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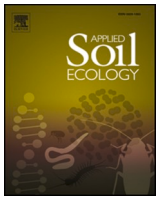

Topographic attributes override impacts of agronomic practices on prokaryotic community structure

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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 conservation agriculture practices (reduced tillage, main crop and cover crop, crop residue retention vs. removal) in treatments amended with 0, 40, and 80 kg ha^{-1} N on soil physicochemical properties and microbiota. Topography imposed profound shifts in soil physiochemical properties and prokaryotic community structure. Foot-slope soils harbored higher prokaryotic richness and diversity compared to the 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 effect of tillage was significant in foot-slope while crop rotation was influential in up-slope soils on structuring the prokaryotic community. The interactive effect 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 overall by agronomic practices. Among the soil physicochemical properties, pH, clay content, total C%, volumetric water content, temperature, cation exchange capacity, and NO_3^--N were relevant factors influencing the soil microbiota. Geomorphic and soil edaphic properties appeared to interact and were the primary triggers of variation in soil microbiota and their responses to the range of agronomic practices that incorporated conservation management outcomes.

1. Introduction

Sloping terrain can modulate different processes and characteristics of agroecosystems such as erosion, soil water content, receipt and redistribution of light, and microclimatic features (Hu and 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, plant litter decomposition, texture, bulk density, redox potential, N mineralization, and 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) driven by changes in the spatial heterogeneity of edaphic properties in soils (Liu et al., 2020). Microbial biogeography is also generated 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). For these reasons, considering soil and landscape

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geomorphic characteristics is a key factor in preserving soil microbial diversity and function, which in turn can address soil health and cropping system productivity (Chaparro et al., 2012; Kibblewhite et al., 2008).

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 for ensuring cropping sustainability. Accumulation of nutrients and organic C at foot-slope sites from erosion/deposition processes can boost C conversion processes and promote microbial diversity (Liu et al., 2020). On the other hand, sediment migration and soil nutrient depletion at eroding upslope positions can have detrimental implications for microbial diversity (Huang et al., 2013). Therefore, the dynamics of microbial communities are tightly related to erosion and erosion-induced changes in soil properties and nutrient status (Liu et al., 2020; Park et al., 2014). The need to investigate the impact of erosion and its underlying impacts on the microbial community is necessary to maximize the productivity of sloping lands.

Farmlands are dynamic environments where soil microbiota are exposed to numerous agronomic practices including tillage, crop rotation, and N fertilizer amendments (Fierer et al., 2012; Lupwayi et al., 2017; Wang et al., 2020b). There is a growing concern on the implications of high-input-conventional agronomic practices on soil health and microbial diversity (Carbonetto et al., 2014; Hartmann et al., 2015). Among conventional practices, plowing can increase the loss of soil organic carbon (SOC) (Horwath, 2007), with increasing loss as intensification increases, particularly from erosion. 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 ammoniacal fertilizers can lead to a pH decline (Adams et al., 2020), and 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), and adversely affects microbial community structure. 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 although no significant shift in bacterial diversity was evident in their study.

Contrary to high-input agronomic practices, conservation practices including reduced tillage, cultivation of cover crops, and optimized fertilizer applications can reduce soil disturbance, while improving soil aggregation and water infiltration (Miner et al., 2020). Positive effects of conservation practices in promoting soil biodiversity have been reported (Hartmann et al., 2015; Williams et al., 2020). In addition, integrated soil fertility management consisting of cover crops often shows a profound influence on soil properties including texture, nutrient cycling, SOM content (Adams et al., 2020), soil bacterial diversity, and biomass (Chavarria et al., 2016; Wang et al., 2020a). Thus, shifting from conventional to conservation practices may help preserve microbial community heterogeneity and thus functionality.

