Soil culturable heterotrophic bacterial composition in natural and artificial forests: Responses to seasonal variations and tree species in a semi-arid forest ecosystem postprint

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Abstract

Soil bacteria are integral to ecosystem functioning, playing key roles in nutrient cycling, organic matter decomposition, and the enhancement of soil structure. This study examined the composition and dynamics of soil bacterial communities under different vegetation types—native *Quercus brantii* Lindl. and *Amygdalus scoparia* Spach, and non-native *Pinus eldarica* Medw. and *Cupressus arizonica* Greene—in the Zagros mountain region of Iran. We conducted a comparative analysis of soil culturable heterotrophic bacterial communities in spring (wet season) and summer (dry season) to elucidate the effects of seasonal variation and vegetation type on soil microbial dynamics.

Soil samples were randomly collected beneath the canopies of the different tree species and from an adjacent control area, yielding a total of 48 composite samples that were analyzed for bacterial composition. In total, 11 Gram-negative (e.g., *Citrobacter freundii*, *Enterobacter cloacae*, *Escherichia coli*, *Klebsiella oxytoca*, *Klebsiella pneumoniae*, etc.) and 2 Gram-positive (*Staphylococcus epidermidis* and *Staphylococcus aureus*) bacterial species were identified, exhibiting significant seasonal variation. Overall, 53.85% of the bacterial species were shared between the two seasons, yet pronounced shifts in community composition were observed from spring to summer, with a higher abundance of Gram-negative species in spring.

Bacterial community structure was significantly influenced by vegetation type, with different tree species supporting distinct microbial assemblages. Furthermore, Pearson’ s correlation analysis showed that soil properties—particularly pH, phosphorus content, and moisture—were critical drivers of bacterial diversity and abundance.

These findings highlight the dynamic nature of soil bacterial communities in response to seasonal changes and vegetation type, and underscore the importance of repeated temporal sampling for accurate assessment of microbial diversity. A better understanding of these microbial dynamics is essential for improving soil management strategies and enhancing ecosystem resilience, especially in arid and semi-arid regions where environmental fluctuations are especially pronounced. This research not only supports our initial hypotheses but also advances our understanding of soil biogeochemical processes and provides guidance for future vegetation management practices.

Full Text

Preamble

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Soil culturable heterotrophic bacterial composition in natural and artificial forests: Responses to seasonal variations and tree species in a semi-arid forest ecosystem

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Abstract: Soil bacteria are integral to ecosystem functioning, significantly contributing to nutrient cycling and organic matter decomposition, and enhancing soil structure. This research examined the composition and dynamics of soil bacterial communities under different vegetation types (native *Quercus brantii* Lindl. and *Amygdalus scoparia* Spach, and non-native *Pinus eldarica* Medw. and *Cupressus arizonica* Greene.) in the Zagros mountain area of Iran. The study involved a comparative analysis of soil culturable heterotrophic bacterial communities in spring (wet season) and summer (dry season) to clarify the effects of seasonal changes and vegetation on the dynamics of soil microorganisms. Soil samples were randomly collected under the canopies of various tree species and a control area, yielding a total of 48 composite samples analyzed for bacterial composition. Results indicated that 11 Gram-negative (e.g., *Citrobacter freundii*, *Enterobacter cloacae*, *Escherichia coli*, *Klebsiella oxytoca*, *Klebsiella pneumoniae*, etc.) and 2 Gram-positive (*Staphylococcus epidermidis* and *Staphylococcus aureus*) bacteria were identified, showing significant seasonal variation. Specifically, 53.85% of bacterial species were common to both seasons, with notable shifts in community composition observed between spring and summer, highlighting a higher abundance of Gram-negative species in spring. Bacterial community structure was significantly influenced by vegetation type, with various tree species shaping distinct microbial assemblages. Moreover, Pearson' s correlations revealed that soil properties, particularly pH, phosphorus, and moisture content, were critical drivers of bacterial diversity and abundance. Our findings underscore the dynamic nature of soil bacterial communities in response to seasonal and vegetation changes, emphasizing the importance of repeated temporal sampling for accurate assessments of microbial diversity. Understanding these microbial dynamics is essential for improving soil management strategies and enhancing ecosystem resilience, particularly in arid and semi-arid areas where environmental fluctuations play a pivotal role. This research not only confirms our hypotheses but also enhances our understanding of soil biogeochemical processes and informs future vegetation management practices.

