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Implications of topography and agronomic practices for soil biogeochemical and microbiological properties in Upper Eastern Ghana hilly farmland

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Summary

While topography can infer erosion potential, implementation of convention practices can trigger accelerated erosion, and both pose major threats to soil abiotic properties and microbiota. The majority of farmlands in the Upper-Eastern of Ghana (UE) are undulating, moderately hilly, comprised of soils with low organic matter and light texture which make them highly susceptible to erosion and accelerated erosion. Considering the importance of erosion and its repercussions on soil C cycle, fertility, and health, this study was conducted to trace the erosion and unravel its consequences for soil biogeochemical. The current study also aims at attaining deeper insights into the effects of topography and various agronomic practices, comparatively and interactively, on the soil microbial community and their plant growth-promoting potentials. Accrual of clay particles, the higher mass of C (MWC%) and N (MWN%), NH_4^+-N, NO_3^--N, and other eroded cations in footslope soils served as evidence of ongoing erosion/deposition processes in the field. Erosion homogenized ^{13}C values along the slope while accelerating N cycling at the footslope positions. The regular occurrence of anoxic conditions in frequently waterlogged footslope soils led to a higher relative abundance of anaerobic bacteria compared to upslope. A higher relative abundance of denitrifiers suggested the presence of an open N cycle within the footslope sediments. Evidently, geomorphic features imposed profound shifts in soil ^{15}N natural abundance, as well as in soil edaphic, and pedoclimatic properties. This in turn fueled spatial heterogeneity in the soil prokaryotic community diversity and composition, as well as in the plant growth-promoting potential of the sorghum rhizobiome. Besides, implications of various agronomic practices (conventional vs. reduced tillage, crop rotation with cover crop cultivation and residue return vs. no cover crop and no residue return, and soil amended with 0, 40, and 80 kg ha^{-1} nitrogen) for soil edaphic properties and microbiota appeared to be modulated by the prepotent impact of topography. Albeit the interactive impact of slope × tillage changed soil physiochemical characteristics and soil ^{13}C values, the given interactive effect was less effective in altering prokaryotic community diversity and assemblages. The potent effect of topography, heterogeneous cropping regimes prior to initiating our experiment, the homogenizing nature of the agricultural practices, and inherited spatial heterogeneity at the study site can explain the diluted implications of agronomic practices for the soil microbiota. Among the soil edaphic properties, pH, clay content, MWC%, volumetric water content, temperature, cation exchange capacity (CEC), and NO_3^--N were identified as the influential factors for structuring soil microbiota, while Fe, Al, CEC, pH, N_{min}, and temperature appeared to be effective on the metabolic potential of the sorghum rhizobiome. Among the plant growth-

promoting potentials of sorghum rhizobacteria, indole production was strongly contingent upon nutrient availability within the rhizosphere and thus improved at the footslope position. However, the phosphate solubilizing potential of rhizobiome gained prominence at the eroding up-slope positions. Noticeably, the prokaryotic biogeographical pattern, community composition, and themetabolic potentials of the sorghum rhizobiome were all primarily shaped by environmental filtering as the underlying factor.

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Zusammenfassung

Die Topographie einer Landschaft ist verknüpft mit dem Erosionspotenzial des Bodens, welches sich durch konventionelle agronomische Praktiken erhöhen kann, mit negativen Auswirkungen auf die abiotischen Eigenschaften des Bodens und dessen Mikrobiota. Die meisten Ackerflächen in der Upper East Region von Ghana (UE) sind hügelig, enthalten wenig organische Bodensubstanz und sind von leichter Textur und daher sehr anfällig für Erosion. Angesichts der Bedeutung der Erosion und ihrer Auswirkungen für die Region wurde diese Studie durchgeführt, um Erosionsprozesse nachzuweisen und Auswirkungen auf die biogeochemischen und mikrobiologischen Eigenschaften des Bodens zu erkennen. Diese Studie zielt somit darauf ab, die Auswirkungen von Topographie und agronomischen Praktiken auf die Bodenmikrobiota und die physiologischen Eigenschaften des lokal adaptierten Hirse-Rhizobioms, insbesondere das pflanzenwachstumsfördernde Potenzial, vergleichend und interaktiv zu beurteilen. Die Ansammlung von Tonpartikeln zusammen mit einer höheren mittleren Masse von C (MWC%) und N (MWN%), NH_4^+-N, NO_3^--N und anderen erodierten Kationen an den Ablagerungsstellen ist Beweis für eine anhaltende Erosionsprozesse, die eine höhere ^{15}N-Fraktionierung hangabwärts förderten. Gleichzeitig homogenisierte die Erosion die ^{13}C-Werte im Boden-C-Pool entlang des Hangs. Das regelmäßige Auftreten von anoxischen Bedingungen in schlechter entwässerten Böden in den unteren Hanglagen führte zu einer höheren relativen Häufigkeit anaerober Bakterien als in den oberen Hanglangen. Ferner indizierte eine höhere relative Abundanz von Nitrifizierern und Denitrifizierern das Vorhandensein eines offenen N-Kreislaufs in den unteren Hanglagen. Geomorphe Merkmale führten somit zu tiefgreifenden Verschiebungen der natürlichen ^{13}C- und ^{15}N-Abundanz sowie von edaphischen und pedoklimatischen Eigenschaften des Bodens. Das wiederum förderte die räumliche Heterogenität der Diversität und Zusammensetzung der Gemeinschaft der Prokaryoten im Boden ebenso wie das metabolische Potential des Hirse-Rhizobioms. Die Auswirkungen verschiedener agronomischer Praktiken (konventionelle vs. reduzierte Bodenbearbeitung, Fruchtfolge mit Zwischenfruchtanbau und Einarbeitung von Pflanzenrückständen vs. Fruchtfolge ohne Zwischenfrucht sowie Entfernung von Pflanzenrückständen, Stickstoffdüngung mit 0, 40, and 80 kg ha^{-1}) auf die physikochemischen Eigenschaften des Bodens und die Mikrobiota schien durch den dominanten Einfluss der Topographie moduliert zu werden. Obwohl der interaktive Einfluss von Hangneigung × Bodenbearbeitung die physikalisch-chemischen Eigenschaften des Bodens und die ^{13}C-Werte des Bodens veränderte, war der gegebene interaktive Effekt weniger effektiv hinsichtlich der

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Verschiebung von Diversität und Zusammensetzung der prokaryotischen Gemeinschaft im Boden. Die kurzzeitige Anwendung neuer agronomischer Managementpraktiken, die homogenisierende Natur dieser Praktiken und die gegebene räumliche Heterogenität am Standort könnten die geringen Auswirkungen agronomischer Praktiken auf die Bodenmikrobiota erklären. Als relevante physikalisch-chemische Eigenschaften des Bodens für die Bodenmikrobiota wurden pH-Wert, Tongehalt, MWC%, volumetrischer Wassergehalt, Temperatur, Kationenaustauschkapazität (CEC) und, NO_3^--N identifiziert, während Fe, Al, CEC, pH, Nmin und Temperatur identifiziert wurden als Faktoren, die das metabolische Potential des Hirse-Rhizobioms beeinflussten. Unter den pflanzenwachstumsfördernden Merkmalen war die Indolproduktion der Rhizobakterien der Hirse stark von der Nährstoffverfügbarkeit im Boden abhängig und verbesserte sich somit in den unteren Hanglagen. Phosphatlösende Aktivitäten hingegen gewannen an den erodierten oberen Hanglagen an Bedeutung. Ich erkannte, dass biogeografische Muster, die Zusammensetzung der Gemeinschaft der Bodenbakterien und das metabolische Potential des Rhizobioms von reifer Hirse hauptsächlich durch zugrunde liegende physiochemische Heterogenitäten des Bodens bestimmt wurden.

List of abbreviations

ADONIS	Analysis of variance using distance matrices
AMR	Ammonification rate
ANOSIM	Analysis of similarity
ANOVA	Analysis of variance
BEA	Bile-esculin agar
BLAST	Basic local alignment search tool
CAS	Chrome Azurol S medium
Cfu/ml	Colony forming units per ml
CT	Conventional tillage
GLM	Generalized linear model
GPS	Global positioning system
IAA	Indole acetic acid
ICP-OES	Plasma-optical emission spectrometry instrument
ISRIC	International soil reference and information centre
LB	Luria Bertani medium
LSD	Least significant difference
MANOVA	Multivariate analysis of variance
N0	No nitrogen
NJ	Neighbor-joining cluster
NMDS	Non-metric multidimensional scaling
NPK	Nitrogen, phosphorus, potassium
OF	Oxidation-fermentation
OTU	Operational taxonomic unit
PCA	principal component analyses
PCNM	Principal coordinates of neighbor matrices
PCoA	principal coordinate analyses
PCR	Polymerase chain reaction
PerManova	Permutational multivariate analysis of variance
PGP	Plant Growth-Promoting trait
PGPB	Plant growth promoting bacteria
PGPR	Plant growth promoting rhizobacteria
PSB	Phosphate solubilizing bacteria
QIIME	Quantitative Insights Into Microbial Ecology
RDA	Redundancy analysis
Re+CP	Residue retained, combined with cowpea as a cover crop
-Re-CP	No residues retained and no cowpea as a cover crop
RT	Reduced tillage
SL	Strigolactone
SOM	Soil organic matter
SOC	Soil organic carbon
SSA	Sub-Saharan Africa
STAMP	Statistical analysis of metagenomic profiles

List of abbreviations

TSA	Trypticase Soy Agar
TSI	Triple sugar iron agar
UE	Upper Eastern Ghana
UTM	Universal Transverse Mercator
WASCAL	West African Science Service Center on Climate Change and Adapted Land Use

1. General Introduction

1.1. Climate and farming in Upper Eastern Ghana

Agriculture remains the foundation of most Sub-Saharan African economies and the population's livelihoods. However, Sub-Saharan is the only region where agricultural growth is lower than the growth of the region population (Muzari, 2016; Shimeles et al., 2018). High temperatures, erratic rainfall (starts in May and ends in September), eroded light texture soils with low buffering capacity, low cation exchange capacity, and low fertility together with limited ability to invest in new technologies are among the major constraints for growing agriculture in this region (Bationo et al., 2007; Danso et al., 2018; Kumasi et al., 2019). Despite the fact that the vast majority of people's livelihoods in the Upper-East regions of Ghana (UE) are contingent upon agriculture, farming in these regions is typically associated with extremely challenging conditions for the farmers. One of the main drawbacks is the topography of the lands. The topography of UE is extremely rugged, dominated by relatively undulating lowlands and some upland slopes with gentle slopes ranging from one to five percent gradient. Due to these specifications, erosion is considered a main challenge in these regions and the main factor leading to soil destruction, degradation and precipitates food insecurity (Folly 1997; Bongo District, 2015; Danso et al., 2018).

Usually, the standard climatic year in UE can be divided into the dry season from November to April/May, with non to only marginal rainfall, and the wet season characterized by erratic rainfalls from June to October (Laube et al., 2012; Danso et al., 2018). Following a long dry spell, characterized by harmattan winds from November to mid-February, for usually six to seven months no rainfed farming is possible. As it has been reported there is a high risk of severe drought in UE on average once in every five years (Dickson and Benneh 1988).

In most parts of the UE, levels of precipitation vary from 1,000 up to 1,300 m per annum in some parts even less with the mean annual temperature of 37.5 °C. (Laube et al., 2012; Danso et al., 2018). The high range of temperature in UE is a coincidence with high precipitation (wet/rainy season). Average precipitation between 0.2-0.9 mm during October, which is concomitant to harvesting yields in the UE, has been reported (Danso et al., 2018). The chosen study site was located near the village Aniabisi (Vea watershed) (10°50′N, 0°54′W), which is in the Bongo district of the UE, containing degraded and poor structured soils of Vea watershed which are predominantly plinthosols and luvisols (Danso et al., 2018).

1.2. Soil C and N biogeochemical cycles

Soils deliver fundamental ecosystem services through biogeochemical processes that rely on soil microbiota to provide regulating, provisioning, and promoting given services, such as soil biodiversity maintenance (genetic diversity, functional diversity, and abundance and dynamics of organisms) (Smith et al., 2015; Dontsova et al., 2020). In fact, microbial communities drive biogeochemical cycles, and biogeochemical processes are eventually preserving microorganisms' functionalities (Ma et al., 2020). This stands to reason that, any shifts in microbial load, activity, and community structure may affect nutrient flows in soil (Schmidt et al. 2011; Markussen et al. 2018; Kuzyakov et al., 2019; Ma et al., 2020).

It is widely recognized that soil carbon (C) cycling is constrained by nitrogen (N) availability, which makes C and N cycles the well-coupled biogeochemical cycles (Hartman et al., 2017). Therefore, to depict a clear picture of these coupled biogeochemical cycles simultaneous study of C and N cycles is advocated. C cycle starts with photosynthesis and converting the inorganic C from the atmosphere into organic C, which later either returns to the atmosphere through plants' respiration or will be stored through plants biomass in the lithosphere. Free-living autotrophic microbes contribute to both forms of C flux and sequestration. On the other side, heterotrophic microorganisms together with soil fauna can act as decomposers and mineralize the majority of stored C in plants' biomass (Horwath, 2007). Similar to C, N is also one of the major nutrients for all living organisms and is generally of limiting availability to plants, resulting in tight competition between microorganisms and plants (Vitousek and Howarth, 1991). The main biogeochemical cycle of N consists of four processes N fixation, ammonification, nitrification, and denitrification processes. The most vital process which regulates N cycling is the redox potential, as certain processes occur aerobically while others are occurring anaerobically (Rosswall, 1982). Net N mineralization will be triggered by the surplus of N, which exceeds microbial demand, either by high N inputs or as a result of limited microbial production, constrained by low C and nutrients availability (Phillips et al., 2012; Winsome et al., 2017).

1.3. Natural erosion and human-induced erosion implications for biogeochemical properties of the soil

Wind and water are the major drivers of natural erosion in the land surface of the Earth. The land surface is dominated by sloping landscapes (Staub and Rosenzweig, 1992), erosion laterally translocates every year the sloping landscapes topsoil on the order of 75 Gt. (Berhe et

al. 2007). Therefore, erosion governs the biogeochemical cycling of elements in the Earth system (Berhe et al. 2018; Guerra et al., 2020). Soil erosion, which is known as the major contributor to the degradation of the global soil resource (Bridges & Oldeman, 1999) poses a huge threat to food security in certain parts of the world especially Africa (Lal, 1995; Scherr, 1999). The coupled biogeochemical cycles of C and N are widely known to be influenced by soil erosion as it affects their fluxes in and out of the soil system. Therefore, their sequestration and distribution within the soil matrix and eventually ecosystem are also affected by the erosion process (Berhe et al., 2018). Key research in the past seven decades has highlighted the specific role of topography and associated processes of soil erosion in the biogeochemical cycling of C (Harden et al., 1999; McCarty and Ritchie, 2002; Berhe et al., 2007; Van Oost et al., 2007; Quinton et al., 2010) and N (Hilton et al., 2013; Houlton and Morford 2015; Weintraub et al., 2015; Berhe and Torn 2017). However, there is a knowledge gap in understanding the combination of erosion and accelerated erosion in shifting agroecosystems' biogeochemical cycling. As exemplified in previous literature, soil erosion/deposition processes affected both eroding and depositional sites through declining SOC content of the perturbed soils while accumulating SOC within the sink area (Schaub and Alewell 2009). The deposition of eroded soils at depositional settings has recently been indicated as a sink of atmospheric CO_2 (Berhe et al., 2007; Galy et al., 2007; Van Oost et al., 2012).

The biogeochemical implications of soil erosion are varied due to multifarious factors such as the travel distance of topsoil, the dissolved soil components, whether erosion is a continuous or episodic process for a given ecosystem, the degree of disturbance experienced by the soils, if sediment accesses a water channel, and so forth (Stallard 1998). Land-use change and agricultural activities are among the major anthropogenic drivers of erosion which are known as the accelerated erosion. In the absence of anthropogenic disturbances such as tillage practice, mass transport is highly episodic around the globe (Carroll et al., 2007) with less severe erosion impacts rather than continuous accelerated erosion induced by anthropogenic activities such as conventional agricultural practices (Borrelli et al., 2017). The rate of soil erosion in an agricultural field that is intensively cultivated is estimated to be an order of magnitude higher than natural rates of erosion (Nearing et al., 2017). Rates of agronomic-induced erosion are influenced by varying site traits and can range from an average of 0.13 ± 0.02 mm yr^{-1} for conservational agriculture to 3.94 ± 0.321 mm yr^{-1} for conventional agriculture (Montgomery 2007, 2012). Thus, the nature and extent of management-induced outcomes are contingent upon the intensity of agronomic perturbation in comparison to pre or intensive agriculture practices (Mann 1986). These manifested differences can be addressed, applying ^{13}C and ^{15}N

soil natural abundance techniques to figure out the extent of shifts in biogeochemical properties of the soil under natural erosion, conservational vs. conventional practices-induced erosion as well as their combination. The ^{13}C and ^{15}N isotopic abundance in soils is a dynamic function of the isotopic composition, which can be used to assimilate the soil C sequestration and loss in ecosystems and gain insights into soil C and N cycles (Wang et al., 2018). $\delta^{13}C$ of soil carbonates corresponds to paleovegetation, and $\delta^{15}N$ refers to the N cycle and the source of N amendment, which commonly ascribes degrees of isotopic fractionation. The $\delta^{13}C$ content of soil organic matter corresponds closely to the $\delta^{13}C$ content of the plant residuals from which it is derived (Gregorich et al., 1995). Noticeably, processes such as N mineralization, nitrification, denitrification, NH_3 volatilization, N leaching, and plant uptake from the soil discriminate against ^{15}N, which eventually leads to various signatures of $\delta^{15}N$ in the soil N pools (Robinson, 2001). Application of stable isotope techniques can reveal the dominant factors controlling N and C cycles and their impact on erosion in soils as well as the origin of decomposed soil organic matter. Thus, can be applied to advocate the appropriate management regimes for sequestering SOM by foreseeing potent SOM turnover under erosion and accelerated erosion.

1.4. Soil prokaryotic community affected by erosion and accelerated erosion

Slope position causes spatial heterogeneity in soil physiochemical properties (Sul et al., 2013). Bearing in mind that soil microbial communities are dependent upon soil edaphic properties, so they would change and adapt to any disruption in the soil swiftly (Malard et al., 2019; Neupane et al., 2019; Zhao et al., 2020a). From this, it is inferred that the dynamics of microbial communities are strongly contingent upon erosion and erosion-induced repercussions for soil abiotic properties and substrate availability (Park et al., 2014; Liu et al., 2020). The accumulation of nutrients and organic C in depositional sediments through erosion/deposition processes can boost the soil C and N conversion process within depositional sites, which favors bacterial diversity and heterotrophic respiration (Wood and Silver, 2012; Xia et al., 2016; Liu et al., 2020). Erosion and sediment migration have detrimental implications for soil microbial properties in eroding sites. These detrimental implications have been attributed to soil nutrient reduction (Xiao et al., 2017). Moreover, during the erosion-deposition processes, soil particles, specifically clay inhabited by multifarious microbial species (Xia et al., 2020), are translocated by the overland runoff. This can lead to higher microbial diversity at the deposition site while promotes homogeneity of the bacterial community in eroding site (Huang et al., 2013).

Farmlands are dynamic environments where soil bacterial communities are exposed to various

management practices including N fertilizers, rotation, and tillage practices (Fierer et al., 2012; Bainard et al., 2016; Lupwayi et al., 2017). The nature and extent of management-induced detriments depend upon the trained agronomic scheme and the virgin properties of the soils. Plowing increases soil disturbance and accelerates organic matter oxidation (Horwath, 2007). Agricultural disruption overall impacts microbial communities (Lee et al., 2020). Evidently, there is growing concern about the implications of conventional-high-input agricultural practices on soil productivity and agricultural sustainability (Knowler and Bradshaw, 2007). Unlike conventional management practices, which adversely impact the microbial community structure and diversity (Carbonetto et al., 2014) and deplete their catabolic variety (Degens et al., 2000), conservational management practices including reduced tillage, cultivation of cover crops, and optimizing fertilizer applications have been reported to sustain long-term crop productivity by protecting microbial community diversity (Vanlauwe et al., 2014; Williams et al., 2020).

Maintenance of microbial functionalities is attained by securing soil microbial diversity (Chaparro et al., 2012). Protecting and responsible utilization of land are key factors in preserving soil biodiversity and health (Kibblewhite et al., 2008). Most farmlands in the Upper Eastern of Ghana are moderately hilly and consist of soils with low organic matter and poor structure which makes them highly susceptible to erosion and accelerated erosion. Therefore, probing the effects of agronomic practices in relation to topography on soil edaphic properties and prokaryotic communities are required to achieve a better understanding of appropriate management practices in order to sustain microbial diversity and soil fertility in this region.

1.5. Sorghum rhizobiome plant-growth-promoting potential under erosion and accelerated erosion

Maize and sorghum producers usually plant them in soils that are nutrient deficient, and therefore, plant-growth-promoting rhizobacteria (PGPR) can be relevant to contribute to the enhancement of plant nutrient uptake and biomass production (Aquino et al., 2019). PGPRs improve plant productivity through multifarious pathways including but not limited to enhancing asymbiotic N_2 fixation (Khan, 2005; Aloo et al., 2019), promoting inorganic/organic phosphate solubilization (Hayat, 2010; Aloo et al., 2019), and producing phytohormones like indole-3-acetic acid (Farina et al., 2012; Goswami et al., 2016). The majority of the discovered host-specific rhizospheric PGPR belong to genera such as *Acinetobacter*, *Agrobacterium*, *Arthobacter*, *Azotobacter*, *Azospirillum*, *Burkholderia*, *Bradyrhizobium*, *Enterobacter*, *Rhizobium*, *Frankia*, *Serratia*, *Bacillus*, *Variovorax*, *Thiobacillus*, *Geobacillus*, *Paenibacillus*,

Lysinibacillus, *Microbacterium*, *Ochrobactrum*, and *Pseudomonads* (da Costa et al., 2014; Goswami et al., 2016; Govindasamy et al., 2017; Kumar et al., 2019). The genera *Acinetobacter*, *Bacillus* (Santana et al., 2020), *Enterobacter*, and *Microbacterium* (Gopalakrishnan et al., 2013; Anwar et al., 2016), have been specifically identified in the endo- and rhizosphere of sorghum, and were reported to be endowed with PGP potential.

Exometabolism or rhizodeposition by plant roots and rhizobiome catabolic/anabolic activities, kindle nutrient cycling, and nutrient uptake by plant roots thus can support plant growth (Glick, 2014; Sasse et al., 2018). It's noteworthy to mention that rhizodeposition varies depending upon plant genotype, growth stage, and other surrounding environmental features, which might consequently alter the plant-microbiome-soil interface. This interaction causes a constant dynamic in the rhizosphere (Bulgarelli et al., 2013; Kai et al., 2016; Chaparro et al., 2013 and 2014). Free-living PGPR diversity and composition are strongly affected by soil substrate availability (Kai et al., 2016; Goswami et al., 2016; Sasse et al., 2018; Flores-Núñez et al., 2018), the pedoclimatic soil conditions, abiotic stresses, and soil pH (Paul and Lade, 2014; Goswami et al., 2016). Besides, microbial biomass and activities are contingent upon soil organic matter, which can also alter following soil surface disruptions like erosion and anthropogenic activities (Paul and Lade, 2014; Xiao et al., 2017). Blom et al., (2011a) examined the efficiency of plant-growth-promoting (PGP) bacteria grown on various media in enhancing plant growth and they observed contrasting effects of these bacteria on plant growth. *Pseudomonas* strains grown on protein-rich media were also shown to have a deleterious effect on plant growth caused by HCN production (Blom et al., 2011b). Thus, it is predictable that biotic and abiotic factors that dominate the soil ecosystem alter their activities and functionalities (Chen et al., 2019; Huang et al., 2019). Thus, bacterial phenotypic characteristics, specifically their PGP characteristics, should be scavenged in association with their surrounding environment. While erosion and agricultural practices, as a trigger of accelerated erosion, are expected to affect the soil microbial community composition, the specific responses of various rhizobacteria and their PGP activities to the given disruptions are not well understood.

1.6. Aims and scope of this study

Soil loss by erosion can be significant in sloping terrains (Lal, 2003). This entitles soil erosion to rank as a worldwide challenge (Pimentel et al., 1995) and has raised more attention recently following its copious adverse effects on soil fertility, water quality as well as enhancing

greenhouse gases emissions (Lal, 2001; Lal, 2021). The large magnitude of erosion repercussions for agroecosystems retains this objective as a trendy topic that merits further exploration and appraisal. Upper Eastern Ghana is among the regions coping with the erosion consequences including but not limited to soil degradation, infertility, and food insecurity (Al- Hassan, 2015). Most farmlands in Upper Eastern Ghana are moderately hilly and comprised of soils with low organic C and poor structure, which exacerbate the erosion risk in the region with an estimated soil loss of 2.6 t ha-1 y-1 (Baatuuwie et al., 2015). Considering the importance of erosion, the current study was conducted on the basis of three chief hypotheses;

1. $\delta^{13}C$ values are decreased and $\delta^{15}N$ values are increased at the footslope position due to soil movement from upslope into depositional site. Conventional tillage on hillslope exacerbates erosion and its consequences for soil organic matter turnover.
2. Topography is the predominant influence on soil edaphic heterogeneity and therewith a major control of prokaryotic community structure in sloping farmlands. The extent that various agronomic practices impact on prokaryotic community structure is also contingent upon topography.
3. Eventually, the plant growth-promoting potential of sorghum rhizobiome are also modified by topography and agronomic disruptions, which consequently can affect sorghum yield indices.

2. Results

2.1. Soil organic matter turnover in Upper Eastern Ghana hilly farmland revealed by changes in soil $\delta^{13}C$ and $\delta^{15}N$

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Abstract

Farming on hillslopes can drastically affect soil organic matter (SOM) maintenance and accumulation. Most hillslope studies to date have been focused on soil movement to characterize SOM turnover under erosive conditions. In this study, we characterize the combined impacts of erosion and accelerated erosion on SOM turnover. We employed soil ^{13}C and ^{15}N natural abundances to detect erosion and unravel erosion repercussions for SOM dynamics. Except for plowing (conventional vs. reduced tillage), other individual agricultural practices (residue removal with no cover crop vs. retaining residuals and adding a cover crop, and mineral N amendments with 0, 40, and 80 kg ha^{-1} nitrogen) caused no significant shifts in $\delta^{15}N$ and $\delta^{13}C$ values but in soil total N %, and C: N ratios. Topography x tillage interaction significantly altered soil ^{13}C values, due possibly to higher contribution of recalcitrant SOM to soil C pool. Despite 30 years of groundnut (C_3) cultivation in upslope, and dominance of C4 crops (rice, millet-sorghum-sorghum, millet-sorghum, millet, millet-sorghum-groundnut sequences) in footslope, a slight $\delta^{13}C$ variation (0.46‰) was seen between upslope and footslope plots. This implies the alleviation impact of erosion following the adaptation of upslope ^{13}C value by deposition site. Unlike soil $\delta^{13}C$, $\delta^{15}N$ was strongly negatively correlated with elevational gradients and positively correlated with enrichment of SOM and enriched along with enhancement of total C%, total N%, soil organic matter% (SOM%) at the deposition site. Graphing $\delta^{15}N$ vs. $\delta^{13}C$ revealed the wider range of ^{13}C values under reduced tillage in the upslope soils, while in the depositional sediments conventional tillage led to a wider range of ^{13}C values, suggesting inefficiency of conservational practices in preserving SOM at the eroding site due to strong geomorphic exogenic movement. This study has implications for sequestering SOM by foreseeing potent SOM turnover under erosion and accelerated erosion.

Keywords: soil $\delta^{13}C$ and $\delta^{15}N$, SOM turnover, eroding site, topography, conventional management practices

1. Introduction

Soil organic matter (SOM) losses are magnified on sloping land where conventional farming introduces soil disturbance and lower residue retention within the soil (Rasmussen and Collins 1991; Liebe et al., 2005; Bationo et al., 2007). A significant portion of C in the soil exists as free organic particles, which are associated with mineral particles or encapsulated in aggregates (De Baets et al., 2012). However, soil erosion and tillage practices both can disrupt soil aggregates resulting in the loss of protection of soil organic C (SOC) (Lal, 2003; Horwath, 2007). Eventually, runoff alters soil C biogeochemical cycling through often decrease SOC along the hillslope while simultaneously increasing it in the depositional sediments (Schaub and Alewell 2009; Wang et al., 2017). The enrichment of SOC in the footslope following soil erosion/deposition can also lead to higher emissions of CH_4, N_2O, and NO_x to the atmosphere through methanogenesis and denitrification, under anaerobic conditions of often poorly drained depositional footslope sites (Moiser et al., 1991). Most farmlands in Upper Eastern Ghana are poorly structured and moderately hilly with an estimated soil loss of 2.6 t ha^{-1} y^{-1} which makes them highly susceptible to natural erosion and accelerated erosion (Baatuuwie et al., 2015). Thus, soil erosion, as well as nutrient depletion are threatening agriculture in these regions (Vanlauwe et al., 2014; Tesfahunegn et al., 2021). Thus, precluding soil erosion and maintaining land productivity in Upper Eastern Ghana are high-priority national goals (Baatuuwie et al., 2015).

Attenuating soil erosion repercussions in upslope environments calls for a better understanding of the shifts in soil C and N balance and SOM turnover following the erosion (Ngaba et al., 2019). The ^{13}C and ^{15}N natural abundance in soils are dynamic characteristics, which are used to assimilate the soil C loss or sequestration in ecosystems, and to reveal the dominant factors controlling soil N and C cycles (Poage and Feng 2004; Garten 2006, Schaub and Alewell 2009; Meusburger et al., 2013; Wang et al., 2017). $\delta^{13}C$ of soil mirrors soil moisture status, and $\delta^{15}N$ isotopic fractionation outcomes can reflect the source of N amendment and inputs such as N-fixation or N losses from volatilization, leaching, and denitrification (Robinson, 2001; Aranibar et al., 2008). Evidently, the $\delta^{13}C$ content of SOM corresponds to the $\delta^{13}C$ content of the plant residuals from which it is derived (Gregorich et al., 1995). For instance, $\delta^{13}C$ signature of C_4 crops is -12.5‰ ±1.5‰ (Hansen et al., 2004; Kristiansen et al., 2005; Fuentes et al., 2010) which differ from that of C_3 vegetation ($\delta^{13}C$ of -28‰±1.9‰) (Balesdent et al., 1990; Gerzabek et al., 2001; Kaler et al., 2018). This disparity enables the identification of distinct C sources in the

SOM. Thus, tracing $\delta^{13}C$ signatures of eroded sediment facilitates understanding of C_3 and C_4 plants' transition and feasible shifts in eroding terrains (Turnbull et al., 2008; Drinkwater et al., 1998; Wanniarachchi et al., 1999; Aranibar et al., 2008). Unlike $\delta^{13}C$, the use of $\delta^{15}N$ in understanding SOM turnover can be complicated due possibly to isotopic fractionation following N cycling processes in the soil. Processes including N mineralization, nitrification, denitrification, NH_3 volatilization, N leaching, and plant uptake which generate various $\delta^{15}N$ signatures in soil N pools (Robinson, 2001; Wang et al., 2021). To date, the soil ^{13}C and ^{15}N isotopic signatures of suspended organic matter have been applied to detect the origin of SOM in rivers and riversides (Masiello and Druffel 2001; McCorkle et al., 2016), runoff waters (Roose and Barthès 2006), a pine forest (Sah and Brumme 2003), a wetland with no transition from C_3 to C_4 vegetation (Schaub and Alewell 2009) or with the transition from C_3 to C_4 vegetation (Turnbull et al., 2008) and in intensive agricultural catchments (Fox and Papanicolaou 2007; Wang et al., 2017).

Topography controls sites' hydrological and pedological processes by controlling soil water content, microbial biomass, N mineralization, nitrification, and denitrification (Sehy et al., 2003; Florinsky et al., 2004). Land use transformation and transition of C4 to the C3 vegetation are among those factors known to increase the risk of surface runoff (Aranibar et al., 2008; Ngaba et al., 2019) and the run-off process translocates the soil surface from up to footslope positions. This increases the biologically available C and N at depositional sediments due to selective transport of light C fraction (Zhang et al., 2006), disturbing of aggregates (Horwath, 2007), and leaching of soluble C and NO_3^-, as long as the C and N can settle and remain at the bottom of the slope (Saha et al., 2017; Lal, 2018; Singh et al., 2019). However, accumulation of C and N at the depositional site is associated with higher soil water content (Lal and Pimental, 2008) which usually is coincident with an increase in microbial respiration and gaseous loss of N and C in the form of CO_2 and N^2O emissions (Paterson et al., 2008). This cycle eventually affects the structure and functioning of soil microbiota (Dungait et al., 2012; Xu et al., 2021) and therefore soil biogeochemical cycles.

The nature and extent of management-induced outcomes are contingent upon the type and intensity of agronomic practices perturbation (Mann 1986). In croplands, the rapid loss of SOC is attributed to exposed soil surfaces and the destruction of soil aggregation as a feature of plowing (Horwath 2007). Since soil disruption can expose SOC to microbial decomposition and mineralization, which eventually incites additional C loss (Dalal et al., 1991; Rasmussen and Collins 1991; Horwath 2007). Reduced soil exposure, applying crop rotation, and residue

management that influences the biomass load of return to the soil that helps to mitigate soil C loss (Rasmussen and Collins 1991). The application of mineral N fertilizer can affect soil ^{15}N values in systems with high N losses compared to the systems characterized by close N-cycles with organic N amendments (Hobbie and Ouimette 2009). Although ammonical N fertilizer can compensate for soil nitrogen deficit, it can also promote soil acidity, denitrification, and nitrogen leaching and lead to the progressive enrichment of soil $\delta^{15}N$ (Aranibar et al., 2008).

Soil edaphic properties strongly correlated with the soil $\delta^{15}N$ and $\delta^{13}C$ patterns (Amundson et al., 2003). The positive correlation between N and C contents of soil with ^{15}N and ^{13}C values, respectively, across elevation gradients, has been reported previously in the literature (Sah and Brumme 2003). Evaluating $\delta^{15}N$ and $\delta^{13}C$ values of soils are applicable tools for tracking down the erosion, recognizing SOM origin, the transport mechanisms, and degree of soil erosion at the various scales of plots (Fox and Papanicolaou, 2007; Aranibara et al., 2008; Schaub and Alewell, 2009; Nadeu et al., 2012; Park et al., 2014; McCorkle. et al., 2016; Wang et al., 2017). Although most studies to date have been focused on the extent of soil organic matter decomposition under natural erosion, or accelerated erosion there is a paucity of knowledge on the simultaneous impacts of both on soil stability and organic matter turnover. Thus, the current study was carried out with the aspiration of covering the missing information and based on three chief hypotheses, 1. sheet erosion induced by topography in combination with conventional tillage practice on upslope enhance SOM decomposition 2. enriched soil $\delta^{13}C$ at footslope position also occurs in tandem with soil movement from up into depositional sediments 3. eventually, the soil $\delta^{15}N$ fractionation occurs at depositional sediments due to N surplus and higher N losses. The results are used to characterize the effects of intensive vs. conservational agricultural practices on upslopes SOM turnover.

2. Material and methods

2.1. Site description, and sampling

The study site was located in Vea catchment (10°50′N, 0°54′W), which is in the Bongo District of Upper-Eastern Ghana (UE). The Vea watershed consists of degraded sandy loam soils which are predominantly plinthosols (upslope/backslope) and luvisols (footslope) (Danso et al., 2018). The average annual temperature of 37.5 °C and mean annual precipitation of around 1054 mm were reported for UE. Precipitation in UE mainly falls during the 5 months of the growing season (May-Sep), which is coincident with high temperatures, harsh and erratic rainfalls in the region (Danso et al., 2018). It has been reported by Olsson (1992) that the UE land surface has leveled

into erosion plateaux or tropical pediplains through erosion and physical weathering. Full details of the experimental site and sampling procedure are given in Ghotbi et al. (2021). In brief, the train's morphometry divides the field into two transects of upslope and footslope sites with an average slope between 3-5%, separated by a ~100 m distance between two positions. The experimental field trial was established in 2012 on fields that were consistently and conventionally cultivated by local farmers for more than 30 years. The crop rotation within each slope position consisted of maize and sorghum between 2012 to 2015 cropping seasons, with/without adding cowpea as a cover crop in the sequence. The local farmers' sequence of cropping in the field was as follows: rice, millet-sorghum-sorghum, millet-sorghum, millet, millet-sorghum-groundnut which were crop sequence of footslop, and groundnut which was merely planted at the upslope position for 30 years. A strip-split plot design was used with slope positions considered as the strips and a combination of three experimental factors was embedded in each slope position: conventional tillage (CT) and reduced tillage (RT) considered as the main plot, improved residue management (residue retained and combined with cowpea as a cover crop (Re+CP)) and standard residue management (no residues retained and no cowpea added (-Re-CP)) as sub-plots, and three dosages of mineral nitrogen fertilizer (no nitrogen (N0P60K60), recommended 40 kg h-1 N (N40P60K60) and high nitrogen 80 kg h-1 (N80P60K60)) constituting the sub-sub-plot factors. Each factor was laid out with four replications for a total of 96 subplots. Sampling was done during Oct using a 100 cm auger with 2.5 cm diameter. Soil sampling (depth of 15 cm) was conducted for 96 plots as described by Ghotbi et al. 2022. Ten soil cores were collected from each plot, combined into a single homogenized sample, and transferred to the lab in a cooler with ice.

