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The Influence of Bioclimates and Soil Physicochemical Properties on Bacterial and Archaeal Communities from Forest Ecosystems in Côte d'Ivoire (West Africa)

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Abstract: Archaea and bacteria communities play pivotal roles in tropical forest ecosystems' functioning, especially nutrient cycling, plant phenology, and health. The objective of this study was to explore the diversity of archaeal and bacterial communities in forest soil ecosystem of Côte d'Ivoire and to identify abiotic factors that influence their composition. Using high-throughput amplicon sequencing targeting the V4V5 hypervariable region of the 16S ribosomal RNA gene, we analyzed 22 soil samples taken from the 2 main forest areas of Côte d'Ivoire, namely the semi-deciduous moist forest and the evergreen moist forest, both of which are located in the humid and sub-humid areas of the country. The analysis revealed that the biodiversity at the phyla level was congruent with previous studies. Richness and Shannon diversity indices revealed the dominance of bacteria over archaea in all studied soils. Moreover, the predominant bacterial community consisted of Proteobacteria (29.8%), Acidobacteria (15.5%), and Actinobacteria (14.2%), while the archaeal community was dominated by Thaumarchaeota (1.93%). However, at the genus level, patterns emerged. The most abundant and ubiquitous members at the genus level included *Bradyrhizobium*, *Rhodoplanes*, *Bacillus* (bacteria), and *Nitrosophaera* (archaea). While bacterial core microbiome members were found in almost all soils, *Nitrososphaera* genus were selective to sub-humid bioclimate and cropland land use. These patterns were correlated to the soils' physicochemical characteristics, bioclimate, and land use. This study sheds light on the intricate relationships between abiotic factors and microbial communities in Côte d'Ivoire's forest soils and helps to identify keys species for future soil management.

Keywords: forest soil ecosystems; archaea; bacteria; abiotic factors; Côte d'Ivoire

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1. Introduction

In Côte d'Ivoire, it is estimated that more than 90% of the original forest cover is lost, mainly due to increasing land conversion from forestlands to agricultural lands [1,2]. The loss of the natural forest ecosystems is critical for the country as it leads to the disappearance of livelihoods in rural communities and land degradation. Overall, Côte d'Ivoire is facing a serious ecosystem functioning issue since forests play a crucial role in ecosystems [3]. Indeed, forests provide a wide range of essential services that are interconnected and vital for the functioning of the overall ecosystem. Firstly, forests regulate water cycling by capturing precipitation and releasing water vapor into the atmosphere, contributing to the distribution of water resources [4]. Secondly, they play a fundamental role in climate regulation by absorbing carbon dioxide through photosynthesis and releasing oxygen [5].

This process helps to mitigate the impact of greenhouse gases and contributes to the overall balance of the atmosphere [6]. Moreover, forests harbor a remarkable diversity of living microorganisms and support vital biological processes. Indeed, numerous studies conducted in forest soil ecosystems have provided valuable insights into various microorganisms' genetic diversity and vital roles. These microorganisms include fungi [7,8], bacteria, and archaea [9–11], which play crucial roles in processes like nutrient cycling, organic matter decomposition, and soil fertility preservation [12–14]. Particularly, arbuscular mycorrhizal fungi are recognized for their roles in enhancing root development, stimulating nutrient cycling, improving soil structure, increasing plant resilience to stress, facilitating the uptake of less mobile ions, and promoting plant community diversity [15]. Since bacteria possess genes that encode plant cell wall-degrading enzymes, they make significant contributions to organic matter decomposition [16–19]. Forest soils act as a reservoir of nutrients that supply trees and other vegetation types with essential elements necessary for their growth and development. They also play a significant role in the regulation of water flow, preventing erosion, and maintaining stable moisture levels within the forest.

Due to their essential roles in ecosystem services, it becomes urgent to explore microbial diversity and structure in the threatened forest environment of Côte d'Ivoire. Indeed, historically, the original forest biome was important and covered more than 45% of the total area of Côte d'Ivoire. It was located mainly in the south and west parts of the country where the climate has an equatorial/subequatorial type with a long rainy season [20]. Unfortunately, these two areas have been intensively converted into cash crop fields, including cocoa and coffee, without appropriate measures of forest conservation. Consequently, today, the forest biome is dominated by degraded forests. This continuous degradation of forest vegetation in Côte d'Ivoire may cause the loss of important ecosystem services. Indeed, it has been evidenced recently that there is a straight link between plant diversity, soil microbial diversity, and the complexity of microbial networks in a tropical rainforest [21]. It means that ecological studies that aim at deciphering the communities of forest soil microorganisms could help to formulate effective policies and strategies for forest conservation and/or restoration, reforestation, and sustainable agriculture in Côte d'Ivoire. Of such services, carbon and nitrogen cycling are important in forest ecosystems [22]. Both archaea and bacteria are key players in carbon and nitrogen cycles [23]. Such studies need not only to focus on the structure, function, and diversity of the microbial communities but also to define the core microbiome which is known to be dependent on environmental factors [24]. The identification of the core microbiome is important since its persistent presence in particular habitats/niches is likely to be essential for their functioning [25,26]. Moreover, recent studies have revealed that the core microbiome is essential for the maintenance of the functional stability of soil microbiomes in reforestation ecosystems [27].

Hence, this study aims to explore (1) the diversity of archaeal and bacterial communities in the soils of Côte d'Ivoire's forest areas, (2) identify the core bacteriobiome and archaeome, and (3) determine the major abiotic drivers influencing archaeal and bacterial richness in the forest biome.

2. Materials and Methods

2.1. Study Sites and Soil Sampling

The study area was located in the Côte d'Ivoire forestry region, which is divided into two parts: the evergreen moist forest and the semi-deciduous moist forest (Figure 1).

The Côte d'Ivoire evergreen moist forest consists of trees and shrubs, ranging in height from 5 to 50 m. The semi-deciduous moist forest formations have been affected by degradation and maintain coverage of only 22% [28]. Most of the country's cash crops are produced in these forest areas, owing to the good fertility of the soils. The main cash crops are cocoa (*Theobroma cacao*), coffee (*Coffea* sp.), hevea (*Hevea brasiliensis*), palm groves (*Elaeis guineensis*), and coconut groves (*Cocos nucifera*). The sampled soils belong to the rhizosphere of all the vegetation types of the forest biome (the evergreen moist and the semi-deciduous moist forests) and either cropland or forestland (Table 1).