Keywords: bacterial abundance; soil properties; coniferous species; deciduous species; semi-arid Zagros forests

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Introduction

Soil bacterial communities are fundamental for nutrient cycling, organic matter decomposition, and maintenance of ecosystem stability [?]. These microorganisms significantly enhance soil structure, fertility, and overall health [?]. The composition and diversity of soil bacterial communities are affected by a multitude of factors, which ultimately affect ecosystem stability [?]. One of the most critical influences is the type of vegetation present in a habitat, such as those resulting from afforestation efforts. Species-specific variations in litter quality, root exudates, and rhizodeposition patterns can modify food availability and habitat conditions for microorganisms, often promoting certain bacterial taxa while inhibiting others [?]. The stark contrast in bacterial abundance observed in barren soils underscores the considerable influence of vegetation on soil microbial composition [?].

Seasonal variations also play a crucial role in shaping soil bacterial communities. Changes in environmental conditions during the growing season, such as reduced rainfall and increased temperatures in summer, can affect microbial dynamics and crop yields [?]. Plants gradually alter various physical, chemical, and biological characteristics of the soil, such as soil pH, the quality and quantity of organic matter, soil structure, respiration rates, and microbial biomass. These changes subsequently influence the composition of bacterial communities [?, ?, ?]. Furthermore, afforestation as a form of land-use change has profound effects on both above- and below-ground biota because it modifies microclimatic conditions and alters the availability of organic resources, significantly influencing the structure and diversity of soil bacterial communities [?].

The composition of soil bacterial communities exhibits significant variability over short-time scales, such as months or growing seasons. These shifts can be attributed to fluctuations in soil temperature, moisture content, organic matter levels, or autecological dynamics like dormancy [?, ?, ?]. Research shows that bacterial diversity typically peaks during wetter periods compared with drier ones [?]. While it remains uncertain whether these temporal dynamics result in major variations in ecosystem functions, some studies suggest that certain soil functions may remain resilient despite declines in microbial diversity or may recover quickly following disturbances [?]. Concurrently, drought events have been shown to increase the abundance of Gram-positive bacteria, which are capable of utilizing recalcitrant carbon sources in arid nutrient-poor soils, while Gram-negative bacteria that prefer labile carbon compounds exhibit less resilience to drought [?].

Soil properties such as pH, nutrient availability, structure, and moisture significantly influence bacterial community composition. Soil pH is particularly critical because extreme pH levels can limit the presence of certain bacterial species. Nutrients like nitrogen, phosphorus, and carbon are vital for bacterial growth and function, and fluctuations in these nutrient levels can lead to shifts in community composition [?, ?, ?, ?].

Despite numerous studies examining microbial community changes across various temporal scales [?], many investigations into soil microbiology have relied on one-time sampling tests. Such approaches capture only a snapshot of microbial communities at a specific moment, neglecting their dynamic nature and temporal patterns [?, ?, ?]. Additionally, the effects of different vegetation types on soil microbial community composition that are crucial for evaluating soil fertility conditions remain insufficiently explored [?]. Therefore, greater emphasis on the timing and frequency of sampling during the growing season is necessary to accurately capture variations in soil microbial community structures. Addressing this knowledge gap could profoundly impact sampling strategies in soil microbiology and enhance monitoring systems for soil biodiversity [?], particularly in arid and semi-arid areas.

This study aimed to investigate the composition of bacterial communities in relation to seasonal changes during spring (wet) and summer (dry) seasons across different tree species. The goal was to enhance our understanding of soil biogeochemical processes in response to environmental variations while linking ecosystem functions to specific microbial groups. The hypotheses of this research were as follows: (1) the composition of bacterial communities would differ with seasonal changes; and (2) different tree species would harbor distinct bacterial community compositions. Additionally, the research would examine how soil properties drive these differences.

2.1 Study Area

The study area is situated near Ilam County in western Iran, within the Zagros mountain region (33°37′-33°38′N, 46°19′-46°21′E). This area is renowned for its distinctive oak forests, yet it lacks natural coniferous tree species. Historically, the forests were predominantly composed of *Quercus brantii* Lindl., a broadleaf species that has thrived in the foothills since the Holocene, as evidenced by pollen records. These oak forests occasionally intermixed with species such as *Pistacia* spp. and *Amygdalus* spp. [**?**, **?**]. In recent decades, however, forest degradation has intensified due to the local population' s reliance on firewood and changes in land use types, which resulted in a drastic reduction in forest cover, with over 90.00% of the Zagros woodlands now exhibiting a coppice structure [**?**, **?**, **?**]. In response to this environmental challenge, afforestation initiatives commenced approximately 30 years ago, targeting the region' s degraded and open areas. Both native species, such as *Quercus brantii* Lindl. and *Amygdalus scoparia* Spach, as well as non-native coniferous species, including *Pinus eldarica* Medw. and *Cupressus arizonica* Greene., were introduced to aid in landscape restoration. The planted stands are located adjacent to one another, sharing similar physiographic characteristics: an elevation of approximately 1350 ($±$50) m a.s.l., a slope of 20.00%-30.00%, and a northern aspect. The semi-arid climate of the area, classified using the De Martonne aridity index, is characterized by an annual precipitation of 590 mm, an average temperature of 17°C, and a dry season that spans from early May to early October [**?**]. The soils in the study area are primarily shallow and calcareous, featuring a sandy clay loam texture.