2.2. Assessing soil edaphic properties and natural abundance of $\delta^{15}N$ and $\delta^{13}C$

Samples were air-dried overnight and used for the physiochemical and isotopic C, N value analyses. Soil samples were sieved through a 2 mm mesh sieve. Small stones and roots were removed by hand. Total C mass% (MWC%) and total N mass% (MWN%) was determined by dry combustion, the soil nitrate-N (NO_3^--N) and ammonium-N (NH_4^+-N) and Soil volumetric water content (cm^3 water/cm^3 of soil = vol. %) and temperature (°C) were measured on-site, Soil clay% was assessed by the hydrometer method as explained in detail by Ghotbi et al. (2022).

Inorganic carbon was removed prior to stable isotope analysis by acid fumigation (HCl) of moistened subsamples in a glass desiccator overnight (Harris et al., 2001; Schaub and Alewell 2009). Soil samples depleted of inorganic C were dried at 40 °C. Samples were ground to a fine

powder in a mortar and pestle. 10 mg of material were transferred into 6 to 4 mm tin cups for analysis of carbon and nitrogen using a continuous-flow isotope ratio mass spectrometer (CF-IRMS). The δ15N content of the inorganic fertilizer of urea (46% N), which was the source of inorganic N input in our study, was 1.2‰ ± 0.1 (n = 4). The $\delta^{15}N$ and $\delta^{13}C$ ratios in soil were determined at the UC Davis Stable Isotope Facility using a continuous flow, isotope ratio Europa Integra mass spectrometer (CF-IRMS, PDZ-Europa Scientific, Sandbach, UK) interfaced to a CN combustion analyzer. Isotope ratios were determined and expressed in ‘‘δ’’ units as the relative difference (in parts per thousand (‰)) among the sample and conventional standards (atmospheric N2 for nitrogen and PD-belemnite [PDB] carbonate for carbon), according to $\delta^{13}C$ or $\delta^{15}N$ (‰) = (Rsample / Rstandard - 1) = 1000 formula where R is the ratio of heavy isotope/light isotope content for the considered element.

$$\delta^{13}C \text{ or } \delta^{15}N_{sample}(‰) = \left(\frac{R_{sample} - R_{standard}}{R_{standard}}\right) x1000$$

2.3. Statistical analyses

Total C mass% (MWC%) and total N mass% (MWN%) were used to assess the C:N ratios. SOM% was estimated following the method recommended by Pribyl (2010) based on the equation below, total carbon % × 2, where average SOM is composed by the stoichiometric percentage of 50% organic carbon, so 100/50= 2.

$$\%SOM = total\ C\% \times 2$$

The effects of slope position, agricultural practice, and farming history on soil δ13C and δ15N natural abundances, the total mass of C% (MWC%), the total mass of N% (MWN%), NO_3^--N, NH_4^--N, C:N ratio, and SOM% were evaluated after Shapiro-Wilk normality test and Bartlett test of homogeneity of variances. A linear mixed model for strip-split plot layout was applied according to Gomez et al. (1984) using the “lmer” function of the “lme4” and summarized by “Anova” function embedded in “lmerTest” package. The factors slope position, tillage system, crop rotation, and N fertilizer rates were considered as fixed factors, while replication ×rotation × N fertilizer interactions were considered as random factors. The “LSD test” function in the “Agricolae” package was applied to assess significant differences between the means of four replicates among the N fertilizer levels ($P < 0.05$), P value adjusted by the Benjamini-Hochberg method (“FSA” package).

Kruskal-Wallis tests and effect size (Dunn, 1964) were applied for assessing the significant differences among the local farming cropping sequence. Dunn tests (Zar, 2010) for multiple comparisons of means were conducted to evaluate the impact of farming history levels, applying the "dunnTest" function in the "FSA" package, and "cldList" functions in the "rcompanion" package. The familywise error rate for controlling the false discovery rate was conducted by the Benjamini-Hochberg method. The $\delta^{13}C$ graphed versus $\delta^{15}N$ to estimate the possible source of degraded SOM under various factors applying tRophicPosition package.Principal component analysis followed by the visualization of the results in PCA biplots helped to understand the correlations between soil edaphic properties, $\delta^{13}C$, and $\delta^{15}N$ under slope position and 30-year local farming history ("Vegan" and "factoextra" packages). We also conducted Spearman correlation coefficient analyses (applying "ggpubr" and "devtools" packages) to intimately evaluate the correlation among all soil elements such as MWC%, MWN%, C:N ratio, NH_4^--N, NO_3^--N, SOM%, with soil ^{13}C, and ^{15}N stable isotope values. The multiple comparisons false discovery rate and P value adjustment were controlled for false discovery concerning both Pearson correlation, and "wilcox.test" results by the Benjamini-Hochberg method applying the "FSA" and "multcompView" packages, respectively. The $\delta^{13}C$ and $\delta^{15}N$ shifts relative to each other and along with their relationships with elevational, latitudinal, and longitudinal gradients were evaluated, applying partial Mantel tests in the "Vegan" package and depicted using the "ggplot2" package. All analyses were conducted in the R v4.0.0 environment.

3. Results

3.1. Topographic repercussions for soil edaphic properties and $\delta^{13}C$ and $\delta^{15}N$ natural abundances

The linear mixed effect model revealed the significant imprints of slope position on soil stable isotope of ^{15}N ($F=110.46$, $P<0.001$), SOM% ($F=102.8$, $P<0.001$), and as have been shown in our previous study (Ghotbi et al., 2021) on NO_3^--N ($F=41.04$, $P<0.001$), NH_4^+-N ($F=41.96$, $P<0.001$), C: N ($F=23.23$, $P<0.001$), MWN% ($F=86.87$, $P<0.001$), MWC% ($F=102.08$, $P<0.001$), temperature ($F=120.5$, $P<0.001$), VWC ($F=8.4$, $P<0.01$), and clay ($F=8.6$, $P<0.01$). However, no significant shift in soil ^{13}C value was detected in response to topography (Table S1). The soil ^{13}C mean values were -18.96 and -18.50‰ and ^{15}N mean values increased from 4.88 to 6.25‰ from upslope to footslope plots, respectively (Table 1). The maximum ^{15}N and ^{13}C values were noticed at deposition sites, with the max ^{15}N value of 7.40‰ and the max ^{13}C value of -16.61‰. The soil MWC% and MWN% were higher in depositional plots with max values of 1.05 for MWC% and 0.81 for MWN%. Compared to the footslope, SOM% was significantly lower in plots of upslope

with a minimum value of 0.41% and mean value of 1.31% in footslope and 0.65% in upslope plots. The mean temperature for west-facing footslope plots was 35.48 °C while the mean value of east-facing upslope temperature was 34.53 (Table 1). The mean value of clay percentage in footslope plots was almost double the clay percentage in upslope plots.

3.2. Soil C and N stable isotopes and edaphic properties affected by agricultural schemes

A linear mixed model revealed the efficacy of tillage practice among the individual agronomic practices in significantly altering soil C: N, NO_3^--N, MWN%, and temperature values. The slope x tillage interaction also led to significant shifts in some measured soil elements specially $\delta^{13}C$ but didn't alter $\delta^{15}N$, NH_4^--N, C.N ratio, temperature, VWC, and clay content of the soils (Table S1). Tillage x fertilizer interaction also significantly altered the clay content of the soils. Except for slope x tillage practice interaction which significantly altered soil ^{13}C value ($F=8.16$, $P<0.001$), the impacts of other individual management practices and their interactions were found nonsignificant in shifting soil ^{13}C, ^{15}N values (Table S1).

3.3. Local farming history impacts on soil $\delta^{13}C$ and $\delta^{15}N$ and edaphic values

The sequences of cropping in the region before establishing the experimental field were as follows: rice, millet-sorghum-sorghum, millet-sorghum, millet, millet-sorghum-groundnut, or groundnut. According to the non-parametric Kruskal-Wallis rank test, 30-year local farming history was among the factors that significantly influenced soil $\delta^{13}C$ ($F=12.1$, $P<0.03$, effect size= 0.08), and $\delta^{15}N$ values ($F=52.5$, $P<0.0001$, effect size= 0.54) and all other measured soil edaphic properties (Table S2). The highest effect size of the Kruskal-Wallis test was relevant to temperature, SOM%, MWN%, MWC%, and ^{15}N variables. Considering the Dunn test multiple comparisons following the Kruskal-Wallis rank test demonstrated that none of the crop sequences could significantly alter soil ^{15}N, ^{13}C values as well as other measured elements (Table 1). The mean $\delta^{13}C$ values of plots with mostly C_3 plants such as groundnut and rice were -18.80‰ and -18.73‰, respectively, while the $\delta^{13}C$ values of soil with C_3 and C_4 type of plants (millet-sorghum-groundnut) and one of the plots with C_4 plants only (millet-sorghum) showed a slight ^{13}C depletion (-19.49‰ to -19.12‰, respectively) (Table 1). $\delta^{15}N$ mean values varied not significanlty among the local farming sequences with millet/sorghum as the effective rotation in slightly enrichment of soil ^{15}N while groundnut sequences led to slight soil ^{15}N depletion. Soil $\delta^{13}C$, and $\delta^{15}N$ shifts under local farmers practice (30-year local farming history) indicated a slight change between ^{13}C and ^{15}N values among C_3, C_4 plants and mixed of both across the field

Results

Table 1 Mean comparison of soil edaphic, 13δC, and 15δN values affected by slope position, agronomic practices, and 30-year local farming history. Mean values (n = 96 for each level of slope position, n = 48 for each level of tillage as well as rotation, n = 32 for each dosage of N fertilizer, and each group of 30-year farming history with unbalanced sample size (groundnut n=54, millet n= 7, millet-sorghum n= 3, millet-sorghum-groundnut n=9, millet-sorghum-sorghum n=15, rice n=8)) and standard errors are given. Significant differences for all factors except for 30-year farming history effects were assessed by linear mixed effect models (type III ANOVA based on strip-split plot design) first and followed by Fisher's Least Significant Difference (LSD) test for N fertilizer levels. Farming history impacts were evaluated applying Kruskal-Wallis rank test, followed by Dunn test. Values followed by the same lower-case letter are not significantly different. P values adjusted by the Benjamini-Hochberg method.

			$\delta^{13}C$	$\delta^{15}N$	NO_3^--N	NH_4^--N	C:N	¥MWC	#MWN	†SOM	††Temp	§VWC	Clay
Units			‰	‰	g kg^{-1}	g kg^{-1}		%	%	%	C°	%	%
Slope position													
Foot-slope			-18.50±0.14	6.25±0.09	5.20±0.08	4.61±0.05	13.39±0.09	0.66±0.02	0.05±0.002	1.31±0.05	35.48± 0.06	0.021± 0.00	11.90± 0.11
Up-slope			-18.96±0.20	4.88±0.13	2.64±0.06	2.87±0.04	12.55±0.15	0.32±0.03	0.03±0.002	0.65±0.06	34.53± 0.05	0.019± 0.00	6.99± 0.08
Management practices													
Tillage													
CT			-18.85±0.16	5.58±0.15	4.53±0.46	3.61±0.20	13.14±0.14	0.46±0.03	0.04±0.003	1.05±0.07	34.13±0.09	0.02±0.00	9.32±0.15
RT			-18.56±0.22	5.51±0.12	3.33±0.21	3.86±0.22	12.79±0.13	0.52±0.05	0.03±0.002	0.91±0.09	34.88±0.09	0.02±0.00	9.57±0.14
Rotation													
Residue+CP			-18.70±0.20	5.49±0.13	3.79±0.37	3.68±0.20	12.98±0.11	0.49±0.03	0.04±0.003	0.98±0.07	35.03±0.09	0.02±0.00	9.22±0.12
NoResidue-NoCP			-18.71±0.19	5.61±0.13	4.08±0.36	3.80±0.22	12.96±0.16	0.48±0.05	0.04±0.004	0.98±0.09	34.97±0.09	0.02±0.00	9.67±0.17
Fertilizer													
N0PK			-18.55±0.17	5.58±0.18	4.10±0.49	3.75±0.24	12.82±0.18	0.49±0.04	0.04±0.003	0.99±0.08	34.98±0.11	0.02±0.00	8.52±0.16 b
N40PK			-18.85±0.25	5.54±0.13	3.41±0.29	3.86±0.23	12.99±0.17	0.49±0.06	0.04±0.003	0.99±0.11	35.00±0.10	0.02±0.00	8.15±0.19 b
N80PK			-18.72±0.25	5.52±0.17	4.25±0.52	3.62±0.31	13.10±0.14	0.48±0.06	0.04±0.003	0.96±0.11	35.02±0.11	0.02±0.00	11.66±0.18 a
30-year local farming history (Dunn test)													
Upslope	C_3	Groundnut	-18.80±0.18	5.00±0.18	2.77±0.02	3.02±0.15	12.68±0.12	0.33±0.03	0.04±0.002	0.67±0.03	34.58±0.07	0.019±0.00	7.49±0.15
		Rice	-18.73±0.50	6.44±0.50	7.26±0.05	4.84±0.42	13.29±0.33	0.86±0.10	0.05±0.008	1.71±0.07	35.55±0.07	0.021±0.00	10.59±0.14
	C_4	Millet	-18.57±0.53	6.50±0.53	4.87±0.05	6.10±0.45	13.13±0.35	0.81±0.02	0.02±0.001	1.61±0.08	35.88±0.11	0.021±0.00	12.67±0.19
Footslope		Millet/Sorghum	-19.49±0.78	7.35±0.78	11.10±0.08	5.32±0.67	12.85±0.52	0.98±0.03	0.03±0.002	1.96±0.11	35.76±0.15	0.021±0.00	11.76±0.36
		Millet/Sorghum/Sorghum	-18.01±0.39	5.93±0.39	3.67±0.04	4.39±0.33	13.48±0.26	0.53±0.02	0.03±0.001	1.06±0.06	35.53±0.10	0.021±0.00	11.93±0.18
Mixed		Millet/Sorghum/Groundnut	-19.12±0.48	6.15±0.48	5.14±0.05	3.78±0.40	13.56±0.32	0.62±0.01	0.02±0.001	1.24±0.07	35.56±0.14	0.021±0.00	10.59±0.18

¥MWC%= total C%, #MWN%= total N%, †SOM%= soil organic matter%, ††Temp= temperature C°, §VWC= volumetric water content%.

Results

The dominant vegetative cover of upslope for 30 years before initiating our experimental field was groundnut (C_3). This precluded us from assessing soil $\delta^{13}C$, and $\delta^{15}N$ shifts affected solely by farming history irrespective of topographic attributes.

3.5. Trophic position and interplay between environmental factors and soil ^{13}C and ^{15}N

To summarize and depict the information relevant to the relationship between soil ^{13}C and ^{15}N pools with soil MWC%, MWN%, SOM%, NH_4^+-N, NO_3^+-N, C.N ratio, VWC%, temperature, and clay% under slope position and local farmers practice (30-year local farming history) principal component analysis (PCA) was applied. PCA revealed the tight relationship between ^{15}N natural abundance and soil edaphic factors such as MWC%, MWN%, SOM%, NH_4^+-N, NO_3^+-N, C.N ratio, and temperature. All evaluated factors except for soil ^{13}C natural abundance were well clustered according to slope positions (Figure 1b). Groundnut was the dominant plant cultivated for 30 years at upslope position while rice, millet-sorghum-sorghum, millet-sorghum, millet, and millet-sorghum-groundnut sequences were the footslope crop sequences. This precluded us from evaluating the crop sequence impacts on ^{13}C and ^{15}N values and soil edaphic properties regardless of topographic features (Figure 1b).

Increasing MWN%, MWC%, SOM%, temperature, and NO_3^--N contents of the soil at footslope plots was in tandem with a significant enrichment of soil ^{15}N. However, soil ^{13}C values were significantly adversely associated with soil MWN%, MWC%, SOM%, NO_3^--N, temperature enhancement at the depositional site (Figure 1 and Figure S1). Given trend was weaker to non-significant at upslope in regard to MWN% and NO_3^--N contents (Figure S1). Additionally, a stronger correlation of ^{13}C and MWC% (R= 0.47) was noticed in the footslope soils, which was weaker at upslope (R= 0.30), suggesting the contribution of recalcitrant SOC% to $\delta^{13}C$ profiles of the upslope soils. NH_4^+-N and C: N ratios showed no significant correlation with soil ^{13}C and ^{15}N irrespective of topography.

To check the spatial distribution of $\delta^{13}C$ and $\delta^{15}N$ values trophic position and partial Mantel test was applied. The mixed source of degraded SOM under reduced tillage was noticed following the wider range of ^{13}C under reduced tillage at the upslope position, while conventional tillage at the footslope position showed the similar result (Figure 1a). Unlike $\delta^{13}C$ values, soil ^{15}N natural abundance was spatially distributed along the field (Figure 2a, c, e). δ15N values had significant strong correlations with latitude ($R=0.48$, $P<0.001$), elevation ($R=0.30$, $P<0.001$), and longitude ($R=0.16$, $P<0.001$) (Figure 2b, d, f).

Results

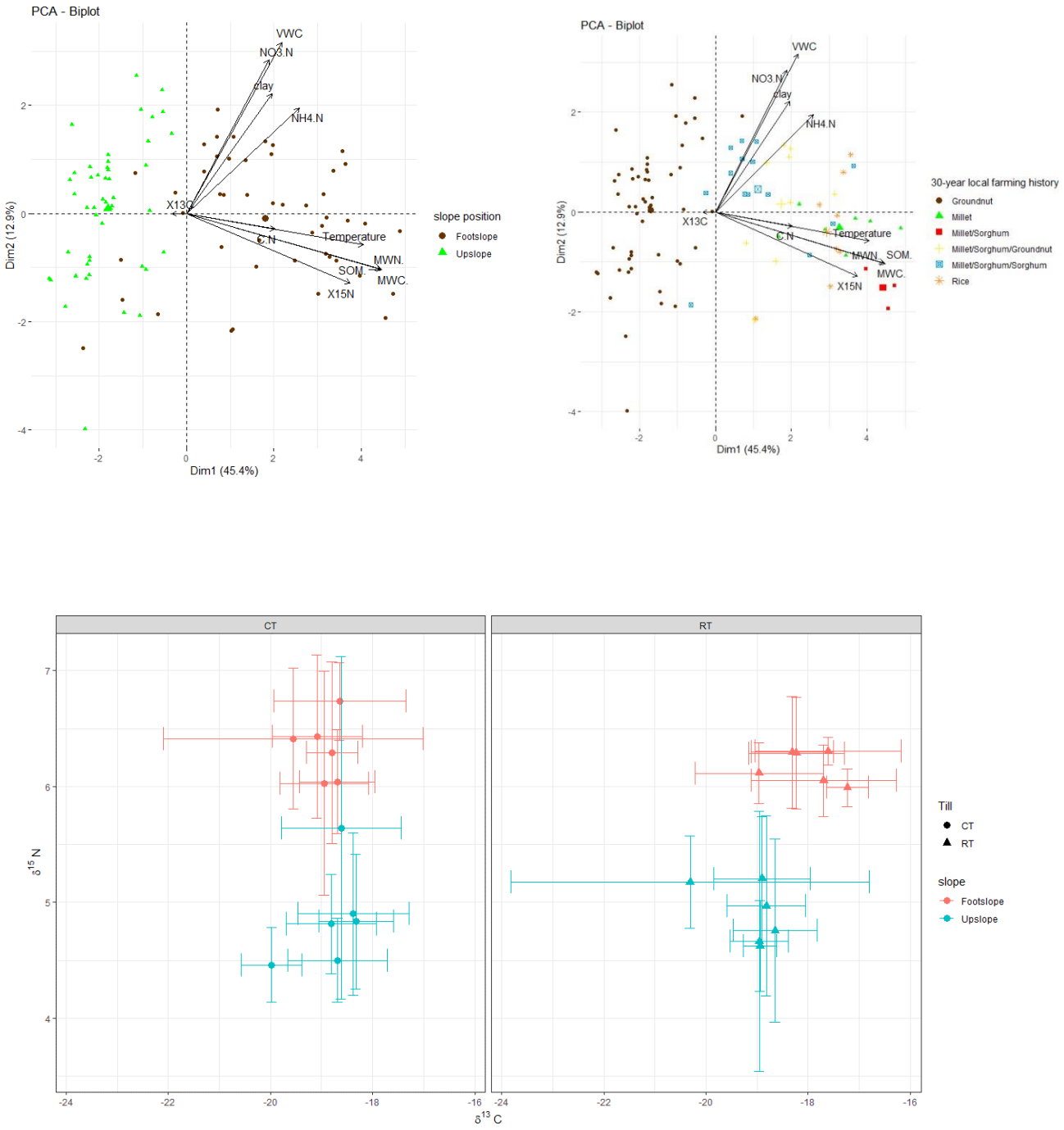

Figure 1 Biplots delineating the clustering of soil chemical elements and stable isotopes of ^{15}N and ^{13}C (a) under topography and (b) under 30-year local farming history of the field, arrows revealing the directions each elements improves (c) trophic position and source of degraded SOM under various tillage system in each slope position.

Results

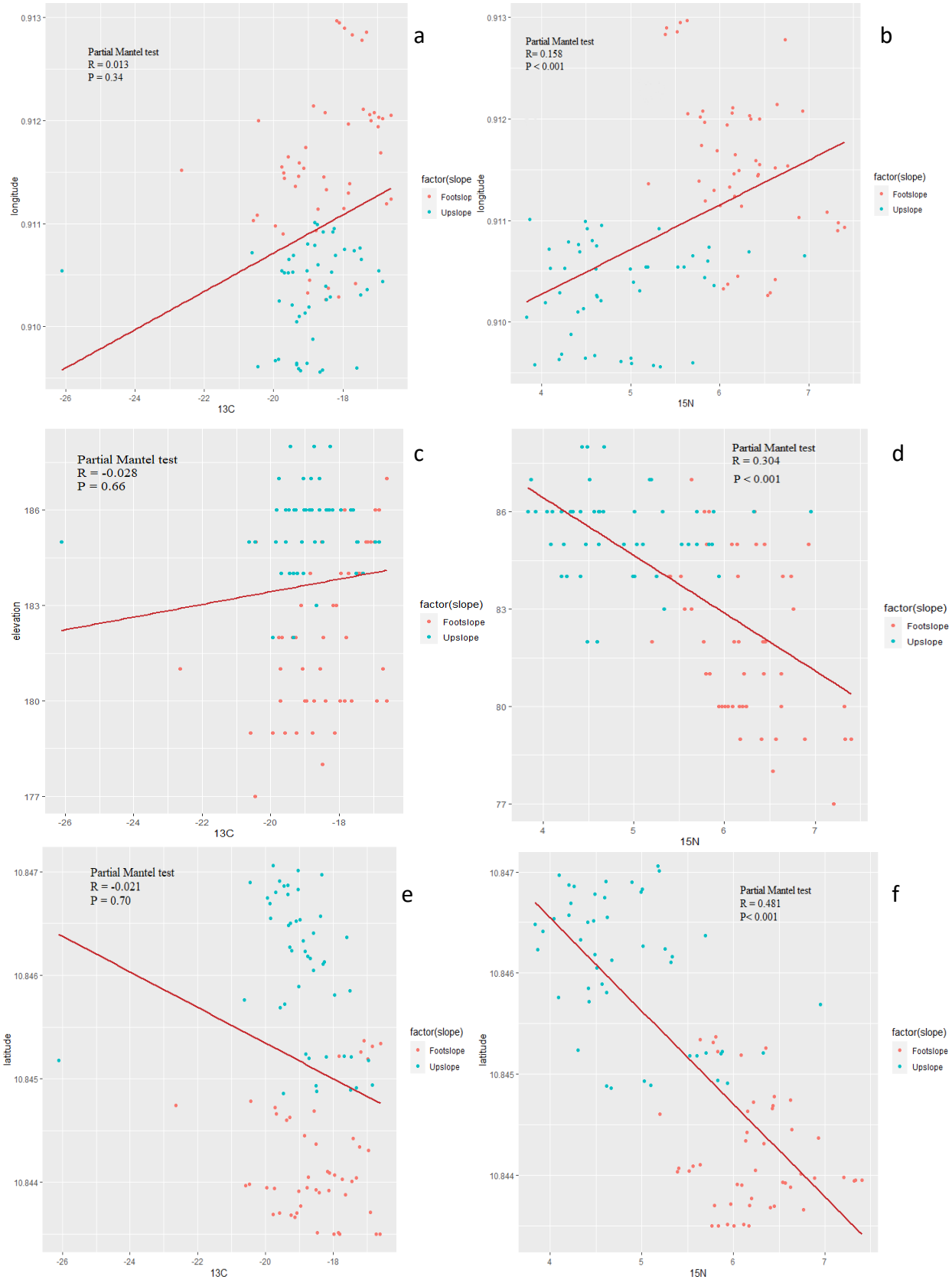

Figure 2 a-f Depicting the spatial correlations between ^{13}C, and ^{15}N with elevational, longitudinal and latitudinal gradients of the field, applying Partial mantel test based on Pearson correlation coefficient.

4. Discussion

4.1. Tracking down erosion

Unlike the ^{13}C isotope, a significant strong linkage between elevation, latitude, longitude, and soil ^{15}N natural abundance was observed, which can be explained by the erosion/deposition consequences and translocation of upslope ^{13}C into the deposition sediments which leads to ^{13}C homogenization along the slope (Figure 2a-f). In line with previous literature, we noticed higher values of $\delta^{15}N$ with higher MWN%, MWC% and NO_3^--N contents at the footslope position, which explains the higher $\delta^{15}N$ fractionation (Bellanger et al., 2004; Aranibar et al. 2008; Wei et al., 2013; Craine et al., 2015; Gómez et al., 2020). Wider spatial distribution of enriched ^{15}N towards agroecosystems is a common event, while soil $\delta^{13}C$ showed weaker spatial correlation compared to ^{15}N of soil (Norra et al., 2005; Boeckx et al., 2006). As reported by Norra et al. (2005) and Gerzabek et al. (2001) the spatial pattern of $\delta^{13}C$ in surface soil is associated with that of the underlying parent material, and disruptions changes such as agronomic activities. As occurred at footslope position, the fractionation associated with nitrification and N mineralization can be remarkable when NH_4^+-N and NO_3^--N are abundant in the soils (Yeatman et al., 2001; Dijkstra et al., 2006; Kawashima and Kurahashi, 2011). Therefore, the positive correlation between ^{15}N value and NO_3^--N enhancement was expected at the depositional site.

Compared to the footslope with an average SOM% of 1.31, upslope contained significantly lower SOM% with an average SOM% of 0.65%. Besides, the accumulation of significantly higher soil MWC%, MWN%, NH_4^+-N, NO_3^--N, and C: N ratio along with enrichment of ^{15}N were detected in our footslope plots (Table S1 and Table 1), which can imply the ongoing erosion/deposition processes in the field. Since, plants $\delta^{15}N$ and their associated surface soils have a very close relationship (Aranibar et al., 2008; Choi et al., 2017) alteration of plants' $\delta^{15}N$ values will shift soils ^{15}N values and vice versa. This pattern is related to N cycling and loss in the soil, and simultaneously reflects the possible isotopic fractionation during transformations of soil N. This explains the higher $\delta^{15}N$ values at footslope suggesting higher overall in situ loss of soil N. $\delta^{15}N$ values changed from 4.88 ‰ to around 6.25 ‰ from upslope to footslope, respectively. Overall, the $\delta^{15}N$ range for cultivated soils has been reported around 6 ‰ and higher than natural soils following various N inputs to the agricultural lands (Choi et al., 2017; Fuertes-Mendizábal et al., 2018). The estimated N isotope fractionation for major N cycle processes is 40-60% for NH_3 volatilization, 35-60% for nitrification, 28-33% for denitrification, 0-19% for NO3, and 9-18% for NH_4 plants assimilation (Robinson, 2000, 2001; Senbayram et al., 2008) which consequently

lead to ^{15}N enrichment in the soil (McCorkle et al., 2016; Choi et al., 2017; Fuertes-Mendizábal et al., 2018; Liu et al., 2019). Shifting in nitrogen isotope dynamics and signatures following erosion among hillslopes compared to associated wetlands have been reported frequently (Alewell et al., 2008; McCorkle. et al., 2016; Xu et al., 2021). The higher range of soil ^{15}N natural abundance in deposited sediments was in tandem with the accumulation of other measured edaphic properties specifically NO_3^--N and SOM%, except for ^{13}C values at the deposition site. The predominance of groundnut as a N fixing C_3 plant at upslope position for 30 years can be one of the explanations for the lower ^{15}N-values of up-slope plots, due to biological nitrogen fixation which can lead to lower ^{15}N values (Hartman & Danin, 2010: Unkovich, 2013). Moreover, nutrient wash off following the erosion process could also increase the depleted-^{15}N at our eroding site while promoted higher ^{15}N values at depositional site following the higher ^{15}N fractionation (McCorkle et al., 2016). As a shred of evidence we noticed the higher accumulation of NO_3^--N and ^{15}N in the depositional sediments which suggests higher N accessibility for the plant's uptake (plant preferential ^{14}N uptake along with higher leaching, volatilization, microbial activities particularly during drying and rewetting of poorly drained footslope and could contribute to the ^{15}N fractionation at the depositional footslope (Dungait et al., 2013; Xu et al., 2021) This explains the occurrence of higher open N cycle and N losses at the depositional site. Landscape topography is known to play a crucial role in soil edaphic characteristics heterogeneity (Doetterl et al., 2016). Consistent with our results, Amundson et al. (2003) also revealed that soils ^{15}N values are dependent upon soil slope and are altered by redistribution of SOM through its removal from topsoil/O horizon upslope and deposition at footslope. During given transportation, SOC is partially decomposed and lost (Doetterl et al., 2012; Doetterl et al., 2016; Wang et al., 2017). This eventually affects the biogeochemical properties of both the eroding upslope and depositional footslope (Park et al., 2014). Previous studies showed more degraded SOM is usually enriched in ^{15}N, and less consistently, ^{13}C-enriched compared to newly added/less decomposed organic inputs (Kramer et al., 2003). Additionally, anaerobic processes in the often-waterlogged soils of depositional sites usually lead to lower ^{13}C values (Krull and Retallack, 2000; Park et al., 2014) whereas well-drained soils with higher aerobic decomposition can contain higher ^{13}C values (Becker-Heidmann and Scharpenseel, 1989; Agren et al., 1996).

We evidenced the maximum natural abundances of both soil ^{15}N (7.40‰) and ^{13}C values (-16.61‰) at the depositional plots. These enrichments were found to be significant solely for 15N in depositional sediments (Table S1 and Table1). In line with Schaub and Alewell (2009) results, we attributed this phenomenon to the ^{15}N, and ^{13}C relocation due to surface run off and deposition

of washed sediments at poorly drained footslope which significantly enhanced ^{15}N while alleviated ^{13}C values at our footslope position.

Generally, the application of $\delta^{13}C$ and $\delta^{15}N$ natural abundances to trace C_3, C_4 pathways and N cycle processes is based on the assumption that the signature of degraded SOM $\delta^{13}C$ and $\delta^{15}N$ are similar to the origin input materials. The dominance of the groundnut (C_3) (with $\delta^{13}C$ signature of -26 to -28‰ (Gregorich et al., 1995) over 30 years of local farmers practice within upslope plots versus the dominance of C_4 within footslope (with $\delta^{13}C$ signature of -12 to -14‰ (Gregorich et al., 1995) could lead to the distinctly different ^{13}C values between upslope and footslope plots. Thus, irrespective of erosion-induced repercussions the C_4-$\delta^{13}C$ signature around -12 to -14‰ was expected at the footslope position. However, our results revealed the $\delta^{13}C$ homogenization along the slope and intermediate $\delta^{13}C$ signatures with a mean range of -18.50‰ at footslope positions, which implies the preponderant role of topography in redistributing $\delta^{13}C$ signature, which was confirmed by McCorkle. et al., 2016 as well.

4.2. Evaluating ^{15}N and ^{13}C natural abundances under agronomic practices

None of the individual agronomic practices led to significant enrichment or depletion of soil ^{13}C and ^{15}N in C and N pools of the soil (Table 1 and Table S1). However, the slope × tillage interaction of erosion and accelerated erosion appeared to be significant in altering soil ^{13}C natural abundance as a function of soil NO_3^--N, MWC%, MWN%, and SOM%. Substantial loss of soil organic matter from soil surface is widely known as a consequence of conventional tillage. However, the highest C concentrations and stocks found in the topsoil under no-tillage practice (Smith and Chalk, 2021). Degradation of mixed source of SOM following the application of reduced tillage at the upslope site can be explained by insufficiency of reduced tillage in preventing accelerated erosion and incomplete incorporation of crop residuals to the soils (Figure 1C). Our results were inconsistent with those of Beniston at al. (2015), estimating the decomposition of higher recalcitrant SOM following the application of conventional tillage on hillslope. Steadily increase of $\delta^{13}C$ with years of corn cropping under no tillage practice has also been reported (Clapp et al., 2000). It is estimated that plowing is effective in stratification in soil C stock and $\delta^{13}C$ values of different depths (Balesdent et al.,1990; Dolan et al., 2006). Besides, as exemplified by Zang et al. (2018) the shifts in the soil $\delta^{13}C$ signature occurred mostly following the significant exchange of newly added C to the old C stock under tillage practice (Zang et al. 2018). Thus, combination of topology and accelerated erosion impact on ^{13}C fractionation can be attributed to the SOM mineralization and enhancement of microbial

dynamics (Werth and Kuzyakov, 2010). As defined by Balesdent et al. (1990) and Xu et al., (2021), there is a possibility of $\delta^{13}C$ enrichment with a higher rate of crop residues and decomposition of SOM. This could explain in part the higher $\delta^{13}C$ content of the soil in those plots affected by slope × tillage interaction (Table S1). In an attempt to trace the source of SOC in an intensive agricultural catchment, Wang et al. (2017) suggested that erosion in sloping cropland can drastically contribute to the total SOC deposited in the sedimentation. The deposited SOC boosted due to the duration of erosion and anthropogenic activities. Consistent with their findings we noticed the significant interactive impacts of tillage × slope on soil ^{13}C values, which manifested the bold implication of erosion when combined with conventional practices in sloping croplands.

In farmlands, the $\delta^{15}N$ signature is strongly affected by various soil N amendments such as N fertilizer through altering N inputs and outputs fluxes (Choi et al., 2017; Liu et al., 2017). Mineral fertilization was reported to either lead to depletion (Serret et al., 2008; Craine et al., 2015), or enrichment (Senbayram et al., 2008; Liu et al., 2017) of soil ^{15}N, or no change (Choi et al., 2003; Kriszan et al., 2009), the latter case being consistent with our findings. The increase of N inputs to 80 kg ha^{-1} did not alter ^{15}N isotopic values compared with the no N fertilizer application (Table 1), despite a lower ^{15}N isotopic signature of the applied fertilizer compared to the soil ^{15}N ratio. The nonsignificant impact of N fertilizer might be partially explained by the contribution of the N fertilizer to the soil N pool due to either erosion impacts or plant uptake or following the loss through paths such as nitrification, denitrification, and volatilization (Flores et al., 2007). Thus, ^{15}N fractionation in the soil can complicate the quantification of N turnover in the soil-plant ecosystem through employing ^{15}N natural abundance (Gerzabek et al., 2001).

The similar ^{13}C values within the upslope and footslope plots, despite their various farming history, might reflect the homogenization of the surface soil resulting from the erosion/deposition processes. Higher ^{15}N values at the depositional site also can confirm the occurrence of erosion/deposition processes. To probe deeper into the feasible causes of ^{13}C homogenization and ^{15}N enrichment at depressional site, finer resolutions are advocated by the new sampling from the deeper soils of upslope and footslope plots. This may illuminate the ^{13}C and ^{15}N values of deeper soil which may still hold the history of C_4 dominated farming at the deposition site.

5. Conclusion

Predictably, soil $\delta^{15}N$ showed a strong correlation with elevation and latitude and therewith

topography. However, soil $\delta^{13}C$ was found to be homogenized as a result of erosion/deposition processes. Accumulation of NO_3^--N, MWN%, MWC%, SOM% and higher temperature at footslope position was strongly correlated with enrichment of soil ^{15}N values. This can present evidence for the occurrence of higher N loss through nitrification, denitrification, leaching, volatilization and plant N uptake and therefore higher ^{15}N fractionation at the depositional footslope position. Plots under conventional vs conservational practices did not differ in $\delta^{13}C$ and $\delta^{15}N$ values. However, the combination of erosion and tillage practice significantly affected soil $\delta^{13}C$ values. SOM% that deposited and decomposed in the footslope plots is mostly comprised of the old C_3-dominated SOC, which was washed off through soil surface erosion and deposited at the footslope position. Since $\delta^{13}C$ and $\delta^{15}N$ values can act as a valuable probe tool for tracing down erosion and turnover of SOM, thus they can be applied to promote managing practices in favor of SOM sequestration in low fertile soils of upper-East regions.

