To explore the effects of forest types on microbial communities, five RMT-based correlations were constructed, and the topological properties of networks are shown (Table 1; Supplementary Figure S4). The PT forest has an edge density of 0.29 and an avgK of 57.29, highlighting the network's exceptional connectivity and compactness. Notably, the APL of PT forest is 1.35, indicating short inter-node distances that facilitate rapid information or material transfer. In contrast, while the RP forest exhibits modest values across most network indexes, its relative modularity reaches up to 2.30, revealing a unique modular architecture that may contribute to network stability. The AA forest shares numerous similarities with the PT forest in network properties, including edge density, APL, and avgCC. Moreover, the degree centrality and closeness centrality in the AA forest are both the highest, highlighting the significance of key nodes and the preferable accessibility among nodes. Meanwhile, the diameter of EU forest is 4.47, suggesting that information or material transfer may involve more intermediary nodes, yet this property also reflects the network with greater robustness.

3.3 Relationship between environmental factors and the soil bacterial community

The Mantel test showed that the bacterial Shannon's diversity index was significantly correlated with DBH, $\text{NH}_4^+\text{-N}$, and BGL across the five forest types (Figure 3). DBH emerged as the dominant factor influencing the composition of the bacterial community, whereas TN was significantly associated with the co-occurrence network of bacteria. Random forest analysis identified DBH and DOC as the key predictors of the soil bacterial community Shannon index, followed by SOC, TN, and BGL (Figure 4). Notably, DBH alone served as the principal predictor of soil bacterial

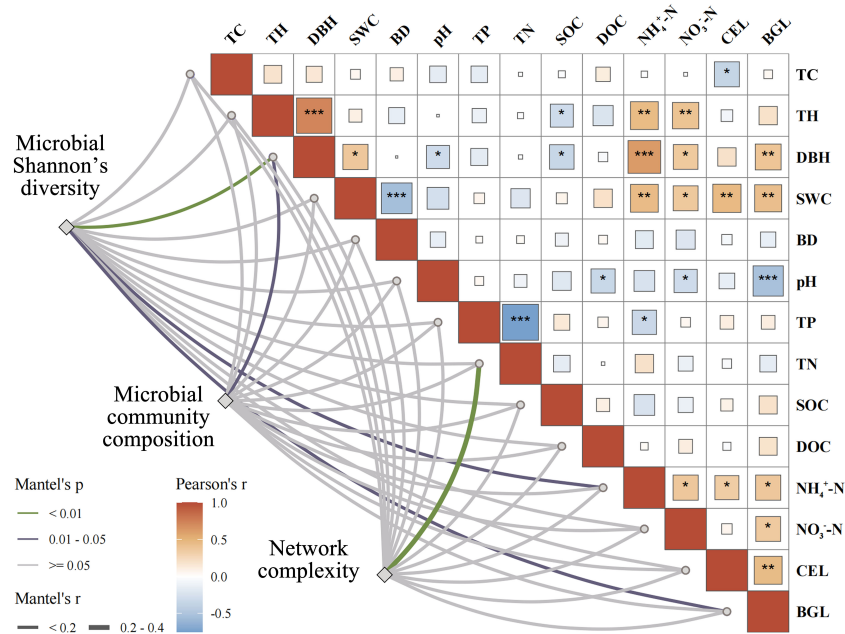


FIGURE 3

Correlations between soil bacterial community Shannon and composition and network complexity and environmental factors. Mantel test (MT) analyzed the relationship between environmental variables and microbial diversity, structure, co-occurrence networks of soil bacterial community. TC, tree canopy size; TH, tree height; DBH, diameter at breast height; SWC, soil water content; BD, bulk density; TP, total phosphorus; TN, total nitrogen; SOC, soil organic carbon; DOC, dissolved organic carbon; NH₄⁺-N, ammonium nitrogen; NO₃⁻-N, nitrate nitrogen; CEL, cellulase; BGL, β -Glucosidase, the same below. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

community composition. TH and TN were the primary factors affecting network complexity, with DBH, TP, and SWC also contributing. These results confirmed that, in addition to soil physicochemical properties, forest structure also played a vital role in shaping microbial community assembly.