The effects of agronomic practices on hillslope farming have so far been addressed primarily for one specific management practice at a time such as tillage (Montgomery et al., 1999; Xu et al., 2021), retention of plant residues (Kok et al., 2009; McCool and Roe, 2005), or changes in N and P fertilization levels (Bouraima et al., 2016). However, there is a dearth of information on the impacts of conventional vs. conservation agronomic practices on hillslope farmlands, particularly effects on soil microbiota. The hillslope farmlands in the Upper-East region of Ghana are low in organic matter and water infiltration making them highly susceptible to erosion with an estimated soil loss of 4.7% annually for sandy soils (Bationo et al., 2007; Veihe, 2002). Our goal was to gain insight into changes in the prokaryotic community structure in relation to topography under conventional vs. conservation agronomic practices. We addressed three hypotheses: 1. Topography is the predominant influence on soil physiochemical heterogeneity 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 potent impact of topography modulates the effects of agronomic practices on the prokaryotic community through shaping soil edaphic properties.

2. Material and methods

2.1. Site description and soil sampling

The study site is 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 (Fig. 1). 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 considered 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 (Fig. 1). An average slope of 3–5% with an average horizontal distance of 100 m separated up-slope and foot-slope plots. A strip-split plot layout was applied with landscape slope position (foot-slope or up-slope) as strip plots and tillage (contour ridge-conventional tillage (CT) and reduced tillage (RT)) as the main plots. Residue management (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 including no N addition (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 nested as split plots across treatments. Treatments were laid out with four replications for a total of 96 sub-plots (Fig. 1). 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 Fig. 1, in the supplementary material, and by Danso et al. (2018).

Soil samples were taken after the sorghum harvest in October 2014. Ten samples were taken from each of the 96 plots using a 15 cm auger with 2.5 cm diameter and their geographical coordinator points noted. The ten merged soil samples from each plot were sieved through a 4 mm mesh to remove stones and plant residues. To avoid contamination, the auger and meshes were cleaned, wiped with 75% ethanol, and rinsed with sterile water after sampling in each plot. The processed soil was 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 and 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 nutrient bases measured in the leachates (Van Reeuwijk, 1993).