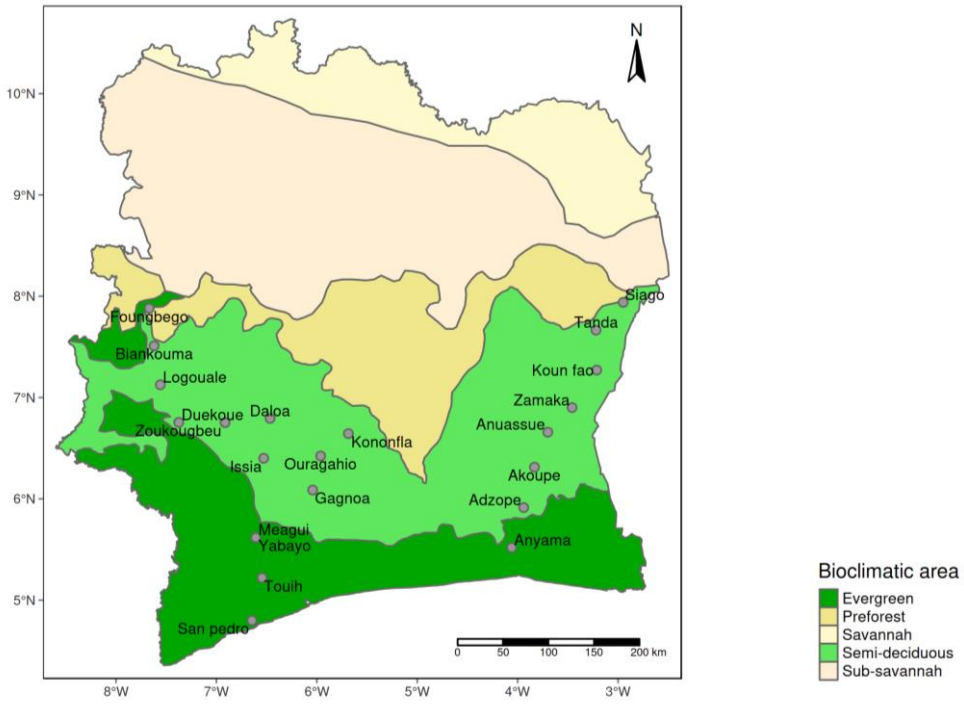

Figure 1. Côte d'Ivoire map with the two forest areas and sampling localities. The evergreen region is in dark green while the semi-deciduous region is in green. The savannah, sub-savannah, and preforest areas are also shown.

Table 1. Forest zones and main characteristics of sampling soils.

Soil ID	Locality (City)	Geographic Position	Forest Zone	Bioclimate	Land Use
CI01	Anyama	5°31′07.2″ N 4°03′33.8″ W	Evergreen	Humid	Cropland
CI02	Adzopé	5°54′49.5″ N, 3°56′24.4″ W	Semi-deciduous	Humid	Cropland
CI03	Akoupé	6°18′46.7″ N, 3°49′51.1″ W	Semi-deciduous	Sub-humid	Cropland
CI04	Anuassué	6°39′29.5″ N, 3°42′00.2″ W	Semi-deciduous	Sub-humid	Cropland
CI05	Zamaka	6°54′02.0″ N, 3°25′23.7″ W	Semi-deciduous	Sub-humid	Forest land
CI06	Koun-Fao	7°39′55.9″ N, 3°13′03.4″ W	Semi-deciduous	Sub-humid	Forest land
CI07	Tanda	7°39′55.9″ N, 3°13′03.4″ W	Semi-deciduous	Sub-humid	Cropland
CI08	Siago	7°56′22.0″ N, 2°56′57.6″ W	Semi-deciduous	Sub-humid	Forest land
CI24	Kononfla	6°38′38.8″ N, 5°41′02.0″ W	Semi-deciduous	Sub-humid	Cropland
CI25	Ouragahio	6°25′23.1″ N, 5°57′43.3″ W	Semi-deciduous	Sub-humid	Cropland
CI26	Gagnoa	6°05′12.9″ N, 6°02′30.7″ W	Semi-deciduous	Sub-humid	Cropland
CI29	Meagui	5°37′04.3″ N, 6°36′28.7″ W	Evergreen	Sub-humid	Cropland
CI27	San Pedro	5°05′13.1″ N 6°02′30.7″ W	Evergreen	Humid	Cropland
CI28	Touih	5°13′12.8″ N 6°32′43.4″ W	Evergreen	Humid	Cropland
CI30	Yabayo	5°37′04.3″ N, 6°36′28.6″ W	Evergreen	Sub-humid	Cropland
CI31	Issia	6°24′01.3″ N, 6°31′46.3″ W	Semi-deciduous	Sub-humid	Cropland

Table 1. *Cont.*

Soil ID	Locality (City)	Geographic Position	Forest Zone	Bioclimate	Land Use
CI32	Daloa	6°47′39.5″ N, 6°27′57.8″ W	Semi-deciduous	Sub-humid	Cropland
CI37	Zoukougbeu	6°45′08.0″ N, 6°54′51.3″ W	Semi-deciduous	Humid	Cropland
CI38	Duekoue	6°45′16.7″ N, 7°22′30.7″ W	Semi-deciduous	Humid	Forest land
CI39	Logouale	7°07′31.6″ N, 7°33′24.3″ W	Semi-deciduous	Humid	Cropland
CI40	Biankouma	7°30′38.1″ N, 7°37′14.4″ W	Semi-deciduous	Humid	Forest land
CI41	Foungbego	7°52′50.5″ N, 7°40′09.7″ W	Evergreen	Humid	Forest land

Soil samples were collected in August–September 2017. A total of 22 soils were obtained of which >70% were located in the semi-deciduous ecosystems. The sampling was carried out following the guidelines of the African Soil Microbiome Project [29]. Briefly, soil samples were collected from 22 sites along national roads. The sampling sites were spread across distances of 50–300 km. Each sampling site covered an area of approximately 100 m × 50 m, with four independent sample locations at the corners of the rectangular area (Supplementary Figure S1) [30]. At each independent sample location, four topsoil cores (2 cm in diameter and 5 cm in depth) were collected as pseudo-replicate samples. These samples were pooled together and homogenized into a composite sample of approximately 25 g (replicate sample). Four independent replicate samples (4 × 25 g) obtained from four sample locations at each sampling site were stored in labeled sterile plastic bags as an independent soil sample. This process was repeated for all twenty-two sites. The resulting samples collected from the forest biome of Côte d'Ivoire (CI) are referred to by the soil numbers CI01 to CI41 (Table 1). After collection, the soil samples were stored at 4 °C in the laboratory before being shipped to South Africa for further analysis.

Land use classification used the categories recognized in FAO's World Census of Agriculture (www.grid.no/climate/ipcc/land_use/045.htm, accessed on 30 November 2023). Bioclimate classification was performed using the Thornthwaite climatogram based on the precipitation effectiveness and temperature efficiency [31,32], as computed in the CHELSA database [33], as follows: humid (Anyama, Adzopé, San Pedro, Touih, Zoukougbeu, Biankouma, Duekoué, Foungbego, Logoualé) and sub-humid (Akoupé, Anuassué, Zamaka, Koun-Fao, Tanda, Siago, Kononfla, Ouragahio, Gagnoa, Meagui, Yabayo, Issia, Daloa). Detailed information about the sampled sites and their geographical positions is reported in Table 1.