2.2.1 Soil Sampling and Laboratory Analysis

Soil sampling locations were randomly determined beneath the canopy of various patches of both non-native woody species plantations, including *P. eldarica* and *C. arizonica*, and native species plantations such as *Q. brantii* and *A. scoparia*, all approximately 30 years old. In addition, natural forests of *Q. brantii* were sampled, encompassing both coppice and standard trees, alongside *A. scoparia*.

A control area, located approximately 20 m away from the tree species of this study, was also included in the sampling.

Soil sampling was conducted during both spring and summer of 2020, resulting in a total of 48 soil samples collected (eight patches (seven species and control) × two seasons × three replicates). Given the significant variability associated with soil sampling, it was essential to collect multiple soil cores for each composite sample, ensuring thorough homogenization [?, ?]. To this end, three random points were designated within each patch, from which three soil samples at a depth of 20 cm were collected at each point and then combined to form a composite sample for analysis.

Since the uppermost soil layer serves as the primary interface for humans and animals, with daily contact occurring regularly, it can provide pathways for exposure to bacterial pathogens via ingestion, inhalation, or dermal contact. Therefore, this layer is of critical importance. In this study, we employed a fully standardized and validated sampling protocol adapted from the U.S. Geological Survey (USGS) procedures [?]. This protocol provides detailed instructions for the preparation, collection, handling, preservation, and shipment of soil samples from potentially contaminated environments, specifically designed to minimize the risk of pathogen transmission to the field. Additionally, the guidelines allow for site-specific adjustments in response to equipment limitations or protocol constraints. These procedures, in line with U.S. Environmental Protection Agency (USEPA)/USGS recommendations [?], not only minimized the potential of direct exposure or inhalation of contaminated particles but also reduced the risk of cross-contamination between sampling sites. Collectively, the adoption of this protocol ensured that the risks associated with clinically relevant soilborne bacteria identified in this study were reduced to the lowest practicable level.

The soil samples were divided into two parts: the first part was directly transported to the soil laboratory in wet flasks and refrigerated at 4°C to preserve moisture and facilitate the assessment of biological properties. The second part was air-dried and sieved through a 2-mm mesh for analysis of physical and chemical properties [?].

Soil texture was determined using the hydrometric method [?], while soil water content (SWC) was measured using the weight method, which involves the ratio of water-saturated soil to dry soil after oven drying at 105°C for 24 h [?]. Additionally, three undisturbed soil cores were collected from each sampling location to determine bulk density (BD) [?]. Soil organic carbon (SOC) was measured using dichromate oxidation and titration [?], while total nitrogen (TN) was assessed via the Kjeldahl method [?]. Calcium carbonate ($CaCO_3$) equivalent was determined using a reverse titration method with NaOH [?], and available phosphorus was extracted using sodium bicarbonate and measured with a spectrophotometer [?]. Soil acidity (pH) was measured using a pH meter at a 1:2 ratio of soil to deionized water, and electrical conductivity (EC) was determined using an electrometer [?].

Soil basal respiration (BR) and substrate-induced respiration (SIR) were measured by the incubation method using 2.00% glucose [?]. Microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were calculated using the chloroform fumigation-extraction method with potassium sulfate, followed by titration and Kjeldahl method [?]. Microbial biomass phosphorus (MBP) was determined through chloroform fumigation and extraction with sodium bicarbonate, measured via spectrophotometry [?]. The activity of alkaline phosphatase (ALP) enzyme was assessed using the method described by [?]. Microbial indices, such as microbial quotient (qmic) and metabolic quotient (qCO_2), were computed by dividing microbial biomass carbon by organic carbon (MBC/organic C) and BR/MBC, respectively [?].

2.2.2 Bacterial Sampling and Laboratory Analysis

To identify soil bacteria, we suspended 1 g of soil from biological samples stored at 4°C in 9 mL of distilled water. The suspension was homogenized by shaking for 10 min in a specialized shaker, then incubated at 28°C for 48 h to promote bacterial growth. For each sample, two types of culture media were prepared: MacConkey Agar (MAC) for Gram-negative bacteria and Mannitol Salt Agar (MSA) for Gram-positive bacteria. After inoculating these selective and differential media, we incubated the Petri dishes again at 37°C for 48 h.