3.4 Pathways of environmental factors affecting microbial community

Soil physicochemical properties emerged as the dominant predictor, accounting for 80% of the explained variance, followed by forest structural attributes (20%) (Figure 5). Adjusted R^2 values (0.502) indicate that the model explains approximately half of the observed variation in bacterial diversity. The proportional contribution analysis demonstrated that TN emerged as the predominant driver, accounting for 36.58% of the explained variation (95% CI [-0.25, -0.12], $P < 0.001$). This was followed by TP (31.39%, 95% CI [-0.15, -0.95], $P < 0.01$) and DOC (25.31%, 95% CI [-0.11, -0.78], $P < 0.01$). SEM revealed distinct environmental drivers of bacterial diversity. Soil BD exhibited moderate direct effects ($R^2 = 0.044$), while NH₄⁺-N displayed stronger associations ($R^2 = 0.226$) (Figure 6). TN exerted the strongest total effect (-0.33), directly suppressing bacterial diversity (path coefficient = -0.33) and indirectly modulating NH₄⁺-N. TD showed a direct positive effect on NH₄⁺-N (path coefficient = 0.29), yet its indirect contributions to microbial diversity were negligible. These findings suggest the predominance of direct pathways—particularly nutrient availability

(TN, NH₄⁺-N)—in shaping microbial community structure, with minimal mediation through secondary environmental interactions.

4 Discussion

4.1 Soil microbial diversity and composition under different forest types

The observed variations in soil microbial diversity and composition among different forest types in this study are consistent with previous findings that highlight the influence of vegetation type on soil microbiomes (39, 40). The higher Shannon diversity index observed in SM forests, compared to other forest types, suggests the presence of distinct ecological conditions favoring a more diverse bacterial community. The lack of significant differences in the Chao1 and ACE indices across forest types suggests that while dominant taxa shift, the underlying richness of rare species remains conserved. This discrepancy between diversity indices is well-documented and underscores that the Shannon index is more sensitive to changes in abundant taxa, whereas Chao1 and ACE better reflect the rare biosphere (41). Local environmental conditions, such as soil type and forest structure, are known to be strong confounding factors in mediating tree species effects on soil microbes (42, 43), which may explain the specific pattern observed here.

The dominance of *Acidobacteria* and *Proteobacteria* across these managed forest ecosystems is a common phenomenon observed in various soil types (44, 45). Recent studies, such as Deltedesco et al. (46),