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Supplemental materials

Table S1 Effect of topography and management practices on soil physiochemical properties, evaluated by statistical analysis using a linear mixed model (Type III Analysis of Variance with Satterthwaite's method is shown). The table shows F-values and indicates the significance of the individual influence factors and their interactions using asterisks.

Treatment Units	$\delta^{13}C$ ‰	$\delta^{15}N$ ‰	NO_3^--N mg kg^{-1}	NH_4^--N mg kg^{-1}	C:N	[††]MWC %	[‡‡]MWN %	[§§]SOM %	Temp C°	VWC %	Clay %
[#]Slope	2.91	110.46***	41.04***	41.96***	23.23***	102.08***	86.87***	102.08***	120.5***	8.4**	8.6**
[†]Tillage	1.42	0.18	7.92**	1.03	4.28*	3.71	4.93*	3.71	6.8*	0.2	1.7
[‡]Rotation	0.10	0.25	0.38	0.18	0.00	0.00	0.00	0.00	0.7	1.3	0.3
[§]Fertilizer	0.29	0.46	1.82	0.21	0.91	0.10	0.15	0.10	0.2	3.1	4.0*
Slope:Tillage	8.16**	0.52	16.68***	0.12	0.05	7.33**	7.05**	7.33**	0.7	0.6	1.1
Slope:Rotation	0.25	0.86	0.03	0.01	0.00	0.05	0.07	0.05	0.0	0.5	2.1
Tillage:Rotation	1.29	0.00	0.10	0.06	0.08	0.03	0.02	0.03	0.1	0.0	0.0
Slope:Fertilizer	1.31	1.48	1.60	0.19	1.22	0.73	0.64	0.73	0.2	0.3	0.5
Tillage:Fertilizer	0.39	0.75	1.09	0.48	1.65	0.02	0.08	0.02	0.1	0.5	3.7*
Rotation:Fertilizer	0.40	0.19	1.89	0.60	0.52	0.42	0.54	0.42	0.1	0.1	1.6
Slope:Tillage:Rotation	0.84	2.77	0.80	0.05	0.00	0.00	0.01	0.00	0.5	0.1	1.2
Slope:Tillage:Fertilizer	1.17	2.03	0.72	1.83	0.15	0.59	0.62	0.59	0.1	0.3	0.3
Slope:Rotation:Fertilizer	0.10	0.42	0.58	0.00	0.10	0.54	0.51	0.54	0.1	0.0	0.0
Tillage:Rotation:Fertilizer	1.11	0.67	1.41	0.02	2.59	1.11	0.65	1.11	0.2	0.6	0.3
Slope:Tillage:Rotation:Fertilizer	0.85	0.31	0.35	0.20	0.96	0.02	0.04	0.02	0.5	0.6	1.4

[#]Slope = up-slope and foot-slope positions, [†]Tillage: conventional tillage and reduced tillage , [‡]Rotation: residual management including a cover crop and no residual management and no cover crop retention , [§]Fertilizer: rates of nitrogen

[††]MWC = total C%, [‡‡]MWN = total N%, and [§§]SOM= soil organic matter %.

* Significant at the 0.05 level.

** Significant at the 0.01 level.

*** Significant at the 0.001 level.

Table S2 30-year farming history implications for soil edaphic properties and natural abundances of ^{15}N and ^{13}C of the soils assessed by Kruskal-Wallis rank tests.

Kruskal-Wallis rank test				
Evaluated elements	Units	¥KW	$P	$$Ef
$\delta^{13}C$	‰	12.1	*	0.1
$\delta^{15}N$	‰	52.2	***	0.5
NO_3.N	mg kg^{-1}	37.8	***	0.4
NH_4.N	mg kg^{-1}	39.6	***	0.4
C:N		15.9	*	0.1
††MWC	%	68.0	***	0.7
‡‡MWN	%	68.1	***	0.7
§§SOM	%	68.0	***	0.7
Temperature	°C	70.9	***	0.8
VWC	%	19.1	**	0.2
Clay	%	20.5	***	0.2

¥KW= Kruskal-Wallis one way ANOVA, and $P= P value in Kruskal-Wallis tests, $$Ef= effect size.
††MWC = total C%, ‡‡MWN = total N%, and §§SOM= soil organic matter %.
#30-year farming history = (groundnut n=54, millet n= 7, millet/sorghum n= 3, millet/sorghum/groundnut n=9, millet/sorghum/sorghum n=15, rice n=8)
* Significant at the 0.05 level.
** Significant at the 0.01 level.
*** Significant at the 0.001 level.

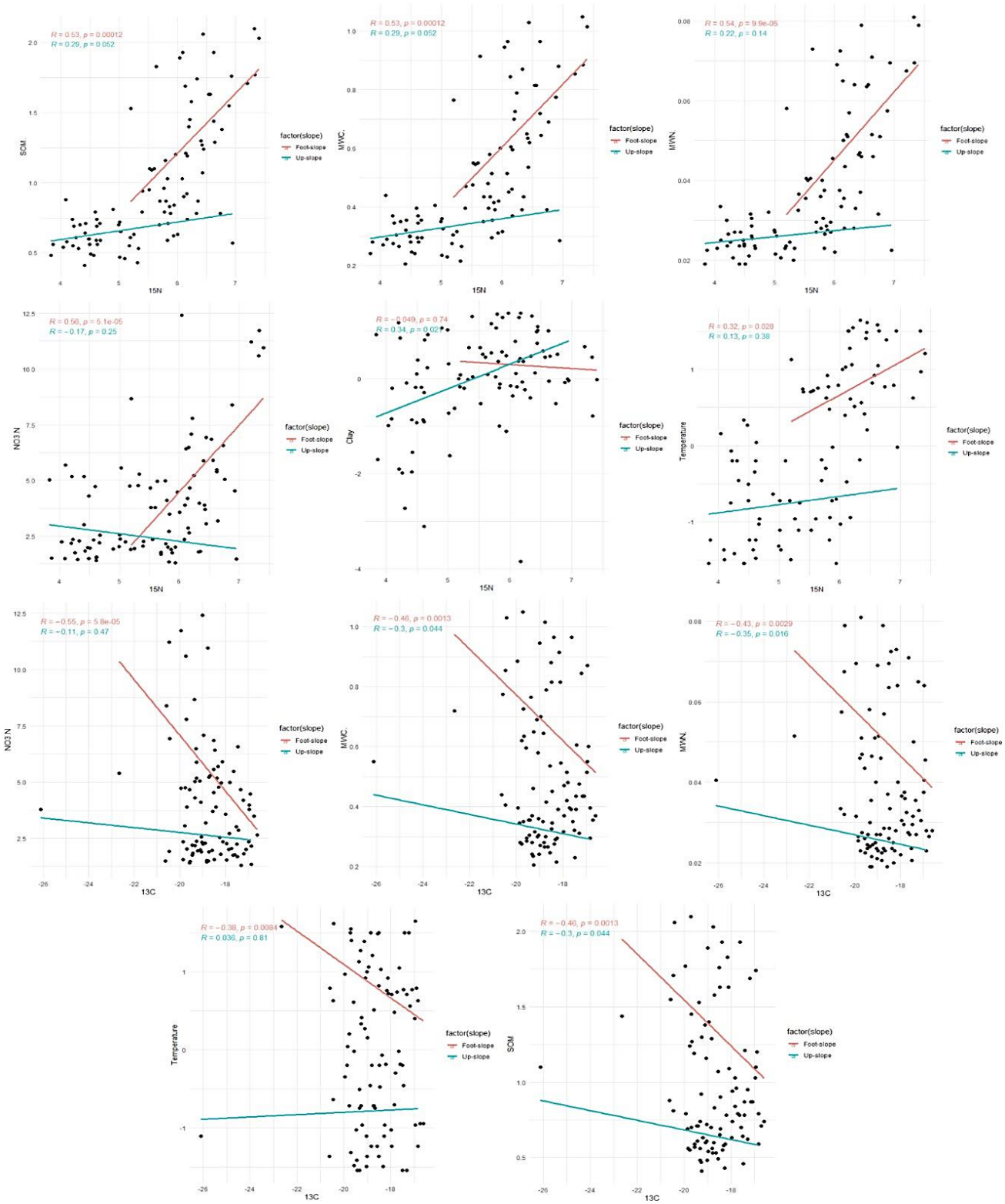

Figure S1 a-k significant Pearson product-moment correlation coefficient between soil edaphic and soil ^{13}C, and ^{15}N natural abundance were shown. The linear regression line also added to show the ascending/descending trend of ^{13}C, and ^{15}N in association with soil edaphic properties and temperature. Correlations were depicted for each slope position separately red shows the value and trend of foot-slope plots and green color refers to up-slope.

2.2. Topographic attributes override impacts of agronomic practices on prokaryotic community structure

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Type of paper: Original paper

ABSTRACT

While topography can infer erosion potential, the practice of conventional agronomic management can trigger accelerated erosion and pose major threats to soil assets such as biodiversity. The majority of farmlands in Upper-Eastern Ghana are moderately hilly and highly susceptible to erosion. This study pioneered the comparative and interactive effects of topography and conventional versus conservational agronomic practices (conventional vs. reduced tillage, rotation including residue removed and no cover crop added vs. cover crop and residue incorporated, and soil amended with 0, 40, and 80 kg ha^{-1} nitrogen) on soil physicochemical properties and microbiota. Topography imposed profound shifts in soil physiochemical properties and prokaryotic community structure. Foot-slope harbored higher prokaryotic richness and diversity than up-slope. *Bacillaceae* (28.95%) and anaerobic bacteria increased in relative abundance in foot-slope soils, while *Micrococcaceae* (25.79%) gained prominence in up-slope soils. The impact of the agronomic practices on prokaryotic community structure was contingent upon topography, evidenced by tillage practice being influential merely in foot-slope and rotation in up-slope soils. The interactive impact of slope × tillage was significant in altering soil physiochemical properties, but not prokaryotic community structure. Variation in prokaryotic community composition was explained by soil physiochemical properties (14.5%), elevation as a proxy for topography (11.3%), and spatial distance (10.8%), but rather weakly by agronomic practices. Among the soil physicochemical properties, pH, clay content, total C mass %, volumetric water content, temperature, cation exchange capacity, and NO_3^--N were relevant factors for the soil microbiota. Geomorphic and soil properties appeared to cooperatively be the primary triggers of variation in soil microbiota and their responses to the various agronomic practices.

Keywords: conservational management, conventional management, crop rotation, erosion, prokaryotic community, soil microbiota, tillage, topography

Highlights

1. Topography was the predominant influence on soil physiochemical heterogeneity and microbiota

2. Impacts of agronomic managements on prokaryotic community structure were dependent upon topography

3. Tillage practice influenced the microbiota at foot-slope and crop rotation at up-slope position

4. A geomorphic pattern contributed to the variation of prokaryotic community structure

1 | INTRODUCTION

Sloping terrain can modulate different aspects of agroecosystems such as erosion, soil water content, receipt and redistribution of light, and microclimatic features (Hu & Si, 2014; Sun et al., 2015; Shi et al., 2019; Liu et al., 2021). Additionally, it has an impact on the storage and translocation of organic matter, on plant litter decomposition, texture, bulk density, redox potential, N mineralization, N immobilization (Silver et al., 1999; Suriyavirun et al., 2019; van Kessel et al., 1993; Liu et al., 2021). Topography is also correlated with microbial community diversity, respiration, and dynamics (Huang et al., 2013; Qiu et al., 2021) due to the fueling spatial heterogeneity of edaphic properties within the soil (Liu et al., 2020). Microbial diversity and biogeography have been reported to be controlled by soil edaphic properties such as soil C and N contents and pH in sloping farmlands (Liu et al., 2018; Neupane et al., 2019; Seibert et al., 2007). Given that, responsible utilization of land through considering soil and landscape geomorphic characteristics is a key factor in preserving soil microbial biodiversity and health, which in turn can guarantee functions such as litter decomposition and soil structure formation (Chaparro et al., 2012; Kibblewhite et al., 2008).

Accumulation of nutrients and organic carbon at foot-slope sites through erosion/deposition processes boosts C conversion processes, which favors bacterial diversity (Liu et al., 2020). On the other hand, sediment migration and soil nutrient reduction at eroding up-slope can have detrimental implications for soil microbial diversity (Huang et al., 2013). Hence, the dynamics of microbial communities are tightly related to erosion and erosion-induced changes in soil abiotic properties and nutrient status (Liu et al., 2020; Park et al., 2014). Surface erosion in sloping farmlands of Upper-Eastern Ghana has been frequently reported to cause soil loss (Baatuuwie et al., 2011; Veihe, 2002). This phenomenon remains a critical issue in this region, which merits further exploration and appraisal. To this end, investigating the impact of erosion and its underlying factors on prokaryotic community variation may offer valuable insights and a promising pathway to conserve soil microbial diversity in sloping farmlands.

Farmlands are dynamic environments where soil bacterial communities are exposed to various agronomic practices such as types of tillage, crop rotation, and N fertilizer amendments (Fierer et al., 2012; Lupwayi et al., 2017; Wang et al., 2020b). Evidently, there is a growing concern on the implications of high-input-conventional agronomic practices for soil health and microbial

biodiversity (Carbonetto et al., 2014; Hartmann et a., 2015). Among conventional practices, plowing can increase soil organic carbon (SOC) loss (Horwath, 2007), with increasing loss as intensification increases. Albeit conventional tillage practice has been reported to have negative impacts on soil microbial communities in some investigations (Kihara et al., 2012; Navarro-Noya et al., 2013), contrasting results have also been published (Jangid et al., 2011; Jiang et al., 2011). The intensive application of mineral fertilizers can lead to a pH decline (Adams et al., 2020), as well as a decrease in soil organic matter (SOM) content (Li et al., 2014). SOM decline contributes to the destruction of soil structure and exacerbates soil degradation (Horwath, 2007). Bacterial community structure also adversely responds to the application of chemical fertilizers, especially nitrogen (N) fertilization. For instance, high levels of N fertilization can facilitate the loss of bacterial diversity and modify bacterial community composition (Zhao et al., 2014). As evidenced by Fierer et al. (2012) long-term N inputs shifted bacterial community composition in favor of copiotrophic groups vs. oligotrophic taxa, though no significant shift in bacterial diversity was evident in their study.

Contrary to high-input agronomic practices, conservational practices including application of reduced tillage, cultivation of cover crops, and optimized fertilizer applications can reduce soil disturbance and organic C oxidation, while improving soil aggregation and water infiltration in the surface soil (Miner et al., 2020). Moreover, positive effects of conservational practices in promoting soil biodiversity have been reported (Hartmann et a., 2015; Williams et al., 2020). Integrated soil fertility management where cover crops are applied shows a profound influence on soil properties including texture, nutrient cycling, SOM content (Adams et al., 2020), and soil bacterial diversity (Wang et al., 2020a). Cover crop usage in crop rotations produces an increase in total bacterial biomass (Chavarría et al., 2016). Additionally, cover crop application can mitigate the detrimental effect of intensive N fertilization on both, soil properties and microbial communities (Verzeaux et al., 2016). Thus, shifting from conventional to conservational practices and including cover crops may help preserve microbial community heterogeneity and functionality.

Effects of agronomic practices in combination with topography have so far merely been addressed for specific management practices including tillage (Montgomery et al., 1999; Xu et al., 2021), retention of plant residue (Kok et al., 2009; McCool & Roe 2005), or application of different N and P fertilization levels (Bouraima et al., 2016). However, the implications of conventional vs.

conservational agronomic schemes associated with topography for soil edaphic properties and microbiota have not yet been explored.

We examined the individual and combined effects of topography and management practices on soil properties and microbial communities in undulating sloping farmland of Bongo in the Upper-East Region of Ghana. Most farmlands in this region are relatively hilly, with low organic matter status, low water filtration rate, and poor structure. Thus, they are highly susceptible to erosion and accelerated erosion with an estimated soil loss of 4.7% annually for sandy soils (Bationo et al., 2007; Veihe, 2002). We aimed at gaining a deeper insight into the prokaryotic community structure in dependence on topography and conventional vs. conservational agronomic practices. To this end, we addressed three hypotheses: 1. Topography is the predominant influence on soil physiochemical heterogeneity and therewith a major control of prokaryotic community structure in sloping farmlands. 2. Various agronomic practices induce specific shifts in the soil microbiota, individually and interactively. 3. The prepotent impact of topography modulates the effects of agronomic practices on the prokaryotic community through altering soil edaphic properties.

2 | MATERIAL AND METHODS

2.1 | Site description and soil sampling

The study site was located in the Sudan Savanna region of Ghana, near the village Aniabisi (Vea watershed) (10°50′N, 0°54′W) in the Upper-East Region of Ghana, Bongo District (Figure S1). The Upper-East Region of Ghana has a tropical climate with an average annual temperature of 37.5 °C and mean annual precipitation of 1054 mm. Precipitation mainly falls in the growing season (May to September), which is coincident with high temperatures. Soils of the Bongo district have a sandy loam texture, are predominantly plinthosols (in up-slope, with mean elevation 188 m) and luvisols (in foot-slope, with mean elevation 177 m), and are mostly degraded (Danso et al., 2018). An experimental field trial was established by WASCAL (West African Science Service Center on Climate Change and Adapted Land Use) in 2012 on farmers' fields, which have been under cultivation for more than 30 years (Danso et al., 2018). The experimental fields were located on a hillslope (Figure S1). An average slope of 3-5% by an average horizontal distance of 100 m separated up-slope and foot-slope plots. A strip-split plot layout was applied with the landscape slope positions (foot-slope or up-slope) as the strip plots and tillage (contour ridge-conventional

tillage (CT) and reduced tillage (RT)) as the main plots, in which rotation (residue retained and combined with cowpea as a cover crop (Residue+CP) versus no residues retained with no cowpea added (NoResidue-NoCP), and N fertilizer levels (N0PK, with 0 kg N ha^{-1}), recommended/optimized N (N40PK, with 40 kg N ha^{-1}) and high N dosage (N80PK, with 80 kg N ha^{-1}) were arranged in replicated plots. Treatments were laid out with four replications for a total of 96 sub-plots (Figure S1). The crop sequence was maize-sorghum-maize-sorghum between 2012 and 2015, with and without cowpea as the cover crop. Contour ridge-conventional tillage, crop rotation, and fertilizer application were performed as specified in figure S1 and by Danso et al. (2018).

Soil samples were taken after harvesting sorghum at the end of October 2014. Ten samples were taken from each of the 96 plots using a 15 cm auger with 2.5 cm diameter. The ten merged soil samples of each plot were sieved through a 4 mm mesh to remove stones, plant residues, clods, and aggregates larger than 4 mm diameter. To avoid contamination, the auger and meshes were cleaned, wiped with 75% ethanol, and rinsed with sterile water after sampling in each plot. The sieved and merged soil cores collected from each plot were immediately placed in a cooler with ice for transportation. A total of 100 g of each soil sample were frozen at -40°C until DNA extraction. The remaining soil was air-dried overnight and stored at 4 °C for measurement of soil physiochemical properties.

2.2 | Characterization of soil physical and chemical properties

Soil volumetric water content (cm^3 water/cm^3 of soil = vol. %) and temperature (°C) were measured directly using a soil temperature and moisture sensor kit (WET kit, along with readout meter, HH150 Meter, Delta-T, UK). Soil textural classification (i.e., % sand, % clay, and % silt) was performed by the hydrometer method with air-dried soil samples (Gee & Bauder, 1979). Soil pH was measured in a 1:5 soil-to-solution ratio suspension in 0.01 M $CaCl_2$. Cation exchange capacity (CEC) was determined by percolating the samples with ammonium acetate (pH 7) and the bases were measured in the leachates as a measure for CEC (Van Reeuwijk, 1993). Determination of mean mass of C in % (MWC%) and mean mass of N in % (MWN%) after dry combustion was performed applying elementary analysis following the procedures of the International Organization for Standardization, ISO N 10694 (1995) and ISO N 13878 (1998). The wet chemical analysis of soil nitrate-N (NO_3^--N) and ammonium-N (NH_4^+-N) was done in KCl (1 mol L^{-1}) extracts and determined by colorimetry using an autoanalyzer (Bran + Luebbe, Germany). Total mineral N (N_{min}) content was estimated

according to Hofer (2003). Total contents of various elements were determined after aqua regia digestion with an inductively coupled plasma-optical emission spectrometry instrument (ICP-OES: Perkin-Elmer OPTIMA 3000). Extraction of trace elements soluble in aqua regia was carried out as described in ISO 11466 (1995).

2.3 | Molecular analysis of the prokaryotic community composition

DNA extraction was done in triplicates per sample from 0.5 g of soil using the PowerSoil DNA Isolation Kit (MoBio, CA), following the manufacturer's protocol. PCR amplification of the V4 hypervariable region of the 16S rRNA was done in 25-µL assays and performed in triplicates per sample. The primer set F515 (5' GTGCCAGCMGCCGCGGTAA 3') and R806 (5' GGACTACVSGGGTATCTAAT '3) was used according to Caporaso et al., 2010b. The reverse PCR primer was barcoded with a 12-base error-correcting Golay code to facilitate multiplexing of all 96 samples. Both forward and reverse primers were tagged with adapter, pad, and linker sequences (Caporaso et al., 2010b). A PCR assay contained 12 µL of MOBIO PCR water, 10 µL of 5 Prime Hot Master Mix containing buffer substances and dNTPs (QIAGEN, USA), 0.5 µL of each primer (1.0 µM final concentration), and 2 µL (concentration of 2 ng/µL) genomic DNA template. Reactions were held at 94 °C for 3 min DNA denaturation, followed by 35 cycles of amplification at 94 °C for 45 s, 50 °C for 60 s, and 72 °C for 90 s, and a final elongation step at 72 °C for 10 min. The integrity of the PCR products was confirmed by 1.5% agarose gel electrophoresis. PCR products of the triplicate assays were pooled, followed by pooling products of the 96 samples in equimolar concentrations according to Qubit (Invitrogen, Life Technologies, CA, USA) quantification. The pooled amplicons were cleaned using the MoBio UltraClean PCR Clean-Up Kit according to the manufacturer's instructions. Library sequencing was carried out by the Genome Center DNA Technologies Core Facility (University of California Davis, USA). Sequencing was performed in paired-end mode (2x250 bp) with the Illumina MiSeq system (Illumina, Inc, CA, USA).

2.4 | Bioinformatics analysis

The raw sequence reads were processed using the Quantitative Insights into Microbial Ecology (QIIME) toolkit (Caporaso et al., 2010b). The sequence reads were de-multiplexed, and adapters, barcodes, and primers were removed. Reads with low-quality values were discarded and paired-end reads were assembled using FLASH (Magoč & Salzberg, 2011). Chimeric sequences were removed

applying VSEARCH (Rognes et al., 2016). Clustering was implemented through the de novo SUMACLUST at a 97% similarity cut-off level (Kopylova et al., 2016). For taxonomy assignment, the most abundant read per OTU was selected as representative sequence and aligned to the Greengenes 13-5 core-set available at (http://greengenes.lbl.gov/) using PyNast (Caporaso et al., 2010a). Singletons were removed and the prepared OTU table was randomly rarefied to 19,000 sequences per sample, owing to the need for an even depth of sampling for diversity assessment. Rarefied datasets were used to calculate the relative abundance of each phylotype at different taxonomic levels. The quality-controlled sequence reads were representing on average 62,780 reads per sample before rarefaction, with a mean read length of 300 bp. Of the different sequences, 95.5% were classified. The raw sequence reads have been deposited in the NCBI (National Center for Biotechnology Information) SRA (Sequence Read Archive) databank as accession number SUB8928620 under Bioproject ID PRJNA695406).

2.5 | Statistical analyses

2.5.1 | Soil physiochemical data

Soil physio-chemical data were z-score-transformed after testing for normal distribution of the data (Shapiro test and bell curve drawing) and homogeneity of variances (Bartlett test) (Snedecor & Cochran, 1989). To estimate the comparative and integrated impacts of topography, tillage practice, crop rotation, and N fertilizer rates a linear mixed effect model analysis was performed, considering the strip-split plot layout on the basis of the method of Gomez and Gomez (1984). We applied the "lmer" function in the "lme4" package and summarized the results by "Anova" function as embedded in the "lmerTest" package. For the linear mixed effect model slope position, tillage practice, crop rotation, and N fertilizer rates and their interactions were considered as fixed factors, while replication and replication × rotation interaction were considered random factors. The linear mixed model effect application was validated with the restricted maximum likelihood estimation method (REML) against the normalized scores of standardized residual deviance of response variables. Lastly, the "emmeans" function in "emmeans" package was applied to assess the differences among mean values of interactive effects.

Assuming that the dominant impact of slope position might conceal the agronomic impacts, we additionally performed the analyses of agronomic impacts for each slope position individually. This

enabled us to evaluate the agronomic practice's impacts irrespective of topology. The impacts of various agricultural management practices on dependent variables were re-analyzed by three-way ANOVA with strip-split plot layout, applying the “agridat” package following Gomez and Gomez (1984). A Fisher’s protected least significant difference (LSD) test was used to detect mean differences between the three levels of N fertilizer treatments ($P < 0.05$), applying the “LSD test” function in the “Agricolae” package. The pure effect of slope position on soil properties was evaluated by one-way ANOVA. The multiple comparisons false discovery rate was controlled by the Benjamini-Hochberg method applying the “FSA” package. All analyses were done using R, version 4.0.3.

2.5.2 | Prokaryotic community structure

Richness (observed OTUs, ACE, and Chao1) and diversity indices (Shannon and evenness) were calculated in QIIME using the rarefied OTU table. We used linear mixed model effect, one-way and three-way analysis of variance (ANOVA) to assess the effects of the different treatments and their interactions on the microbial richness and alpha diversity indices in analogy to the analysis of soil properties. Fisher’s LSD post-hoc tests were applied to assess significant differences between the means of N fertilizer level (“LSD” package in R language). Variation in beta-diversity was assessed based on Bray–Curtis dissimilarity matrices using Vegan and visualized in non-metric multidimensional scaling (NMDS) plots, applying the ggplot2 package (Wickham, 2016). To test for significant differences between groups of samples, analysis of similarity (ANOSIM) was conducted with 999 permutations based on the Bray-Curtis dissimilarity matrix in Vegan. Impacts of topography and agronomic practice interactions (i.e., slope × tillage × rotation × N fertilizer) on prokaryotic community structure were further assessed by applying permutational analysis of variance (ADONIS function) on Bray–Curtis dissimilarity matrices (Vegan package) (Oksanen et al., 2016). To identify taxa being responsive to slope position, the statistical analysis of metagenomic profiles (STAMP) software was used (Parks et al., 2014). The significant differences were proven by Kruskal-Wallis tests and Scheffé post-hoc tests along with a False Discovery Rate assessment after Benjamini–Hochberg.

2.5.3 | Distance decay relationship and interplays between prokaryotic community composition and environmental factors

To further analyze the spatial pattern of the prokaryotic community, we plotted community similarities based on the Bray-Curtis indices against distance matrices of Universal Transverse Mercator (UTM) coordinators (m), slope positions defined by the elevational gradient (m above sea level), and z-score scaled soil edaphic variables chosen through the “ordiR2step” function including pH, clay, temperature, NO_3^--N, MWC%, CEC, P, and VWC (“betapart”, "Vegan", “lattice”, and “permute” packages). For accurately representing the geographical distances with meter as unit, geographic coordinator points were converted to the projected coordinate system of UTM applying the “rgdal” and “sp” packages. UTM coordinators and elevational gradient distance matrices were fitted with the Bray-Curtis distance matrix using the generalized linear model (GLM) and plotted using the plot.decay function of the “betapart” package (Nekola & McGill, 2014). This was likewise done for the edaphic data and complemented by additional application of a power-law decay model. The goodness of decay model fits was computed as pseudo-R^2. GLM adjusted R^2 values (R_{adj}^2) were used as the coefficient determination and P values were calculated applying the F test. The relationships were additionally tested by Mantel tests based on Pearson's product-moment correlation coefficient applying the Bray-Curtis dissimilarity matrix against the respective environmental distance matrices. Plots were generated using the “ggplot2” package.

To identify the chief driving forces for individual bacterial families, Spearman correlations were computed between taxa and edaphic factors using the “Hmisc” package. Geographic distances (longitude, latitude, and slope position) of each field plot were included to capture additional spatial variables. Likewise, species richness estimators and alpha-diversity indices were correlated with these edaphic and spatial factors. P values were adjusted for multiple comparisons applying the Benjamini-Hochberg method with the “FSA” package. A clustered heatmap was drawn based on the calculated correlation coefficients applying the “pheatmap” package.

Redundancy analysis (RDA) was conducted to estimate the proportion of variation in prokaryotic community structure induced by environmental features (Vegan package). First, geographical coordinator points were included by constructing vectors of principal coordinates of neighbor matrices (PCNM). Later, the function “ordiR2step” in vegan (for z-score scaled edaphic variables) and “forward.sel” from the “adespatial” package (for PCNM vectors) was applied with 999 permutations for both functions to select a set of significant and nonredundant predictors for the spatial structuring of the soil prokaryotic community. Significant factors were selected for RDA to

determine the correlations between soil bacterial community structure and selected soil edaphic properties. Site and species scores were extracted from the RDA results and significant variables were plotted using the package "ggplot2".

The effects of four major factors (edaphic factors, spatial distance, slope position, agricultural management) on shaping prokaryotic community composition were comparatively assessed through variation partitioning analysis (VPA) based on RDA using the "Vegan" package. The significant vectors of weighted PCNM and significant soil edaphic variables were selected by the "ordiR2step" function and were included in this analysis. To add the impact of the agronomic practices, the "model.matrix" function in the vegan package was applied. R_{adj}^2 values were reported due to the unbalanced number of variables in each variable category. The significance of each R_{adj}^2 value was tested using ANOVA ("anova.cca" function of the vegan package). The proportions of variation in prokaryotic community composition were expressed by the R^2_{adj} values and attributed to the individual factors as well as spatially structured environmental variance (the interaction between spatial distance and soil edaphic properties), environmental variance structured by management practices (the interaction between soil physiochemical properties and management practices), and residual variance. Results are presented as Venn diagram using the "varpart" function of the "Vegan" package.

3 | RESULTS

3.1 | Implications of topography for soil physiochemical properties

Evaluation of the effect of slope position on soil physiochemical properties revealed that soils from up-slope and foot-slope plots differed significantly in most analyzed parameters except for Al, Na, Fe, and P contents (Table 1). Higher values for Ca, K, and Mg contents were observed in foot-slope plots (Table 1). Likewise, pH (ranging from 5.7 to 6.2 across entire samples), CEC (451 to 1033 cmol kg^{-1}), VWC (4.3 to 7.0%), NH_4^+-N (2.9 to 4.6 g kg^{-1}), and NO_3^--N (2.6 to 5.2 g kg^{-1}) mean values increased in foot-slope compared to up-slope plots. In agreement with N components, MWN% as well as MWC% were also significantly increased at the foot-slope position. Soil temperature was 1 °C higher in the west-facing foot-slope plots compared to the east-facing up-slope soils. Clay and silt contents were also significantly higher in the foot-slope soils, while sand content was increased among up-slope plots.

3.2 | Implications of agronomic practices for soil physiochemical properties

TABLE 1 Comparison of soil physiochemical properties associated with slope positions. Mean values (n = 48) and standard errors are given. Significant differences were assessed by one-way ANOVA. P_{adj} refers to a P-value corrected by the Benjamini-Hochberg method

Soil physiochemical properties		Foot-slope	Up-slope	ANOVA	
				F	P_{adj}
N_{min} [a]	g kg^{-1}	9.84 ± 0.47	5.54 ± 0.26	62.971	0.014**
NH_4^+-N	g kg^{-1}	4.61 ± 0.05	2.87 ± 0.04	48.718	0.010**
NO_3^--N	g kg^{-1}	5.20 ± 0.08	2.63 ± 0.06	32.236	0.010**
C/N [b]		13.39 ± 0.01	12.50 ± 0.02	23.123	0.025*
pH		6.19 ± 0.01	5.66 ± 0.01	53.015	0.010**
Ca	mg kg^{-1}	218.63 ± 0.88	37.15 ± 0.32	135.800	0.000***
K	mg kg^{-1}	14812.12 ± 0.40	1179.12 ± 0.71	16.207	0.001***
Al	mg kg^{-1}	4779 ± 23	4389 ± 16	1.769	0.229
Na	mg kg^{-1}	398 ± 0.95	303 ± 0.49	1.466	0.229
Fe	mg kg^{-1}	7796 ± 0.56	8010 ± 0.35	3.871	0.156
Mn	mg kg^{-1}	150.68 ± 0.33	219.26 ± 0.54	11.021	0.010**
Mg	mg kg^{-1}	827.89 ± 0.52	454.60 ± 0.20	50.945	0.014**
P	mg kg^{-1}	117.59 ± 0.22	134.17 ± 0.22	5.560	0.080
MWC [c]	%	0.65 ± 0.02	0.32 ± 0.01	90.133	0.000***
MWN [d]	%	0.05 ± 0.01	0.03 ± 0.00	105.670	0.000***
Clay	%	11.90 ± 0.11	6.99 ± 0.08	30.826	0.000***
Silt	%	8.54 ± 0.08	6.45 ± 0.08	9.811	0.014**
Sand	%	79.56 ± 0.06	86.58 ± 0.03	33.374	0.000***
CEC [e]	cmol kg^{-1}	1032.80 ± 0.93	451.10 ± 0.73	81.606	0.014**
VWC [f]	%	0.021 ± 0.00	0.019 ± 0.00	96.640	0.000***
Temperature	°C	35.48 ± 0.06	34.53 ± 0.05	125.350	0.000***

Significance codes: P < 0.05 '*', P < 0.01 '**'; P < 0.001 '***'

[a] N_{min} = mineral N

[b] C/N = C to N ratio

[c] MWC = mean mass of C %

[d] MWN = mean mass of N %

[e] CEC = cation exchange capacity

[f] VWC = volumetric water content

The initial assessment of the impact of agronomic practices on soil physicochemical properties was performed based on the full dataset, which unraveled the lower impact of agronomic practices on deriving soil edaphic variation compared to topography. We noticed very few significant changes related to the individual or interactive effects of agronomic practices (Table S1). Most remarkable was the interactive effect of slope × tillage on soil edaphic traits including pH, C/N, P, Mg, MWC%, and MWN%. Hence, the impact of the agronomic practices was further assessed for each slope position independently. The individual management regimes had limited impact and were only detected at foot-slope, evidenced by clay content responding to fertilizer treatments (Table 2).

However, ANOVA accompanied with LSD test did not ascertain significant differences for clay content at a specific N level (Table S2).

In addition to the individual effects, we noted a few interactive effects which significantly altered soil physiochemical characteristics, especially at the foot-slope position (Table 2). This included a tillage × rotation impact on N_{min}, NO_3^--N, MWN%, MWC%, and VWC. Besides, tillage × rotation affected the C/N ratio at the up-slope position. Tillage × rotation × fertilizer interactions merely changed the pH value of the soils in up-slope soils, while it affected clay content in foot-slope soils. A rotation × fertilizer effect was seen on NO_3^--N and clay content in foot-slope and on K content in up-slope soils.

3.3 | Effect of topographic attributes on prokaryotic community structure

Our results indicated significant impacts of slope position on prokaryotic diversity with higher richness ($F = 59.01$, $P < 0.001$), Chao1 ($F = 64.7$, $P < 0.001$), ACE ($F = 73.8$, $P < 0.001$), Shannon ($F = 33.1$, $P < 0.001$), and evenness ($F = 28.7$, $P < 0.001$) indices in foot-slope compared to up-slope soils (Table 3). Likewise, prokaryotic community composition was affected by topography as depicted in an NMDS plot (Figure 1a), with a distinct clustering of samples under slope position, whereby foot-slope samples deciphered a broader variation compared to up-slope soils. The slope position potential in driving variation of prokaryotic community composition was validated by ANOSIM with an R-value of 0.39 ($P = 0.001$) (Table 4). Irrespective of treatments Firmicutes, Actinobacteria, Proteobacteria, Acidobacteria, Bacteroidetes, Chloroflexi, Verrucomicrobia, Planctomycetes, Gemmatimonadetes, and some unclassified phyla accounted for almost 98% of all sequences in the samples (Figure 2). At the family level, Bacillaceae (29%) and Micrococcaceae (25.9%) dominated prokaryotic community composition (Figure S2). Remarkably, the relative abundance of Bacillaceae decreased (29.0% to 23.6%) from foot-slope toward up-slope plots while that of Micrococcaceae increased (9.1% to 25.8%).