For the identified Gram-positive *Staphylococcus* species, a coagulase test was performed, distinguishing *S. aureus* as coagulase-positive and *S. epidermidis* as coagulase-negative. The IMViC test (an acronym derived from the first letters of four distinct biochemical tests: indole, methyl red, voges-proskauer, and citrate) was then conducted for Gram-negative bacteria, comprising four biochemical tests for the Enterobacteriaceae family. Following the IMViC tests, we performed the Triple Sugar Iron (TSI) agar test, a solid differential medium used to identify Enterobacteriaceae based on their sugar fermentation preferences [?].

2.3 Data Analysis

The Kolmogorov-Smirnov and Levene tests were conducted to assess the normality and homogeneity of variances of the soil data, respectively. We employed the Duncan test ($P<0.05$) to compare means, and used multidimensional scaling (MDS) to ordinate bacterial species for spring and summer seasons based on Euclidean distances, using SPSS v.23.0 software. Additional statistical analyses included calculating the relative abundance of Gram-positive and Gram-negative bacteria, determined by dividing the number of individuals of each bacterial species by the total number of identified individuals and expressing the relative abundance as a percentage. Heatmap hierarchical clustering of dominant soil bacterial species in relation to woody plant species was performed, along with an analysis of the correlation between physical-chemical and biological properties of the soil and the identified bacterial species. These analyses were conducted using R v.3.1.3 software with the "pheatmap," "tidyr," "ggplot2," "reshape2," and "VennDiagram" packages.

3.1 Relative Abundance of Identified Bacterial Species

Bacterial identification across all treatments, which included two seasons (spring and summer) and seven tree species (including non-native plantations such as *P. eldarica*, *C. arizonica*, and native species plantations *Q. brantii*, *A. scoparia*, natural forest species of *Q. brantii* encompassing both coppice and standard trees, and *A. scoparia*), revealed a total of 11 Gram-negative and 2 Gram-positive bacteria. In both seasons, 5 Gram-negative bacteria (*C. freundii*, *E. cloacae*, *E. coli*, *K. oxytoca*, and *K. pneumoniae*) and 2 Gram-positive bacteria (*S. epidermidis* and *S. aureus*) were identified, accounting for 53.85% of the total. In spring, 5 additional Gram-negative bacteria (*Citrobacter diversus*, *Pseudomonas aeruginosa*, *Serratia marcescens*, *Shigella sonnei*, and *Yersinia enterocolitica*) were found, contributing 38.46%, while 1 Gram-negative bacterium (*Enterobacter aeruginosa*) was exclusive to summer, representing 7.69%. Overall, the data indicated a higher distribution of Gram-negative bacteria in spring compared with summer (Figs. 1 and 2).

[FIGURE:1] Venn diagram illustrates the distribution of bacterial species between spring and summer seasons. Cit.fre, *Citrobacter freundii*; Ent.clo, *Enterobacter cloacae*; Esc.col, *Escherichia coli*; Kle.oxy, *Klebsiella oxytoca*; Kle.pne, *Klebsiella pneumoniae*; Sta.aur, *Staphylococcus aureus*; Sta.epi, *Staphylococcus epidermidis*; Cit.div, *Citrobacter diversus*; Pse.aer, *Pseudomonas aeruginosa*; Ser.mar, *Serratia marcesense*; Shi.son, *Shigela sonnei*; Yer.ent, *Yersinia enterocolitica*; Ent.aer, *Enterobacter aeruginosa.*

[FIGURE:2] Relative abundance of identified Gram-negative (a) and Gram-positive (b) bacterial species in spring and summer seasons

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3.2 Dominant Bacterial Species Under Tree Species

The MDS results, characterized by low normalized raw stress values, Dispersion Accounted For (DAF) explaining 94.00% and 97.00% of the data variability in spring and summer seasons, respectively, and a Tucker' s coefficient indicating excellent correlation between observed and predicted distances, demonstrated that in both seasons, the model provided a valid and robust representation of bacterial community structures with a very strong fit (Fig. 3 [FIGURE:3]; Table 1).