2.2. Soil Physicochemical Analyses

All physicochemical analyses were carried out by Bemlab (Strand, Cape Province, South Africa) using standard methods and 10 g sieved air-dried soil as in Cowan et al. [29]. The soil pH (aqueous) was measured according to the Thomas method [34], and the oxidizable carbon was analyzed using the Walkley–Black method [35]. Soil exchangeable and soluble Na, K, C, Mg, Al, Fe, Mn, and P were analyzed using the Mehlich No. 3 soil test extractant with the inductively coupled atomic emission spectrometry method [36]. The extractable ion concentration was quantified using inductively coupled plasma optical emission spectrometry (Spectro Genesis, SPECTRO Analytical Instruments GmbH & Co. KG, Kleve, Germany). The soil particle size distribution (sand/silt/clay percentage) was measured using the Bouyoucos method [37]. The total nitrogen (TN) and soil organic carbon (SOC) (as a percentage) were measured using the catalyzed high-temperature combustion method [38].

2.3. Molecular Methods and Bioinformatics

DNA was extracted from 0.25 g of lyzed and homogenized soil using the DNeasy PowerSoil DNA isolation kit (QIAGEN GmbH, Hilden, Germany) at the Centre for Microbial Ecology and Genomics (University of Pretoria, Pretoria, South Africa). Archaeal and bacterial sequences were amplified from soil DNA extracts using the 16S ribosomal RNA V4-V5 hypervariable region-specific alternative primer 515F-Y (5′-GTGYCAGCMGCCGCGGTAA-3′; [39]) and the universal reverse primer 909–928 (5′-CCCCGYCAATTCMTTTRAGT-3′; [40]). PCR and sequencing were conducted following the process described in Gnangui et al. [30] and Cowan et al. [29]. Raw reads were demultiplexed using Sabreur v0.4.1 (https://github.com/Ebedthan/sabreur, accessed on 1 August 2022). Primer sequences were removed using cutadapt v2.10 [41]. After the removal of barcode and primer sequences, the trimmed sequences were denoised using the DADA2 algorithm [42] that resolves Illumina sequencing amplicon errors to generate amplicon sequence variants (ASVs). Obtained ASVs were subjected to a taxonomic classification using the trained naive Bayes RDP classifier v2.13 [43].

2.4. Statistical Analysis

All statistical analyses were conducted in R v4.3.2 [44]. The vegan package v2.6.4 [45] and phyloseq package v1.44 [46] were utilized to generate the ASV table. Alpha diversity and beta diversity analyses involved multiple rarefaction and estimation of average diversity using the metagMisc package v0.5 (https://github.com/vmikk/metagMisc, accessed on 1 March 2023). Taxa abundance differences were computed using the non-parametric Kruskal–Wallis test and pairwise Wilcoxon rank-sum test, with p-value correction using the Benjamini and Hochberg method (False Discovery Rate, FDR) [47]. Core microbiome analysis was performed by selecting the 1% most abundant ASVs and most ubiquitous of 100% across the entire dataset, following standard recommendations [48–50]. The relative abundance is expressed as a percentage of the total number of sequences in each soil sample or locality. Tests for association between genus abundance, using Spearman's rho, were conducted using the R function cor.test. Abundance was first centered log ratio transformed using the propr package [51]. Results were considered significant at $p < 0.05$.

3. Results

3.1. Characteristics of Sampling Sites and Soil Physicochemical Properties

The soil sampling data indicated that nearly 73% of the 22 soil samples were located in the semi-deciduous ecosystems, while 60% of them were located in the sub-humid areas as for the bioclimates. Additionally, a significant proportion (16 out 22) of the sampled sites were primarily used as cropland, with only 6 sites used as forest land (Table 1). Consequently, variations in physicochemical properties were evident across the sampled sites (see Table S1). Principal component analysis of the environmental variables unveiled distinct environmental conditions corresponding to different land uses and bioclimates. The forest land soils were split into two groups differentiated mainly by mean annual precipitation (MAP) influence, while all the cropland soils showed similar environmental conditions (Figure 2).

Forest soils exhibited higher pH levels, ranging from 5.43 to 7.78 (mean = 6.44, sd = 0.923), in contrast to cropland soils that ranged from 4.94 to 6.93 (mean = 5.77, sd = 0.55). A similar trend was observed for soil organic carbon (SOC), which varied from 1.15 to 2.5% in forest soils compared to cropland soils, where the range was from 0.69 to 2.04%. The variation extended to total nitrogen (TN), soluble and exchangeable sodium (Na), phosphorus (P), silt percent (silt), clay percent (clay), and sand percent (sand).

Regarding climatic variables, forest soils exhibited two subgroups. The first subgroup (Koun-Fao, Siago, Zamaka), located in the eastern part of the country, was characterized by a higher mean annual temperature (MAT) ranging from 26.4 to 26.8 °C and a lower mean annual precipitation (MAP) ranging from 1113 to 1175 mm. The second subgroup (Biankouma, Foungbego, Logouale), located in the western part of the country, displayed

an inverse pattern with MAT ranging from 24.1 to 25.5 °C and MAP ranging from 1517 to 1675 mm.

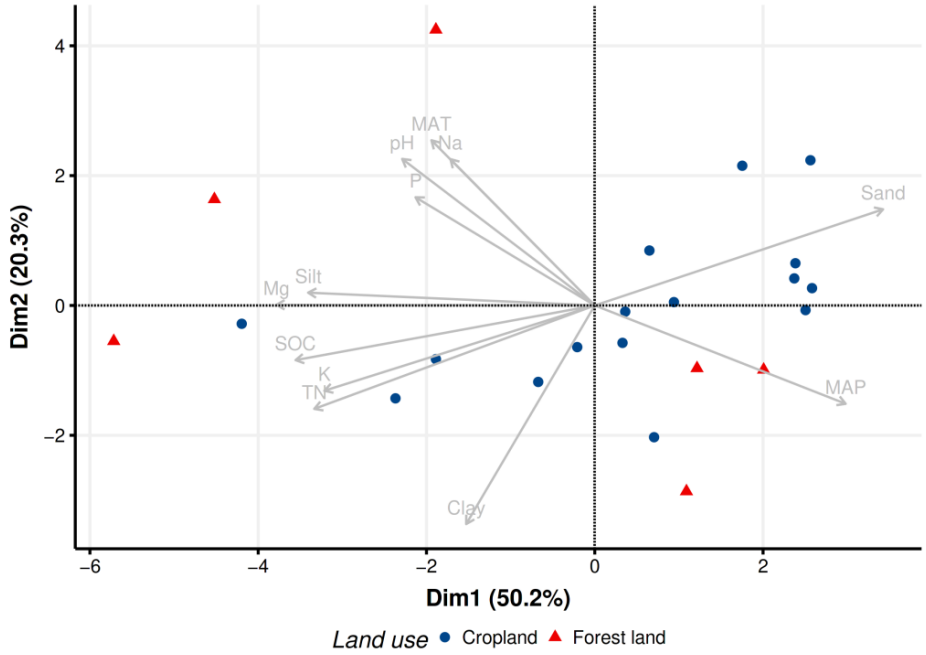

Figure 2. Principal component analysis of the environmental data. Sampled sites are colored according to land use.