TABLE 2 Statistical evaluation of the effect of agricultural practices on soil physiochemical properties in each slope position. Differences were assessed by three-way ANOVA, considering the strip-split-plot layout. The table reports F values with asterisks indicating significant P-values based on n = 24 for each level of tillage as well as rotation and n = 16 for each dosage of N fertilizer

Treatments	N_{min} [a] g kg^{-1}	C/N	K mg kg^{-1}	Na mg kg^{-1}	Fe mg kg^{-1}	MWN [b] %	MWC [c] %	pH	NO_3^--N g kg^{-1}	$^+NH_4$-N g kg^{-1}	Temperature °C
Up-slope											
Tillage	0.29	0.07	0.54	0.01	1.20	0.78	0.84	1.16	0.06	0.75	0.13
Rotation	0.13	1.59	0.04	0.17	0.20	0.09	0.18	0.36	0.08	2.08	0.73
Fertilizer	0.70	0.35	0.56	1.76	0.15	1.54	1.47	1.81	0.36	1.07	0.78
Tillage × Rotation	0.01	**6.25***	0.01	1.40	2.70	0.15	0.01	0.05	1.16	3.18	3.18
Tillage × Fertilizer	0.77	0.27	0.26	0.71	0.12	2.57	2.63	0.10	0.74	1.56	1.38
Rotation × Fertilizer	1.93	1.21	**3.60***	0.17	2.63	2.66	2.29	1.96	3.02	0.11	0.20
Tillage × Rotation × Fertilizer	1.88	1.29	0.83	0.74	3.31	3.08	2.80	**3.68***	2.19	0.49	1.25
Foot-slope											
Tillage	0.33	0.12	0.35	0.35	0.26	0.00	0.01	1.20	1.23	0.10	0.51
Rotation	0.00	0.00	1.28	1.23	0.62	0.06	0.07	0.46	0.00	0.00	0.33
Fertilizer	0.19	1.58	0.53	0.90	0.25	0.46	0.47	0.41	0.27	0.03	0.83
Tillage × Rotation	**4.59***	0.57	1.70	0.00	0.06	**3.63***	**3.75***	2.23	**5.22***	1.55	0.09
Tillage × Fertilizer	0.23	2.29	0.54	1.58	0.51	0.17	0.27	0.66	0.55	0.06	0.58
Rotation × Fertilizer	2.59	2.08	0.04	0.01	2.53	0.79	0.66	0.29	**4.29***	0.26	2.12
Tillage × Rotation × Fertilizer	0.78	3.25	0.44	1.35	2.77	1.24	1.53	0.75	0.40	1.25	1.09

Treatments	Mn mg kg^{-1}	Al mg kg^{-1}	Ca mg kg^{-1}	Mg mg kg^{-1}	P mg kg^{-1}	CEC [d] cmol kg^{-1}	Clay %	Silt %	Sand %	VWC [e] %
Up-slope										
Tillage	0.69	0.83	0.04	0.04	0.80	0.01	0.41	0.26	0.06	0.62
Rotation	0.73	0.02	0.62	0.05	1.19	0.26	0.18	0.02	0.06	0.21
Fertilizer	0.16	0.38	2.35	2.20	0.52	1.37	0.93	1.64	1.41	1.77
Tillage × Rotation	0.52	0.54	0.44	0.88	0.57	0.04	0.06	0.35	0.01	0.01
Tillage × Fertilizer	0.53	0.95	0.78	1.62	1.82	0.12	1.49	0.22	1.18	0.05
Rotation × Fertilizer	0.09	0.02	1.14	1.37	0.76	0.30	0.24	0.06	0.15	0.73
Tillage × Rotation × Fertilizer	0.18	1.22	1.44	1.58	2.29	0.42	1.05	0.16	0.35	1.12
Foot-slope										
Tillage	0.33	0.16	0.07	0.00	0.71	0.14	0.03	0.04	0.00	0.08
Rotation	0.63	0.04	0.20	0.88	0.72	0.05	1.36	0.34	0.09	0.81
Fertilizer	0.30	0.40	0.22	0.55	0.39	0.60	**8.76***	0.08	2.86	0.85
Tillage × Rotation	2.47	0.20	1.96	1.33	0.30	1.35	3.06	2.09	3.11	**4.15***
Tillage × Fertilizer	0.18	0.10	0.28	0.58	0.23	0.03	1.54	0.73	1.52	0.51
Rotation × Fertilizer	0.26	0.87	0.66	0.47	0.83	0.08	**8.47***	0.21	3.45	1.47
Tillage × Rotation × Fertilizer	0.63	1.06	0.73	1.40	0.15	2.05	**5.23***	0.93	1.86	0.11

Significance codes: P < 0.05 '*', P < 0.01 '**'; P < 0.001 '***'

[a] N_{min} = mineral N, [b] MWN = mean mass of N%, [c] MWC = mean mass of C%, [d] CEC = cation exchange capacity, [e] VWC = volumetric water content

Results

STAMP analysis was performed to systematically identify prokaryotic genera that contributed to the variation of community composition between foot- and up-slope soils. The analysis revealed a significantly higher abundance of 310 genera in foot-slope soils. However, merely 92 genera were more prominent in up-slope soils. An enrichment of diverse genera in the orders *Clostridiales, Bacillales, Rhizobiales,* and *Actinomycetales* (between 19 and 34 genera per order) was observed in foot-slope soils (Figure S3). In contrast, several other genera of the order *Actinomycetales* including the *Micrococcaceae* gained prominence in up-slope plots. Further genera that were enriched in foot-slope soils included ammonium-oxidizing archaea (*Nitrososphaeracae*) and bacteria (*Nitrosovibrio*), the nitrite-oxidizing genus *Nitrospira* and the N-fixing diazotrophic genera *Rhizobium* and *Bradyrhizobium*, as well as some methane cycling genera (*Methylosinus, Methylocaldum, Methylomicrobium*). Additionally, various anaerobic taxa appeared with higher relative abundance in soils of foot-slope plots (e.g. *Anaeroliinea, Anaerobacillus, Anoxybacter, Anaerovorax,* diverse members of the *Clostridiales*). Likewise, potential denitrifiers (e.g. known within the genera *Bacillus, Cytophaga, Flavobacterium, Geobacillus, Geobacter, Hyphomicrobium, Paracoccus Pseudomonas,* or *Rhizobium*), iron reducers (members of the family *Geobacteraceae* and *Anaeromyxobacter*), and sulfate reducers (*Desulfovibrio* and unclassified members of the *Desulfobacteraceae* and *Desulfobulbaceae*) were enriched there.

3.4 | Impacts of agronomic practices and their interactions on prokaryotic community structure

Similar to what we observed for soil physiochemical properties, topography had a striking stronger effect on prokaryotic diversity than the agronomic practices (Table S3). The impacts of the agronomic practices were also evaluated in detail within each slope position. The alpha diversity indices Chao1 and ACE responded significantly to the fertilizer application in up-slope soils (Table 5), with the highest dosage of N supporting higher diversity (Table S4). Furthermore, evenness and Shannon indices were affected by rotation × fertilizer interaction effects in up-slope plots (Table 5). No significant effects on richness and diversity were noticed following the agronomic practices in the foot-slope soils.

Results

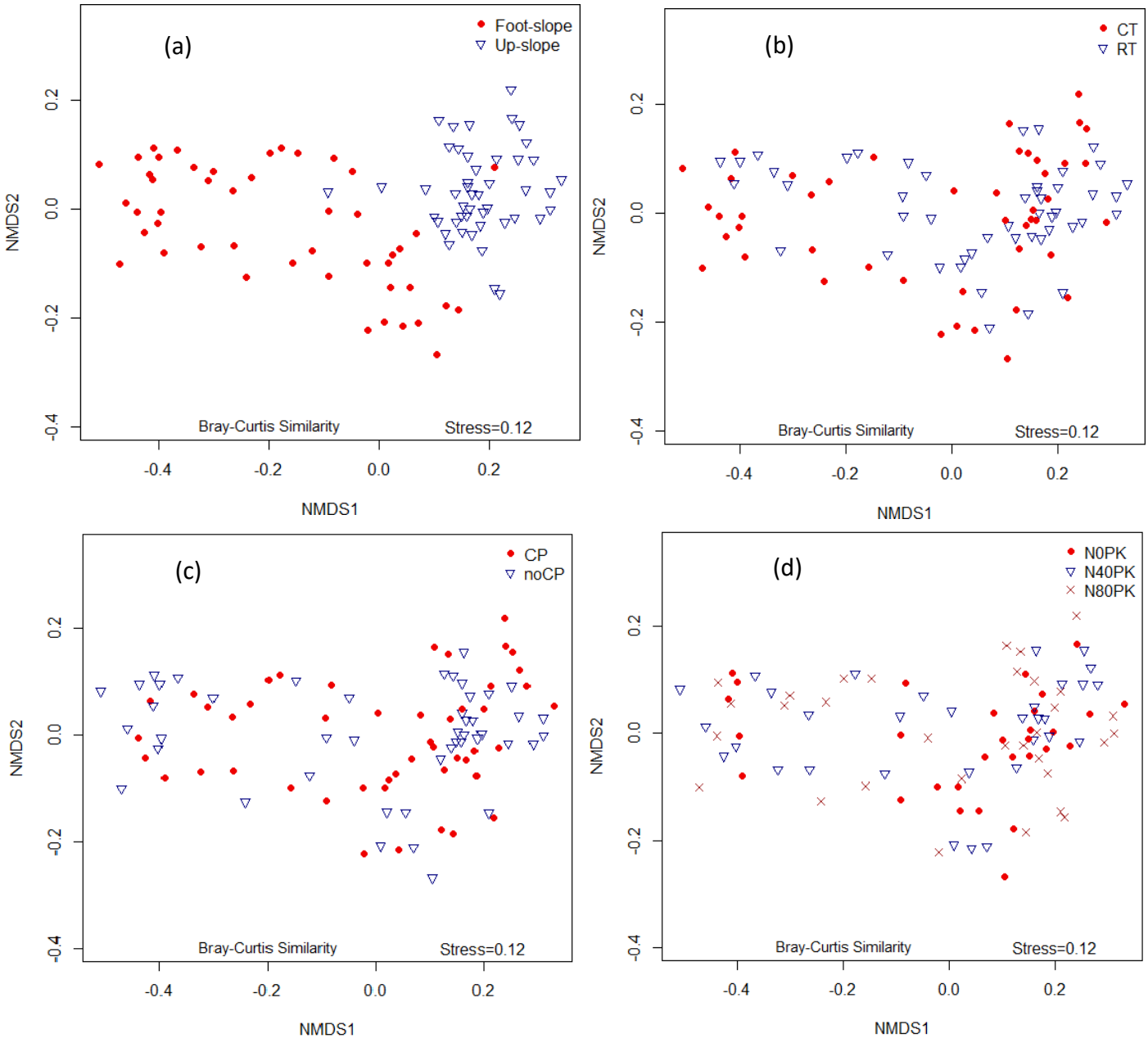

Figure 1 Non-metric multidimensional scaling (NMDS) plots to show variation in beta-diversity. Color coding according to slope position (a) or management practices (b-d). Agronomic practices include different tillage practices (b), rotation practices (c), and fertilizers with different rates of nitrogen (d). Tillage: conventional tillage (CT), reduced tillage (RT), rotation practices: residual management including cover crop (CP) and no residual management and no cover crop retention (noCP), fertilizers with different rates of nitrogen (N0PK, N40PK, and N80PK

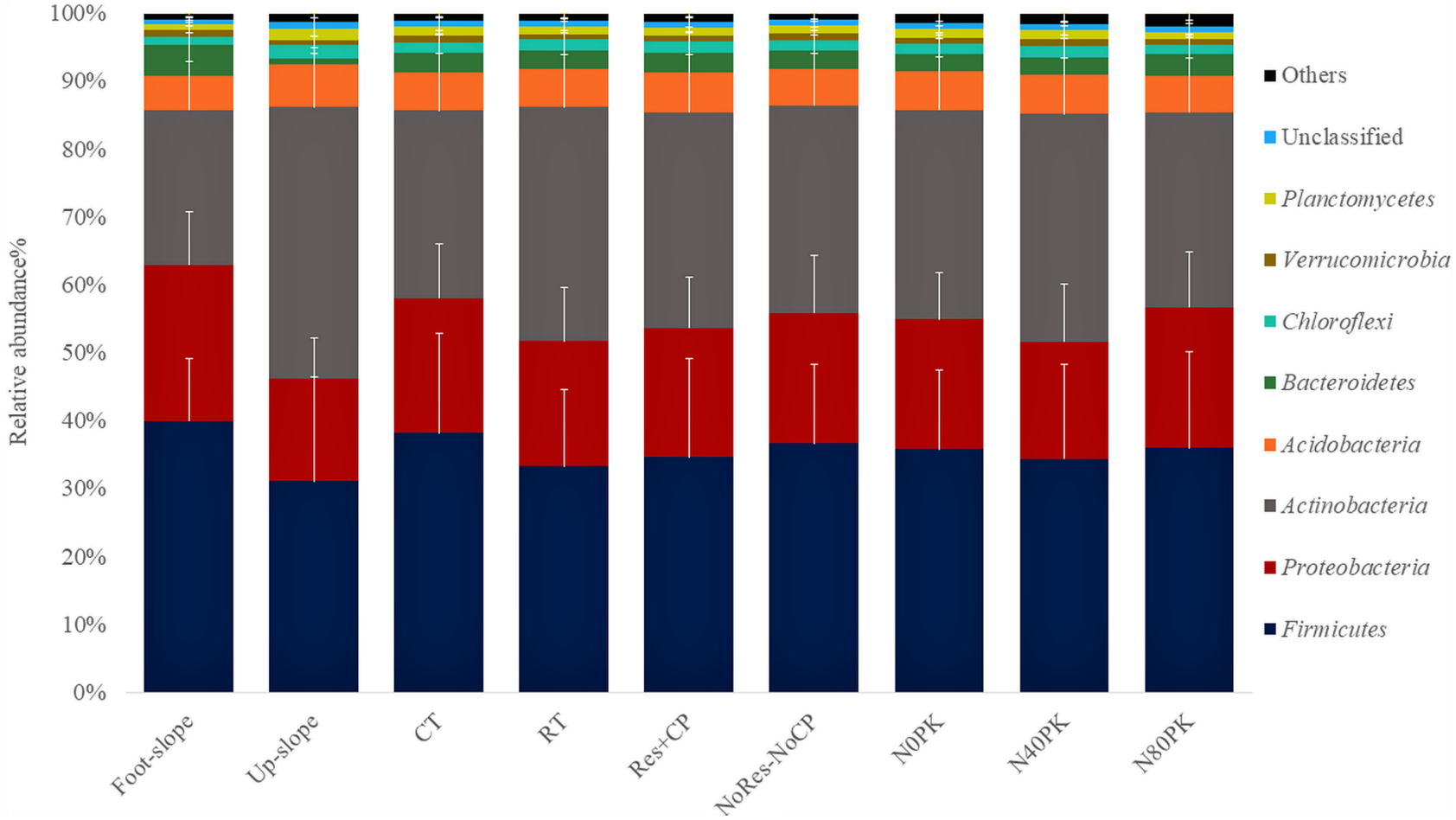

Figure 2 Taxonomic distribution of the eight dominant phyla (> 1%) in soil samples based on 16S rRNA gene sequence analysis. Samples are grouped by slope position (Foot, Up), tillage: conventional tillage (CT) and reduced tillage (RT), different crop rotation regimes: residual management including a cover crop (Res+CP) and no residual management and no cover crop retention (NoRes-NoCP), and fertilizers with different rates of nitrogen (N0PK, N40PK and N80PK). Phyla with ≤ 1% relative abundance are grouped as "Others"

TABLE 3 Comparison alpha diversity indices affected by slope position. Mean values (n = 48) and standard errors are given. Differences were assessed by one-way ANOVA (P_{adj} calculated by Benjamini-Hochberg method)

Alpha diversity indices	Foot-slope	Up-slope	ANOVA	
			F	P_{adj}
Richness	4826 ± 73	3913 ± 98	59.069	0.000***
Chao1	16194 ± 27	12895 ± 32	64.700	0.000***
ACE	18275 ± 31	14264 ± 36	73.811	0.000***
Evenness	0.70 ± 0.01	0.63 ± 0.01	28.676	0.000***
Shannon	5.20 ± 0.12	5.07 ± 0.07	33.095	0.000***

*** Significant with P < 0.001

TABLE 4 Variation of prokaryotic community structure affected by field topography and individual agronomic practices. Analysis of similarity (ANOSIM) was done based on taxonomic similarity using a Bray-Curtis distance matrix. Significant differences are highlighted in bold

Factors	n	R	P
All samples			
Slope position	96	**0.391**	**0.001**
Tillage	48	**0.066**	**0.006**
Rotation	48	0.033	0.051
Fertilizer	36	-0.007	0.617
Up-slope samples			
Tillage	24	0.020	0.190
Rotation	24	**0.110**	**0.009**
Fertilizer	16	0.011	0.303
Foot-slope samples			
Tillage	24	**0.109**	**0.003**
Rotation	24	-0.021	0.793
Fertilizer	16	0.023	0.183

Ordinating community similarities in NMDS plots (Figure 1b-d) showed no manifested separation of samples according to agronomic practices, while ANOSIM indicated a significant though weak effect of tillage ($R = 0.07$, $P < 0.006$) (Table 4). ANOSIM performed for each slope position independently revealed that tillage affected beta-diversity solely in the foot-slope samples ($R = 0.11$, $P = 0.003$). Additionally, this data subset showed that the prokaryotic community structure responded to the rotation treatment in up-slope soils ($R = 0.11$, $P = 0.009$) (Table 4). These findings were confirmed by ADONIS (Table S5), which was performed in addition to ANOSIM to evaluate interactive effects. However, no significant interactions between management practices were noticed.

3.5 | Interplay between environmental features, and prokaryotic community structure

As topography imposed profound changes on soil edaphic properties and the prokaryotic community, possible correlations between soil physiochemical shifts and prokaryotic community structure were studied. The alpha diversity indices showed significant positive correlations to several soil properties according to Spearman's rank correlation coefficient analysis (Figure S4). All indices showed positive correlations with soil MWC%, MWN%, VWC, pH, Ca, Mg, K, CEC, N_{min}, NH_4^+-N, NO_3^--N contents, and temperature (Figure S4). Moreover, they were all negatively correlated with latitude and elevation, the latter as a proxy for topography.

To evaluate the relationship between the variation of soil physiochemical properties and prokaryotic beta-diversity, an environmental distance matrix was fitted to the OTU Bray-Curtis distance matrix. The negative slope of a best fitted power model (slope = -0.25, $R^2 = 0.215$, $P < 0.001$) significantly explained the decay in prokaryotic community similarity with increasing soil edaphic heterogeneity (Figure 3a). Redundancy analysis (RDA) was carried out to identify soil traits that were strongly linked to the variation in prokaryotic community composition. The most important explanatory variables according to "ordiR2step" included MWC% ($R^2_{adj} = 0.08$, $P < 0.002$, $F = 9.21$), temperature ($R^2_{adj} = 0.12$, $P < 0.01$, $F = 1.72$), P ($R^2_{adj} = 0.11$, $P < 0.002$, $F = 2.61$), pH ($R^2_{adj} = 0.10$, $P < 0.002$, $F = 2.64$), NO_3^--N ($R^2_{adj} = 0.13$, $P < 0.018$, $F = 1.60$), VWC ($R^2_{adj} = 0.09$, $P = 0.002$, $F = 9.21$), CEC ($R^2_{adj} = 0.13$, $P < 0.002$, $F = 1.59$), and clay content ($R^2_{adj} = 0.13$, $P < 0.068$, $F = 1.33$).

TABLE 5 Management practices and their interaction effects on alpha diversity and richness indices in fields within each slope position. Statistical differences are reported as F-values with asterisks indicating significance levels according to three-way ANOVA, considering the strip-split-plot design

Treatments	Richness	Chao1	ACE	Evenness	Shannon
Up-slope					
Tillage	0.027	0.015	0.091	0.005	0.011
Rotation	0.198	0.160	0.066	0.777	0.711
Fertilizer	2.872	**4.685***	**4.873***	2.741	2.796
Tillage × Rotation	0.084	0.118	0.998	0.037	0.049
Tillage × Fertilizer	0.414	0.052	0.091	0.575	0.563
Rotation × Fertilizer	**3.009***	2.136	2.605	**4.613***	**4.438***
Tillage × Rotation × Fertilizer	1.267	0.652	1.136	1.031	1.077
Foot-slope					
Tillage	0.017	0.022	0.039	0.151	0.106
Rotation	0.600	0.058	0.059	1.147	1.107
Fertilizer	1.543	1.751	1.750	0.832	0.964
Tillage × Rotation	0.096	0.674	0.722	0.235	0.148
Tillage × Fertilizer	0.634	0.825	0.705	0.181	0.150
Rotation × Fertilizer	0.854	0.399	0.244	0.585	0.651
Tillage × Rotation × Fertilizer	0.665	0.822	1.085	0.502	0.510

* Significant with $P < 0.05$

The significant soil physiochemical properties explained 31.6% and 11.1% of the variation in community composition as resolved along the first two axes in an RDA biplot (Figure 4), where samples were distinctly clustered according to slope position. Soil temperature showed the best fit with the sample clustering, whereby foot-slope samples were characterized by higher temperature. Likewise, MWC%, P, pH, NO_3^--N, VWC, CEC, and clay content showed a correlation with higher values linked to foot-slope samples. P content did not rely on topography, which became evident through the rectangular arrangement of its arrow in relation to other arrows.

Lastly, the relationship between the relative abundance of dominant families to the variation of soil physiochemical properties was investigated by Spearman's correlations (Figure 5). The symbiotic diazotrophic *Bradyrhizobiaceae* and the anaerobic *Syntrophobacteraceae* showed the strongest positive correlations, primarily to soil MWN%, MWC%, Mg, Ca, K, NO_3^--N, N_{min}, pH, CEC, and temperature. Other *Proteobacteria* such as *Erythrobacteraceae*, *Hyphomicrobiaceae*, *Xanthomonadaceae*, *Comamonadaceae*, as well as *Paenibacillaceae*, and *Planococcaceae* (both *Firmicutes*) showed such positive relationships to most of these soil traits. The *Micrococcaceae* showed opposite correlations to several of these soil properties including MWN%, MWC%, Mg, Ca, pH, K, NO_3^--N, N_{min}, and temperature. Such opposite correlations were also seen for *Koribacteraceae*, and *Intrasporangiaceae* (Figure 5). Due to the limited impact of management

practices on prokaryotic community composition, correlations between soil edaphic properties and community compositional data were not further explored for agronomic practices within each slope position.

3.6 | Identification and comparative assessment of major deterministic factors shaping prokaryotic community composition

Effects of spatial distance and slope position on prokaryotic community assemblage were assessed based on correlations between distance matrices (Figure 3b-c). Mantel tests revealed significant findings with $R = 0.25$ ($P < 0.001$) for the correlation of community compositional differences with spatial distance and $R = 0.38$ ($P < 0.001$) with elevation, which reflects topography. Plots displaying community similarity versus geographic or elevational distances revealed negative relationships in both cases. The generalized linear model confirmed the slightly negative slope for spatial distance (slope = -0.001, $R^2 = 0.07$, $P < 0.01$) and a stronger significant negative relationship with elevational gradients (slope = -0.03, $R^2 = 0.15$, $P < 0.01$). Following these findings, the relevance of spatial and elevational distance to the other influential factors, i.e. edaphic factors and agronomic practices, was investigated comparatively by VPA (Figure 6). To this end, the six selected significant PCNM vectors, the eight most relevant soil edaphic properties as identified by RDA, as well as elevation and management practices were included as major deterministic factors. The analysis revealed that the prokaryotic community structure was dependent upon all four intercorrelated variable groups, which overall explained 38% of the variation in prokaryotic community composition, while 62% was left unexplained. All evaluated variable groups except for agronomic practices (1.3%) had statistically significant roles in structuring the prokaryotic community assemblages with soil edaphic properties (14.5%) being most relevant, followed by slope position (11.3%), and spatial distance (10.8%). The pure effects of these four factors accounted for 2.1%, 1.5%, 6.0%, and 0.14% of the variation, respectively. The highest co-variation (9.2%) was seen between soil physicochemical traits and slope position.

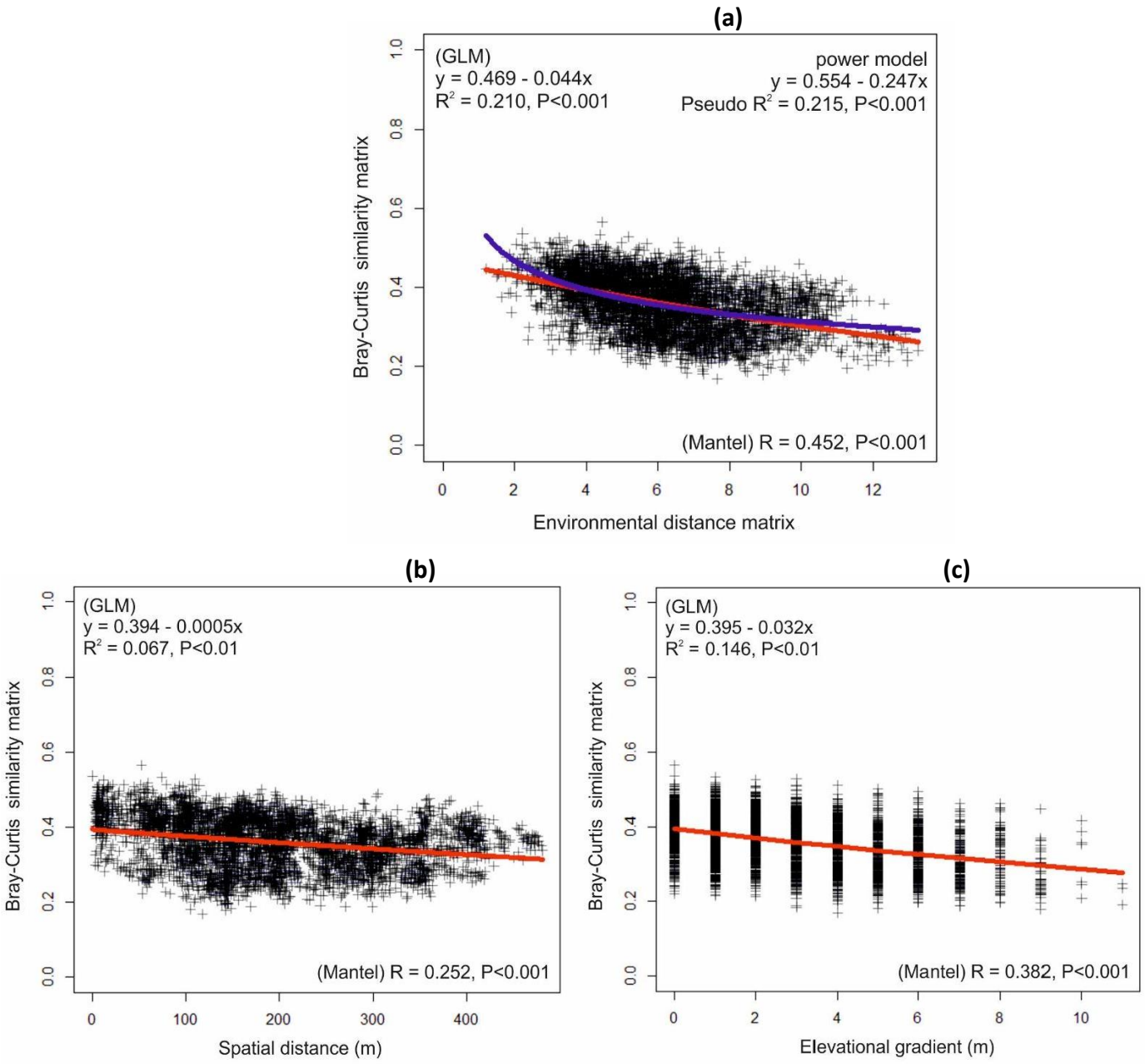

Figure 3 Distance-decay curves showing the relationship between bacterial community similarities (based on comparisons of OTU profiles using the Bray-Curtis dissimilarity index) against distance matrices reflecting soil physiochemical properties (a), spatial distances between plots of sampling (b), and slope positions defined by the elevational gradient (c). Distance-decay curves were calculated based on linear regression (red) and for soil properties additionally based on the best-fitted power model (blue). The regression slopes of the linear relationships based on the Gaussian generalized linear model (GLM) are shown with (statistically non-significant) lines. Linear regressions were tested with a probability estimate for significance. Mantel tests with 9999 permutations, using the Bray-Curtis dissimilarity matrix, were additionally performed

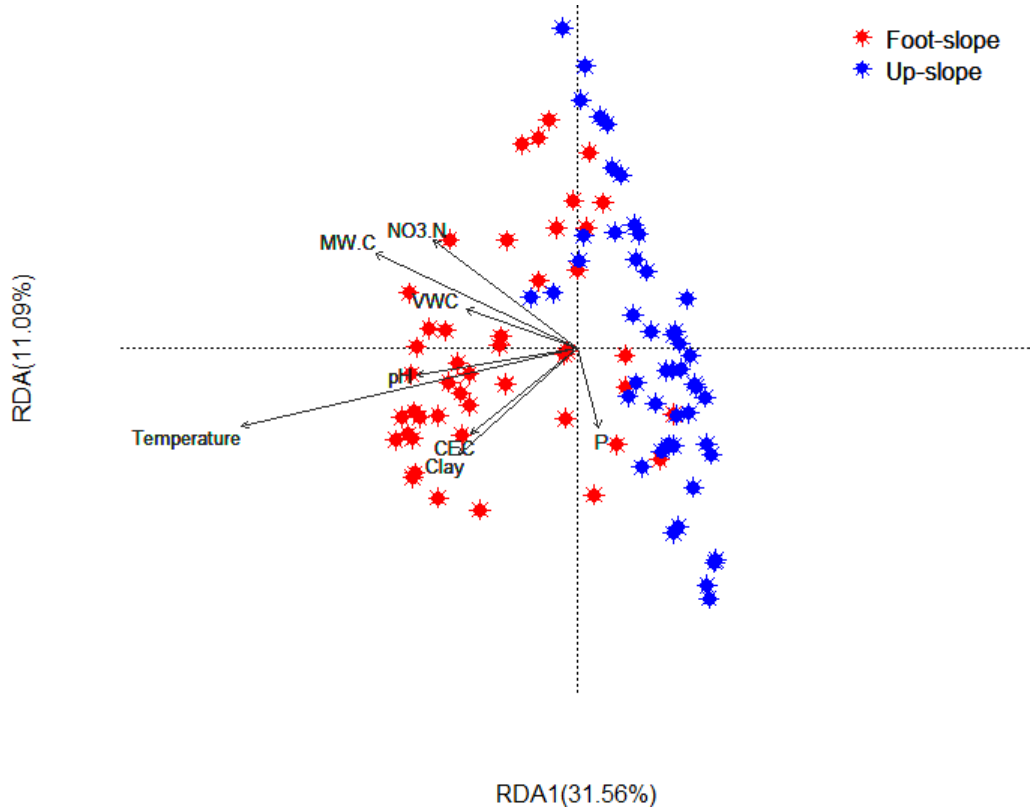

Figure 4 Redundancy analysis (RDA) of soil bacterial community composition constrained by soil physio-chemical properties. Red dots represent the foot-slope and blue dots the up-slope sites. Relevant soil properties were chosen based on the "ordiR2step" function and are shown as arrows. They represent quantitative explanatory variables with arrowheads indicating the direction of increasing "bp" scores. MW.C= mean C%, NO3.N = NO_3^--N, CEC = cation exchange capacity, VWC = volumetric water content, and P = phosphorus

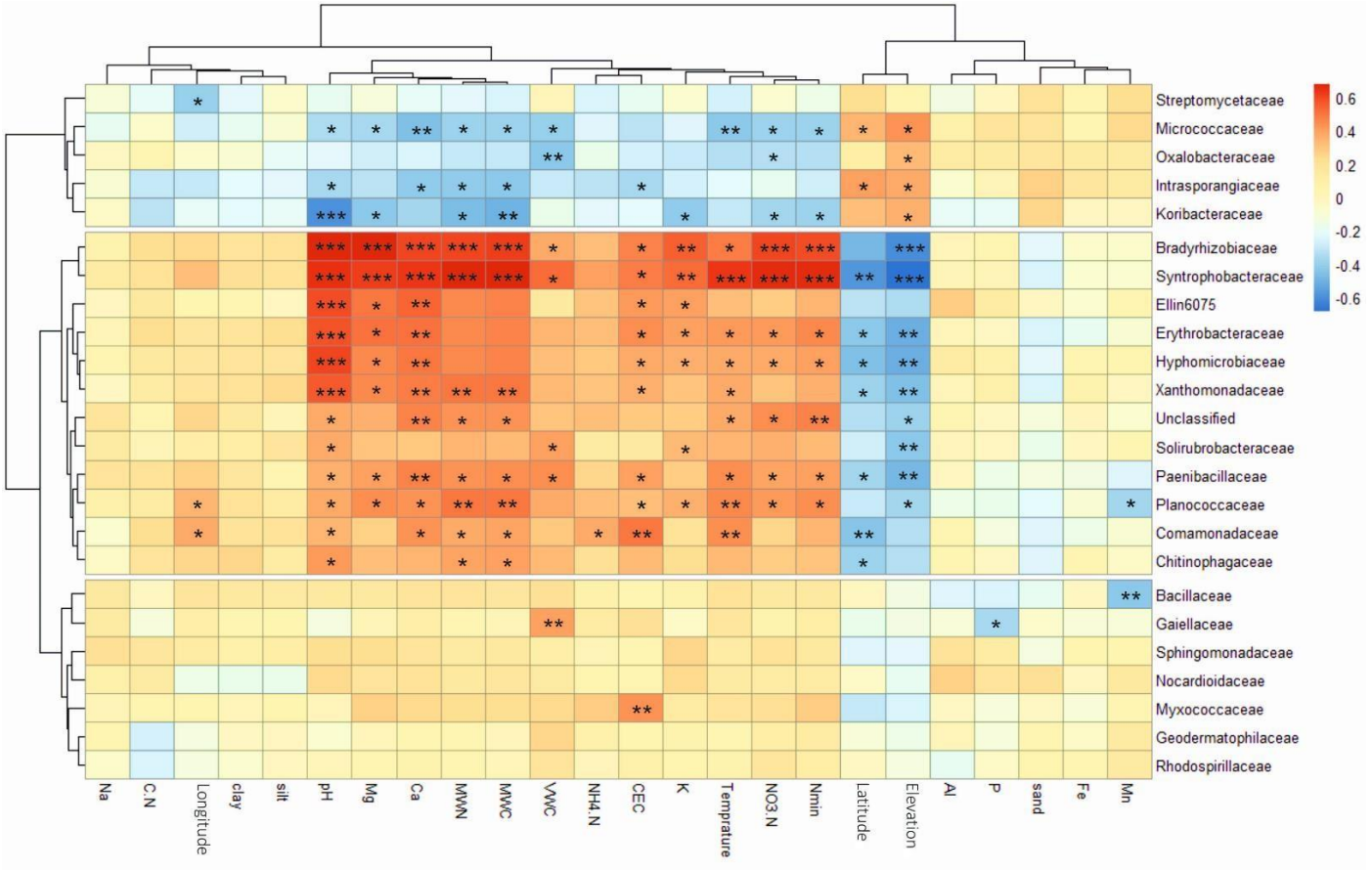

Figure 5 Heatmap showing the correlation of the abundant (>1% relative abundance) soil bacterial families with environmental factors applying Spearman correlation analysis. Values of Spearman correlation coefficients are colored from red (positive) to blue (negative). Slope positions are defined by elevation. Dendrograms indicate the grouping of bacterial families with similar response patterns to the environmental parameters. Likewise, environmental parameters with similar correlation patterns to bacterial families are clustered. Both dendrograms are based on Euclidean distances and were constructed by the complete method of agglomerative hierarchical clustering, hclust, algorithm. P values were adjusted for multiple comparisons by the Benjamini-Hochberg method.
(*Significant at the 0.05 level,
**Significant at the 0.01 level,
***Significant at the 0.001 level)

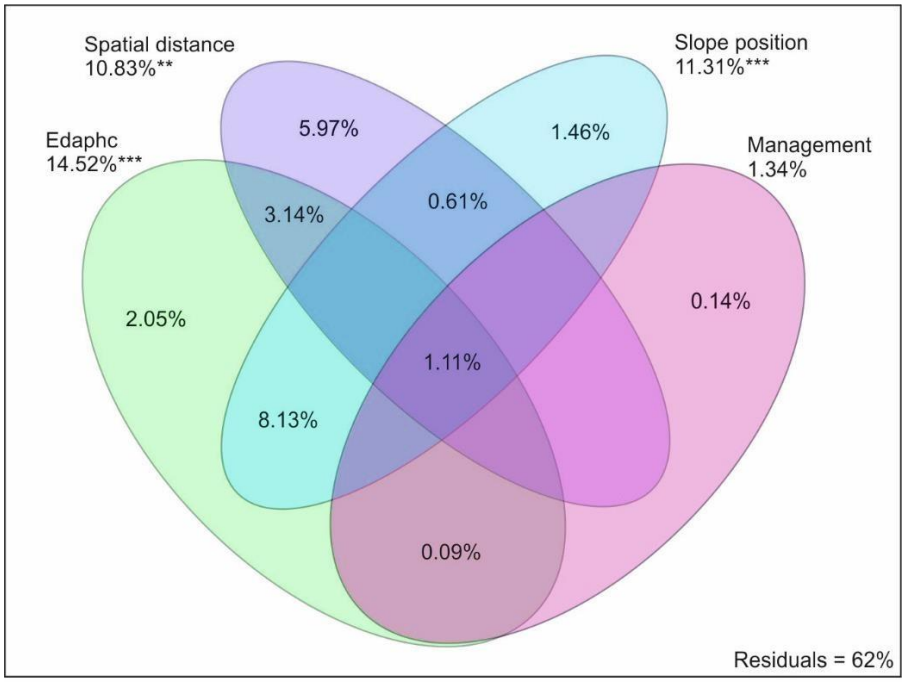

Figure 6 Venn diagram representing the contribution of soil edaphic properties (significant chemical and physical properties including MWC%, temperature, P, pH, NO_3^--N, VWC, CEC, and clay content), management practices, spatial distance (6 significant PCNM vectors), and slope position on the variation of bacterial community composition. The values outside the overlapping circles represent the total contribution of each group of variables. Adjusted R^2 values are reported for individual contributors. Asterisks show the significance on each contributor according to ANOVA ($P < 0.01$ '**' ; $P < 0.001$ '***')

4 | DISCUSSION

4.1 | Topography induced shifts in the soil abiotic properties and the soil microbiota

Topography caused striking differences in soil physiochemical properties among foot-slope and up-slope soils. The higher content of clay particles and basic elements such as Mg, K, Mn, and Ca at the depositional position (Table 1) suggests that erosion is likely to have occurred at our study site. Translocation and deposition of basic elements into foot-slope position has been reported previously (Seibert et al., 2007; Lal & Stewart, 2019). These and the further observed shifts in soil physiochemical properties between foot-slope and up-slope are in agreement with literature reports, therewith emphasizing the profound potential of slope position in explaining soil physiochemical heterogeneity including soil organic C (Lal, 2003; Mayer et al., 2018), moisture (Western et al., 2004), texture (Xu et al., 2016), total C and N, C/N ratio as well as pH (Seibert et al., 2007) at our

study site. Erosion processes reduce the physical protection of SOC at eroding sites and simultaneously accumulate higher C and N contents at the depositional sites (Gómez et al., 2020; Shi et al., 2019). This can explain the higher MWC% and MWN% values determined at our foot-slope plots (Table 1).