[FIGURE:3] Multidimensional scaling (MDS) of dominant bacterial species in spring (a) and summer (b) seasons

Goodness of fit in spring and summer

Test index	Spring	Summer
Normalized raw stress		
Dispersion Accounted For (DAF; %)		
Tucker' s coefficient		

Hierarchical clustering of dominant bacterial species associated with woody plant species revealed that the presence and abundance of certain bacteria were influenced by seasonal changes, despite the tree species remaining constant (Fig. 4 [FIGURE:4]). For instance, *C. freundii* was detected in the understory of plantation species *C. arizonica* and *A. scoparia* in spring, with the highest abundance observed in *A. scoparia*. In summer, however, it shifted to the understory of natural species (*A. scoparia* and *Q. brantii* coppice). Similarly, *E. cloacae* was found in the understory of natural species (*A. scoparia* and *Q. brantii* coppice) in spring but moved to the understory of plantation species (*C. arizonica* and *Q. brantii*) in summer. The abundance of *E. coli* increased in summer. *Klebsiella* genera showed consistency across both seasons, with *K. oxytoca* prevalent in the understory of *P. eldarica* and *K. pneumoniae* found in the understory of natural *Quercus* species (*Q. brantii* coppice and standard tree). *P. aeruginosa* was only observed in spring under plantation species (*C. arizonica*, *A. scoparia*, and *Q. brantii*). Notably, *S. marcescens* exhibited the highest abundance under *A. scoparia* and was exclusively present in spring. *S. sonnei* was identified in *Quercus* species (*Q. brantii* plantation and *Q. brantii* standard tree). *E. aeruginosa* appeared solely in summer and was found in the soil of all tree species, with its highest abundance noted under *A. scoparia*.

Gram-positive bacteria also demonstrated seasonal patterns. *S. epidermidis* was identified in the understory of *Quercus* during both seasons, specifically under natural *Quercus* species (*Q. brantii* coppice and standard tree) in spring and under *Q. brantii* plantation in summer. *S. aureus* was more prevalent in plantation areas, appearing under *A. scoparia* across both seasons, under *C. arizonica* in spring, and under *P. eldarica* in summer.

In conclusion, the clustering of tree species based on bacterial composition indicated that in spring, all forms of *Q. brantii* (including *Q. brantii* plantation, *Q. brantii* coppice, and *Q. brantii* standard tree) exhibited similar bacterial profiles. Additionally, *A. scoparia* (both *A. scoparia* plantation and *A. scoparia* natural tree) shared a comparable bacterial community. In contrast, no distinct pattern was observed for non-native needle leaf species, with *P. eldarica* showing greater similarity to the control treatment (CK) (Fig. 4a). In summer, bacterial composition of natural trees (*Q. brantii* coppice, *Q. brantii* standard tree, and *A. scoparia*) became more homogenous among themselves, but became distinctly separated from all afforested groups of both native and non-native species (*Q. brantii*, *A. scoparia*, *P. eldarica*, and *C. arizonica*) (Fig. 4b).

[FIGURE:4] Heatmap illustrating the hierarchical clustering of dominant bacterial species identified in samples of woody plant species in spring (a) and summer (b) seasons. CUP, *Cupressus arizonica* Greene.; AMP, *Amygdalus scoparia* Spach plantation; AMN, *A. scoparia* natural standard tree; QNC, *Quercus brantii* Lindl. natural coppice; QP, *Q. brantii* plantation; QNS, *Q. brantii* natural standard tree; PIN, *Pinus eldarica* Medw.; CK, control.

3.3 Relationship Between Bacterial Species and Soil Properties

The Pearson' s correlation between bacterial abundance and soil properties in spring indicated that among the physical properties, soil texture (clay, silt, and sand) had a stronger effect on bacterial abundance, especially Gram-negative bacteria like *E. coli* and *K. oxytoca*, as well as the Gram-positive bacterium *S. aureus*, compared with BD and SWC. Among the chemical properties, phosphorus (P) content had the greatest positive effect on the abundance of Gram-negative bacteria (*C. diversus*, *K. oxytoca*, and *Y. enterocolitica*) and Gram-positive bacterium *S. epidermidis*. Additionally, SOC, TN, and EC showed positive correlations with Gram-negative bacteria such as *P. aeruginosa*, *S. marcescens*, and *S. sonnei*. Regarding biological properties, the qmic index had the most significant and negative effect on Gram-negative bacteria (*K. oxytoca*, *P. aeruginosa*, and *S. sonnei*) and Gram-positive bacterium *S. epidermidis*. Following qmic, microbial biomass indicators (MBP and MBC), microbial respiration (BR and SIR), ALP, and qCO_2 influenced the abundance of Gram-negative bacteria, but had no effect on Gram-positive bacteria. Furthermore, results showed that Gram-negative bacteria *K. oxytoca*, *S. sonnei*, and *Y. enterocolitica* and Gram-positive *S. aureus* were the most strongly influenced by soil properties in spring (Fig. 5a [FIGURE:5]).