Similarly, soils mapped into the different bioclimates also showed a distinct pattern. Indeed, the soil from the sub-humid area was characterized by higher levels of pH, MAT, Na, P, Mg, silt, SOC, K, TN, and clay, while the soils from the humid area were mostly influenced by MAP and sand percentage (Figure S2).

3.2. Proteobacteria and Thaumarchaeota Dominate Bacteria and Archaea Communities in Forest Soil Ecosystems of Côte d'Ivoire

After sequencing, a total of 1,815,112 barcoded sequences were obtained. Following the filtering step, 1,626,802 sequences were retained, resulting in 12,752 amplicon sequence variants (ASVs). A subsequent taxonomic classification revealed that 97.94% of all ASVs belonged to bacteria, while only 2.06% were identified as archaea. The analysis of all ASVs revealed the presence of 43 archaeal and bacterial phyla in total, of which 11 could be considered major taxa based on criteria of a relative abundance of at least 1% and a prevalence of 100%. These major phyla could be divided into two groups, namely major phyla group 1 (relative abundance > 6.47%)—which included Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes, Planctomycetes, and Chloroflexi (Figure 3)—and major phyla group 2 (relative abundance > 1.0%)—which included Verrumicrobia, candidate division WPS-1, Firmicutes, Thaumarchaeota, and Gemmatimonadetes (Supplementary Table S1). Specifically, the Proteobacteria phylum was the most abundant group, at 29.8%, followed by Acidobacteria at 15.4%, and Actinobacteria at 14.2%, while Thaumarchaeota represented the only archaeal phylum in this group at 1.93% (Figure 3).

At the genus level, *Gp6*, *Gaiella*, and *Zavazinella* were the most abundant in terms of the average relative abundance of ASVs for bacteria (respectively 4.75%, 3.75%, and 2.83%) and were found in all bioclimates and soils. *Nitrososphaera* was the most abundant archaea, with an average relative abundance of 1.90% and a prevalence of 100%.

Richness indices and alpha diversity analyses confirmed the highest diversity of bacteria compared to archaea in the Ivorian forest soil ecosystem with a Shannon index of 6.72 and 2.67 for bacteria and archaea, respectively (Figure 4).

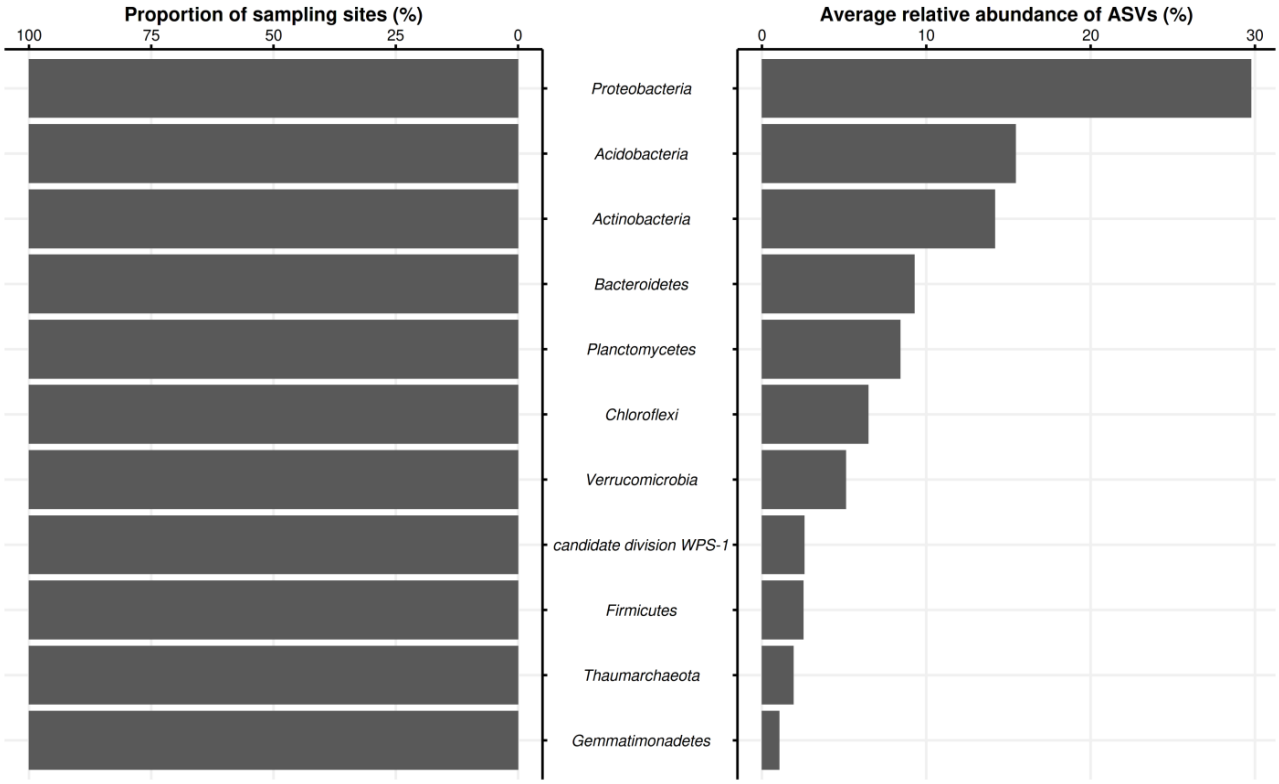

Figure 3. Archaeal and bacterial major taxa across the forest ecosystem.