It is widely known that eroding sites adversely impact soil microbial diversity, primarily due to the redistribution of sediments and soil nutrients along the slope (Du et al., 2020; Huang et al., 2013; Liu et al., 2018). We noticed higher bacterial richness and diversity at our depositional site (Table 3), which was closely associated with the accrual of soil nutrients at the foot-slope position (Figure S4). Enrichment of organic matter and soil nutrients are known to support bacterial diversity at foot-slope sites (Du et al., 2020; Neupane et al., 2019). Other processes that can support diverse prokaryotic communities at the depositional sites are related to the translocation of soil particles during erosion. Specifically, clay, which is inhabited by multifarious microbial species, will be translocated by the overland runoff (Huang et al., 2013), and can introduce new bacterial species to the depositional sites. Simultaneously, the translocated sediment can provide secure niches for colonization of the introduced prokaryotes (Du et al., 2020). Moreover, higher clay contents at the depositional sites can contribute to the formation of more anoxic microsites in the more frequently waterlogged depositional sites (Keiluweit et al., 2018). This can support the development of a more diverse bacterial community (Pett-Ridge & Firestone, 2005).

Slope position also appeared to be the chief underlying force behind shifts in prokaryotic community structure at our field scale, evidenced by NMDS plots and ANOSIM results (Table 4 and Figure 1). This is in line with other studies reporting a tight association between topography and prokaryotic community structure (Huang et al., 2013; Hargreaves et al., 2015; Neupane et al., 2019). Differences in prokaryotic life strategies can explain such topographic-induced discrepancies (Hargreaves et al., 2015; Neupane et al., 2019; Suriyavirun et al., 2019).

In the current study, *Bacillaceae* (with the prevalence of *Anaerobacillus*) were dominant in fortified foot-slope soils, which corresponds to their copiotrophic life strategy (Mandic-Mulec et al., 2015). Contrarily, *Micrococcaceae* (with a prevalence of *Arthrobacter*) as a subdivision of *Actinomycetales* were favored in up-slope soils. *Actinobacteria* are known to be excellently capable of surviving under growth-limiting, harsh, and drought conditions (Delgado-Baquerizo et al., 2018), which can support their higher abundance in eroding up-slope soils. We also evidenced an increase in the

relative abundance of nitrogen cycling prokaryotes at foot-slope positions in tandem with higher availability of NH_4^+-N and NO_3^--N. This may come along with higher nitrification and denitrification rates in the foot-slope plots (Pett-Ridge & Firestone, 2005; Xu et al., 2021). In addition to the higher relative abundance of the denitrifiers, other anaerobic bacteria such as fermentative microorganisms, iron-, and sulfate-reducing bacteria were also enriched in foot-slope soils, which indicates a recurrent occurrence of anoxic conditions in the foot-slope soils. Anoxic conditions are tightly linked to higher soil water contents (Pett-Ridge & Firestone 2005). In this study, differences in VWC were slightly higher at the depositional site compared to the up-slope position (Table 1). However, we did only a one-time measurement and differences might be periodically stronger over a whole season. In line with our findings, similar changes in prokaryotic community structure in relation to topography including enrichment of anaerobic bacteria in depressional soils have been reported elsewhere (Frindte et al. 2019, Suriyavirun et al. 2019). Taken together, soil physiochemical characteristics, including soil carbon and nutrient status, VWC, as well as soil texture, are affected by topography and have consequences for the soil prokaryotic community structure. These were evident as shifts in soil diversity and physiological adaptations to nutrient redistribution and oxygen availability.

4.2 | Slope-specific agricultural induced changes in soil abiotic properties and the prokaryotic community

The effects of agronomic practices on soil abiotic properties were largely slope-dependent, e.g. evident from several slope × tillage interaction effects that were observed (Table S1). Merely a handful of soil traits were significantly altered due to the application of agronomic practices with no consistent response in both slope positions (Table 2). In the same manner, the effects of agronomic practices on the prokaryotic community structure became evident merely for a restricted number of agronomic practices and solely among up-slope plots, where the application of N fertilizer increased the Chao1 and ACE indices at the highest N-level. Moreover, rotation × N fertilizer interaction affected bacterial richness, evenness, and Shannon indices (Table 5). Copious studies have exploited the fact that crop residues along with the application of N fertilizer are capable of boosting soil C and N inputs due primarily to higher organic residue deposition within the field (Adiku et al., 2008; Lupwayi et al., 2018; Verzeaux et al., 2016; You et al., 2020). According to Lupwayi et al. (2018), the appropriate application of mineral N fertilizer accompanied with the effective turnover of organic

amendments such as cover crops is vital in supporting the diversity of soil bacteria. Likewise, the application of cover crops for the fallow period in Ghanaian agricultural systems has been reported to favor fostering a diverse bacterial community (Asuming-Brempong et al., 2008; Sul et al., 2013). These effects are likely to be more relevant to the more nutrient deficient up-slope soils rather than to the foot-slope soils. Furthermore, an impact of rotation management was seen in the prokaryotic community composition in up-slope soils (Table 4 and Table S5). Such changes can be expected and are often explained by higher SOM levels, which occur upon residue incorporation into the soil, leading to the increase in soil microbial diversity and shifts in community structure (Lupwayi et al., 2018; Navarro-Noya et al., 2013; Sul et al., 2013).

In foot-slope soils, the effects of management practices on the prokaryotic community structure were primarily seen in response to tillage practice (Table 4). Although soil properties were not responsive to the pure tillage practice in the same soils, the tillage × rotation interaction affected MWC%, MWN%, N_{min}, and NO_3^--N as well as VWC (Table 2) and modulated the soil nutrient and possibly the oxygen status at the foot-slope position. It is well known that plowing leads to a change in anoxic-oxic transitions and can alter the quality and physical accessibility of C, thus stimulating heterotrophic microbial activities and SOC oxidation (Horwath & Paul, 2015; Zhao et al., 2020b). Moreover, tillage causes closer contact between unprotected organic matter and fast-growing bacteria as well as other consumers (Horwath, 2007; Horwath & Paul, 2015) and therefore facilitates the incorporation of SOC by the soil microbiota. These facts correspond well to a recent study, reporting elevated CO_2 emissions and higher denitrification rates at foot-slope positions in response to tillage, in tandem with nutrient enrichment at the depositional site (Xu et al., 2021). These effects can induce shifts in the soil microbial life strategies in favor of copiotrophic taxa and therewith community compositional changes (Lupwayi et al., 2017; Navarro-Noya et al., 2013; Ramirez-Villanueva et al., 2015; Wang et al., 2020a), which were more predominant in the foot-slope than upslope-soils in our study, as discussed before. The exclusive response of the prokaryotic community to tillage practice at the foot-slope position might thus be related to the resident soil microbiome and the higher carbon stock stored within foot-slope soils (Table 1), which may support faster growth and stronger microbial responses to tillage than in up-slope soils (Horwath, 2007; Horwath & Paul, 2015; Xu et al., 2021).

4.3 | Combined and comparative effects of topography and agronomic practices on soil abiotic properties and microbiota

Despite the rather weak impact of agronomic practices, our data clearly manifested that the effects of the agronomic practices were largely slope-dependent, as hypothesized. This is reflected in different interactive responses of the soil properties. Among the interactive effects slope × tillage and slope × rotation interactions effectively altered soil physiochemical characteristics, whereby especially slope × tillage affected several soil edaphic properties (Table S1). This was in part reflected in the soil prokaryotic community structure, which was solely responsive to tillage at foot-slope (Table 4). However, the effect of slope × tillage interaction on the soil microbiota remained just above the significance threshold (Table S5). A similar topographic-dependent response in the soil microbiota was noted for the rotation management, which was revealed to be significant merely at the up-slope position (Table 4). However, crop rotation with residue return at the up-slope position did not lead to a shift in soil edaphic properties (Table 2). This contrast may be explained by the 4-year-period the field experiment was ongoing before sample collection and the fact that samples were taken six months after the latest sorghum and cowpea residues were incorporated into the soil. Residue return may have left a detectable footprint on the prokaryotic community structure as a kind of legacy effect, but it may not yet have induced long-lasting shifts in soil edaphic properties.

Unexpectedly, the effects of the agronomic practices remained rather weak, and the pertinent interactive effects were sporadically observed. These overall rather weak implications of agronomic practices for the soil microbiota can be defined through some theories. Homogenization of soil microbiota which may be ascribed to a homogenizing nature of the agronomic practices (Rodrigues et al., 2013). In addition, spatial heterogeneity at the study site, which explained 11% of the variation in community composition (Figure 6), might have concealed the effects of other factors. Moreover, heterogenous cropping regimes prior to initiating our experiment may have modulated responses in individual plots, resulting in plot-specific and thus heterogeneous responses. Lastly, the period of four years over which the new management regimes were applied to the field until sample collection occurred placed the focus on short-term responses of the prokaryotic communities.

4.4 | Underlying factors for variation in soil prokaryotic community composition

To shed light on all possible factors affecting prokaryotic community composition, we additionally explored the role of spatial patterns (Frey, 2015) at the scale of our study field. The distance decay relationship was significant (Figure 3b) and spatial distance explained 10.8% of the variation in prokaryotic community composition (Figure 6). Our findings concurred with those of Chen et al. (2017), Durrer et al. (2017), Liu et al. (2020), Malard et al. (2019), Neupane et al. (2019), and Zhao et al. (2020a) who reported the presence of spatial autocorrelation and microbial biogeographical patterns in farmlands. The high contribution of soil edaphic heterogeneity was the common aspect between their findings and ours. We also observed a high overlap of soil edaphic properties with slope position (9.2%, Figure 6), which agrees with the clear effects of topography on soil physiochemical properties, and presence of strong bonds between soil properties and prokaryotic community composition (Figure 5). This underlines the relevance of geomorphic patterns in distributing prokaryotic community composition in sloping farmlands, which shapes soil microbiota primarily via soil edaphic properties.

Among the soil physiochemical properties, soil pH, clay, temperature, MWC%, VWC, CEC, and NO_3^--N were the key elements in shaping prokaryotic community composition and diversity (Figure 4, Figure 5, and Figure S4). The given soil properties are known to influence bacterial community composition, e.g. pH (Neupane et al., 2019; Wang et al., 2020a; Zhao et al., 2020a) MWC% and MWN% (Xue et al., 2020; Zhang et al., 2016), NO_3^--N (Shen et al., 2016; Zhao et al., 2020a), CEC (Docherty et al., 2015; Holland et al., 2016), temperature (Bahram et al., 2018; Frindte et al., 2019), and soil texture (Holland et al., 2016; Neupane et al., 2019). These soil physiochemical properties determine the soil nutrient and redox status, which correspond very well to the enrichment of anaerobic as well as copiotrophic microorganisms at the foot-slope position, as discussed above. This dependency is also reflected in strong correlations between dominant families and these soil physicochemical properties (Figure 5). The strongest positive correlations with diverse soil physiochemical properties were observed for the anaerobic sulfide-reducing *Syntrophobacteraceae*. Besides, a strong positive correlation of several taxa was seen with soil pH, which is a well-known influential factor for soil microorganisms (Delgado-Baquerizo et al., 2018; Rousk et al., 2010). Families that responded negatively to increasing soil nutrient levels (e.g. MWC%, MWN%, N_{min}, NO_3^--N or NH_4^+-N), were primarily members of the phyla *Actinobacteria* (*Micrococcaceae*, *Intrasporangiaceae*) or *Acidobacteria* (*Koribacteraceae*), which have been reported to represent

rather oligotrophic phyla adapted to harsh environments (Delgado-Baquerizo et al., 2018; Fierer et al., 2007; Zhang et al., 2016). This correlative analysis at the family level confirms our conclusions on selective mechanisms resulting in topographic-induced variations in the prokaryotic community composition. However, as correlations are not necessarily the result of causality and adaptations not necessarily manifested at the family level, this aspect deserves further appraisal in future studies.

5 | CONCLUSION

Topography was found to be the predominant influence on soil physiochemical heterogeneity and thus prokaryotic community structure. The extent of agronomic management impacts was contingent upon topography for the soil properties. The integrated impact of slope × tillage, known as a trigger of accelerated erosion, changed the soil physiochemical properties most evidently. The responses of the prokaryotic community to agronomic managements were brightly dependent upon topography. This was evident from the effectiveness of tillage, merely at the foot-slope position, and residue management at the up-slope position in structuring prokaryotic community. Compared to up-slope, depositional foot-slope soils featured higher bacterial richness and diversity. The higher relative abundance of copiotrophic *Bacillaceae* and anaerobic genera in occasionally waterlogged foot-slope soils vs. the predominance of *Micrococcaceae* in up-slope soils asserted our hypothesis regarding the striking imprints of topography on prokaryotic community assemblages. We also delineated a geomorphic pattern of distribution for prokaryotic communities at our field scale with soil physiochemical properties as relevant underlying factor of this systematic distribution. Overall, the soil microbiota was in a tight relationship with soil edaphic properties. Together, these findings help to retain soil microbiota in favor of sustainable agriculture in sloping farmlands by implementing appropriate management practices, which needs to be defined in relation to farmland geomorphic characteristics.

DECLARATION OF COMPETING INTEREST

The authors state that there is no conflict of interest.

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Supplemental materials

TABLE S1 Individual and combined effects of topography and management practices on soil physiochemical properties, evaluated by statistical analysis using a linear mixed model (Type III Analysis of Variance with Kenward-Roger method is shown). The table shows F-values and indicates the significance of the individual influence factors and their interactions using asterisks

Fixed factors	pH	C/N	VWC [a] %	Temp [b] °C	CEC [c] cmol kg^{-1}	N_{min} [d] g kg^{-1}	NO_3^--N g kg^{-1}	NH_4^+-N g kg^{-1}	Na mg kg^{-1}	K mg kg^{-1}	Fe mg kg^{-1}	Mn mg kg^{-1}	Al mg kg^{-1}	Ca mg kg^{-1}	Mg mg kg^{-1}	P mg kg^{-1}	MWC [e] %	MWN [f] %	Clay %	Silt %	Sand %
Slope	14.3***	17.8***	8.4**	120.5***	6.1*	12.9**	8.5**	10.8**	5.5*	10.0**	0.1	0.2	4.7*	10.0**	7.7**	0.0	16.7***	13.7***	8.6**	2.3	8.6**
Tillage	0.3	0.2	0.2	6.8*	0.0	0.4	1.7	0.7	0.6	0.1	0.0	0.0	1.2	0.1	0.1	0.3	0.0	0.1	1.7	0.0	0.8
Rotation	0.3	3.0	1.3	0.7	0.0	0.1	0.1	0.0	0.0	0.1	0.2	0.0	0.0	0.4	1.3	0.0	0.5	0.3	0.3	0.3	0.5
Fertilizer	2.0	1.1	3.1	0.2	2.4	1.1	0.8	0.8	3.2*	1.1	0.0	0.6	1.1	1.4	3.4*	1.2	1.3	1.4	4.0*	1.5	4.0*
Slope × Tillage	12.2***	7.9**	0.6	0.7	0.0	2.2	3.5	0.0	1.6	2.3	2.1	2.2	1.2	1.8	3.2*	19.6***	3.7*	3.8*	1.1	1.2	1.7
Slope × Rotation	0.1	0.0	0.5	0.0	0.5	0.4	0.0	2.1	2.2	0.0	0.1	0.0	0.1	0.7	0.0	4.3*	0.5	0.5	2.1	1.7	3.1
Tillage × Rotation	2.0	0.1	0.0	0.1	2.0	3.0	3.0	1.0	0.4	0.7	0.0	0.0	0.0	2.4	1.5	1.7	1.5	1.7	0.0	2.4	0.9
Slope × Fertilizer	0.8	0.0	0.3	0.2	0.2	0.8	0.4	1.0	0.1	0.5	1.0	0.9	0.1	1.0	0.1	0.2	0.6	0.6	0.5	1.5	0.7
Tillage × Fertilizer	0.8	0.9	0.5	0.1	0.1	0.4	0.3	0.3	0.3	0.6	0.2	0.1	0.1	0.1	0.9	0.7	0.2	0.2	3.7*	0.8	2.9
Rotation × Fertilizer	2.1	0.8	0.1	0.1	0.3	0.4	1.1	0.4	0.6	1.8	1.3	0.7	0.5	0.2	0.3	0.5	0.0	0.1	1.6	1.6	0.9
Slope × Tillage × Rotation	0.0	0.0	0.1	0.5	0.2	0.0	0.4	1.1	1.4	1.5	0.2	0.6	0.6	0.0	0.2	1.5	0.1	0.1	1.2	0.1	0.9
Slope × Tillage × Fertilizer	0.4	0.4	0.3	0.1	0.1	0.5	0.7	0.0	1.5	0.3	0.5	0.1	0.6	0.4	0.7	1.6	0.3	0.3	0.3	0.9	0.5
Slope × Rotation × Fertilizer	0.1	0.9	0.0	0.1	0.7	0.1	0.1	1.0	1.0	0.1	0.3	0.9	0.3	0.5	0.3	2.6	0.1	0.0	0.0	0.1	0.0
Tillage × Rotation × Fertilizer	0.7	1.7	0.6	0.2	2.2	1.0	0.3	2.6	0.2	3.2*	0.0	0.5	0.5	2.2	3.2*	0.1	1.6	1.7	0.3	1.4	0.5
Slope × Tillage × Rotation × Fertilizer	1.3	0.0	0.6	0.5	0.1	0.0	0.2	0.4	0.2	1.3	0.2	1.5	1.3	0.0	0.1	0.5	0.1	0.1	1.4	1.1	1.9

Significance codes: $P < 0.05$ '*', $P < 0.01$ '**'; $P < 0.001$ '***'

[a] VWC = volumetric water content, [b] Temp= temperature, [c] CEC = cation exchange capacity, [d] N_{min} = mineral N, [e] MWC = mean mass of C, and [f] MWN = mean mass of N

TABLE S2 Variation in soil physio-chemical properties under different agricultural management practices in fields within each slope position. Mean values and standard errors were calculated by grouping the data of the 48 plots within each slope position according to the different management practices tillage (n = 24), rotation type (n = 24) and N fertilizer treatment (n = 16). Differences were assessed by ANOVA for treatments as summarized in table 2. Fisher's Least Significant Difference (LSD) test was applied as post-hoc test for the comparison of the different N fertilizer levels. Values followed by the same lower-case letter are not significantly different (±LSD protected, $P \leq 0.05$)

Treatment		NH_4^+-N	N_{min} [a]	NO_3^--N	P	Ca	K	Al	Na	Fe	Mn	Mg
Fixed factors and their levels		g kg^{-1}	g kg^{-1}	g kg^{-1}	mg kg^{-1}	mg kg^{-1}	mg kg^{-1}	mg kg^{-1}	mg kg^{-1}	mg kg^{-1}	mg kg^{-1}	mg kg^{-1}
Up-slope												
Tillage	CT	3.06±0.20	2.70±0.29	5.19±0.36	147±8	464±23	11228±598	4766±269	326±60	8048±70	272±33	274±12
	RT	2.68±0.18	2.58±0.27	5.86±0.37	122±5	410±14	10929±508	4012±123	280±57	7973±108	166±9	269±7
Rotation	Res+CP	3.03±0.22	2.55±0.29	5.43±0.34	141±7	444±18	10755±705	4441±215	315±58	8094±81	230±30	275±10
	NoRes-NoCP	2.72±0.72	2.72±0.27	5.67±0.41	128±7	431±22	11402±335	4337±231	291±60	7926±97	208±23	268±10
Fertilizer	N0PK	2.85±0.19	2.47±0.30	5.70±0.53	135±11	447±23	10963±920	4434±298	267±76	8017±113	214±28	278±14
	N40PK	3.11±0.28	3.00±0.38	5.71±0.44	134±8	440±28	11314±598	4512±268	320±61	8007±112	245±41	274±14
	N80PK	2.66±0.22	2.44±0.34	5.23±0.40	134±8	425±21	10958±459	4221±257	322±78	8006±113	199±27	262±8
Foot-slope												
Tillage	CT	4.78±0.27	11.05±0.73	6.60±0.63	130±7	1431±98	16644±1372	4928±408	461±83	7907±148	163±13	512±41
	RT	4.44±0.30	8.58±0.48	3.80±0.29	105±5	1007±60	12974±817	4630±188	336±108	7686±112	139±11	398±19
Rotation	Res+CP	4.63±0.27	9.63±0.71	5.37±0.62	119±8	5008±103	14872±1330	5008±196	327±94	7953±168	156±11	460±41
	NoRes-NoCP	4.59±0.30	10.05±0.64	5.04±0.52	116±6	4550±80	14746±1036	4550±401	470±98	7640±72	145±13	450±26
Fertilizer	N0PK	4.67±0.28	10.20±0.90	5.54±0.40	113±5	1284±102	16817±1545	4920±409	560±134	8031±17	163±11	480±38
	N40PK	4.61±0.28	8.84±0.40	4.17±0.80	128±8	11967±114	13977±1151	4788±371	349±114	7748±58	146±19	443±38
	N80PK	4.56±0.47	10.51±1.02	5.90±0.76	112±10	1175±125	13634±1555	4628±401	286±99	7609±215	143±12	441±49

Treatment		MWC [b]	MWN [c]	C/N	pH	CEC [d]	VWC [e]	Temperature	Clay	Silt	Sand
		%	%			(cmol kg^{-1})	%	°C	%	%	%
Up-slope											
Tillage	CT	0.55±0.20	0.15±0.002	12.62±0.26	5.70±0.03	477±47	0.02±0.00	34.58±0.08	7.24±0.61	6.49±0.75	87.85±0.20
	RT	0.58±0.01	0.16±0.003	12.49±0.14	5.63±0.04	426±43	0.02±0.00	34.48±0.07	6.73±0.53	6.41±0.54	86.30±0.73
Rotation	Res+CP	0.57±0.02	0.16±0.003	12.61±0.23	5.67±0.03	469±42	0.02±0.00	34.52±0.08	7.13±0.64	6.73±0.75	87.73±0.70
	NoRes-NoCP	0.56±0.02	0.16±0.002	12.49±0.18	5.66±0.03	433±48	0.02±0.00	34.54±0.07	6.85±0.50	6.18±0.53	86.42±0.65
Fertilizer	N0PK	0.55±0.02	0.16±0.003	12.77±0.26	5.64±0.04	495±61	0.02±0.00	34.52±0.09	**8.08±0.64 a**	6.51±0.57	88.14±0.69
	N40PK	0.59±0.02	0.17±0.004	12.46±0.29	5.69±0.04	441±56	0.02±0.00	34.56±0.09	**6.45±0.77 b**	5.48 ±0.12	87.04±0.72
	N80PK	0.55±0.02	0.16±0.002	12.42±0.21	5.67±0.04	417±49	0.02±0.00	34.54±0.09	**6.44±0.63 b**	7.37±0.51	85.56±0.47
Foot-slope											
Tillage	CT	0.84±0.04	0.22±0.002	13.55±0.12	6.34±0.11	1145±95	0.02±0.00	35.63±0.04	13.36±0.31	8.85±0.54	80.71±0.61
	RT	0.75±0.04	0.16±0.003	13.23±0.11	6.03±0.07	920±48	0.02±0.00	35.53±0.11	11.44±0.77	8.22±0.78	79.42±0.22
Rotation	Res+CP	0.79±0.04	0.23±0.007	13.40±0.11	6.21±0.11	1082±65	0.02±0.01	35.49±0.10	12.12±0.97	8.78±0.77	80.59±0.44
	NoRes-NoCP	0.80±0.04	0.20±0.008	13.38±0.13	6.16±0.09	983±89	0.02±0.00	35.52±0.08	12.68±0.18	8.29±0.55	80.59±0.42
Fertilizer	N0PK	0.82±0.05	0.22±0.009	13.40±0.16	6.21±0.10	1114±84	0.02±0.00	35.49±0.11	15.13±0.90	9.58±0.36	82.02±0.16
	N40PK	0.79±0.05	0.22±0.008	13.40±0.12	6.21±0.13	1046±104	0.02±0.00	35.51±0.11	11.02±0.78	8.07±0.63	83.38±0.20
	N80PK	0.79±0.06	0.22±0.010	13.37±0.17	6.15±0.13	938±98	0.02±0.00	35.48±0.10	10.55±0.57	8.96±0.20	77.29±0.23

[a] N_{min} = mineral N, [b] MWC = mean mass of C, [c] MWN = mean mass of N, [d] CEC = cation exchange capacity, and [e] VWC = volumetric water content.

TABLE S3 Individual and interaction effects of topography and management practices on soil prokaryotic richness and alpha diversity indices, evaluated by statistical analysis using a linear mixed model effect (Type III Analysis of Variance with Kenward-Roger 's method is shown). F-values are given, and significance is indicated by asterisks

Fixed factors	Richness	Chao1	ACE	Evenness	Shannon
Slope	58.03***	62.96***	72.76***	26.85***	31.16***
Tillage	2.66	1.57	1.87	0.69	0.92
Rotation	2.97	4.48*	4.01*	1.39	1.63
Fertilizer	1.39	0.68	0.89	1.20	1.22
Slope × Tillage	0.27	0.01	0.02	0.47	0.44
Slope × Rotation	0.57	0.06	0.06	0.99	0.99
Tillage × Rotation	0.05	0.40	0.27	0.14	0.13
Slope × Fertilizer	0.27	0.36	0.13	1.41	1.19
Tillage × Fertilizer	1.92	1.42	1.21	1.28	1.39
Rotation × Fertilizer	0.58	0.70	0.53	0.38	0.42
Slope × Tillage × Rotation	0.07	0.00	0.00	0.21	0.19
Slope × Tillage × Fertilizer	0.56	0.45	0.70	0.26	0.31
Slope × Rotation × Fertilizer	0.61	0.50	0.89	0.49	0.51
Tillage × Rotation × Fertilizer	0.72	1.51	2.01	0.19	0.23
Slope × Tillage × Rotation × Fertilizer	0.85	0.89	0.86	0.91	0.89

Significance codes: P < 0.05 '*', P < 0.01 '**'; P < 0.001 '***'

TABLE S4 Comparison of species richness and alpha-diversity indices associated with agricultural management practices in up-slope and foot-slope soils. Mean values and standard errors were calculated by grouping the data according to tillage (n = 24 per treatment), rotation (n = 24) and fertilizer treatments (n = 16). Differences were assessed by ANOVA considering the strip-split-plot design. Fisher's Least Significant Difference (LSD) test was applied for the comparison of different rates of nitrogen application. Values followed by different lower-case letters indicate significant differences upon a specific treatment (LSD protected, $p < 0.05$)

Treatments	Levels	Richness	Chao1	ACE	Evenness	Shannon
Up-slope						
	Conventional	3930 ±142	12981 ± 470	14301 ± 510	0.63 ± 0.02	5.21 ± 0.15
Tillage	Reduced	3923 ± 139	12808 ± 443	14226 ± 520	0.63 ± 0.02	5.18 ± 0.18
	Res+CP	4071 ± 148	12270 ± 363	13532 ± 427	0.61 ± 0.02	5.33 ± 0.17
Rotation	NoRes-NoCP	3755 ± 123	13520 ± 503	14995 ± 550	0.64 ± 0.02	5.06 ± 0.16
	N0PK	3832 ± 153	**12668 ± 475 b**	**13921 ± 532 b**	0.62 ± 0.02	5.12 ± 0.19
Fertilizer	N40PK	3890 ± 182	**12519 ± 598 b**	**13998 ± 680 b**	0.63 ± 0.02	5.24 ± 0.21
	N80PK	4017 ± 180	**13497 ± 583 a**	**14872 ± 663 a**	0.63 ± 0.02	5.24 ± 0.22
Foot-slope						
	Conventional	4954 ± 104	16418 ± 371	18556 ± 436	0.72 ± 0.01	6.08 ± 0.09
Tillage	Reduced	4698 ± 98	15970 ± 392	17993 ± 451	0.69 ± 0.01	5.86 ± 0.11
	Res+CP	4877 ± 98	16549 ± 346	18655 ± 397	0.70 ± 0.01	5.99 ± 0.09
Rotation	NoRes-NoCP	4776 ± 109	15838 ± 406	17894 ± 480	0.70 ± 0.01	5.96 ± 0.11
	N0PK	4750 ± 103	16258 ± 355	18203 ± 420	0.70 ± 0.01	5.91 ± 0.11
Fertilizer	N40PK	4902 ± 98	16334 ± 416	18624 ± 487	0.72 ± 0.01	6.08 ± 0.07
	N80PK	4826 ± 171	15989 ± 613	17997 ± 703	0.70 ± 0.02	5.93 ± 0.18

TABLE S5 Individual and interactive effects of slope position and agronomic practices on prokaryotic beta-diversity assessed by ADONIS, applying a Bray-Curtis distance matrix; number of permutations=999

Treatment	n	R^2	P
All samples			
Slope	**96**	**0.1102**	**0.001 *****
Tillage	**48**	**0.0143**	**0.04 ***
Rotation	48	0.0105	0.25
Fertilizer	32	0.0193	0.45
Slope × Tillage		0.0125	0.11
Slope × Rotation		0.0103	0.39
Tillage × Rotation		0.0080	0.76
Slope × Fertilizer		0.0195	0.41
Tillage × Fertilizer		0.0167	0.84
Rotation × Fertilizer		0.0175	0.73
Slope × Tillage × Rotation		0.0076	0.98
Slope × Tillage × Fertilizer		0.0168	0.85
Slope × Rotation × Fertilizer		0.0159	0.94
Tillage × Rotation × Fertilizer		0.0171	0.78
Slope × Tillage × Rotation × Fertilizer		0.0169	0.88
Residuals		0.6868	
Total		1.0000	
Up-slope samples			
Tillage	24	0.0189	0.864
Rotation	**24**	**0.0405**	**0.049 ***
Fertilizer	16	0.0404	0.697
Tillage × Rotation		0.0182	0.962
Tillage × Fertilizer		0.0377	0.940
Rotation × Fertilizer		0.0390	0.851
Tillage × Rotation × Fertilizer		0.0432	0.424
Residuals		0.7622	
Total		1.0000	
Foot-slope samples			
Tillage	**24**	**0.0308**	**0.011 ***
Rotation	24	0.0196	0.861
Fertilizer	16	0.0417	0.688
Tillage × Rotation		0.0190	0.954
Tillage × Fertilizer		0.0425	0.573
Rotation × Fertilizer		0.0401	0.864
Tillage × Rotation × Fertilizer		0.0415	0.695
Residuals		0.7647	
Total		1.0000	

Significance codes: P < 0.05 '*', P < 0.01 '**'; P < 0.001 '***'

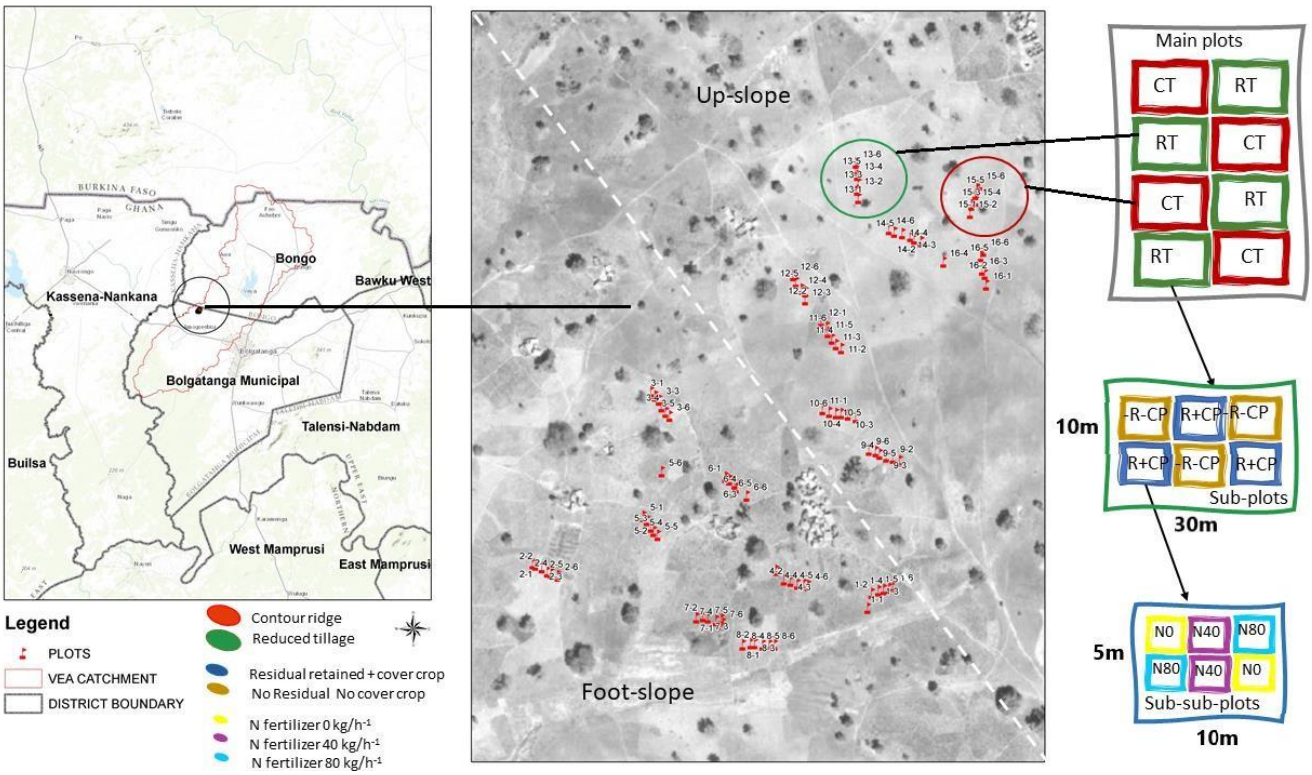

Figure S1 Map (left) showing the location of the study site in Upper-Eastern Ghana, satellite image (middle) showing the location of the fields in the terrain, and schematic drawings (right) explaining the strip-plot design and the plot sizes. The study area was established along a 1.2 km elevational transect. Tillage: conventional tillage (CT) and reduced tillage (RT), rotation: residual management including a cover crop (R+CP) and no residual management and no cover crop retention (-R-CP), and fertilizer rates of nitrogen (N0, N40 and N80)

Explanation of the treatments

The experiment had a strip-split plot design with foot-slope and up-slope as strip plots. The tillage treatment as the main plot comprised reduced tillage and contour ridge-conventional tillage. In contour ridge the tillage orientation and crop cultivation was perpendicular to the runoff direction, which helps to protect growing crops from damage by runoff and mitigates soil erosion. Hand hoeing (hand tool for cultivating the soil) was applied for conventional tillage to make contour ridges. The amount of residue returned to the plots was depending on the amount of biomass that accrued from the previous cropping season (average of 5 t ha^{-1} for all cropping seasons). Cowpea was planted as cover crop and added to the plots in which crop residuals were retained, while in other plots no residual was returned and no cover crop planted in their crop sequence. As emphasized by Danso et al. (2018) the fertilizers used were urea (46% N), triple super phosphate (46%P_2O_5) and muriate of potash (60% K_2O). Fertilizers were broadcast and worked into in the soil immediately. Optimum P and K amounts (60 kg ha^{-1}) were fix in all plots. For N fertilizer 50% N were applied 25 days after planting the crops and the remaining N 45 days after planting in all plots (Danso et al., 2018). Three dosages of N amendment were applied, 0 kg ha^{-1} as control, 40 kg ha^{-1}, and 80 kg ha^{-1}. The cultivars of early maturing (90 days) Dorke SR (maize variety), Padi Tuya (cowpea variety), and Kadaga (sorghum variety) were planted as crop sequence in this experiment.