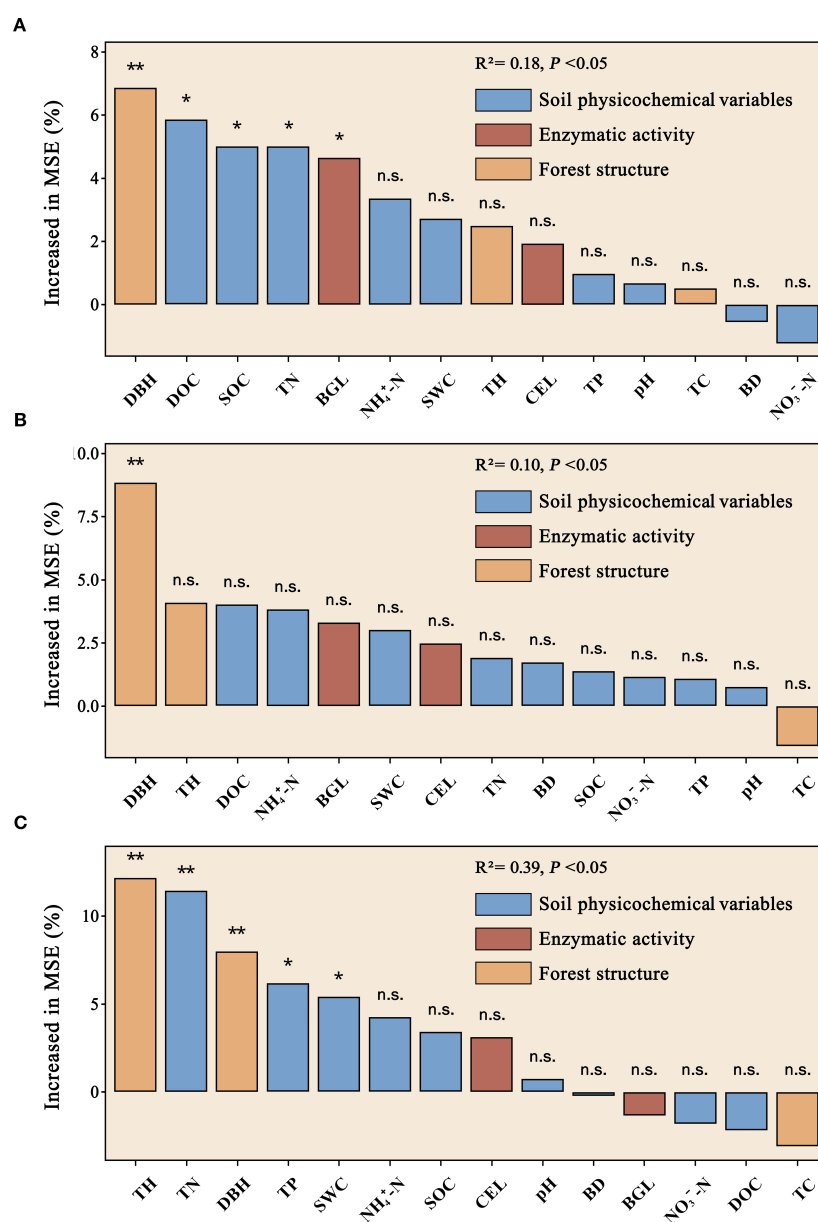


FIGURE 4

Random Forest (RF) determined the role of environmental variables in microbial diversity (A), structure (B), and co-occurrence networks (C). The thickness of the lines represents the partial Mantel's r statistic, while the color denotes the correlation between influencing factors. * means $P < 0.05$, ** means $P < 0.01$, ns means not significant. Significance levels denoted by asterisks (* $P < 0.05$; ** $P < 0.01$; n.s. means not significant).

have also highlighted the consistent dominance of these phyla in different forest ecosystems, reinforcing their ecological importance. The SM forest exhibited the highest Shannon diversity index, accompanied by a significantly higher relative abundance of *Proteobacteria*. This finding suggests that the soil environment of the SM forest may be particularly conducive to the growth and proliferation of this phylum. The reason may be that the microbial community in SM forest harbors positive interactions, such as symbiosis or mutualism, that promote the growth of *Proteobacteria* (47, 48). These interactions could involve nutrient exchange, signaling molecules, or other forms of cooperation that benefit both *Proteobacteria* and their associated microbes. The stable relative abundance of *Acidobacteria* across all

forest types indicates its broad ecological adaptability, likely due to its extensive metabolic versatility and niche breadth within acidic to neutral soils (49, 50). This underscores that forest type shifts primarily restructure dominant community components rather than alter rare species pools in these managed ecosystems.

4.2 Soil microbial co-occurrence network in different forest types

The high complexity and connectivity of the microbial network in PT forests may be attributed to the high resource availability and