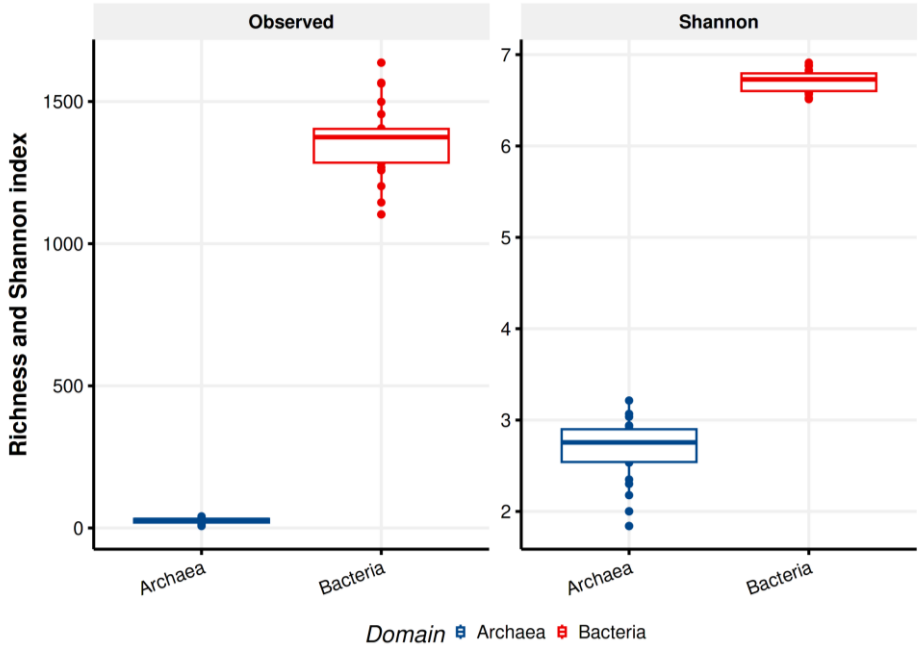

Figure 4. Comparison of indices of richness (observed) and alpha diversity (Shannon) between archaea and bacteria. Upper and lower whiskers of the boxplots extend from the hinge to the largest or smallest value at the most 1.5× interquartile range.

When examining the alpha diversity differences between archaea and bacteria, no consistent patterns emerged across land uses. However, variations were observed between bioclimates. Specifically, the mean bacterial Shannon index was 6.73 in sub-humid areas and 6.70 in humid areas. In comparison, the mean archaeal Shannon index across bioclimates was 2.81 in sub-humid areas and 2.48 in humid areas. The Kruskal–Wallis test,

comparing archaeal and bacterial abundance between bioclimates, revealed that archaeal communities exhibited differential abundance between bioclimates based on their richness and Shannon index (FDR-corrected $p < 0.05$). Further confirmation was provided with pairwise comparisons using the Wilcoxon test, indicating that the archaeal abundance and Shannon index were lower (FDR-corrected $p > 0.05$) in humid bioclimates compared to sub-humid bioclimates (Figure S3).

3.3. Bradyrhizobium and Nitrososphaera Dominate the Core Bacteriobiome and Archaeome in Forest Soil Ecosystems of Côte d'Ivoire

By selecting the 1% most abundant ASVs across all samples, the relative abundance of the core microbiome ranged from 0.12% to 1.17%.

The core microbiome consisted of eighteen ASVs representing thirteen different bacterial genera (core bacteriobiome) dominated by the nitrogen-fixing bacterium genus *Bradyrhizobium* (3 ASVs), the genus *Rhodoplanes* (3 ASVs), and the genus *Bacillus* (2 ASVs). The core archaeome consists of the ammonia-oxidizing archaea genus *Nitrososphaera* with one ASV (Table 2).

Table 2. List of core microbiome found in the soil of forestry areas of Côte d'Ivoire. This list contains information on the relative abundance (rounded at two decimals after comma) and taxonomic identity of each taxon. Each ASV is present in 100% of soils.

Taxa	Relative Abundance (%)	Genus	Phylum
ASV_1	1.17	*Bradyrhizobium*	Proteobacteria
ASV_2	0.94	*Spartobacteria*	Verrucomicrobia
ASV_4 [1]	0.53	*Nitrososphaera*	Thaumarchaeota
ASV_5	0.51	*Rhodoplanes*	Proteobacteria
ASV_9	0.40	*Bradyrhizobium*	Proteobacteria
ASV_10	0.40	*Gaiella*	Actinobacteria
ASV_15	0.34	*Tepidimonas*	Proteobacteria
ASV_17	0.34	*Bacillus*	Firmicutes
ASV_22	0.32	*Terrimonas*	Bacteroidetes
ASV_32	0.25	*Burkholderia*	Proteobacteria
ASV_33	0.25	*Gp6*	Acidobacteria
ASV_34	0.25	*Sphingomonas*	Proteobacteria
ASV_36	0.23	*Rhodoplanes*	Proteobacteria
ASV_37	0.23	*Sphaerobacter*	Chloroflexi
ASV_41	0.21	*Bradyrhizobium*	Proteobacteria
ASV_44	0.21	*Rhodoplanes*	Proteobacteria
ASV_46	0.21	*Mycobacterium*	Actinobacteria
ASV_53	0.20	*Flavobacterium*	Bacteroidetes
ASV_105	0.12	*Bacillus*	Firmicutes

[1] In bold: only this single ASV out of the eighteen ASVs forming the Ivorian forest soil core microbiome belongs to the core archaeome.

3.4. Archaeal and Bacterial Communities in Soils Forest Ecosystems Are Shaped by Bioclimates

In terms of relative abundance per sampling site of the core microbiome, the analysis showed the dominance of *Bradyrhizobium*, *Rhodoplanes*, and *Spartobacteria* (bacteria), as well as *Nitrososphaera* (archaea) (Figure 5). However, while the three bacterial genera co-dominate in the humid bioclimate, they are joined by the *Nitrososphaera* genus in the sub-humid bioclimate. Indeed, *Nitrososphaera* is very poorly present in soils collected in the humid area, except for the soil of Duekoué. Thus, the presence of the archaeal genus *Nitrososphaera* could be seen as a signature associated with the sub-humid climatic area in the forest zone of Côte d'Ivoire.

In addition, when analyzing the transformed abundance correlation using the centered log ratio, an inverse correlation was observed between *Bradyrhizobium* and *Nitrososphaera*. Spearman's rank correlation applied to the transformed abundance values indicated a value of -0.73.