In summer, the correlation between bacterial abundance and soil properties revealed that bacterial abundance was less influenced by physical soil properties, with chemical and biological properties gaining more importance. Unlike in spring, P was less significant in shaping bacterial species composition in summer, while EC emerged as the most critical chemical property in determining bacterial abundance. SOC and TN had positive effects on Gram-negative bacteria (*C. freundii* and *K. pneumoniae*) and negative effects on Gram-positive bacterium *S. aureus*. Additionally, microbial respiration indicators (BR and SIR) and microbial biomass (MBC, MBN, and MBP) had similar impacts on Gram-negative bacterial composition. Gram-negative bacteria *K. oxytoca* and *K. pneumoniae*, along with Gram-positive *S. epidermidis*, were more strongly influenced by soil properties in summer compared with other bacterial species (Fig. 5b). The comparison of soil properties (physical, chemical, and biological) for all studied treatments (seven plant species and control) across two seasons and three replicates (Table S1) showed that season and species had a significant effect on most soil chemical parameters including $CaCO_3$, P, pH, and EC. In addition, the season and species had a significant effect ($P<0.05$) on SWC. The effect of woody species on soil biological attributes was greater than season as different woody species significantly changed BR, SIR, MBC, MBN, MBP, and ALP. Duncan' s multiple mean comparison showed that SWC, SOC, TN, P, MBC, MBN, MBP under *Q. brantii* trees (natural and plantation) were more than those of *A. scoparia*, and for *A. scoparia*, those values were more than those of *P. eldarica* and *C. arizonica.* In addition, the amount of nutrients and soil biological activity beneath these non-native plantations decreased compared with native plantation species.

[FIGURE:5] Pearson' s correlation heatmap illustrating the relationships between soil properties (physical, chemical, and biological) and the abundance of dominant bacterial species in spring (a) and summer (b) seasons. EC, electrical conductivity; P, phosphorous; TN, total nitrogen; SOC, soil organic carbon; SWC, soil water content; BD, bulk density; qmic, microbial quotient; qCO_2, metabolic quotient; ALP, alkaline phosphatase; MBP, microbial biomass phosphorous; MBN, microbial biomass nitrogen; MBC, microbial biomass carbon; SIR, substrate-induced respiration; BR, basal respiration. *, $P<0.05$ level; **, $P<0.01$ level.

4.1 Relative Abundance of Identified Bacterial Species

The results of this study underscore the significant impact of seasonal variations and vegetation cover on the composition and abundance of soil bacterial species. Due to their shorter generation cycles compared with larger organisms, such as plants and animals, bacteria can rapidly respond to environmental changes. This rapid response facilitates quicker adaptive and genetic shifts within bacterial populations [?]. Consequently, even over relatively brief time frames, fluctuations in biotic and abiotic factors can lead to both gradual and abrupt alterations in the composition of soil microbial communities [?].

Seasonal changes play a crucial role in regulating temperature and soil moisture balance, which includes factors such as precipitation and evapotranspiration. These conditions significantly affect bacterial transport within soil ecosystems. For instance, heavy rainfall events can lead to the downward movement of bacteria into deeper soil layers [?]. The mobility of bacteria also varies: motile bacteria tend to move more freely than their non-motile counterparts, especially under stagnant water conditions. In contrast, flowing water becomes a dominant factor in bacterial transport dynamics. Research indicates that under saturated and stagnant water conditions, motile species like *E. coli* exhibit enhanced transport capabilities compared with non-motile species [?]. This observation may help explain the increased abundance of *E. coli* in summer.

The study observed a notable increase in Gram-negative bacteria in spring, which aligns with the findings from [?]. This increase can be attributed to favorable moisture and temperature conditions, coupled with higher nutrient availability in the soil. Soil moisture not only influences the physiological activity of bacterial communities but also regulates plant growth. Enhanced plant growth leads to increased root exudation, further enriching the soil environment for bacterial proliferation [?]. Conversely, periods of soil dryness can result in increased compaction and reduced porosity, which amplify temperature fluctuations and limit nutrient availability for fast-growing bacterial groups [?, ?]. Additionally, certain bacterial species exhibit higher survival rates in cooler soils. For example, bacterial mortality rates can double with every 10°C increase in temperature within the range of 5°C–30°C [?].