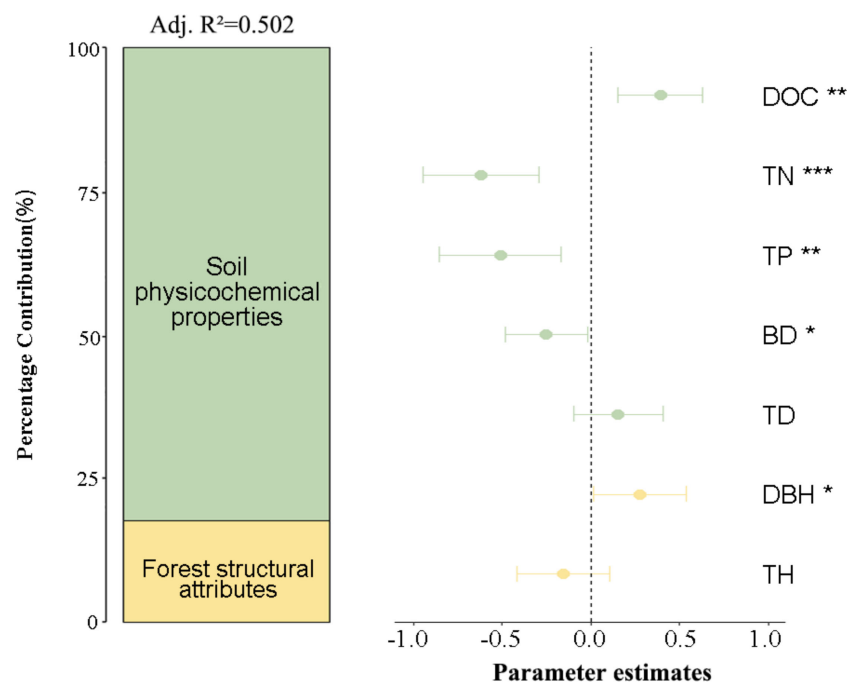


FIGURE 5

Proportional contributions of environmental drivers to bacterial diversity variation. Standardized regression coefficients with 95% CIs demonstrate the effect magnitude hierarchy among predictors. Variable importance is expressed as percentage contribution derived from coefficient ratios. Significance levels denoted by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). TD, tree density; detailed abbreviation are given in Figure 3.

diverse ecological niches. As a fast-growing species, *Populus tomentosa* likely provides abundant carbon and nitrogen sources for soil microbes through root exudates and litterfall, promoting microbial diverse microbial interactions (47, 51–53). This high ecological diversity likely contributes to the high connectivity and short average path length of the microbial network, enhancing network complexity and information transfer efficiency (20). The high modularity of the microbial network in RP forests may be associated with ecological niche differentiation. Modules can act as ‘firewalls’ containing disturbances, enhancing ecological stability (54). In RP forests, different microbial species may form relatively

independent modules due to niche differentiation, with microbes within these modules sharing similar ecological requirements and functions, thereby fostering close interactions within modules (55, 56). Furthermore, variations in soil nutrient distribution, light intensity, and other environmental factors in RP forests may further drive the modular distribution of microbial communities. In ecological co-occurrence networks, modularity (Q) values in RP forests typically range from 0.3 to 0.7, with values exceeding 0.4 generally indicating a significant modular structure. The exceptionally high value observed in this study (2.30) strongly implies a hyper-modular architecture, which may substantially