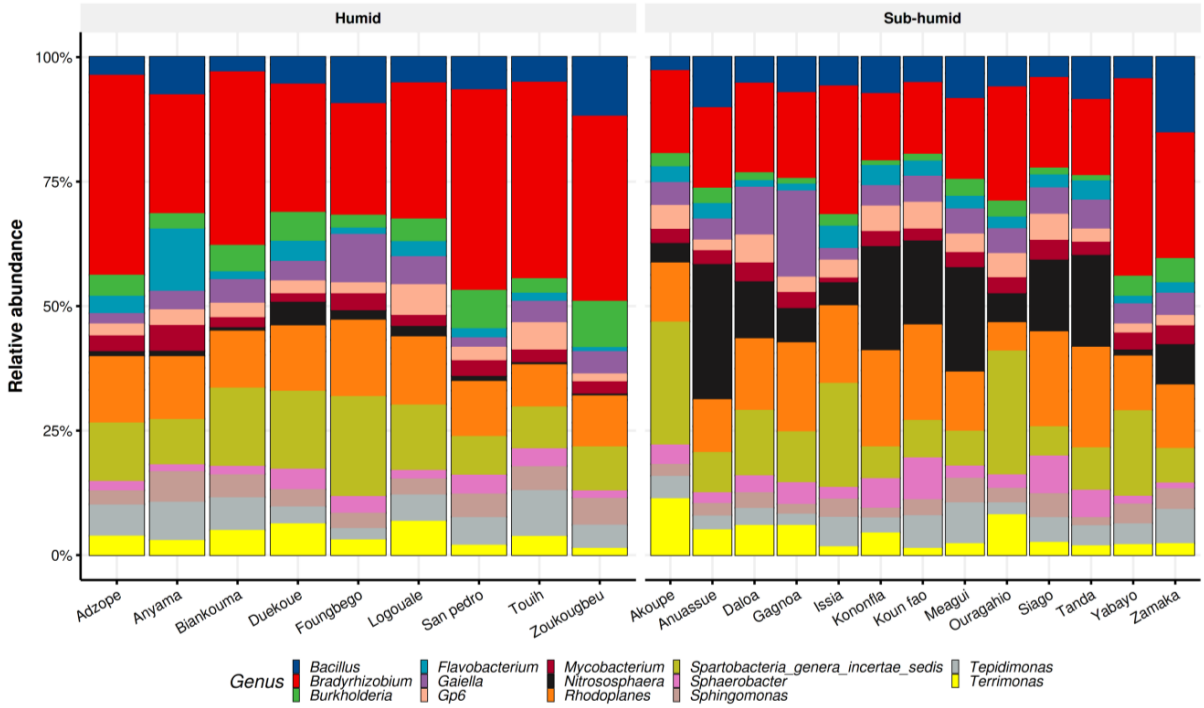

Figure 5. The relative abundance of the core microbiome across geographical sampling sites in the forestry area of Côte d'Ivoire.

Moreover, the two bioclimates shared 30.16% ASVs, while the humid area specifically had 34.83% ASVs and the sub-humid area had specifically 34.99% ASVs. The shared ASVs primarily belonged to the Proteobacteria phylum.

The Bray–Curtis dissimilarity index between bioclimates was statistically significant (FDR-corrected $p < 0.01$) and relatively significant differences in bacterial and archaeal community composition were found. However, no significant beta diversity was observed between land use (FDR, $p > 0.05$) and between bioclimates separated into cropland and forest land (FDR, $p > 0.05$) (Figures S3 and 6).

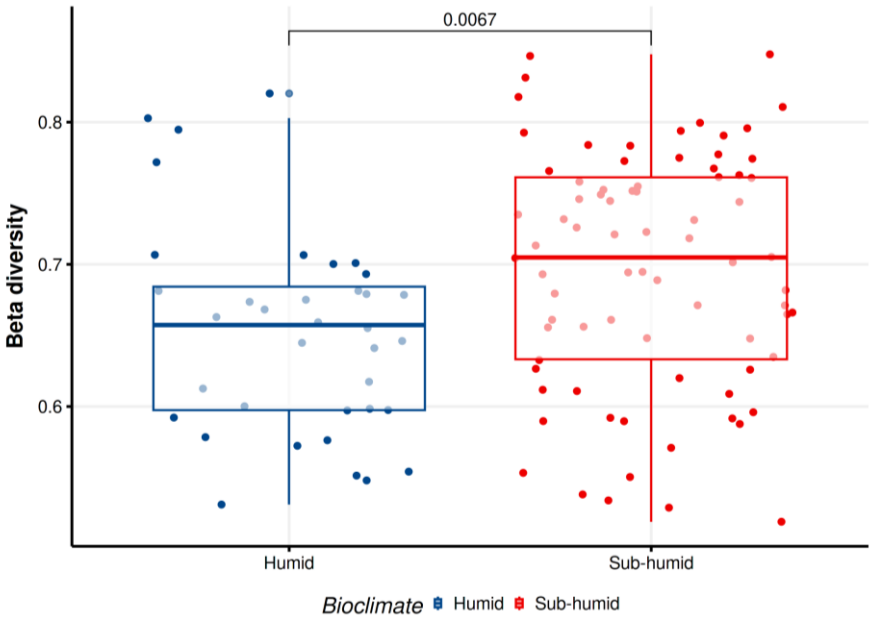

Figure 6. Beta diversity per bioclimate comparison with multiple pairwise comparisons.

3.5. Total Nitrogen, Soil Organic Carbon, and Magnesium Are the Main Drivers of Microbial Community Diversity

The range of total explained variance in major phyla diversity varied from 40.04% (Firmicutes) to 77.25% (Thaumarchaeota) (Figure 7, Supplementary Table S2). The total variance consisted of three sets of explanatory factors: soil properties, climate properties, and land management. Across all considered phyla, the influence impact of soil properties outweighed that of land management and climate properties. Specifically, soil properties emerged as the main driver in the selection process, explaining 40.04% to 64.28% of the total variance, whereas land management accounted for 0% to 21.79% of the total variance.