Increased sunlight exposure in summer can have detrimental effects on bacterial survival due to the sterilizing impact of ultraviolet radiation and subsequent soil desiccation [?]. As a result, temperature serves as a selective pressure that favors microbial communities better adapted to local thermal conditions [?]. On a temporal scale, it has been posited that species sorting is likely the primary mechanism for community adaptation within soil ecosystems [?, ?]. Higher temperatures are expected to favor microbial communities that thrive under warmer conditions, while cooler temperatures will support communities that are better suited to lower thermal environments. The term "community adaptation" is employed here to describe the enhanced functional performance of microbial communities following shifts in temperature [?, ?, ?, ?]. Understanding these dynamics is essential for predicting how soil microbial communities will respond to ongoing environmental changes, particularly in the context of climate variability and its effects on ecosystem health and functionality.

4.2 Dominant Bacterial Species Under Tree Species

The relationship between plant and soil bacterial communities is one of mutual dependence, where plants significantly influence the composition and dynamics of soil microbial populations. Through the diversification of root exudates, plants can modulate microbial communities in the surrounding soil [?, ?]. These exudates not only serve as substrates for bacterial growth but also facilitate the recruitment of specific bacterial taxa that are essential for meeting plant nutritional needs, particularly in terms of P and nitrogen supply [?, ?].

The findings of this study corroborate existing research, highlighting the influence of vegetation on soil bacterial community composition. This result aligns with studies conducted by [?] and [?], who found that changes in plant phenology, including litter inputs and root exudates, can significantly alter microbial community structures [?, ?]. These alterations are driven by various factors such as plant nutrient uptake, root exudate profiles, and litter decomposition, all of which contribute to shifts in soil chemistry and resource availability for soil microbes [?, ?].

Drought conditions present a significant challenge by reducing nutrient availability and impairing plant growth, which can have cascading negative effects on ecosystem functions [?]. While environmental fluctuations are crucial in shaping bacterial communities, the turnover rates for bacteria tend to be stronger and more specific to individual plant species. Despite seasonal variations, a stable subset of microbial species persists, which is affected by consistent features, for example root exudates and decomposition of organic matter [?]. This stability is exemplified by the consistent presence of *K. oxytoca* under the canopy of *P. eldarica* species and *K. pneumoniae* under the canopies of natural *Quercus* species (*Q. brantii* coppice and standard tree) across both seasons in our study. In summer, the bacterial composition beneath natural trees (*Q. brantii* coppice, *Q. brantii* standard tree, and *A. scoparia*) was notably more similar to one another, but remained distinct from all afforested groups containing both native and non-native species (*Q. brantii*, *A. scoparia*, *P. eldarica*, and *C. arizonica*). The observation that bacterial colonization occurred beneath tree canopies suggests that in summer, older natural tree canopies provide favorable moisture and temperature conditions that enhance soil bacterial activity. These conditions lead to more homogeneous bacterial compositions under these standard trees. Furthermore, as forests mature over time, the accumulation of litter increases, enriching soil nutrients that serve as additional energy sources for microbial metabolism and synthesis [?]. In conclusion, the interplay between tree species and soil bacterial communities is complex and dynamic. The stability of certain bacterial species under specific tree canopies highlights how vegetation influences microbial diversity and function within forest ecosystems. Grasping these interactions is crucial for the development of effective forest management and conservation measures that seek to preserve healthy soil ecosystems.

4.3 Relationship Between Bacterial Species and Soil Properties

4.3.1 Effects of Soil Physical and Chemical Properties on the Abundance of Dominant Bacterial Species

This study confirms a significant correlation of soil texture and BD with the abundance of both Gram-negative and Gram-positive bacteria. Physical properties of soil, particularly mineral composition and particle size, play a crucial role in influencing bacterial movement and survival [?]. Additionally, chemical properties such as electrochemical surface characteristics and bacterial morphology further affect these dynamics.

Our findings indicate that fine-textured soils provide more favorable conditions for bacterial survival compared with coarse-textured soils [?, ?]. The adsorption of bacteria to soil particle surfaces is influenced by their physiological and surface properties, including growth stage, surface charge, hydrophilicity or hydrophobicity, and the presence of polysaccharides. For example, polysaccharides can create a negative surface charge on bacteria, which leads to attraction to positively charged soil particles or repulsion from negatively charged ones. Negatively charged *E. coli* demonstrates a strong attraction to positively charged surfaces [**?**, **?**, **?**]. This interaction likely explains the observed correlation between soil texture and bacterial abundance.

Among the chemical properties analyzed, P had the most significant and positive effect on the abundance of Gram-negative bacteria, particularly in spring. This result aligns with previous research, confirming that P addition can significantly increase Gram-negative bacterial populations under warmer temperatures and higher rainfall conditions [**?**, **?**]. P limitation in soils is a common issue due to its low concentration, poor mobility, and high heterogeneity [**?**, **?**]. In response to this limitation, soil microorganisms may enhance their P acquisition strategies by releasing organic anions to solubilize inorganic P or producing enzymes that mineralize organic P—processes that often require additional carbon sources [**?**].