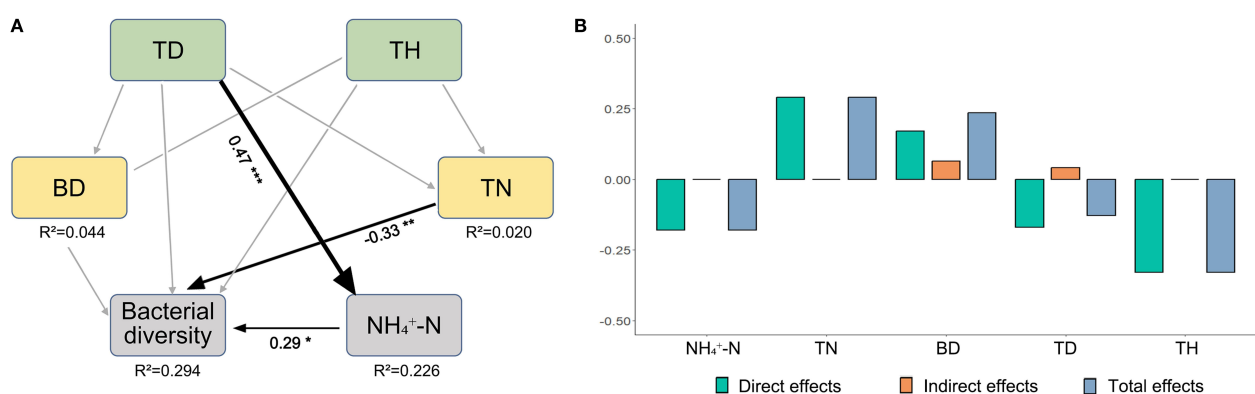


FIGURE 6

The effects of environmental factors on the soil bacterial diversity using SEMs (A). Line thickness indicates effect size. Bar graphs illustrate the standardized effects of each factor on soil bacterial diversity (B). Significance levels denoted by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

enhance network stability through the compartmentalization of ecological interactions (54).

The prominence of key nodes in the microbial network of AA forests is likely related to competitive dominance and niche overlap. In AA forests, certain dominant microbial species may influence the growth and distribution of other microbes by producing inhibitory compounds or competing for resources, thus forming highly connected key nodes (57, 58). These key nodes play pivotal roles in the network, serving as crucial hubs for information transfer, material cycling, or energy flow. Simultaneously, niche overlap and competition among microbes may prompt some species to enhance interactions to consolidate their ecological niches, thereby becoming key nodes in the network (59, 60). The robustness of the microbial network in EU forests may be attributed to its large diameter and redundant paths. EU forests may face severe environmental pressures such as nutrient-poor soils and drought. EU's large diameter creates redundant pathways for nutrient cycling, allowing microbial functions to persist. These pressures may prompt microbial communities to develop more robust network structures to cope with adverse conditions (61–63). A large diameter implies the existence of multiple redundant paths and alternative routes in the network, ensuring that information or materials can be transmitted through other paths when certain nodes or links are disrupted, thereby maintaining network stability and continuous functioning (64, 65).

4.3 Relationships between environmental factors and microbial communities

The results of Mantel tests and Random Forest analysis highlight the significance of DBH as a primary predictor of soil bacterial community composition. This is consistent with previous studies indicating a positive correlation between DBH and soil bacterial diversity (66, 67). Mature trees, defined as those with a DBH greater than 20 cm, release labile carbon compounds, such as succinic acid and fructose, as well as antimicrobial phenolic substances higher than that of saplings. This differential secretion contributes to the formation of distinct microbial niches. However, several studies suggest that the influence of DBH on soil bacterial communities may be modulated by other environmental factors (52, 66). Despite the conflicting opinions, the majority of these studies support the notion that larger trees provide more stable and diverse habitats for soil microorganisms (68). These studies emphasize how tree size and age indirectly shape bacterial communities by influencing soil microenvironments, including BD, SOC, and TN. Moreover, our study identified significant correlations between $\text{NH}_4^+\text{-N}$, TN, DOC, and bacterial diversity and network complexity, emphasizing the importance of soil nitrogen content on bacterial community structure (69, 70). Nevertheless, concerning the role of TP in contributing to network complexity, our findings differ from those of previous studies, which posited a minimal effect of phosphorus availability on bacterial network structure (71). Our research has underscored the significant roles of nitrogen and carbon, the impact of

phosphorus may be contingent upon various ecosystem types, soil conditions, and additional environmental factors.

Our study found a significant correlation between BGL and soil bacterial diversity, emphasizing the crucial role of soil enzymes in driving bacterial community dynamics. The main reason is that soil enzymes, as products of microbial activity and drivers of nutrient cycling, play a vital role in bacterial community dynamics. However, several studies have pointed out that different soil enzymes may have varied impacts on bacterial communities, influenced by soil types (72, 73). In addition, our study reveals that forest structure and soil physicochemical properties jointly shape microbial community assembly and network complexity, which is consistent with previous studies (48, 74). However, some researches have emphasized the dominant role of single factors, such as soil pH, in shaping bacterial communities, contrasting with our findings (75). The formation and maintenance of microbial communities in forest ecosystems are multifactorial processes. Our results emphasize the synergistic effects of forest structure and soil physicochemical properties, but this does not diminish the importance of other single factors. Rather, these studies may reveal differences and complexities in microbial community assembly mechanisms across different ecosystems. Urban-specific pressures, such as nitrogen deposition from traffic, soil compaction due to human activities, and residual heavy metal contamination, collectively intensify the suppression of diversity mediated by TN and alter the structure of microbial networks.