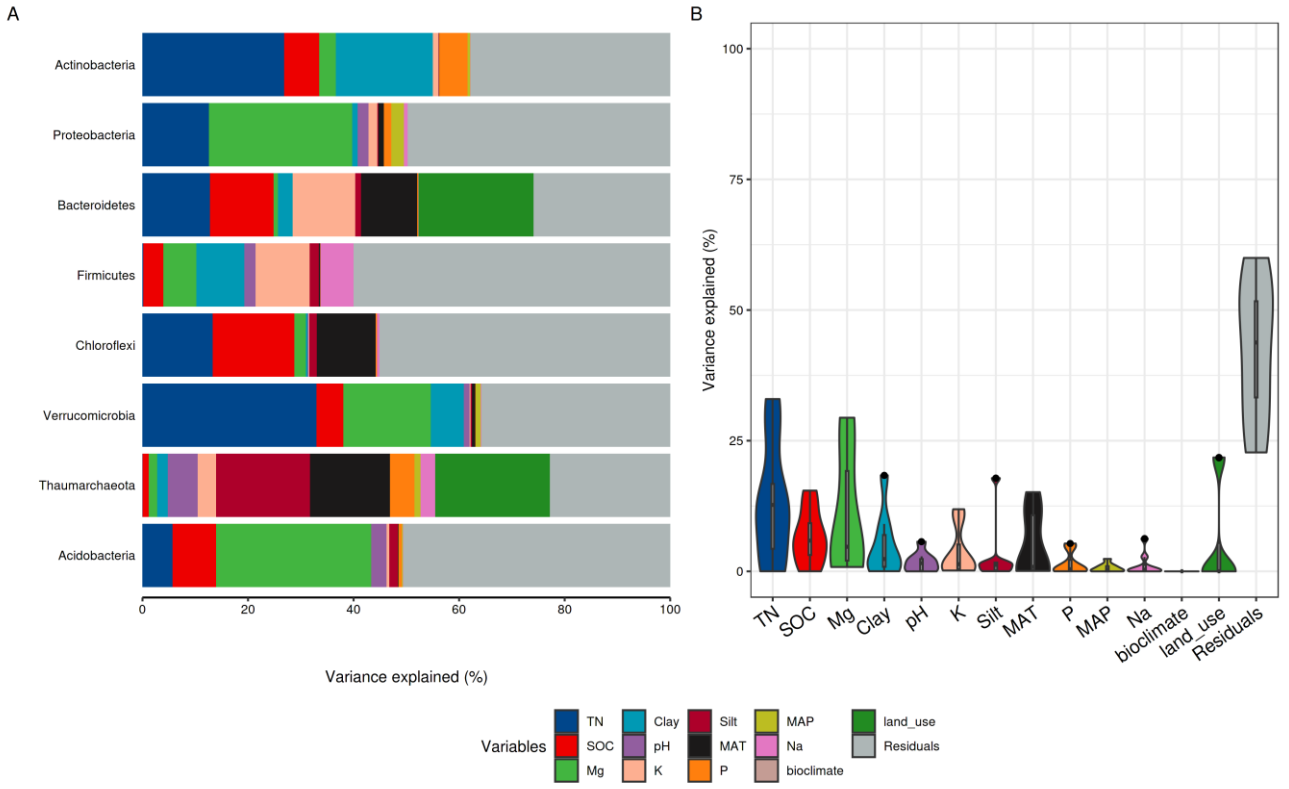

Figure 7. Variance partitioning of major microbial phyla across forest soil ecosystem. (**A**) Total variance for each phylum is partitioned into the fraction due to environmental properties. (**B**) Violin and box plot of percent variation in phylum diversity explained by each variable.

When examining the impact of each environmental parameter, it was observed that the distribution of each major phylum was influenced by three to six parameters. Based on their cumulative influence on major phyla, the drivers can be ranked as follows: total nitrogen (TN) > soil organic carbon (SOC) > magnesium (Mg) > clay > pH > potassium (K). Thus, total nitrogen appeared as the main driver, explaining the diversity variation in six out of eight phyla, closely followed by SOC and Mg. However, land management was also a strong explainer of the diversity variation of Bacteroidetes (21.79%) and Thaumarchaeota (21.72%).

At the genus level, considering the core microbiome, the total explained variance in taxa diversity ranged from 25.56% to 94.6% (Figure S4) and the major drivers were ranked as follows: SOC > MAT > Mg > clay > TN > pH. Thus, the soil organic carbon was the main driver for *Gp6* (34.28%), *Flavobacterium* (33.78%), and *Terrimonas* (25.22%), while mean annual temperature drove *Burkholderia* (15.96%), *Bacillus* (11.16%), and *Bradyrhizobium* (10.06%) diversity. The remaining genera were influenced by a multifactorial effect of the different variables included in the analysis.

4. Discussion

In this study, we used the sequencing of the V4-V5 16S rRNA gene hypervariable region of soil DNA collected in 22 localities to analyze the diversity and structure of the archaeal and bacterial communities present in the forest soil ecosystems in Côte d'Ivoire. Indeed, this region of the 16S rRNA gene is recognized as a discriminant region for the joint study of bacteria and archaea microbial communities although it can influence the internal diversity of certain bacterial taxonomic groups [52]. Our analysis revealed a significant difference in microbial diversity between bacteria and archaea as well as their main drivers in the soils.

4.1. Environmental Conditions in Forest Soil Ecosystems

The analyzed soils exhibited distinct conditions with respect to bioclimates and land uses. Notably, several physicochemical parameters such as pH, soil organic carbon, total nitrogen, sodium, potassium, phosphorus, and magnesium displayed variations regarding both bioclimate (humid vs. sub-humid) and land use settings. This finding is congruent with numerous studies on forest soil ecosystems, which consistently demonstrate the impact of bioclimates [53] and land uses [54] on the creation of distinct environmental conditions. The influence of bioclimate and land use on soil physicochemical properties is due to various complex factors, including biogeochemical cycles, microbial and macrofauna taxa, as well as interactions with plants [55–57].

4.2. Distribution of Bacterial and Archaeal Taxa

Concerning the prevalence of detected phyla in forest soil ecosystems in Côte d'Ivoire, the most widespread phyla (Proteobacteria and Actinobacteria for bacteria, and Thaumarchaeota for archaea) were generally the most abundant, being consistent with previous findings [11,58]. Examining the bacterial community at the genus level revealed several dominant taxa, including *Rhodoplanes*, *Spartobacteria*, *Gaiella*, and *Bradyrhizobium*, all of which have been consistently identified as significant components of soil microbial communities in previous studies [9,29], including in Côte d'Ivoire [26]. Similarly, *Nitrososphaera* emerged as the predominant genus within the archaeal community, a finding which is in line with other reports [59,60].

Two hypotheses could explain these observations: (i) the easy detection of these taxa with the current high-throughput amplicon sequencing procedure, as suggested by previous studies [52,61], or (ii) a potential correlation between microorganisms with larger population sizes and greater dispersal capabilities. These phyla, with a relative abundance higher than 1%, have been identified as dominant in several environments, including in temperate zone soils [9], marine sediments and oceans [62], and mammalian gut microbiota [63]. The observed dominance might also be related to the sampling strategy, which, by collecting soils at 0 to 15 cm depth, selectively favored cosmopolitan microorganisms capable of colonizing multiple soil horizons and adapting to diverse environmental conditions. For instance, Actinobacteria and Firmicutes thrive in hostile environments by forming resistant physiological stages, making them generalists for habitat and substrate [64,65]. In contrast, less abundant taxa appear associated with more restricted ecological niches, potentially limiting their ability to colonize or adapt to new environments [66].

The predominant bacterial composition across various studies consistently highlights the prevalence of Acidobacteria, Actinobacteria, Proteobacteria, and Bacteroidetes within microbial communities, showcasing a stable pattern across different biomes. For instance, a study by Onyango et al. [67] in Kenya's forest soil ecosystem revealed the dominance of Proteobacteria and Acidobacteria. A similar trend was observed in the bacteriobiome of Côte d'Ivoire, where Proteobacteria and Actinobacteria stood out as the most abundant phyla [26]. In the Songshan Forest Reserve area of China, Liu et al. [68] reported that Proteobacteria, Acidobacteria, Actinobacteria, and Verrucomicrobia collectively constituted over 70% of the soil bacterial sequences. This consistent observation suggests that Pro-

teobacteria, Acidobacteria, and Verrucomicrobia may play pivotal roles in responding to variations in plant population richness.