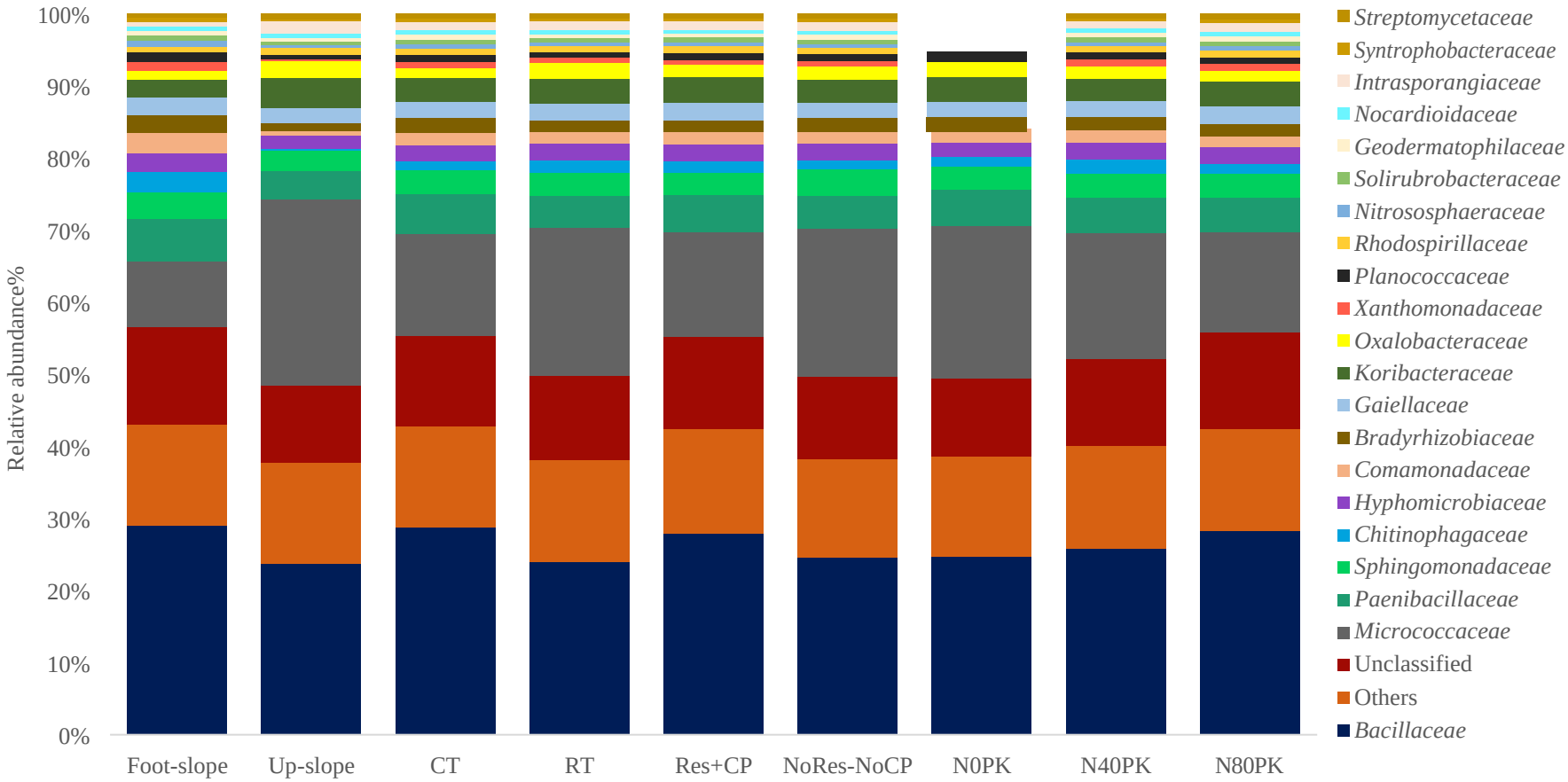

Figure S2 Taxonomic distribution of OTUs at the family level in soil samples influenced by slope position (Up-slope and Foot-slope), tillage: conventional tillage (CT) and reduced tillage (RT), rotation: residual management including a cover crop (Res+CP) and no residual management and no cover crop retention (NoRes-NoCP), and fertilizer rates of nitrogen (N0PK, N40PK and N80PK). The 21 most abundant families (> 0.5 % relative abundance) are shown, lower abundant families are summarized as "others"

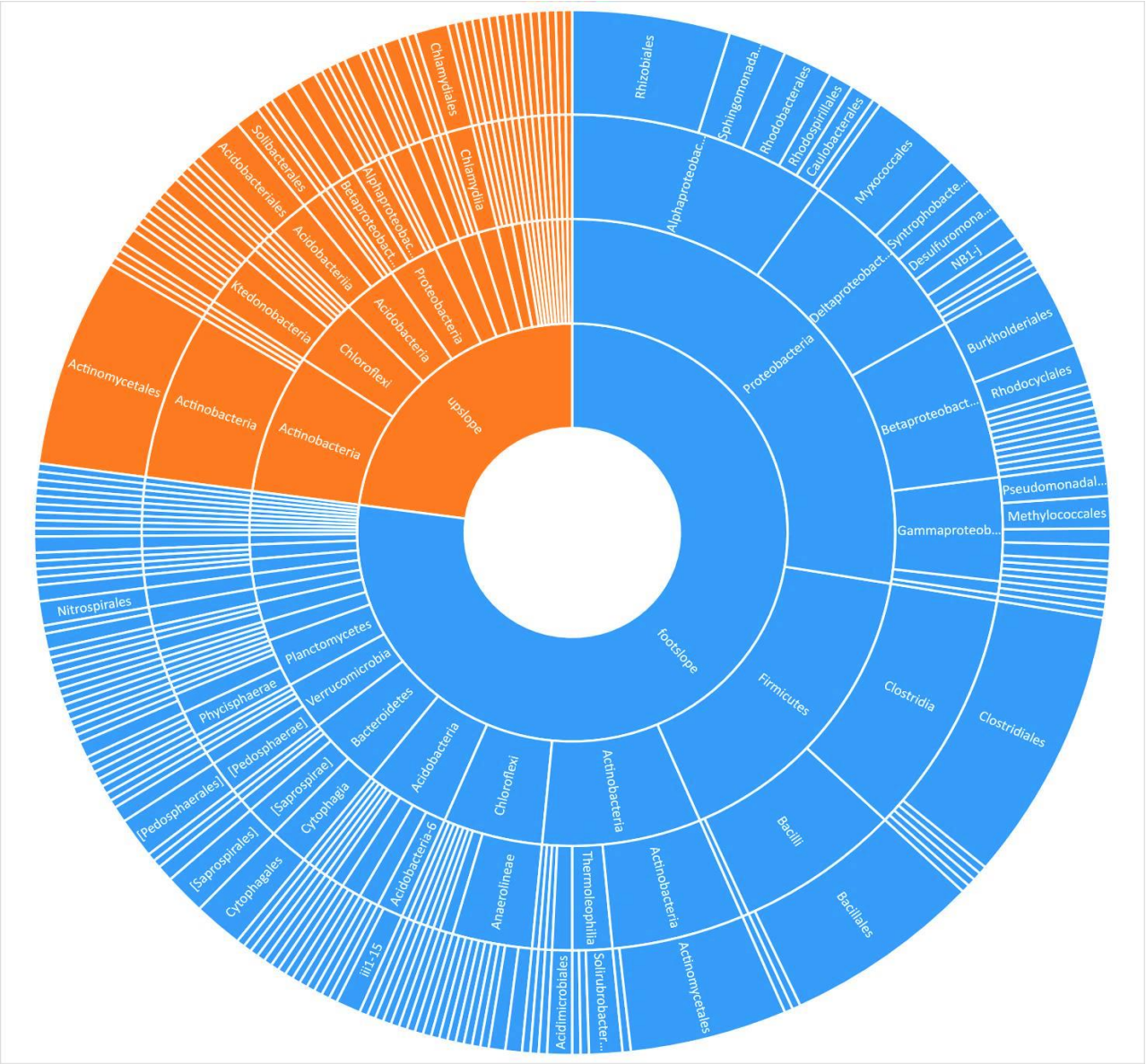

Figure S3 Sunburst diagram showing the number of genera per order, class, and phylum with significantly higher abundance in foot-slope (blue) or up-slope (orange). Responsive genera were identified based on STAMP analysis. Number of genera within different taxonomic groups are illustrated by segment size. The circles represent phylum, class, and order levels from inside to outside. Orders representing three or more genera are labeled by name

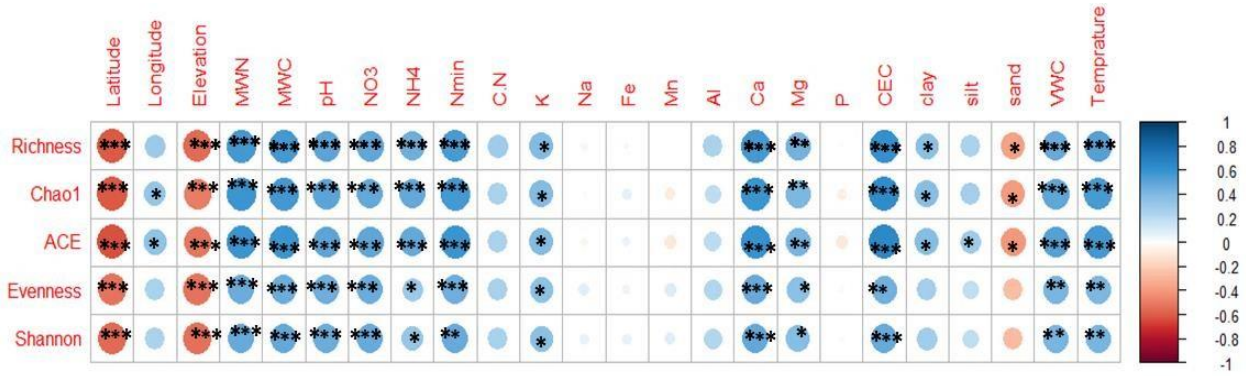

Figure S4 Spearman's rank correlation analysis between prokaryotic alpha-diversity indices and soil physiochemical properties. Color code indicates positive (blue) or negative (red) correlations (n = 96). P-values were adjusted for multiple comparisons by the Benjamini-Hochberg method

Significance codes: P < 0.05 '*', P < 0.01 '**'; P < 0.001 '***'
MWC% = mean mass of C%, MWN% = mean mass of N%, CEC = cation exchange capacity, VWC = volumetric water content, NO3 = NO_3^--N, NH4=NH_4^+-N and Nmin = mineral N

2.3. Plant-growth-promoting potential of sorghum rhizobiome affected by soil substrate availability and pedoclimatic status

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Abstract

The rhizosphere-microbiome (rhizobiome) is essential in regulating plant growth. Rhizobiome wellbeing is preserved by the plant root exudates, and soil substrates availability. Abiotic stresses such as erosion and accelerated erosion adversely affect the rhizobiome diversity and functionalities. The mature sorghum rhizobacteria (MSR) were isolated and characterized based on their colony morphology and biochemical characters. Isolates were screened for their plant-growth-promoting (PGP) potential under topography and agronomic disruptions (conventional vs. reduced tillage, rotation including residue removed and no cover crop added vs. cover crop and residue incorporated, and soil amended with 0, 40, and 80 kg ha^{-1} nitrogen). MSR endowed with multiple PGP traits were clustered, and their representatives were subjected to molecular identification. *Bacillus* was the most abundant genus with multiple PGP traits. Phosphate-solubilizing activities (PSB) contributed to 35.56% of the total PGPP with Enterobacter, Variovorax, Pantoea, Bacillus, and Acinetobacter showing high proficiency in solubilizing mineral-phosphate. MSR showed a 10.18% positive reaction to ammonia production, while merely 5.7% and 0.5% were capable of indole-3-acetic-acid (IAA) and siderophore production, respectively. Physiological and PGP activities of MSR at our field- scale were systematically distributed, with soil edaphic properties as the primary underlying factor. Although foot-slope MSR comprised higher IAA production, PSB declined significantly at the deposition site. Overall, 44.3% of MSR physiological and PGP activities were explained by the distribution of soil Fe, Al, CEC, pH, Nmin, and temperature. Unlike agronomic practices (1.4%), edaphic properties (19.5%), spatial distance (16.7%), and slope position (7.1%) significantly contributed to the MSR dynamics. Sorghum weight of head and grains weight were significantly positively correlated with ammonification rate, while significantly negatively associated with PSB. Under this study sorghum-PGP, rhizobacteria, and their interactions with their surroundings for the better maintenance of soil fertility and environment conservation are discussed.

Keywords: Biochemical tests, phenotypic characteristics, plant growth-promoting, rhizosphere microbiome, sorghum

1. Introduction

Maize and sorghum producers in parts of the world such as West Africa and Brazil plant them in soils that are nutrient deficient, and therefore, plant-growth-promoting rhizobacteria (PGPR) can support and contribute to the enhancement of plant nutrient uptake and biomass production (Danso et al., 2018; Aquino et al., 2019). Part of plants' photosynthetic product is secreted by roots that feed microbial populations (Glick, 2014; Goswami et al., 2016). This root exudation and the composition of rhizodeposits shapes rhizobiomes (Sasse et al., 2018). Subsequent exometabolism in tandem with rhizobiome catabolic/anabolic activities, can kindle nutrient cycling, and nutrients uptake by plant roots in the rhizosphere (Glick, 2014; Sasse et al., 2018). Rhizodeposition varies depending upon plant genotype, growth stage, and other surrounding environmental features which might alter the plant-microbiome-soil interactions. This interaction causes a constant dynamic in the rhizosphere (Bulgarelli et al., 2013; Kai et al., 2016; Chaparro et al., 2013 and 2014). It is known that free-living PGPR diversity and composition are profoundly affected by the soil substrate availability (Kai et al., 2016; Goswami et al., 2016; Sasse et al., 2018; Flores-Núñez et al., 2018).

PGPR improve plant productivity through multifarious pathways such as enhancing N_2 fixation (Khan, 2005; Aloo et al., 2019), promoting inorganic/organic phosphate solubilization (Hayat, 2010; Aloo et al., 2019), or producing phytohormones like indole-3-acetic acid (Farina et al., 2012; Goswami et al., 2016). To preserve environment and sustain field productivity stimulating plant growth by rhizobacteria endowed with PGP potential is advocated (Aloo et al., 2019). The genera *Acinetobacter, Agrobacterium, Arthobacter, Azotobacter, Azospirillum, Burkholderia, Bradyrhizobium, Enterobacter, Rhizobium, Frankia, Serratia, Bacillus, Variovorax, Thiobacillus, Geobacillus, Paenibacillus, Lysinibacillus, Microbacterium, Ochrobactrum,* and *Pseudomonas* have been reported as PGPRs (da Costa et al., 2014; Goswami et al., 2016; Govindasamy et al., 2017; Kumar et al., 2019). Ammonifying bacteria can generate NH_4^+ from organic N monomers and make it available for the plant's uptake. Given bacteria comprise the vast group of microbial taxa (Isobe et al., 2020), and are affected by surrounding environmental features, e.g. temperature, soil organic C, and clay content (Mukai et al., 2019).

Appreciation of microbial community diversity and functionality in the soil is a challenging assignment that requires reliable methods to overcome existing barriers (Ettema and Wardle, 2002; Fierer, 2017). Albeit new technologies have contributed much to advance our understanding of soil microbial community structure, yet disentangling bacterial physiological

traits rely also on culture-dependent techniques (Kirk et al., 2004), which has its pertinent restrictions (Bing-Ru et al., 2006). PGP activities are driven by the pedoclimatic soil conditions, abiotic stresses and strongly depend upon nutrient source availability and pH (Paul and Lade, 2014; Goswami et al., 2016). The rhizobiome from salty and arid ecosystems can develop evolutionary adaptations related to more rigorous stress responses of their host plants, compared to the rhizobiome of common cultivated land (Bonatelli et al., 2021). Cook and Stall (1969) reported a nutrient-dependent effect of bacteria since only those bacteria grown on nutrient agar (NA) or Kings B medium (KBM) caused necrosis in leaf tissues. Blom et al., (2011a) also examined the efficiency of PGP bacteria grown on various media in enhancing plant growth and they observed contrasting effects of these bacteria on plant growth. Pseudomonas strains grown on protein-rich media have also been shown to have deleterious effects on plant growth caused by HCN production (Blom et al., 2011b). Thus, it is predictable that biotic and abiotic factors that dominate the soil ecosystem not only alter the structure of the soil microbial community (Liu et al., 2020) but also their activities, potentials and functionalities (Chen et al., 2019; Huang et al., 2019). The cultivability of bacteria is still essential for revealing their functionalities and physiological potentials (Borsodi et al., 2005). Besides, bacterial phenotypic characteristics, specifically their PGP characteristics, should be scavenged in association with their surrounding environment and feasible abiotic stresses.

It is noteworthy to mention that microbial biomass and activities are contingent upon soil organic matter, which alters following the soil surface disruptions like erosion and anthropogenic activities such as agronomic practices (Paul and Lade, 2014; Xiao et al., 2017). Several studies outline the effects of erosion-induced alteration in microbial properties due primarily to the reduction of soil nutrients in eroding sites, and oxygen deficiency in poorly drained depositional sites (Xiao et al., 2017; Nitzsche et al., 2017). Changes in soil water content, pH, soil nutrient status, plant variations, and growth stage (Schlemper et al., 2017) have been shown to influence soil microbial communities, their functionalities (Gianfreda et al., 2005; Allison and Martiny, 2008; Liu, 2016; Ipek et al., 2019; Carney and Matson, 2006; Fierer, 2017), and their PGPP (Gianfreda et al., 2005; Ipek et al., 2019). Disturbing the soil structure, and occurrence of salinization are among the destructive impacts of agronomic practices (Ipek et al., 2019). While erosion and agricultural practices, as a cause of accelerated erosion, are expected to affect the soil microbial community composition, the specific responses of various rhizobacteria and their PGP potentials to the given disruptions are not well understood. Since the molecular approach has become the main analytical method to study soil bacterial ecology and diversity (Nocker et

al., 2007), many queries regarding rhizobacterial physiologic and PGPP remain open with no answer. Here we investigated sorghum PGP rhizobacteria, and their physiological potential, focusing on variation of PGPPs in relation to field topography and agronomic practices. We anticipate that topography affects soil substrate and pedoclimatic heterogeneity and thus regulates sorghum rhizobacteria physiology and PGPP therewith affects sorghum yield indices.

2. Material and Methods

2.1. Site description and soil sampling

A field trial was established through a corporation with agronomists in the WASCAL (West African Science Service Center on Climate Change and Adapted Land Use) project. The village selected for the study was Anabisi located in Upper-Eastern Ghana (UE). UE has a tropical climate with an average annual temperature of 37.5 C° and a mean annual precipitation of 1100 mm which mainly falls during the growing season (May-Sep) and coincides with high temperatures in the region (Danso et al., 2018; Ghotbi et al., 2021). The farming sequence was maize-sorghum during 2012 to 2015 cropping seasons respectively, with and without cowpea in rotation. The experimental field was divided into two transects of up-slope and foot-slope with a max 10m elevation difference (min 177 m- max 188 m) and 3 to 5% slope gradient. The study design layout was strip-split plot with four replications, comprised of three experimental fixed factors: 1) tillage conventional tillage (CT), and reduced tillage (RT) as the main plot, and 2) rotation (residue incorporation with cowpea as a cover crop (Res+CP), and no residues retained with no cowpea (NoRes-NoCP) constituting the sub-plot factors and 3) nitrogen fertilizer level (no nitrogen (N0P60K60), recommended (N40P60K60), and high nitrogen (N80P60K60) as sub-sub plot factors as described by Ghotbi et al. (2021). Sampling spots recorded using global positioning system (GPS) coordinates. Sampling was done from the loosely and tightly adhered soils to the roots, during the harvesting season in early Oct with 4 replications for each plot (Table 1). The root systems were carefully separated from the soil. All samples were placed in sterile bags and transferred to the lab under cold conditions within 24h to initiate the phenotypic and physiological characterization of sorghum rhizobacteria. The four samples of each plot were mixed after discarding plant residues, shoots, clods, and aggregates larger than 4 mm diameter (Peixoto et al., 2006). Samples kept at 4 ◦C for subsequent analyses.

2.2. Characterization of soil edaphic properties

Soil physiochemical characteristics results were adapted from our previous study (Ghotbi et al., 2021). Briefly, soil volumetric water content (cm3 water/cm3 of soil = vol. %), temperature (°C),

soil texture, pH, cation exchange capacity (CEC), total C % (MWC%), total N % (MWN%), nitrate-N (NO_3^--N), ammonium-N (NH_4^+-N), total mineral N (Nmin) content, and contents of various elements were determined.

Mineralized ammonium (MA) assessment: triplicates consisting of 5 g soil for each sample were incubated with 25 ml of deionized H_2O under anaerobic conditions at 37 °C. After 168 h, 25 ml of 4 M KCl was added and the samples were then extracted with 2 M KCl at a liquid/soil ratio of 5:1. The samples were shaken for 1 h on a reciprocating shaker, centrifuged, and the supernatant was collected (Burger and Jackson, 2003). NH_4^+-N of supernatant was determined by the Lachat flow injection analyzer (Lachat 8000, Zellweger, Milwaukee, WI). Gross ammonification rates of NH_4^+ were calculated according to Kirkham and Bartholomew (1954). Immobilization of NH_4^+ (ug N/g soil/ day) by microbes was estimated from consumption rates of NH_4^+ by microbes (ug N/g soil/ day), assuming that gaseous N losses and other feasible inorganic N fates were negligible.

2.3. Isolation and enumeration

Four independent replicates per treatment were analyzed as follows: ten gram of soil was homogenized in Erlenmeyer flasks in 90 mL of sterile 0.1% (w/v) distilled water by shaking at 290 rpm for one hour. The mixture was vortexed for 3 min (200rev/min), rocked horizontally for 10 min, allowing the dissolved aggregates to settle (Burns, 2005). This solution was ten-fold diluted (10-1 to 10-7) and 0.1 mL aliquots of dilutions 10-4, 10-5, 10-6, and 10-7 were pipetted onto 10% Tryptone Soy Agar (TSA) in triplicates. The plates were incubated at 28 °C for five days until the appearance of visually different colony types (Govindasamy et al., 2017). Each of those morphologically differentiable bacterial colonies (based on their size, shape, color, surface, margin, and elevation) was repeatedly streaked on plates of TSA media (with no modification) to effect purification until isolation was achieved. Plates containing 30 to 200 colonies were taken into account and total viable colony forming units per ml (cfu/ml) for each sample were enumerated (Burns, 2005). Consequently, 10 morphologically different colonies of each sample were isolated, which led to harvesting 960 colonies on TSA. For any further test, isolates were cultured on trypticase soy agar and incubated for 48 h at 28°C.

2.4. Phenotypic characterization

Gram-staining, urease test (Schaad et al., 2001; Anwar et al. 2016), amylose hydrolyzing (Lonsane and Ramesh, 1990) and oxidative-fermentative (OF) tests were performed (Porres and Stanyon, 1974). Moreover, the degradation of organic compounds like mannitol was tested

(Stiles and NG, 1981; Schaad et al., 2001). Gelatin and esculin hydrolyzing, and catalase tests were also carried out (Tabatabai 1994; Stiles and NG 1981; Schaad et al., 2001). Citrate utilization test (Tabatabai, 1994), and triple sugar iron agar fermentation test (TSI) (sucrose/lactose and glucose) were also performed. The formation of neutral or alkaline pH products in the slanted area of the tube revealed the utilization of glucose, while acid production at the bottom showed the utilization of lactose and/or sucrose (Kolmos and Schmidt, 1987). PGP potential evaluation was performed applying the indole-3-acetic-acid (IAA) production ability (Leveau and Lindow, 2005; Ji et al., 2014), phosphate solubilizing (PSB) (Pikovskaya, 1948), and siderophore production tests (Ji et al., 2014; Govindasamy et al., 2017).

Each test was carried out on ten selected isolates to figure out the physiological characteristics of representative isolates in each plot. Overall, garnered information was applied for further phenotypic classification and clustering of the isolates. The slant bottles containing the representative bacteria were preserved in 15% glycerol at −80 °C until the molecular study. Consequently, the percentage of positive reactions for each test was reported as 1 versus no reaction, which was reposted as 0. Later 1 and 0 in each sample converted to a percentage and used for downstream analyses, applying R toolkit. Eventually, characterized colonies were clustered based on their phenotypic characteristics which enabled us to group similar isolates and classify the strains to 35 representatives for taxonomic studies and to prevent redundant screening efforts (Pathom-Aree et al., 2006).

2.5. Phylogenetic assessment of sorghum cultivable rhizobacteria

Representatives of phenotypically clustered isolates were chosen for further identification. Twenty-two unique isolates were selected out of 960 isolates for molecular analyses. DNA extraction of pure isolates was performed through “freeze and thaw” protocol. For freeze and thaw protocol, appropriate volume of cell material was diluted, using 100 µL of DNA-free water. The suspension was kept frozen over night at -20 °C, and eventually thawed in a Thermoblock (Eppendorf, US). The supernatant was extracted by centrifuging the suspension for 5 min at 8000 x g. The supernatant was kept frozen for the molecular analysis. The supernatant later was used for 16S rRNA gene amplification, each in triplicate, nearly full-length (~ 1500 bp) products of the 16S rRNA genes were obtained by polymerase chain reaction (PCR) using universal bacterial primers 8F (5’-AGAGTTTGATCCTTGGCTCAG-3’) and 1492R 5'-GGTTACCTTGTTACGACTT-3' according to Lane (1991). Amplification was done in reaction mixtures that contained 1µl of supernatant as DNA template, 1x PCR buffer, 1.25 mM MgCl2, 0. 5 µM of the forward and reverse primer, and 2U of Taq DNA Polymerase (ThermoFisher,

ThermoFisher, Carlsbad, California). A final volume of 25 µl for each reaction was adjusted with PCR water. PCR was performed in a gradient thermocycler (Eppendorf, US) through a program consisting of 94 °C for 1 min initial denaturation, followed by 30 cycles of 94 °C for 1 min, annealing at 55 °C for 1 min 30 sec, 72 °C for 1 min and a final extension at 72 °C for 10 min. Following PCR amplification, the quality of the PCR products was confirmed by 1.5% agarose gel electrophoresis. Samples exhibiting weak bands were re-amplified and qualified DNA was stored at -40 C. The PCR products were purified through the CleanSweep™ PCR Purification Reagent (ThermoFisher, Carlsbad, California) following the manufacturer's procedures. Purified amplicons were sent to Macrogen Inc. (Seoul, Korea) for sequencing on both strands using both primers in order to attain the nearly complete sequence for each strain.

2.6. Bioinformatic analysis

Bacterial isolates were identified after sequence analysis. The homology search was carried out using BLAST search (Basic Local Alignment Search Tool, http://blast.ncbi.nlm.nih.gov) to compare the sequences obtained with databases of the National Center for Biotechnology Information (NCBI). Sequences of all species were retrieved to derive the nomenclature of the selected isolates. Multiple sequence alignments with the most closely related bacterial sequences were performed applying Muscle (https://www.ebi.ac.uk/Tools/msa/muscle/). Estimation of phylogeny was performed by the Maximum Likelihood approach according to the Tamura three-parameter model and the neighbor-joining method (Saitou and Nei, 1987; Tamura et al., 2013), using MEGA 6.0 (http://www.megasoftware.net/). Phylogenetic tree topology was evaluated by bootstrap analysis on the basis of re-sampling 1000 times the neighbor joining data set. The gene sequences were submitted to NCBI GenBank and the accession numbers were assigned.

2.7. Statistical analyses

2.7.1. Linear mixed effect model

Overall, 960 isolates out of 96 plots were chosen for the biochemical tests. The positive/negative results of the physiological characterization and PGP potential were converted into a numerical dataset (0 and 1), and the percentage of positive and negative reactions in each plot was calculated, which was used to estimate the correlations between soil edaphic properties and sorghum rhizobiome physiological characteristics. The harvested percentage file was used to generate the Bray-Curtis similarity matrices. Soil physio-chemical data, sorghum yield indices, and percentages of physiological/PGP traits data were z-score-scaled after testing for normal distribution (Shapiro test), and homogeneity of variances (Bartlett test).

The Sorghum yield indices, raw data was adapted from Danso et al. (2018), and PGPP data were subjected to a linear mixed model with strip-split plot layout (Gomez et al., 1984) using the "lmer" function in the "lme4" package of R environment. Summarized the results by "Anova" function as embedded in the "lmerTest" package. Slope position, tillage system, crop rotation, and N fertilizer rates were considered as fixed factors in this model, while replication and replication × rotation interactions were treated as random factors. The linear mixed model effect application was validated with the restricted maximum likelihood estimation method (REML) based on the normalized scores of standardized residual deviance of response variables. To evaluate the differences among mean values of interactive effects the "emmeans" function embedded in "emmeans" package was applied. Significant differences of means were compared by the least significant difference multiple-comparison Fisher LSD tests for N fertilizer rates with 3 levels. Significance was determined at 5% ($p \leq 0.05$) probability level.

2.7.2. Interplays

The square root transformation of biochemical tests used as physiological and PGPP data. Principal Component Analysis (PCA) was conducted to depict the responses of physiological traits and PGPP to factors and their interactions. Redundancy analyses (RDA) were also performed to estimate the interplays between soil physio-chemical characteristics and physiological and PGP traits of sorghum rhizobacteria.

Sorghum yield indices interactions with rhizobacterial physiological traits and PGPP were evaluated through Spearman correlation analysis and delineated through clustered heatmaps applying the "pheatmap" package. P-values adjusted by the Benjamini-Hochberg method, applying FDR package. Sorghum yield index data were adopted from Danso et al., (2018). Sorghum was harvested at maturity by the WASCAL agronomy group and shelled, air-dried to 15.5%% moisture content, and weighed.

2.7.3. Distance decay relationship and variation partitioning

Sampling spots geographical coordinator points were converted to universal transverse Mercator (UTM) coordinators applying the "rgdal" function in R and used to plot distance-decay relationships between geographic distance, slope position (defined by elevational gradients), and soil edaphic properties distance matrices with the physiological traits and PGPPs distance matrices using the generalized linear model (GLM) of Millar et al. (2011). Therefore, an environmental, geographical, and elevational gradients distance matrices were fitted to the Bray-Curtis similarity matrix of physiological and PGP potentials. "ordiR2step" function in Vegan

package with 999 permutations was applied to select a set of significant and non-redundant predictors of the edaphic factors in structuring the physiological traits and PGPPs. Vectors of principal coordinates of neighbor matrices (PCNM) were constructed as well, using the "Packfor" package, the significant vectors were determined through "OrdiR2step" function. Significant edaphic variables are shown in RDA plots, which were created using the package "ggplot2" (Wickham, 2009). To figure out proportion of each factor in driving the physiological traits and PGPPs of sorghum rhizobacteria at our field scale, variation partitioning analysis (VPA) was applied. Significant vectors of principal coordinates of neighbor matrices (PCNM) along with significant vectors of soil edaphic properties used to for variation partitioning analysis (VPA). The agronomic practices impacts were added, using "model.matrix" function in the vegan package was applied. Due to the unbalanced number of variables R^2 values were reported for each contributor. The significance of each Radj2 value was tested applying ("anova.cca" function of the vegan package). Results of VPA are presented as Venn diagrams.

3. Results

3.1. Phenotypic and phylogenetic characterization of sorghum rhizobacteria

Among 960 collected isolates out of 96 plots (10 in each plot) a big portion of bacterial physiological and PGP potentials comprised phosphate solubilizing and Bile-esculin utilizing capacities. Overall, 35.6% of isolates demonstrated the capacity of solubilizing mineral phosphate (PSB), 50.8% could hydrolyze esculin (mostly gram-negative), 51.9% amylose, 28.3% gelatine, 15.6% fermented mannitol, and 17.7% utilized citrate (Figure 1b). IAA formation was detected solely in 5.8% of the isolates and 0.5% of isolates showed the ability to produce siderophores. 10.2% of isolates showed a positive reaction in the urease test and thus, could hydrolyze urea and produced ammonia and carbon dioxide in their reactions. 20.1% of the isolates were defined as gram-negative and 79.9% gram-positive. 20.9% of isolates had fermentative metabolism. 31.1% of isolates utilized sucrose/lactose and 15.1% used glucose as their source of energy.

Clustered isolates based on their phenotypic characteristics yielded 32 distinct groups, of which representatives were identified by 16S rRNA gene sequence analysis. This resulted in the identification of 14 genera and 36 species in soil samples (Figure 1a and Table 2). Irrespective of treatments, MSR was primarily composed of *Acinetobacter, Arthrobacter, Bacillus, Rhizobium, Curtobacterium, Enterobacter, Microbacterium, Rhodococcus, Pantoea,*

Pedobacter, Planococcus, Planomicrobium, Variovorax, Xanthomonas at the genus level. *Arthrobacter agilis, Arthrobacter luteolus, Arthrobacter sp., Curtobacterium sp., Curtobacterium oceanosedimentum, Curtobacterium flaccumfaciens, Curtobacterium luteum, Curtobacterium citreum, Microbacterium sp., Microbacterium testaceum, Nocardia corynebacterioides, Rhodococcus corynebacterioides, Pedobacter sp., Bacillus pumilus, Bacillus sp., Bacillus safensis, Bacillus safensis strain, Bacillus subtilis subsp. Inaquosorum, Bacillus subtilis, Bacillus aryabhattai, Bacillus megaterium, Bacillus tequilensis, Bacillus mojavensis, Planococcus maritimus, Planomicrobium sp, Candidatus Rhizobium massiliae, Rhizobium sp., Variovorax paradoxus, Acinetobacter sp., Pantoea agglomerans, Pantoea anthophila, Xanthomonas sp., and Enterobacter soli were among unique identified species (Table 2).*

Overall, all detected genera could highly solubilize mineral phosphate. Genera *Enterobacter, Variovorax, Pantoea,* and *Bacillus* as the representative of their cluster exhibited strong PSB compared to other identified genera. IAA and siderophore production were low among MSR evaluated potentials. Siderophore production capacity showed a descending trend in *Rhizobium, Bacillus, Enterobacter, Xanthomonas, and Arthrobacter* clusters, respectively. Rhizobacteria isolates clustered under *Rhizobium, Enterobacter, Microbacterium, Pedobacter, Variovorax, Acinetobacter, Xanthomonas, Bacillus, and Pantoea* genera showed the IAA production capabilities (Table 3). High urea hydrolyzing capability was mostly relevant to the cluster with *Enterobacter* genus as its representative.

3.2. Sorghum rhizobacteria PGP potential affected by topography and agronomic disruptions

Depicting the implications of treatments for forming bacterial physiological and PGP activities revealed the preponderant role of slope position in this regard (Figure S1).

Results

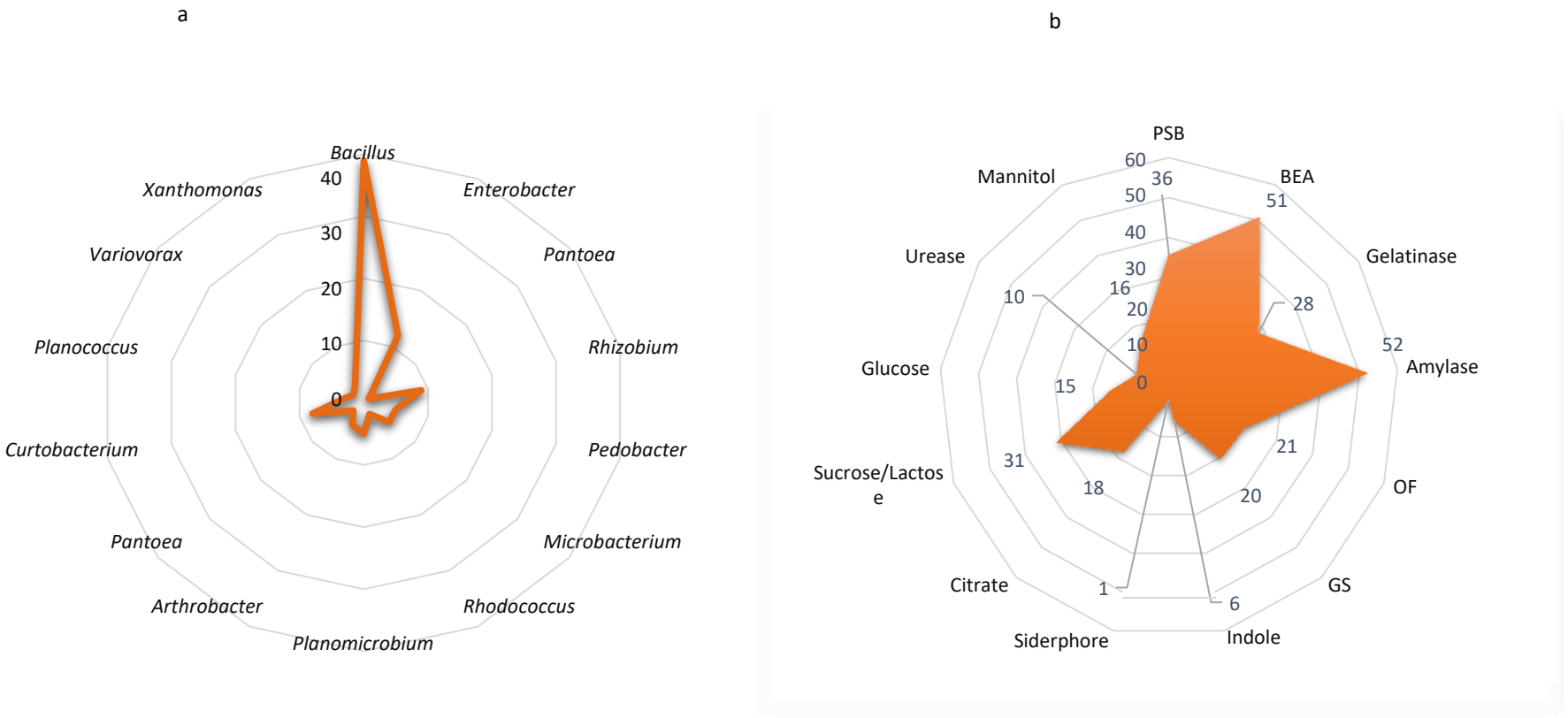

Figure 1 (a) Locally adapted mature sorghum rhizobia endowed with PGP potential and their frequency (%), (b) mature sorghum rhizobiome physiological activities % and their PGP traits. CFU = colony-forming units, MA = mineralized ammonium (ppm), PSB = phosphate solubilizing bacteria activities, IAA= indole-3-acetic-acid, BEA= bile-esculin agar, OF = oxidation fermentation, GS- = gram stain negative.