4.4 Environmental drivers and their pathways in shaping microbial communities

Our findings on the pathways through which environmental factors affect microbial community assembly provide valuable insights into the mechanisms underlying microbial dynamics in urban forest ecosystems. The SEM analysis revealed distinct hierarchical pathways through which environmental factors regulate soil bacterial diversity in urban forest ecosystems. The predominance of direct effects, particularly through nutrient availability (TN and $\text{NH}_4^+\text{-N}$), suggests that microbial communities in these managed ecosystems are primarily shaped by bottom-up resource control rather than secondary environmental interactions. This finding is consistent with recent studies demonstrating the central role of nitrogen dynamics in structuring microbial communities in urban green spaces (51, 70). The strong negative direct effect of TN on bacterial diversity (-0.33) contrasts with previous observations in natural forests, potentially reflecting the unique nutrient dynamics of urban ecosystems where nitrogen deposition and management practices may create distinct selective pressures (69).

Moreover, the moderate direct effects of BD on bacterial diversity, coupled with the strong association of $\text{NH}_4^+\text{-N}$ with diversity, underscore the complex interplay between physical and chemical soil properties. While BD influences microbial habitat structure and oxygen

availability, its relatively weaker effect compared to nutrient factors indicates that chemical properties, particularly nitrogen dynamics, may override physical constraints in shaping microbial communities in these managed systems. This contrasts with observations in natural forests, where physical soil properties often play a more dominant role (68, 75). The negligible indirect contributions of TD through environmental mediation further emphasize the primacy of direct nutrient pathways, suggesting that in urban forests, tree size effects on microbial communities are less mediated by secondary environmental factors. This finding has important implications for urban forest management, suggesting that nutrient management strategies, particularly targeting nitrogen dynamics, could be effective in modulating microbial community assembly and functions in these ecosystems. For instance, they could enable the prediction of network collapse risks under warming scenarios and enhance the optimization of green infrastructure to enhance carbon sequestration rates.

5 Conclusions

This study provides a comprehensive assessment of how different forest types influence soil microbial community structures in plain ecological forests of Beijing, China. Soil nitrogen dynamics emerge as the primary selector of bacterial diversity (TN path coefficient = -0.33), overriding physical constraints like BD, reflecting intensified nutrient cycling in anthropogenic systems. Forest structural attributes—particularly TD and TH—mediate microbial composition through cascading effects on soil chemistry, redefining plant-soil feedback mechanisms in managed landscapes. Crucially, microbial networks exhibit adaptive topological signatures across forest types: *Populus* stands' hyperconnectivity (edge density = 0.29) enhances metabolic coordination, while *Robinia*'s modular architecture (modularity = 2.30) confers resilience against environmental perturbations. These insights advocate for targeted afforestation strategies—prioritizing *Salix* for diversity enhancement and *Robinia* for stability—while highlighting network properties as novel bioindicators for urban ecosystem health. Future research must unravel how climate change alters these structure-function hierarchies through long-term experimental manipulations. Implementation of our species-network matching strategy could enhance ecosystem functions in Beijing's urban forest spaces.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: NCBI SRA, accession PRJNA1313477.

Author contributions

YZ: Conceptualization, Methodology, Writing – original draft, Writing – review & editing. CH: Data curation, Writing – review & editing. JC: Project administration, Writing – review & editing. YW:

Project administration, Writing – review & editing. HH: Data curation, Writing – review & editing. DY: Resources, Writing – review & editing. YSZ: Visualization, Writing – review & editing. XZ: Resources, Writing – review & editing. WD: Visualization, Writing – review & editing. ZL: Investigation, Writing – review & editing. XD: Investigation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fsoil.2025.1573531/full#supplementary-material>

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