Turning to archaeal communities, our study aligns with others by emphasizing the dominance of the Thaumarchaeota phylum. This finding echoes similar trends documented in various studies. Truu et al. [23], for instance, reported the prevalence of Thaumarchaeota over Euryarchaeota and Nanoarchaeota in the forest soils of Järvselja in Estonia. However, it is noteworthy that contrasting results exist; Onyango et al. [67] found that the forest soil archaeal community was primarily dominated by the Crenarchaeota phylum. These variations underscore the complexity of archaeal community structures in different environments.

Furthermore, it is crucial to delve into the notion of the core microbiome, a term denoting microorganisms consistently present in a specific ecological niche, playing a pivotal role in host health and wellbeing [69]. In the context of forest soil ecosystems, the core microbiome holds particular importance. It represents a cohort of microorganisms widely distributed across diverse locations, contributing significantly to the overall stability, and functioning of soil microbiomes, including their role in reforestation endeavors [27] and other essential functions [70]. This study sheds light on the prevalent dominance of *Bradyrhizobium* in the core bacteriobiome, aligning with numerous studies highlighting its cosmopolitan nature [71,72]. Concurrently, the core archaeome was characterized by the dominance of *Nitrosophaera*, echoing similar trends observed elsewhere [73,74]. Both dominant genera play roles in the nitrogen cycle, albeit at different levels. *Bradyrhizobium* includes species forming symbiosis with plants, facilitating nitrogen fixation, although the identified genera in this study may contain non-symbiotic ecotypes [75], thus contributing to the fixation level. On the other hand, *Nitrososphaera* is involved in ammonia oxidation [76].

4.3. Which Drivers for Which Phyla and/or Genus?

Microbial community variations in terms of diversity and abundance in the studied soils were primarily influenced by physicochemical factors, which is consistent with previous findings that highlighted the substantial impact of soil chemistry on microbial abundance [9]. Among the physicochemical parameters, soil organic carbon emerged as the main driver of major phyla diversity, a finding supported by multiple studies [77,78].

While soil pH is commonly cited as a significant contributor to phyla diversity, this study emphasized the more influential role of soil organic carbon on phyla diversity and total nitrogen on core taxa diversity, as reported elsewhere [79]. However, concerning core taxa, pH emerged as the main driver of *Bradyrhizobium* diversity, which is consistent with earlier reports in the soil of Côte d'Ivoire [26].

The ecological niches occupied by both bacteria and archaea are shaped also by agricultural land use in our sampled areas. This outcome is likely associated with the observed land use conversion from forest soils to agricultural soil in Côte d'Ivoire [1] and is consistent with similar studies on the influence of land use changes on microbial structure in Amazonian tropical forest soils [80]. Land use practices, characterized by various amendments and fertilization techniques, reshape common microbial communities, leading to alterations in soil physicochemical properties such as soil organic carbon, total nitrogen, and pH [78,81].

A noteworthy discovery is the reciprocal relationship between the prevalence of *Nitrososphaera* and *Bradyrhizobium*, mirroring findings in agricultural versus non-agricultural soils, as documented by Zhalnina et al. [82]. This implies a conversion of the sub-humid forest areas in Côte d'Ivoire into agricultural lands. The observed distinction is likely rooted in biochemical processes, specifically the inhibition of nitrogen fixation and nitrogenase's coding gene expression by elevated nitrogen levels [83,84]. In regions where a nitrogen fertilizer is applied, the abundance of nitrogen-fixing bacteria like *Bradyrhizobium* may be suppressed due to sufficient nitrogen levels. These outcomes align with recent research that highlighted a decline in forested areas and a corresponding shift towards agricultural land

use [1,85,86]. Furthermore, the substantial difference in *Nitrososphaera* abundance between sub-humid and humid areas implies that *Nitrososphaera* is a potential microbial signature of the former region.

5. Conclusions

In the threatened forest environment of Côte d'Ivoire, it becomes urgent to explore the patterns of microbial biodiversity owing to their role in the overall ecosystem functioning and putative contribution to reforestation. This study deciphered the structure of the archaeal and bacterial diversity in forestland and cropland (degraded forest) soils and revealed the dominancy of bacterial community, with Proteobacteria, Acidobacteria, and Actinobacteria as major taxa. While the results obtained at the phylum level were consistently congruent with previous studies, some patterns that can be correlated to bioclimatic and land uses were found at the genus level. Indeed, while the bacterial core microbiome members that consist of *Bradyrhizobium*, *Rhodoplanes*, and *Bacillus* were detected in all soils, the ammonia-oxidizing archaea genus *Nitrososphaera* was generally absent in soils collected in humid climatic area and showed an inverse correlation with an abundance of the N-fixing bacteria genera (e.g., *Bradyrhizobium*) in soils of the sub-humid areas. This latest result suggests that the presence of the archaeal genus *Nitrososphaera* is a signature mark associated with the sub-humid climatic area in Côte d'Ivoire and may help to further study the core bacteriobiome and archaeome in Côte d'Ivoire forests and their relationship with nitrogen cycling in forest landscapes. The overall data could be valuable in the development of effective strategies for forest management in Côte d'Ivoire.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15030396/s1, Figure S1: Covering area of each sampling site and its corresponding features (not to scale); Figure S2: Principal component analysis of the environmental data. Sampled sites are colored according to bioclimates; Figure S3: Beta diversity per soil type with multiple pairwise comparisons; Figure S4: Variance partitioning of core genus across forest soil ecosystem; Table S1: Average ASV abundance and occurrence per phylum; Table S2: Total variation of microbial phylum explained by physicochemical properties and climatic variables.

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Data Availability Statement: The sequence data generated are publicly available in the NCBI SRA database under the accession numbers SRR13623327 (CI02), SRR13623316 (CI03), SRR13623305 (CI04), SRR13623339 (CI05), SRR13623333 (CI06), SRR13623332 (CI07), SRR13623331 (CI08), SRR13623312 (CI24), SRR13623311 (CI25), SRR13623310 (CI26), SRR13623309 (CI27), SRR13623308 (CI28), SRR13623307 (CI29), SRR13623306 (CI30), SRR13623304 (CI31), SRR13623303 (CI32), SRR13623298 (CI37), SRR13623297 (CI38), SRR13623341 (CI39), SRR13623340 (CI40), and SRR13623338 (CI41). The datasets and code generated during this study are available in the Zenodo repository (https://zenodo.org/record/8024933, accessed on 20 December 2023).

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