Carbon and nitrogen emerged as influential factors affecting bacterial abundance, especially in spring. High organic matter content during this season supports water retention, soil aggregation, and favorable biological conditions for bacterial diversity and survival [**?**, **?**, **?**]. Available nitrogen significantly impacts active bacterial communities and increases the number of taxonomic groups specializing in nitrogen compounds [**?**]. These groups exhibit distinct seasonal dynamics and play crucial roles in nitrification and denitrification processes related to plant community development [**?**].

Specific bacterial genera such as *Pseudomonas* and *Enterobacter* facilitate essential soil bioprocesses such as P solubilisation and nitrogen mineralization [**?**, **?**], indicating the prevalence of key ligninolytic bacteria usually present in rhizosphere and forest soils [**?**, **?**]. Additionally, the composition of microbial communities undergoes alterations throughout the decomposition process, as microbes employ various strategies for resource acquisition. Fast-cycling microbes capitalize on easily accessible carbon at the initial stages, whereas slow-cycling microbes are responsible for the breakdown of more resistant carbon compounds at later stages [**?**, **?**].

EC was positively correlated with bacterial abundance, with its influence being most pronounced in summer. The decomposition of woody biomass and litter under tree canopies enhances microbial activity by increasing EC and nutrient release [**?**], which positively affects bacterial populations. High temperatures in summer may result in greater evaporation, resulting in decrease in soil moisture and increase in salinity. This dynamic strengthens the relationship between EC and bacterial abundance [**?**]. $CaCO_3$ also exhibited a positive effect on bacterial abundance across both spring and summer. In arid and semi-arid areas, $CaCO_3$ accumulates on soil particles due to hot and dry climates. This accumulation alters pore size and reduces the surface charge of both Gram-negative (*E. coli* and *P. aeruginosa*) and Gram-positive bacteria (*S. aureus*) [**?**].

Soil pH emerged as a significant factor influencing bacterial abundance, shaping community composition across different ecosystems [?, ?, ?]. Although bacteria can survive across a wide pH range, their activity tends to decrease in acidic conditions. The higher pH observed in spring compared with summer likely creates more favorable conditions for bacterial growth during this season [?].

4.3.2 Effects of Soil Biological Properties on the Abundance of Dominant Bacterial Species

The correlation between biological properties and bacterial abundance revealed that in spring, microbial biomass (MBP and MBC), respiration (BR and SIR), ALP activity, and qCO_2 significantly affected Gram-negative bacteria abundance. In contrast, no notable effects were observed on Gram-positive bacteria. Biological soil properties such as microbial respiration are positively associated with bacterial abundance and are commonly considered indicators of high soil quality [?]. Increased microbial respiration in spring, driven by favorable climatic conditions regarding moisture, stimulates microbial activity leading to enhanced bacterial populations. While some studies have reported a positive correlation between MBC and SOC [?], our study did not observe consistent patterns regarding their effects on bacterial abundance. Similarly, other microbial biomass properties did not exhibit distinct patterns, potentially reflecting the intrinsic characteristics of the bacteria themselves. This study illustrates the complex interplay between various soil properties—physical, chemical, and biological—and their influence on bacterial species. Understanding these relationships is crucial for managing soil health and enhancing ecosystem functions through targeted agricultural practices.

5 Conclusions

This study highlighted the dynamic nature of soil bacterial communities in response to seasonal variations and different vegetation types, specifically within natural forests of *Q. brantii* and *A. scoparia*, as well as afforested stands of non-native species like *P. eldarica* and *C. arizonica*. Our findings demonstrated significant shifts in bacterial composition and abundance between spring and summer seasons, emphasizing the critical role of environmental factors such as soil moisture, temperature, and nutrient availability. The results confirm our hypotheses that seasonal changes profoundly influence microbial community composition and that specific tree species shape distinct bacterial assemblages. The research underscores the importance of repeated temporal sampling for accurately assessing microbial diversity, which is essential for effective soil management and ecosystem resilience, particularly in arid and semi-arid areas. Investigating soil bacterial interactions with other soil biota and assessing the impacts of environmental stressors will be crucial. Long-term studies on vegetation management practices and their effects on soil health and microbial diversity will also provide valuable insights for ecosystem restoration.

Conflicts of 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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Figure 13

Figure 1: Figure 13

Figure 34

Figure 2: Figure 34

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Figures

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Figure 39

Figure 3: Figure 39