Foot-slope soils possessed a significantly higher CFUs and higher number of gram-negative rhizobacteria compared to up-slope soils (Table 4). Although topography led to significant shifts in CFUs, PSB, BEA, GS-, IAA, sucrose/lactose, urease test, and mannitol utilization, no significant change was detected in siderophore production in response to slope position (Table S1). Urea hydrolyzation, mannitol, and sucrose/lactose utilization activities were found to be significantly higher at the foot-slope position while Bile-esculin hydrolyzing, gelatin and phosphate solubilizing rhizobacteria potential detected drastically higher at the eroding up-slope position (Table 4).

The agricultural practices' implications for rhizobacteria physiological and PGPP were investigated, applying a linear mixed model. Among the individual agronomic practices mostly tillage practice led to significant shifts in CFU's, and BEA hydrolyzing capabilities of the isolated rhizobacteria (Table S1). The number of CFUs increased following the application of reduced tillage (Table 4). Physiological and PGPPs under agricultural practices didn't cluster distinctly evidenced by PCA analysis (Figure S1). Slope: fertilizer interaction altered CFUs, and slope: rotation affected on siderophore production of MSR.

3.3. Interplays and factors contributing to MSR shifts and sorghum productivity

3.3.1. Rhizobacteria PGPP across environmental heterogeneity

The distance decay relationship between the variation of MSR physiological and PGP activities and soil physiochemical properties was examined. The power model (best fit) showed a very gentle negative slope but a significant relationship (slope = -0.05, R^2 = 0.006, $P < 0.01$) which explained the weak decay of MSR physiological and PGP activities by increasing soil edaphic heterogeneity (Figure 2a).

The chief underlying soil edaphic properties in driving MSR shifts were estimated, applying redundancy analysis (RDA). Strong relationships were detected between MSR shifts and the soil physiochemical properties pH (R^2_{adj}=0.03, F= 4.27, p<0.002), Fe (R^2_{adj}=0.06, F= 3.65, p<0.002), Al (R^2_{adj}=0.11, F= 2.28, p<0.01), temperature (R^2_{adj}=0.08, F= 2.80, p<0.008), and Nmin (R^2_{adj}=0.12, F= 1.89, p<0.04). The first and second axes of the RDA triplot explained 32.5% and 11.8% of the constrained variation in MSR shifts, respectively (Figure 3). A strong correlation was seen between pH and gram-negative (GS-) population of LARSR. The higher temperature and mineral N were correlated with higher mannitol, sucrose/lactose, and urease hydrolyzing capacity, as well as higher IAA production of MSR. AMR increase was

associated with enhancement of the number of CFUs, utilizing higher amylase, and citrate by MSR and in direction of higher Fe (Figure 3).

3.3.2. Sorghum rhizobacteria physiological and PGP potential across space

GLM revealed the existence of significant spatial autocorrelation for rhizobacteria physiological and PGPP within the field. GLM performed between rhizobacteria physiological and PGP activities distance matrices and geographic distances (UTM coordinators) (slope = -0.0001, R^2 = 0.002, P < 0.01), as well as slope position, defined by elevational gradients, (slope = -0.008, R^2 = 0.006, P < 0.01) distance matrices showed the slight rate of decay and the existence of geographical pattern for MSR physiological and PGP activities at our field scale (Figure 2b- c).

3.3.3. Contribution of factors in forming rhizobacteria physiological and PGP traits

To assess the variance and contribution of each factor in structuring rhizobacteria physiological and PGP activities, we applied variation partitioning base on RDA. The significant vectors of PCNM were determined and applied in variation partitioning analysis. The five most important explanatory geographic vectors were as follows: PCNM1 (R^2_{adj}=0.06, P<0.002, F= 7.23), PCNM3 (R^2_{adj}=0.13, P<0.01, F=2.23), PCNM4 (R^2_{adj}=0.08, P<0.004, F= 2.89), PCNM5 (R^2_{adj}=0.4, P<0.03, F= 1.97), and PCNM25 (R^2_{adj} =0.11, P<0.01, F= 2.49). VPA revealed that geographical coordinators (in the form of PCN vectors) led to 19.86% and slope position to 7.83% of the variation in MSR physiological traits and PGP activities, respectively (Figure 4). Overall, explained variation within bacterial activities was 44.70%, while 55.3% was left unexplained. The chief significant explanatory factor was soil edaphic properties, accounting for 19.50% of the variation, whereby 6.4%, 5.6%, and 0.7% were due to the joint/co-variation effects of geographic distances, slope position, and management practices, respectively (Figure 4). The co-variation between soil physicochemical features and management practices was less than 1.00% of the variation. The individual geographic fraction irrespective of joint effects accounted for 16.70% of the variation. Thus, except for the agricultural practices fraction, all other evaluated fractions appeared to play a statistically significant role in forming MSR physiological traits and PGP potential.

Table 2 Phylogenetic analysis of isolates constructed based on the neighbor-joining method and bootstrap values (indicated at the nodes) which were calculated from 1, 000 trees.

Phylum	Class	Order	Family	Genus	Accession	Identity	Species
Actinobacteria	*Actinobacteria*	*Micrococcales*	*Micrococcaceae*	*Arthrobacter*	*KF306343*	*94*	*Arthrobacter agilis*
					DQ486130	*99*	*Arthrobacter luteolus*
					HF565368	*100*	*Arthrobacter sp.*
				Curtobacterium	*HM459850*	*100*	*Curtobacterium sp.*
					EF592577	*96*	*Curtobacterium oceanosedimentum*
					JN689336	*94*	*Curtobacterium flaccumfaciens*
					JQ660320	*96*	*Curtobacterium luteum*
					AB506119	*98*	*Curtobacterium citreum*
				Microbacterium	*HM459850*	*100*	*Microbacterium sp.*
					KC329834	*99*	*Microbacterium testaceum*
		Actinomycetales	*Nocardiaceae*	*Rhodococcus*	*AY438619*	*98*	*Nocardia corynebacterioides*
					AB685427	*98*	*Rhodococcus corynebacterioides*
Bacteroidetes	*Sphingobacteriia*	*Sphingobacteriaceae*	*Sphingobacteriaceae*	*Pedobacter*	*HE603499*	*100*	*Pedobacter sp.*
Firmicutes	*Bacilli*	*Bacillales*	*Bacillaceae*	*Bacillus*	*EU369175*	*90*	*Bacillus pumilus*
					EU239356	*90*	*Bacillus pumilus*
					EU912461	*100*	*Bacillus sp.*
					HF570094	*90*	*Bacillus safensis*
					JF411317	*90*	*Bacillus safensis strain*
					KF668463	*90*	*Bacillus subtilis subsp. inaquosorum*
					KF929418	*90*	*Bacillus subtilis*
					JQ673559	*90*	*Bacillus aryabhattai*
					KF933685	*90*	*Bacillus megaterium*
					KF668464	*100*	*Bacillus tequilensis*
					HM753629	*90*	*Bacillus mojavensis*
			Planococcaceae	*Planococcus*	*EU624446*	*100*	*Planococcus maritimus*
				Planomicrobium	*JX524485*	*100*	*Planomicrobium sp*
Proteobacteria	*Alphaproteobacteria*	*Rhizobiales*	*Rhizobiaceae*	*Rhizobium*	*KF687011*	*100*	*Candidatus Rhizobium massiliae*
		Rhizobiales			*HG423546*	*100*	*Rhizobium sp.*
					KC236663	*100*	*Rhizobium sp.*
	Betaproteobacteria	*Burkholderiales*	*Comamondaceae*	*Variovorax*	*JQ291591*	*100*	*Variovorax paradoxus*
	Gammaproteobacteria	*Pseudomonadales*	*Moraxellaceae*	*Acinetobacter*	*KC257046*	*100*	*Acinetobacter sp.*
					KC257041	*100*	*Acinetobacter sp.*
		Enterobacteriales	*Enterobacteriaceae*	*Pantoea*	*AY924374*	*100*	*Pantoea agglomerans*
					JN644500	*100*	*Pantoea anthophila*
		Xanthomonadales	*Xanthomonadaceae*	*Xanthomonas*	*JN628980*	*100*	*Xanthomonas sp.*
		Enterobacteriales	*Enterobacteriaceae*	*Enterobacter*	*JQ682636*	*100*	*Enterobacter soli*

Table 3 Mature sorghum rhizobacteria physiological and PGP potential, values are given in percentage.

Representative genera	GS-	PSB	BEA	Gelatinase	Amylase	OF	Indole	Siderophore	Citrate	Glucose	Sucrose/Lactose	Urease	Mannitol
Rhodococcus	14.290	16.665	33.335	41.665	75.000	0.000	0.000	3.335	0.000	58.335	66.665	17.140	41.665
Xanthomonas	40.000	14.290	0.000	0.000	20.000	0.000	16.670	6.670	0.000	0.000	0.000	0.000	0.000
Pedobacter	33.330	11.110	40.000	80.000	40.000	0.000	16.670	0.000	0.000	20.000	20.000	20.000	0.000
Rhizobium	41.665	33.330	75.000	91.670	91.670	0.000	33.330	16.670	2.000	25.000	16.670	14.280	8.330
Planococcus	12.290	12.700	42.860	0.000	14.290	14.290	6.670	0.000	0.000	28.570	28.570	14.280	14.280
Bacillus	8.330	58.573	42.857	22.223	49.407	4.763	13.337	12.543	0.000	22.023	31.547	9.520	4.760
Enterobacter	48.660	75.000	50.000	50.000	50.000	0.000	16.670	6.670	0.000	50.000	0.000	75.000	0.000
Pantoea	28.570	58.330	79.165	87.500	54.170	0.000	16.670	3.335	1.000	20.835	25.000	25.000	4.165
Arthrobacter	14.290	27.777	72.220	61.113	66.667	0.000	6.670	4.447	0.000	0.000	8.333	25.000	0.000
Microbacterium	14.290	42.500	45.000	52.500	57.500	14.290	16.670	3.335	0.000	35.000	25.000	20.000	0.000
Planomicrobium	14.000	4.730	0.000	0.000	40.000	0.000	6.670	0.000	0.000	0.000	40.000	8.330	0.000
Variovorax	28.570	71.430	85.710	66.670	71.430	0.000	16.670	0.000	0.000	0.000	28.570	14.280	0.000
Curtobacterium	12.330	41.270	85.710	76.190	57.145	0.000	0.000	3.335	0.000	7.145	14.285	14.280	7.140
Acinetobacter	33.330	50.000	41.670	41.670	33.330	18.330	16.670	0.000	0.000	16.670	8.330	8.330	16.670

CFU = colony-forming units, PSB = phosphate solubilizing bacteria activities, IAA= indole-3-acetic-acid, BEA= bile-esculin agar, OF = oxidative-fermentative test, GS- = gram stain negative.

Table 4 variation of physiological activities affected by slope position and management practices. Mean values and standard errors were calculated by grouping the data according to slope position and the different management practices, tillage (n = 24), rotation type (n = 24) and N fertilizer treatment (n = 16). Fisher's Least Significant Difference (LSD) test was applied as post-hoc test for the comparison of the different fertilizer treatments.

	Physiological characteristics of rhizobacterial isolates							
	†††PSB	¥BEA	Gelatinase	Mannitol	Amylase	§§OF	§§§GS-	Siderophore
#Slope positions	%	%	%	%	%	%	%	%
Foot-slope	24.80±0.37	42.22±0.36	30.06±0.53	21.40±0.41	52.93±0.31	2.90±0.15	23.66±0.33	0.58±0.08
Up-slope	47.70±0.40	60.70±0.51	28.72±0.51	11.85±0.35	50.82±0.43	6.03±0.23	17.47±0.35	0.79±0.11
Management practices								
†Tillage								
CT	36.56±0.40	55.99±0.39	24.80±0.48	18.84±0.40	52.91±0.33	5.72±0.21	17.96±0.34	0.43±0.09
RT	35.93±0.44	46.94±0.51	33.99±0.55	14.41±0.37	50.84±0.42	3.21±0.17	23.17±0.34	0.83±0.13
‡Rotation								
Residue+CP	36.70±0.42	48.33±0.47	29.15±0.52	16.94±0.39	47.14±0.38	6.80±0.23	22.16±0.32	0.27±0.09
NoResidue-NoCP	35.80±0.42	54.60±0.45	29.63±0.53	16.31±0.39	56.61±0.37	2.13±0.12	18.97±0.37	1.01±0.13
§Fertilizer								
N0P60K60	40.51±0.50	52.32±0.52	34.68±0.65	16.90±0.50	51.04±0.45	2.56±0.18	22.60±0.40	0.22±0.12
N40P60K60	29.22±0.51	46.63±0.59	24.68±0.61	16.57±0.47	50.39±0.52	4.31±0.24	18.42±0.42	0.83±0.16
N80P60K60	39.01±0.53	55.44±0.57	28.81±0.66	16.40±0.47	54.20±0.41	6.01±0.27	20.67±0.45	0.83±0.16
	Physiological characteristics of rhizobacterial isolates						Tested on soil samples directly	
	##IAA	Citrate	Sucrose/Lactose	Glucose	Urease Test		‡‡MA	††CFUs×10^6
Slope positions	%	%	%	%	%		ppm	
Foot-slope	5.71±0.20	19.85±0.34	21.09±0.38	21.62±0.36	16.09±0.40		1.95±0.02	5.49±0.67
Up-slope	0.85±0.14	28.48±0.44	13.86±0.38	22.85±0.44	6.10±0.26		1.91±0.02	3.38±0.94
Management practices								
Tillage								
CT	2.78±0.06	23.78±0.38	23.12±0.41	22.39±0.41	13.45±0.38		1.90±0.17	5.77±0.16
RT	2.54±0.12	24.545±0.41	13.84±0.37	22.08±0.40	8.74±0.31		1.96±0.02	3.04±0.09
Rotation								
Residue+CP	2.20±0.07	18.36±0.40	17.31±0.36	20.71±0.39	12.37±0.36		1.93±0.02	4.38±0.12
NoResidue-NoCP	3.13 ±0.13	29.97±0.37	19.50±0.41	23.82±0.42	9.83±0.33		1.93±0.02	4.49±0.15
Fertilizer								
N0P60K60	5.20±0.08	21.97±0.48	20.26±0.46	22.86±0.50	13.76±0.48		1.95±0.02	5.63±0.16
N40P60K60	1.67±0.16	25.83±0.49	20.09±0.49	23.02±0.50	12.16±0.45		1.93±0.02	4.16±0.16
N80P60K60	2.21±0.09	24.70±0.49	14.92±0.46	20.86±0.48	7.37±0.34		1.91±0.02	3.51±0.17

#Slope positions = up-slope and foot-slope positions, †Tillage: conventional tillage (CT) and reduced tillage (RT), ‡Rotation: residual management including a cover crop (Residue+CP) and no residual management and no cover crop retention (NoResidue-NoCP), §Fertilizer: rates of nitrogen (N0P60K60, N40P60K60 and N80P60K60).
†††PSB = mineral-phosphate solubilizing activities, ¥BEA= bile esculin agar, §§OF = oxidation fermentation, §§§GS- = gram stain negative, ##IAA= indole-3-acetic-acid,
‡‡AMR = Mineralized ammonium (ppm), ††CFU = colony forming units.

3.3.4. Rhizobacteria PGPP and sorghum productivity

Sorghum yield indices (the row data adapted from Danso et al. (2018)) significantly improved in foot-slope position and under conventional tillage (Table S2). Linear mixed model analysis unraveled the significance of slope position and tillage practice, specifically conventional tillage, besides slope: tillage interaction on alteration of sorghum yield of grain and weight of the head (Table S2). The CFUs, frequency of gram-negative bacteria, IAA production, urea, mannitol hydrolyzation, and AMR were found to be significantly positively correlated with the sorghum weight of the head. Whereas PSB, BEA, amylase hydrolyzing capabilities were significantly negatively correlated with sorghum yield of grain, and weight of the head (Figure 5), IAA production significantly negatively affected the sorghum number of heads.

4. Discussion

4.1. Phenotypic and phylogenetic diversity of sorghum rhizobiome, screening their feasible PGPP

PGP rhizobacteria could contribute to the enhancement of sorghum yield indices which highlights the importance of preserving sorghum rhizobacteria PGPP for attaining sustainable agriculture. We identified the genera *Bacillus*, *Rhizobium*, *Enterobacter*, *Planococcus*, *Microbacterium*, *Rhodococcus*, *Planomicrobium*, *Acinetobacter*, *Variovorax*, *Arthrobacter*, *Pedobacter*, *Curtobacterium*, *Xanthomonas*, and *Pantoea* in MSR with the dominance of *Bacillus* (Table1, Fig 1a). The bacterial modification of plant metabolism, exudates, and hormones have shown the potential to modify rhizosphere microbial community assembly, activities, and interplays (el Zahar Haichar et al., 2014; Vurukonda et al., 2016; Schlemper et al., 2017). PGP bacteria have been identified to date in many crops such as cereals and legume families (Fierer et al., 2007; Backer et al., 2018), sorghum (Govindasamy et al., 2017), wild plants, and tomato (Leontidou et al., 2020). *Acinetobacter*, *Bacillus* (Santana et al., 2020), *Enterobacter*, *Microbacterium*, (Gopalakrishnan et al., 2013; Anwar et al., 2016), genera in the endo- and rhizosphere of sorghum, have been shown to be endowed with PGP potential. The parameters that might affect the plant rizobiome comprise plant genotype, growth stage, and soil substrate availability (Chiarini et al., 1998; da Costa et al., 2014; Schlemper et al., 2017; Chaparro et al., 2013, 2014). As suggested by Chaparro et al. (2014) young plants exude sugars which are widely used by the vast diversity of microorganisms, while plants release more specific exudates at maturity stages which possibly lead to more specific microbes' selection. This can

be one possible explanation of having high population and potential of inorganic phosphate solubilizing bacteria among the identified genera.

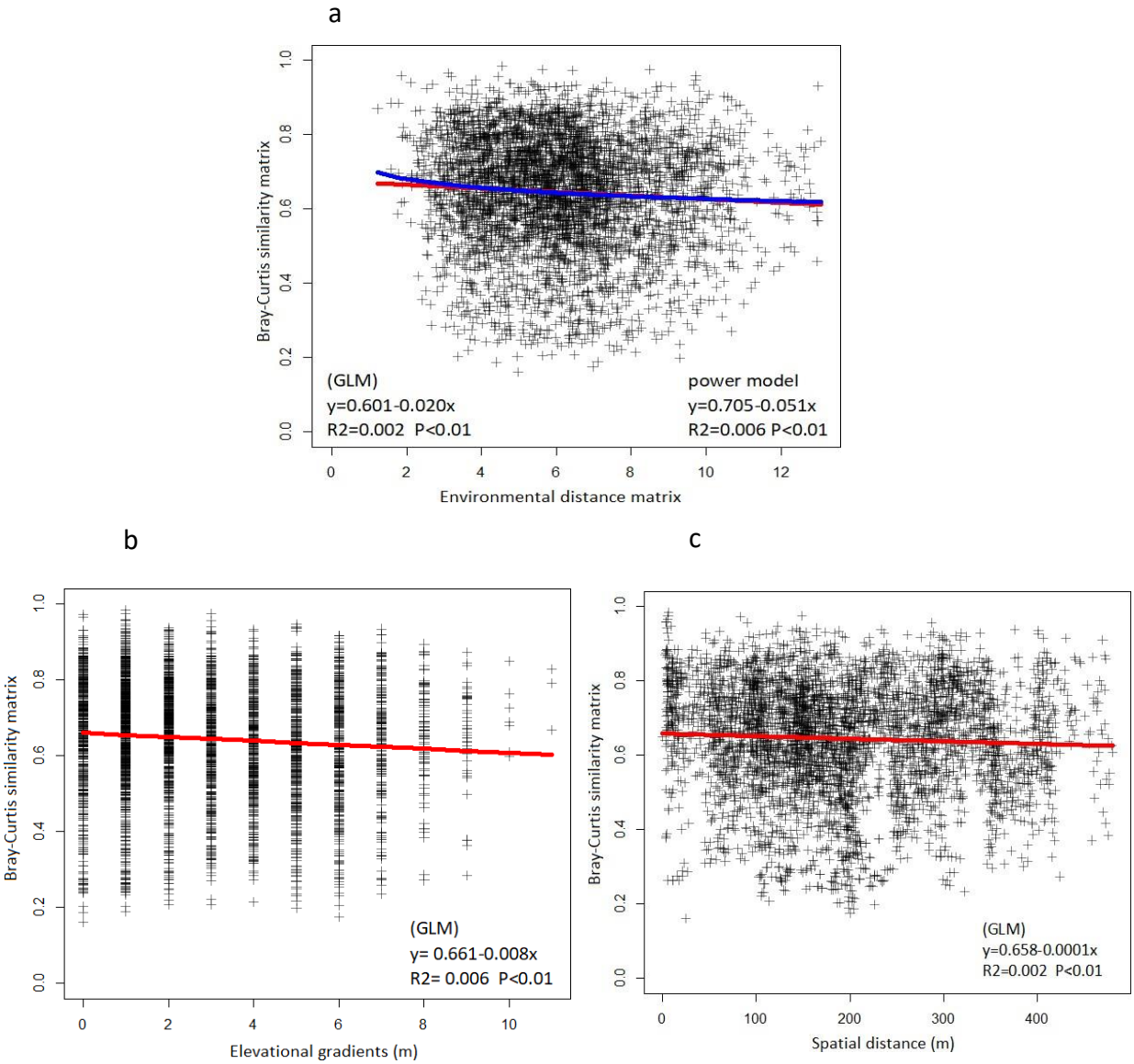

Figure 2 Distance–decay curves showing the relationship between locally adapted mature sorghum rhizobia physiological activities (based on the Bray-Curtis similarity index) against distance matrices reflecting (a) environmental heterogeneity, (b) elevational gradients (c) and spatial distance between all samples. Distance-decay curves were calculated based on linear regression (blue) and best-fitted power model (blue). The regression slopes of the linear relationships based on the Gaussian generalized linear model (GLM) are shown with (statistically non-significant) lines. Linear regressions were tested with a probability estimate for significance.

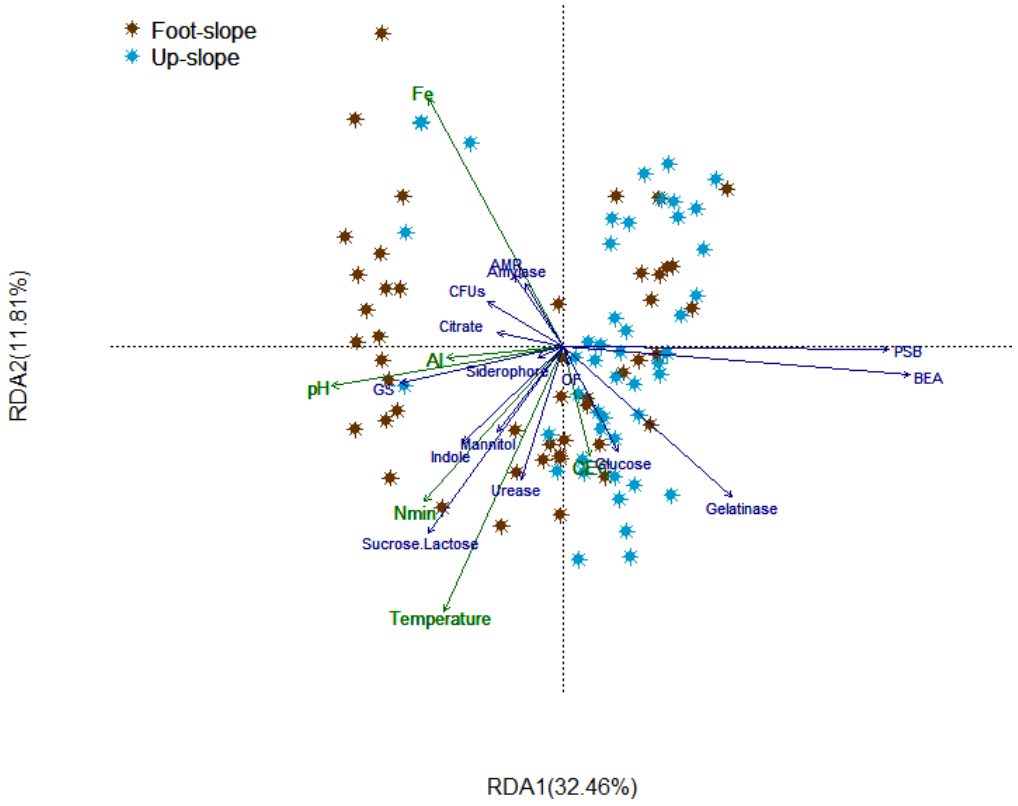

Figure 3 Redundancy analysis (RDA) of mature sorghum rhizobacteria physiological activities constrained by soil physio-chemical properties. Brown dots represent the foot-slope and blue dots the up-slope sites. Relevant soil properties were chosen based on the "ordiR2step" function and are shown as green arrows. Green arrows are representative of physiological characteristics of sorghum rhizobiome. They represent quantitative explanatory variables with arrowheads indicating the direction of increasing "sp" and "bp" scores.

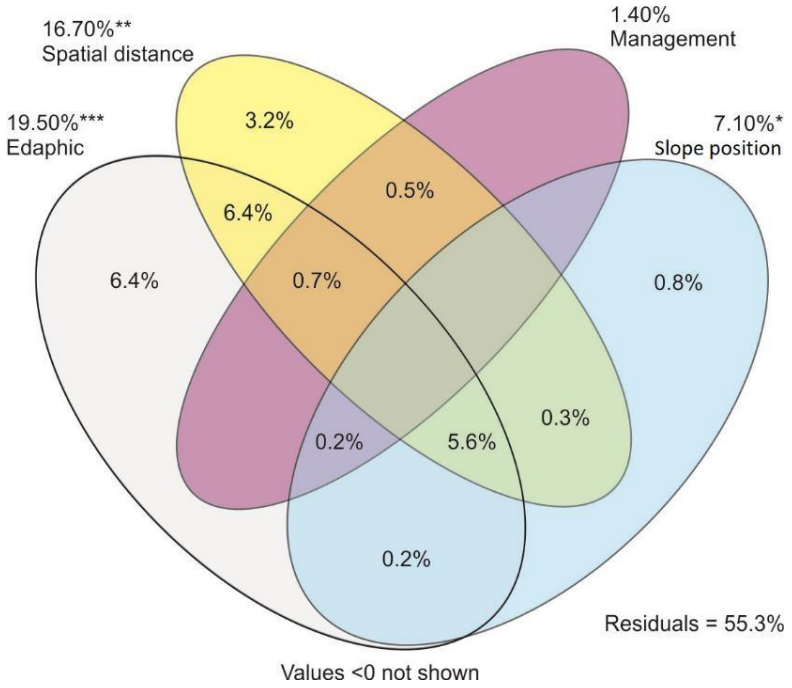

Figure 4 Venn diagram representing the contribution of soil edaphic properties (significant chemical and physical properties), management practices, spatial distance (significant PCNM vectors), and elevation on the variation of rhizobacteria physiological activities. The values outside the overlapping circles represent the total contribution of each group of variables. Adjusted R^2 values are reported for individual contributors. asterisks show the significance on each contributor according to ANOVA ($P < 0.05$ '*'; $P < 0.01$ '**' ; $P < 0.001$ '***'). P values were adjusted for multiple comparisons by the Benjamini-Hochberg method.

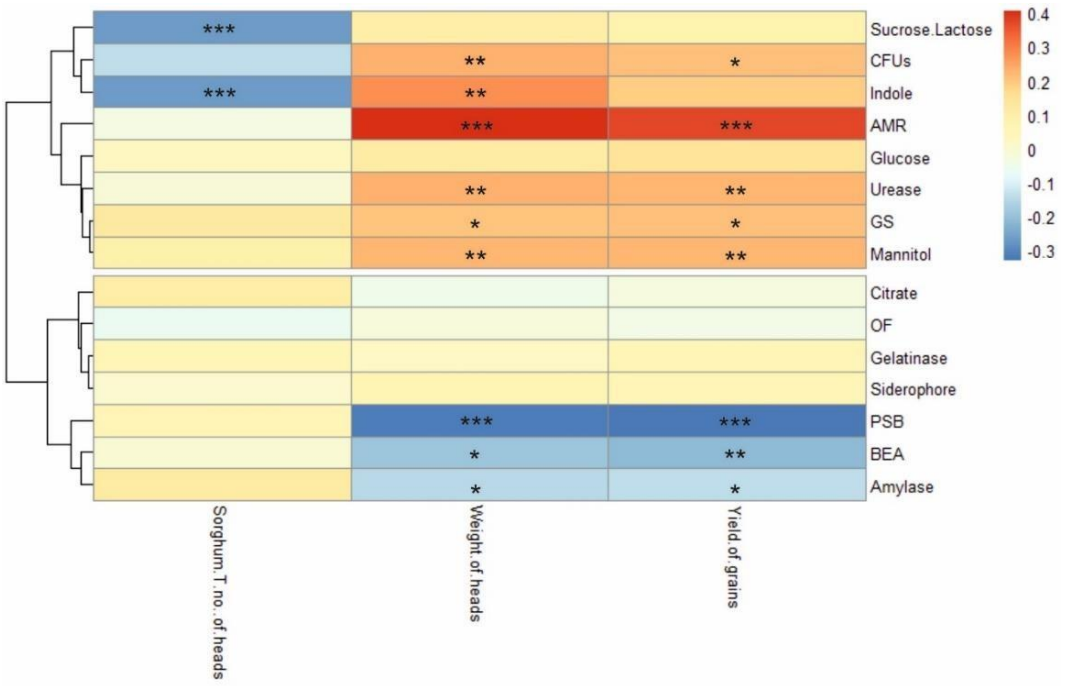

Figure 5 Heatmap showing the correlation of the soil bacterial physiological and PGP activities% with sorghum yield indices applying Spearman correlation analysis. Values of Spearman correlation coefficients are colored from red (positive) to blue (negative). Dendrogram indicates the grouping of bacterial physiological activities% with similar correlation patterns to sorghum yield indices. Dendrogram is based on Euclidean distance and was constructed by the complete method of agglomerative hierarchical clustering, hclust, algorithm. P values were adjusted for multiple comparisons by the Benjamini-Hochberg method. AMR= Ammonium mineralization rate. (*Significant at the 0.05 level, **Significant at the 0.01 level, ***Significant at the 0.001 level)

Enterobacter, Variovorax, Pantoea as subgroups of *Proteobacteria,* and dominant *Bacillus* as a subdivision of *Firmicutes* showed the highest capability of solubilizing phosphate (Figure 1c). In line with our findings *Bacillus* has been frequently reported in various soil types, making up to 95% of the gram-positive rhizobacterial population, and possessed strong PSB capability in croplands (Prashar et al., 2013; Kumar et al., 2017; Aloo et al., 2019). The *Bacilli* rhizobacteria have found wide applications in several sectors because of the unique properties they possess (Ongena and Jacques, 2008). The efficiency of *Bacillus* species over other rhizobacteria has constantly been attributed to their ability to produce spores that are resistant to environmental stresses (Rayavarapu and Padmavathi, 2016). Evidence suggests that many of the *Bacilli* rhizobacteria promote plant growth in multifarious ways. For instance, *Bacillus polymyxa* BFKC01 could improve nutrient availability for plants, produced phytohormones, and enhanced plant host resilience to biotic and abiotic stresses (Zhou et al., 2016).

Phosphate solubilizing (35.6%), and urea hydrolyzing (10%) capacities contributed the most to the PGP potentials of sorghum rhizobacteria, while IAA (5.8%) and siderophore production (0.5%) had the lowest contribution to the overall rhizobacteria PGPPs in recent investigation (Figure 1b). Urease and phosphatase enzymes can contribute to soil fertility by mineralizing nitrogen and phosphorous compounds (Gianfreda et al., 2005). The 80% of bacteria detected at our field found to be gram-positive bacteria (Fig 1b). Thus, relative to Gram-negative bacteria, Gram-positive bacteria can flourish and survive in resource-poor soils due to thicker cell walls and being capable of decomposing complex substrate for survival (Lennon et al., 2012; Cao et al., 2021). This result is in accordance with Govindasamy et al. (2017) results, which confirmed the dominance of *Bacillus* among other identified genera in the sorghum rhizosphere. We noticed that the ammonification rate was increased with increasing CFUs, which can be attributed to the capability of the vast majority of genera in contributing to ammonification within the soil (Isobe et al., 2020).

The phosphate solubilizers need a distinct ambient to grow compared to other physiological potentials, evidenced by the direction of the arrows in RDA plot relevant to the phosphate solubilizing and those that occurred to be capable of hydrolyzing Bile-esculin and gelatin which was apart from other potentials (Figure 3).

4.2. Topography shapes rhizobacteria PGP potential

We noticed that topography played a chief role in driving bacteria PGP and physiological potentials. Topographic features consist of slope position and aspect, affect the field's

microclimate. Soil edaphic properties are influenced by topography, which evidenced in our previous study as well (Ghotbi et al., 2021). The physiochemical properties of sloping farmland can be influenced by runoff and soil contemporary conditions. Thus, topography as a trigger of erosion can alter soil microbial community composition (Liu et al., 2020) and microbial biomass, their enzyme activities (Hou et al., 2014) which helps to anticipate the possible shifts in physiological and PGP potentials of bacteria as well. Erosion/deposition led to the enrichment of soil cations along with clay particles in foot-slope plots and left the eroding site drained with lower pH. This process justifies our findings on the dynamic of phosphate solubilizing bacteria in eroding up-slope plots. Phosphate solubilizers are found in the majority of soils and their performance is influenced by environmental factors (Pal, 2000). The growth of phosphate-solubilizing bacteria results in phosphorus solubilization and can lead to soil acidification (Anwar et al., 2016). We observed the huge number of PSB in up-slope plots, while other activities were drastically low in up-slope soils. Overall, high PSB and BEA in this study can partially be explained by the sorghum maturity stage, since plant developmental stages can markedly impact on the plants rhizobiome, and soil substrate status. da Costa et al. (2014) modeled the rhizobacteria PGP expression based on the soil nutritional status and revealed that nutrient solubilized bacteria can be favored by the plants under the nutrient-poor condition of soils. While the phytohormone producers such as IAA rhizobacteria gained prominence and favored in plant-rhizobiome interaction under the nutrient-rich condition of the soil. Likewise, we detected the manifested increase of phosphate solubilizing potential towards up-slope while the IAA producing potential of rhizobacteria was promoted towards nutrient enriched foot-slope position. Besides, RDA plot proved the dominance of all physiological and PGP potentials specially IAA production in foot-slope plots except for PSB, Bile-esculin degradation, and gelatin hydrolyzing potential, which improved toward eroding up-slope (Figure 3). This indicates the preponderant role of topography in forming soil substrate availability and rhizobacterial activities.

We evidenced no manifested paradigm of clustering in rhizobacterial physiological and PGP potentials due to management practices (Figure S1). Enzymatic activities evaluation is indicative of the presence of physiological activities within the organisms (Levine et al., 2011). Higher bacterial enzymatic activities can be concomitant to their higher physiological potentials (xxxx). We noticed no shifts in rhizobacteria physiological potentials following the agronomic practices (Table 3). It has been reported that differences in organic agroecosystem management have strongly influenced soil nutrients and enzyme activities, but without a major effect on the soil microbial community (Bowles et al., 2014). Investigating how agricultural practices might influence the soil microbiota and their PGP potential can lead to designing efficient strategies to

enhance plant productivity in parallel with preserving the environment.

4.3. Factors contributed to the rhizobacteria PGPPs, and promotion of sorghum yield

PGPP, and most of the assessed physiological potentials were promoted within the foot-slope plots, suggesting the higher substrate availability can affect presence of rhizobacteria metabolic capabilities. Specifically, PGPPs and other physiological potential of MSR shaped by the heterogeneity of soil edaphic properties (Figure 3). Similarly, the optimum conditions of temperature, pH, and ionic strength were found to augment soil enzymatic activities (Tabatabai, 1994) and thus microorganisms' metabolites. Although we couldn't find similar studies for the comparison, we referred to the enzymatic activities as the indicator of bacterial metabolic capabilities. It's widely known that activities of specific microbial enzymes may change depending on the soil amendments and the relative availability of soil nutrients, and other soil unique characteristics such as soil pH, cation exchange capacity, and temperature (Sinsabaugh et al., 2008; Griffiths & Philippot, 2013; Bowles et al., 2014; Docherty et al., 2015). Correlations between soil enzyme activities and organic C and/or total N contents have been reported in other studies (Dodor and Tabatabai, 2002; Taylor et al., 2002; Gianfreda et al., 2005). Similarly, we noticed the positive correlation of most rhizobacteria physiological potentials, except for PSB, gelatinase, and BEA, with soil substrate availability at the deposition site. A proposed model by da Costa et al. (2014) on soil-plants-microbiome interactions, revealed the tight bond between plant roots microbiome PGPPs and soil nutrient availability. They revealed that under nutrient rich condition plants can favor phytohormone producing rhizobacteria while soil's nutrient deficiency promotes solubilizing activities of rhizobacteria. In line with da Costa et al. (2014) we noticed IAA production and urea hydrolyzing capacity of rhizobacteria enhanced in tandem with the enhancement of soil nutrients and temperature toward depositional site (Figure 3).

The C:N:P ratios of microbial biomass is relatively constrained (Cleveland and Liptzin, 2007). Enzymatic activity helps to boost the accessibility of soil limiting nutrients to meet microbial physiological and metabolic demands (Sinsabaugh et al., 2008; Allison et al., 2011). Consequently, higher rhizobiome metabolic potentials as well as higher fermentative reaction potentials can be attributed to the physiological adaptation of rhizobiome to the higher nutrient and water accessibility in footslope soils. Distance decay relationship confirmed the systematic distribution of rhizobiome PGP and physiological potentials. Slope position (7.1%) defined by elevational gradient also had a significant portion in causing MSR physiological variations. However, the most effective factors in this regard found to be soil edaphic properties (19.5%) and spatial distance (16.7%), respectively. We concluded that topography led to soil

physiochemical heterogeneity in the field which shaped sorghum rhizobacterial physiological and PGP potentials (Fig. 4).

The high capability of the *Enterobacter*, *Variovorax, Pantoea,* and *Bacillus* genera in producing IAA, and solubilizing phosphate and hydrolyzing urea was detected in this study. Besides, sorghum weight of head showed a significant positive correlation with the rate of ammonification, number of CFUs, indole production, the population of gram-negative rhizobacteria, mannitol, and urea hydrolyzation (Figure 5). PGP rhizobacteria have been reported to promote growth and yield of maize (Araujo and Guerreiro, 2010) and sorghum (Schlemper et al., 2017). In a study conducted by Govindasamy et al., (2017) *Acinetobacter, Bacillus, Enterobacter, Geobacillus, Lysinibacillus, Microbacterium, Ochrobactrum, Paenibacillus,* and *Pseudomonas* were the major genera present in the endo-rhizosphere of sorghum. According to authors the identified genera were endowed with at least one PGP trait and were correlated with the sorghum growth. *Pseudomonas*, and *Bacillus* genera were also reported as the most effective genera to improve growth of sorghum through increasing availability and uptake of less bioavailable soil nutrients (Abbaszadeh-Dahaji et al., 2019). Matching beneficial bacteria with their preferred host crops and preferential nutritional conditions might optimize root colonization, and their productivity (Weller et al., 2002; da Costa et al., 2014). Appreciating the PGPP knowledge can pave the way to enhance sorghum productivity while supporting sustainable agriculture.

5. Conclusion

Topography fueled soil edaphic heterogeneity whereby shaped rhizobacteria phenotypic, phylogenetic potentials. Significant spatial autocorrelation in PGP/physiological potentials of MSR at our field scale was attributed to rhizobiome physiological adaptation to oxygen deficiency and nutrient accessibility at the depositional site and water and nutrient drained condition of upslope site. Physiological and PGPPs of sorghum rhizobacteria showed a tight association with soil edaphic factors and harvested sorghum yield indices. Together, soil edaphic properties of 19.50% and geographic distance of 16.70% governed about 36.20% of the variation in rhizobacterial physiological and PGPPs. The higher hormone-producing potential was correlated with nutrient enrichment in the depositional soils, while the higher proportion of phosphate solubilizing potential was seen in eroding up-slope site. Phosphate solubilizers' promotion in our field can be explained by the sorghum maturity stage since plant developmental

stages can markedly impact on the plants rhizobiome composition and physiological potentials. Studying phosphate solubilizing activities in association with various sorghum stages of growth is advocated for offering a more confident reason for improving PSB in the field. Besides, more work should be carried out to gain insight into the factors that improve and regulate species PGP potentials and consequently sorghum productivity while preserving the environment.

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Supplemental materials

Table S1. Implications of field topography and agricultural practices for physiological properties of rhizobacteria, assessed by statistical analysis using a linear mixed model.

physiological	††CFUs	‡‡MA	†††PSB	¥BEA	Gelatinase	Amylase	§§OF	§§§GS-	Siderophore	##IAA	Citrate	Sucrose/Lactose	Glucose	Urease	Mannitol
#Slope	12.01***	3.79*	15.11***	9.42**	0.02	0.06	1.03	3.42*	0.44	12.27***	1.12	5.74*	0.21	5.43*	5.53*
†Tillage	7.31**	4.92*	1.64	4.89*	0.05	0.18	0.65	1.37	1.60	1.80	0.11	2.96	0.00	1.29	2.21
‡Rotation	0.50	1.16	0.04	0.24	0.30	4.45*	0.02	0.24	0.00	0.21	0.82	0.16	0.19	1.86	0.60
§Fertilizer	1.66	1.63	0.08	0.34	0.25	0.44	0.99	0.89	0.16	2.06	0.27	1.07	0.76	0.41	0.56
Slope:Tillage	0.04	2.44	0.88	5.32*	0.52	0.26	0.00	0.13	1.45	1.66	0.03	0.01	0.59	0.27	0.76
Slope:Rotation	1.97	0.15	0.55	0.00	0.25	0.02	0.94	0.53	0.46	0.67	4.33*	0.01	3.16	0.44	0.58
Tillage:Rotation	0.69	0.91	0.87	0.54	0.10	1.20	1.49	0.63	0.08	1.11	1.55	1.75	0.79	0.14	0.44
Slope:Fertilizer	3.15*	0.13	0.16	0.11	0.06	0.76	2.46	0.28	0.52	0.59	1.84	0.74	0.68	0.86	0.60
Tillage:Fertilizer	0.12	0.86	2.00	0.82	0.40	1.99	1.00	0.40	1.48	1.21	2.58.	2.11	0.22	0.73	0.73
Rotation:Fertilizer	0.41	0.23	0.28	1.38	2.28	0.94	2.09	0.69	3.91*	2.55	0.06	0.08	0.99	0.45	0.20
Slope:Tillage:Rotation	0.66	0.04	0.09	0.01	0.00	0.01	0.27	0.12	0.13	2.85	0.85	0.14	0.01	0.08	0.64
Slope:Tillage:Fertilizer	0.20	0.19	0.40	2.00	0.19	0.03	2.20	0.83	0.74	0.58	0.68	1.03	0.27	0.36	0.85
Slope:Rotation:Fertilizer	1.40	0.20	0.14	0.08	0.03	0.36	0.74	0.59	0.05	0.98	0.08	0.28	0.47	0.65	0.91
Tillage:Rotation:Fertilizer	1.73	0.11	0.63	0.09	1.65	0.02	0.41	0.01	2.01	1.76	0.22	0.32	0.66	0.46	0.45
Slope:Tillage:Rotation:Fertilizer	1.06	0.45	0.13	0.54	0.48	0.18	0.20	0.34	0.24	0.52	0.96	0.51	0.46	0.35	1.54

#Slope = up-slope and foot-slope positions, †Tillage: conventional tillage (CT) and reduced tillage (RT), ‡Rotation: residual management including a cover crop (Residue+CP) and no residual management and no cover crop retention (NoResidue-NoCP), §Fertilizer: rates of nitrogen (N0P60K60, N40P60K60 and N80P60K60).
††CFU = colony forming units, ‡‡MA = mineralized ammonium, †††PSB = phosphate solubilizing bacteria activities, ¥BEA= bile esculin agar, §§OF = oxidation fermentation, §§§GS- = gram stain negative, ##IAA= indole-3-acetic-acid.
* Significant at the 0.05 level.
** Significant at the 0.01 level.
*** Significant at the 0.001 level.

F-values are given, and significance is indicated by asterisks.

Table S2. Impact of field topography and agricultural practices on sorghum yield indices evaluated by statistical analysis using a linear mixed model. F-values are given, and significance indicated by asterisks

		Sorghum yield indices	
Treatments and their interactions	Total no of heads	Weight of head	Yield of grain
[#]Slope	8.26**	60.62***	53.01***
[†]Tillage	0.76	13.32**	8.92**
[‡]Rotation	1.22	2.48	2.26
[§]Fertilizer	1.19	0.21	0.57
Slope:Tillage	0.00	5.57*	4.94*
Slope:Rotation	0.12	1.19	2.12
Tillage:Rotation	0.07	3.05	1.80
Slope:Fertilizer	2.29	0.99	0.89
Tillage:Fertilizer	0.42	0.06	0.38
Rotation:Fertilizer	1.31	0.49	0.52
Slope:Tillage:Rotation	0.32	2.10	1.25
Slope:Tillage:Fertilizer	0.02	0.64	0.50
Slope:Rotation:Fertilizer	0.38	0.71	0.54
Tillage:Rotation:Fertilizer	2.20	0.29	0.27
Slope:Tillage:Rotation:Fertilizer	0.21	0.03	0.24

[#]Slope = up-slope and foot-slope positions, [†]Tillage: conventional tillage (CT) and reduced tillage (RT), [‡]Rotation: residual management including a cover crop (Residue+CP) and no residual management and no cover crop retention (NoResidue-NoCP), [§]Fertilizer: rates of nitrogen (N0P60K60, N40P60K60 and N80P60K60).
* Significant at the 0.05 level.
** Significant at the 0.01 level.
*** Significant at the 0.001 level.

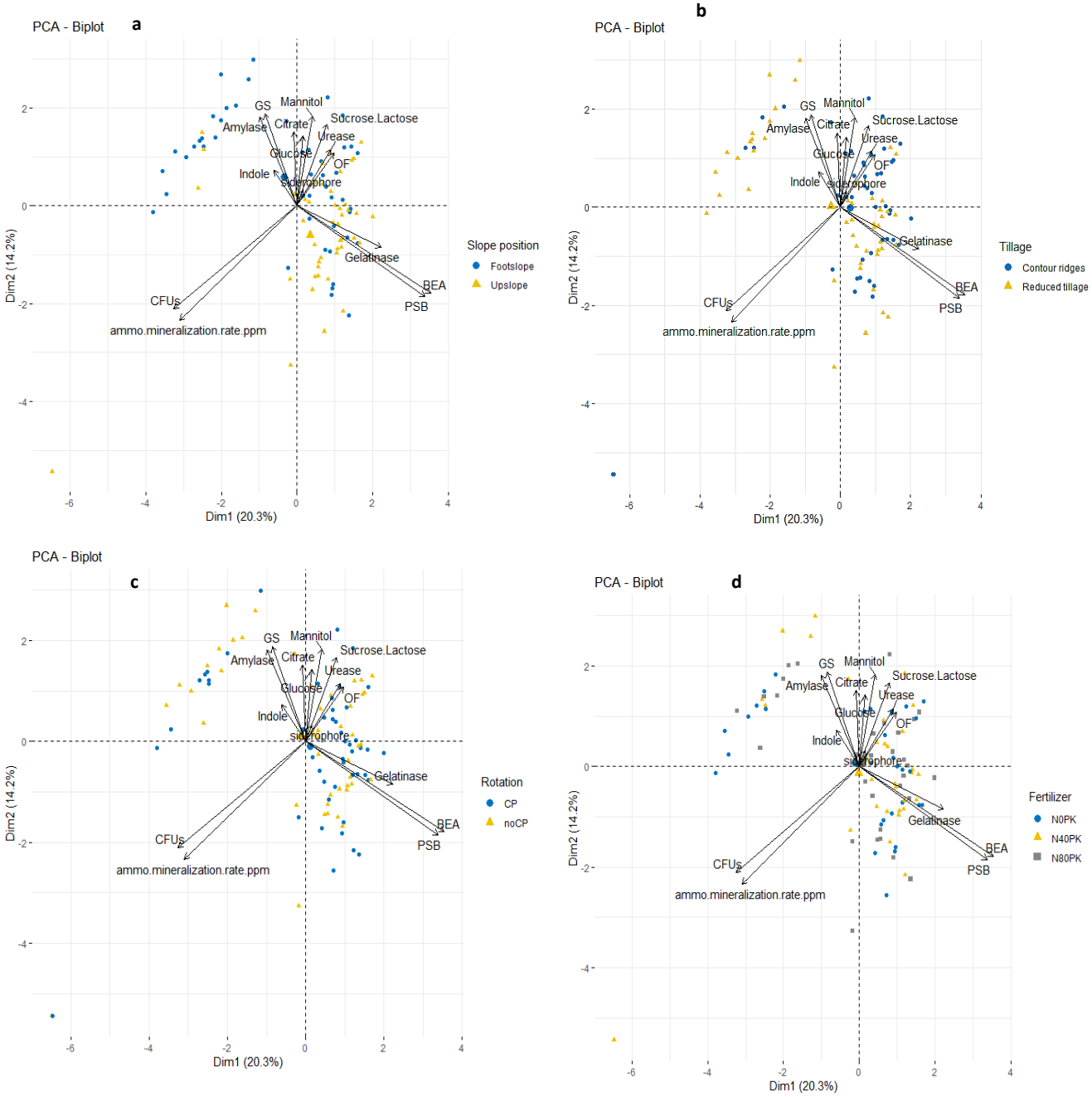

Figure S2 Visualizing treatment implications for bacterial physiological activities%, applying unconstrained principal component analysis. Physiological activities influenced by slope position (a), and agronomic practices including, tillage practice (b), rotation (c) N fertilizer rates (d). CFU = colony forming units, MA = mineralized ammonium, PSB = phosphate solubilizing bacteria activities, IAA= indole-3-acetic-acid, BEA= bile-esculin agar, OF = oxidation fermentation, GS- = gram stain negative.

3. Overarching discussion

Precluding erosion and preserving soil fertility in Upper Eastern Ghana call for a better understanding of erosion and accelerated erosion implications for soil biogeochemical and microbial assets and their possible responses to erosion and accelerated erosion. To garner insights into these objectives, erosion and accelerated erosion in sloping farmland were initially tracked down by evaluating SOM turnover in the field, employing ^{13}C and ^{15}N signature tracing techniques. To this end, the individual and interactive effects of topography in association with common agronomic schemes in the region on soil prokaryotic community composition, and rhizobiome plant growth-promoting potential were determined. This study may support the farmers of the region with the knowledge on the appropriate selection of the management schemes for their sloping farmlands to preserve soil health and fertility in the long run.

3.1. Soil organic matter turnover in Upper Eastern Ghana hilly farmland revealed by changes in soil $\delta^{13}C$ and $\delta^{15}N$

3.1.1. Tracing down erosion and retrieving the origin of deposited soil organic matter

The accumulation of significantly higher soil organic matter%, MWC%, MWN%, NO_3^--N, NH_4^+-N, and C: N ratio along with enrichment of ^{15}N at the depositional site, suggesting the occurrence of sheet erosion and translocation of light soil organic C to the depositional sediments (chapter 2.1. Table 1 and Table S1). It's widely known that topography in association with rainfall can imply erosion potential. Surface runoff removes soils O horizon, consist of soil organic C, from the eroding sites and deposits them within the depositional sediments. During this translocation process, SOC is partially decomposed and lost along the slope (Polyakov and Lal 2004; Doetterl et al. 2016; Wang et al. 2017). SOC removal from eroding site and its storage at the depositional site can imply that erosion/deposition processes simultaneously can alter the biogeochemical properties of both eroding and depositional sites (Park et al. 2014). Tracing possible changes in the eroding lands over runoff events, tracking down C_3 and C_4 vegetation transit of the land (Turnbull et al., 2008; Drinkwater et al., 1998; Wanniarachchi et al., 1999; Aranibar et al., 2008), and retrieving the origin of transported soil components (Fox and Papanicolaou 2007, Park et al. 2014; Wang et al. 2017; Lal, 2001) are among advantages of applying $\delta^{15}N$ and $\delta^{13}C$ techniques in studying soil erosion. Although shifts in soils $\delta^{13}C$ were negligible between slope positions, $\delta^{15}N$ values significantly enhanced

within the depositional sediments. Distinctively different nitrogen and carbon isotope signatures between hillslopes compared with the associated depressional sites have been reported in the literature (Alewell et al., 2008; McCorkle. et al., 2016). Evidently, the degraded SOM is commonly enriched in ^{15}N, and less consistently enriched in ^{13}C compared to the less degraded organic matter (Kramer et al., 2003).

We evidenced the ascending trend of $\delta^{15}N$ values from upslope to footslope (6.25±0.09‰ to 4.88±0.13‰) (Chapter 2.1. Table 1). The maximum natural abundances of soil ^{15}N (7.40‰) at depositional plots were attributed to the accumulation of eroded nutrients and organic matter at the foot-slope plots which can stimulate ^{15}N fractionation (Chapter 2.1. Table S1 and Table1). To date, soil $\delta^{15}N$ values have been applied for recognizing the sources of soil N amendment and N utilized by the plants, since C_3 plants contain significantly higher $\delta^{15}N$ than C_4 plants taken from the same location (Aranibar et al., 2008; Gatica et al., 2017). The $\delta^{15}N$ range around 6 ‰ for cultivated soils was reported (Choi et al., 2017; Fuertes-Mendizábal et al., 2018), which is normally higher than natural soils following various N inputs to the agricultural lands. Current findings concur with that of Schaub and Alewell (2009) emphasizing the occurrence of sheet erosion and redistribution of ^{15}N and ^{13}C along the slope, which was evidenced by the intermediate values of soil $\delta^{13}C$, and enrichment of ^{15}N values at the depositional site. $\delta^{15}N$ showed a tight correlation with latitude and elevational gradients in the current result which also helped to postulate the preponderant imprints of slope and erosion on alteration of $\delta^{15}N$ values (Chapter 2.1. Figure 2 d-f). Shifts in $\delta^{15}N$ values elucidate the N cycling and N loss in the soil, which reflect the possible isotopic fractionation during transformations of soil N (Schaub and Alewell, 2009). The higher range of soil ^{15}N natural abundance in depositional sediments which is associated with the accumulation of other evaluated edaphic properties is compelling evidence for the existence of the open N cycle and higher N loss at the depositional site.

The application of $\delta^{13}C$ and $\delta^{15}N$ natural abundance for tracing C_3 and C_4 assimilation pathways and understanding the N cycle are based on the presumption that the decomposed SOM $\delta^{13}C$ and $\delta^{15}N$ imprints are reflecting those of the origin. According to the history of local farming, the groundnut (C_3) ($\delta^{13}C$ signature of -26 to -28‰ (Gregorich et al., 1995)) has been the dominant crop at the up-slope position over 30 years. At the foot-slope position, irrespective of erosion repercussions, the $\delta^{13}C$ signature of around -28‰ was anticipated due to the dominance of C_4 plants over 30 years (Gregorich et al., 1995). However, our results unraveled

the intermediate $\delta^{13}C$ signature with a mean value of -18.50‰ along the slope suggesting the possible erosion implications for redistributing of soil $\delta^{13}C$ signature and SOM along the slope. The similar ^{13}C values within the up-slope and foot-slope plots reflected the homogenization of the surface soil following the erosion/deposition processes which complicated the detection of sediments source at the depositional sites (McCorkle et al., 2016). The turnovers of both labile and recalcitrant SOM were estimated at up-slope plots, which indicated the ongoing SOC turnover and lower sequestration of SOM within the field (Horwath, 2007; Hammad et al., 2020).

3.1.2. ^{13}C and ^{15}N natural abundance under accelerated erosion

None of the individual agronomic practices significantly affected the enrichment or depletion of soil ^{13}C and ^{15}N (Chapter 2.1. Table S1 and Table 1). However, the slope × tillage interaction as a combination of erosion and anthropogenic erosion appeared to have a significant impact on soil ^{13}C natural abundance. Therefore, the potent impact of erosion when combined with accelerated erosion in inciting ^{13}C fractionation was manifested, which was also reported in other studies (Werth and Kuzyakov, 2010). As the C remaining after mineralization contains richer $\delta^{13}C$ in comparison with its initial point, the higher rates of SOM decomposition enrich soil $\delta^{13}C$ values (Mariotti and Balesdent, 1990). The higher $\delta^{13}C$ content of the soil in plots affected by slope × tillage interaction can be defined through higher mineralization of soil organic C (Chapter 2.1. Table S1). In line with our finding Wang et al. (2017) suggested that sloping cropland can contribute up to 81.3% to the total SOC deposited in the sediments, which illustrates the higher detrimental implications of erosion when combined with intensive agronomic practices in sloping farmlands. Learning about the terrain characteristics, farming history, and N and C cycles can be of assistance to manage the field efficiently towards the improvement of SOC and SON sequestration. It's noteworthy to mention that, in most farmlands, the $\delta^{15}N$ signature is strongly affected by the application of various N fertilizers, which disturbs the balance of soil total N and $\delta^{15}N$ by altering N inputs and outputs (Choi et al., 2017; Liu et al., 2017). However, the increase of N dosage to 80 kg ha^{-1} did not alter soil ^{15}N isotopic values compared to the plots that received no N fertilizer in the recent study (Chapter 2.1. Table 1). This can be assigned to the negligible contribution of the N fertilizer to the soil N pool due basically to the erosion impacts or plant uptake or following the N loss through multifarious pathways such as nitrification, denitrification, leaching, plants uptake, and volatilization (Flores et al., 2007; Quan et al., 2021).

3.2. Topographic attributes override impacts of agronomic practices on prokaryotic community structure

3.2.1. Topography and erosion induced shifts in the soil abiotic properties and microbiota

Accrual of clay particles along with basic elements such as Mg, K, Mn, Ca, as well as higher MWC, and MWN% in the depositional sediments (Chapter 2.2. Table 1), suggests the ongoing erosion-deposition processes with a striking footprint on soil edaphic properties of both foot- and up-slope positions. The occurrence of soil surface removal with the profound repercussions on SOC elimination from eroding sites has been reported previously (Li et al., 2015; Negasa et al., 2017, Shi et al., 2019; Gómez et al., 2020). During the erosion-deposition processes, soil light particles, specifically clay are translocated by the overland runoff and deposited downslope (Huang et al., 2013). Higher clay content at the foot-slope position contributes to the higher chance of anoxic microsites formation at the frequently waterlogged depositional sites, which eventually reinforces the life of a higher number of anaerobic microorganisms (Keiluweit et al., 2018; Du et al., 2020). The presence of diverse bacterial taxa being adapted to anoxic conditions at the foot-slope position was markedly contributed to the higher bacterial diversity at the deposition site in the current study (Chapter 2.1. Table 3) which is consistent with previous studies (Neupane et al., 2019; Du et al., 2020). The decline in bacterial community homogeneity in flooded paddy soils, recurrently facing anoxic conditions, has also been reported in the literature (Maarastawi et al., 2018; Wang et al., 2020). However, there is a knowledge scarcity on poorly drained depositional sites of hilly farmlands.

It is known that the redistribution of sediments at the eroding sites adversely impacts soil microbial diversity, their network complexity, and soil nutrients status at up-slope position (Du et al., 2020; Huang et al., 2013; Liu et al., 2018; Qiu et al., 2021). We noticed higher bacterial richness and diversity at the depositional site (Chapter 2.2. Table 3), which was tightly bound to the accrual of soil nutrients downhill (Chapter 2.2. Figure S4). Enrichment of soil nutrients at depressional sites is known to promote soil bacterial diversity (Du et al., 2020; Neupane et al., 2019). Topography also appeared to be the chief force behind structuring bacterial community, evidenced by NMDS plots and ANOSIM results (Chapter 2.2. Table 4 and Figure 1). Similarly, Huang et al. (2013), Hargreaves et al. (2015), Xiao et al. (2017), and Neupane et al. (2019) reported the association between topography and bacterial community structure. Various bacterial life strategies were used

to define the predominance of major bacterial taxa in different positions of hilly farmlands (Hargreaves et al., 2015; Neupane et al., 2019; Suriyavirun et al., 2019). The *Bacillaceae* (with the prevalence of *Anaerobacillus*) were dominant in the depositional sediments, corresponding to their copiotrophic life strategy (Mandic-Mulec et al., 2015). In contrast, *Micrococcaceae* (with a prevalence of Arthrobacter) as a subdivision of *Actinomycetales* were favored by water and nutrients drained condition of up-slope. The *Actinobacteria's* higher abundance in up-slope plots can also be attributed to their excellent survivability under growth-limiting, harsh and drought conditions (Gittel et al., 2014; Barka et al., 2016). The higher relative abundance of nitrifying and denitrifying prokaryotes along with higher availability of NH_4^+-N and NO_3^--N, as well as other obligate and facultative anaerobic prokaryotes i.e. fermentative microorganisms, iron, and the sulfate- reducing community reinforced the regular occurrence of anoxic conditions in poorly drained depositional soils. Various methanotrophic genera, known to rely on the activities of strictly anaerobic methanogens, were also detected at the foot-slope position (Knief, 2019; Conrad et al., 2020). Similar microtopographic associated shifts in bacterial community structure and enrichment of anaerobic bacteria in depressional soils have been reported in other studies (Frindte et al. 2019, Suriyavirun et al. 2019). Together, topography showed potent capacity in formatting soil prokaryotic community structure and composition.

3.2.2. Agricultural-induced changes in abiotic and biotic soil properties in the hilly field

The limited impact of agricultural schemes in shifting soil edaphic properties implied the preponderant impacts of topography in concealing agronomic practices' effects on soil edaphic properties. Agronomic practices' implications for soil abiotic properties were largely slope-dependent, this assumption was reinforced by slope × tillage interaction effects which altered soil edaphic properties (Chapter 2.2. Table S1). Likewise, the effects of agronomic practices on the prokaryotic community structure appeared to be slope dependent. For instance, the application of N fertilizer promoted the Chao1 and ACE indices at the highest N-level merely at the up-slope position. Additionally, under rotation × N fertilizer interaction bacterial richness, evenness, and Shannon indices were altered (Chapter 2.2. Table 5). This phenomenon can be explained by nutrient deficiency acting as the main constraint for microbial life at eroding up-slope soils, and therewith these soils are more responsive to nutrient enrichment. Assessment of beta-diversity through ANOSIM also revealed the efficacy of the crop rotation regime (plus residue

management) in altering the up-slope prokaryotic community structure (Chapter 2.2. Table 4). Incorporating crop residue with soil through plowing could increase the soil organic matter mineralization by microorganisms (Horwath, 2007). According to Lupwayi et al. (2018), the appropriate application of mineral N fertilizer in tandem with an effective turnover of organic amendments such as cover crops is vital for soil bacterial diversity maintenance. The application of cover crops for the fallow period in Ghanaian agricultural systems was found to be effective in fostering a diverse microbial community (Asuming- Brempong et al., 2008; Sul et al., 2013). Studies have exploited the fact that crop residues along with the application of N fertilizer and tillage practice are capable of increasing soil C and N inputs due to higher organic residue added in the field (Adiku et al., 2008; Verzeaux et al., 2016; Lupwayi et al., 2018; Tang et al., 2019; You et al., 2020). Eventually, higher SOM increases soil microbial diversity and shifts bacterial community structure (Sul et al., 2013; Navarro-Noya et al., 2013; Lupwayi et al., 2018).

At the depositional site, the management practices' implications for the bacterial community structure were seen in response to tillage practice (Chapter 2.2. Table 4). Turning the soil through plowing can lead to a change in anoxic-oxic transition which is associated with higher SOC oxidation and the accessibility of C for heterotrophic microbial utilization (Horwath, 2007; Zhao et al., 2020b). Tillage also causes closer contact between unprotected organic matter and the consumers (Horwath, 2007; Sul et al., 2013) and therefore facilitates the incorporation of SOC within the soil, which all can favor the copiotrophic taxa (Navarro-Noya et al., 2013; Ramirez-Villanueva et al., 2015; Lupwayi et al., 2017; Wang et al., 2020). The higher efflux of CO_2 and higher denitrification rate at foot-slope positions in response to tillage practice corresponds to the mentioned shifts in depositional soils following the plowing (Xu et al., 2021). Overall, the impact of agronomic practices on bacterial community structure was contingent upon topography/slope position and the agricultural impacts remained rather weak.

3.3. Plant growth-promoting potential of mature sorghum rhizobome affected by soil substrate availability and pedoclimatic status

3.3.1. Phenotypic and phylogenetic diversity of sorghum rhizobiome, screening their feasible plant growth-promoting potential

Overall, phosphate solubilizing (35.6%) contributed the most to the PGP potential of the mature locally adapted sorghum rhizobacteria, while IAA (5.8%) and siderophore production (0.5%) had the lowest contribution to these potentials (Chapter 2.3. Figure 1b). The majority of isolated rhizobacteria were gram-positive (~80%). Relative to Gram-negative bacteria, Gram-positive bacteria can decompose complex substrates for survival and flourish in resource-poor soils.

Moreover, they are more resistant to water and nutrient deficiency due to thicker peptidoglycan cell walls (Lennon et al., 2012; Cao and Lin, 2021). This can explain the dominance and major contribution of gram-positive *Bacillus* (29% of rhizobacterial isolates) to the physiological and PGP traits in the field (Chapter 2.3. Figure 1a-b). Maize and sorghum in parts of the world such as Western Africa, and southern America are planted in nutrient-poor soils. Thus, plant growth-promoting rhizobacteria (PGPR) can contribute to the enhancement of maize and sorghum yield and improvement of their nutrient uptake (Gopalakrishnan et al., 2013). This gives great value to the screening and exploration of sorghum rhizobacteria.

The identified genera included *Bacillus, Rhizobium, Enterobacter, Planococcus, Microbacterium, Rhodococcus, Planomicrobium, Acinetobacter, Variovorax, Arthrobacter, Pedobacter, Curtobacterium, Xanthomonas*, and *Pantoea* which were endowed with multiple PGPP in mature sorghum rhizosphere with the dominance of *Bacillus* (39%) (Chapter 2.3. Figure 1a). According to the literature *Acinetobacter, Bacillus* (Santana et al., 2020), *Enterobacter, Microbacterium* (Gopalakrishnan et al., 2013; Anwar et al., 2016), *Streptomyces* (Gopalakrishnan et al. 2013; Anwar et al. 2016) genera have been identified in the endosphere and rhizosphere of sorghum with PGP capabilities. The dominance of *Bacillus* among other identified genera in sorghum endo-rhizosphere was reported by Govindasamy et al. (2017). Among the representative genera, *Rhizobium, Enterobacter, Pantoea, Microbacterium, Pedobacter, Variovorax, Acinetobacter, Xanthomonas, Bacillus, Planococcus, Planomicrobium, Arthrobacter* could produce indole acetic acetate (IAA). However, in the current research merely *Rhizobium* and *Bacillus* clusters showed the potential of iron-chelating. *Enterobacter, Variovorax, Bacillus, Pantoea,* and *Acinetobacter* genera were found to be highly involved (>50%) in solubilizing inorganic phosphate potential

(Chapter 3.1. Figure 1c). Young plants exude sugars, which are used by vast microorganisms, while at their maturity stages, plants release more specific exudates, which leads to a more specific selection of microbes in their rhizosphere (Chaparro et al., 2013 and 2014). The highest PSB activities can be attributed to the sorghum maturity stage and the dominance of gram-positive *Bacillus* (39%), with high phosphate solubilizing potential. *Bacillus* is abundant in various soil types, making up to 95% gram-positive rhizobacteria population, and has a tight bond with P-solubilizing capability in farmlands (Prashar et al. 2013; Kumar et al. 2017; Aloo et al. 2019). The efficiency of *Bacillus* species over other isolated rhizobacteria has been constantly explained by their abilities to produce spores that are resistant to environmental stresses (Rayavarapu and Padmavathi, 2016). This grants them the benefit of surviving in unpleasant conditions. Additionally, being gram-positive, resistant to environmental stresses, adopting to the N, and C rich conditions, having the high capacity of mineralizing inorganic phosphate, and producing indole and siderophore can lend support to the interface that the genus *Bacillus* among other isolated rhizobacteria can be advocated as a highly competent PGPR.

3.3.2. Erosion, and agronomic-induced erosion shapes rhizobacteria PGP potential

As evidenced in our previous study (Chapter 3.1.), the physio-chemical properties of the sloping field were significantly affected by the run-off process and soil contemporary environmental statutes (Chapter 2.3. Table 2). Topography as a trigger of erosion has shown the potential of structuring soil bacterial communities (Zhang et al., 2013; Liu et al. 2020), and their biomass (Liu et al., 2007). Thus, alteration of bacterial phenotypic characteristics can also be expected under topography. The growth of phosphate-solubilizing rhizobacteria can be in tandem with phosphorus solubilization and soil acidification (Anwar et al. 2016). The high phosphate solubilizing potential in this study was detected at the up-slope position comprise of lower soil pH. da Costa et al. (2014) concluded that nutrient solubilizing bacteria are favored by plants under nutrient-deficit conditions. While the phytohormone producers are gaining prominence under the nutrient-rich situation in soils. Higher indole production capacity of rhizobacteria at the foot-slope position can be compelling evidence for the theory put forward by Costa et al. (2014) (Chapter 2.3. Fig S1a).

Rhizodeposition is the interface between plants, soil, and microbial communities, which can cause a constant dynamic in the rhizo-ecosystem (Bulgarelli et al., 2013; Kai et al. 2016). Thus, shifts in

the rhizosphere can precipitate shifts in rhizobacteria phenotypic characteristics and PGP potential. However, we noticed no shifts in rhizobacteria activities following the agronomic practices (Chapter 2.3. Table 3). This can be ascribed to the short term of applying management practices, time of sampling, and the potent impact of topography which concealed other factors' impacts on the physiological capabilities of rhizobacteria.

3.3.3. PGPP and sorghum yield indices

Sorghum weight of the head had a significant positive correlation with the number of CFUs, indole production, the load of gram-negative rhizobacteria, mannitol, and urea hydrolyzation% (Chapter 2.3. Figure 5). Likewise, positive impacts of plant-growth-promoting rhizobacteria on the growth rate and yield of maize (Araujo and Guerreiro, 2010) and sorghum have been reported by other researchers (Schlemper et al., 2017). According to Govindasamy et al., (2017) *Acinetobacter*, *Bacillus*, *Enterobacter*, *Geobacillus*, *Lysinibacillus*, *Microbacterium*, *Ochrobactrum*, *Paenibacillus*, and *Pseudomonas* were the major genera presented in the endo- rhizosphere of sorghum. All of these strains showed at least one PGP trait and were correlated with the sorghum growth indices.

Overall Conclusion

Topography due primarily to erosion and deposition processes drives spatial heterogeneity of soil ^{13}C, ^{15}N natural abundance, edaphic properties, which in turn regulates prokaryotic community diversity, structure, and physiological activities. The observed variations in prokaryotic community structure and assemblages are manifested through their physiological adaptations to the distinct nutrient and oxygen availabilities at each slope position. Agronomic practices' impact on soil prokaryotic community was contingent upon the topography and concealed by the preponderant role of topography in shaping soil edaphic properties and prokaryotic community. The combination of erosion and accelerated erosion following the application of tillage can lead to ^{13}C fractionation and loss. Meanwhile, the accumulation of clay particles, and the higher amount of total C (MWC%) and N (MWN%), NH_4^+-N, NO_3^--N, and other eroded cations at the depositional sediments empowered the higher ^{15}N fractionation and N loss at the foot-slope position. Expectedly, the regular occurrence of the anoxic conditions in poorly drained foot-slope soils led to the higher relative abundance of nitrifying and denitrifying prokaryotes compared to up-slope. This also justified the occurrence of higher ^{15}N fractionation in the depositional sediments. Indole production among plant growth-promoting traits of sorghum rhizobiome appeared to be strongly dependent upon nutrient availability and thus, improved at the depositional site, while phosphate solubilizing potential gained prominence in eroding up-slope. Due to the importance of erosion and erosion-induced changes in soils of Upper-Eastern Ghana this topic continues to merit further exploration and appraisal.

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