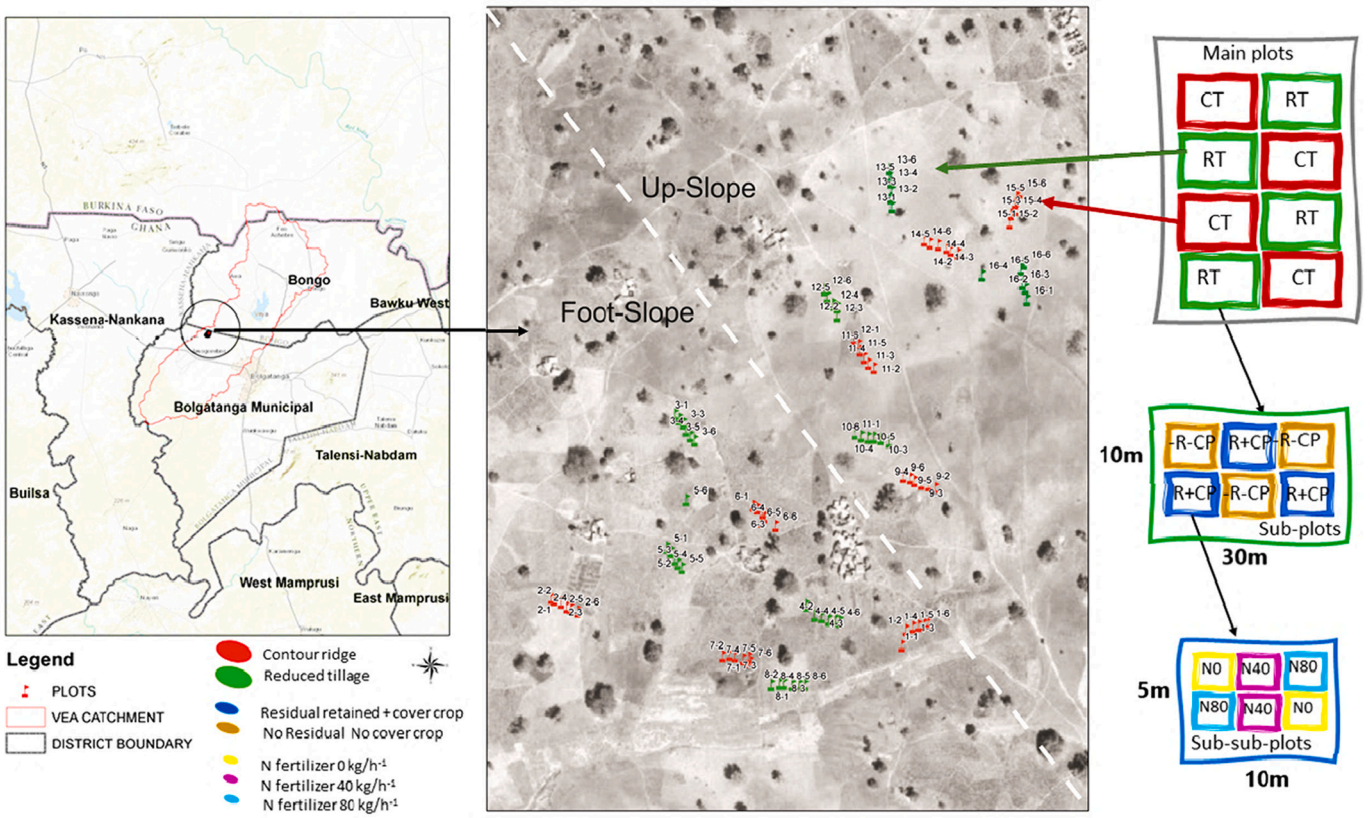

Fig. 1. Map (left) showing the location of the study site in Upper-Eastern Ghana, satellite image (middle) showing the location of the fields in the terrain, and schematic drawings (right) explaining the strip plot design and the plot sizes. The study area was established along a 1.2 km elevational transect. 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).

Total C % (MWC%) and N % (MWN%) were determined after dry combustion following the procedures of the International Organization for Standardization, ISO N 10694 (1995a) and ISO N 13878 (1998). Soil nitrate-N (NO_3^--N) and ammonium-N (NH_4^+-N) were determined following KCl (1 mol L^{-1}) extraction on an autoanalyzer (Bran + Luebbe, Germany). Total mineral N (N_{min}) content was estimated according to Hofer (2003). Total trace elements were determined after aqua regia digestion with an inductively coupled plasma-optical emission spectrometry instrument (ICP-OES: Perkin-Elmer OPTIMA 3000; ISO 11466 (1995b)).

2.3. Molecular analysis of the prokaryotic community composition

DNA extraction was done in triplicate per sample to minimize DNA extraction bias 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 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 (2 × 300 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 and 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 13-8 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, when necessary, after testing for normal distribution of the data (Shapiro test and bell curve drawing) and homogeneity of variances (Bartlett test) (Snedecor and Cochran, 1989). To estimate the comparative and integrated impacts of topography, tillage practice, crop rotation, and N fertilizer rates on soil physiochemical properties linear mixed effect models (LMM) fitted by maximum likelihood were performed, considering the strip-split plot layout on the basis of the Gomez and Gomez (1984) method. We applied the "lmer" function in the "lme4" package and summarized the results by "anova" function as embedded in the "lmerTest" package to summarize the results and obtain *P*-values. Before selecting the model, diagnostic tests such as normal distribution of residuals for both fixed and random effects and multicollinearity tests were conducted applying "performance" package. The effect sizes of the parameters were calculated, using "effectsize" package. To select the best fit model, models with different nested random factors were compared through "anova" function and the Akaike information criterion (AIC) (Akaike, 1998). As a result, slope position, tillage practice, rotation, N fertilizer rates and their interactions were considered as fixed factors, while replication and replication × rotation interaction were considered as random factors in our LMMs. Slope position was considered as a fixed factor since each transect was representative of different soils in our hilly field. Rotation was considered as a random factor since the amount of residue returned to each plot was unpredicted and dependent upon the biomass that accrued from the previous cropping season, which could provoke the inter-individual differences in our rotation subplots. Additionally, we were mostly interested in between groups' effects of rotation with other fertility management practices such as N fertilizer levels. The linear mixed model effect application was validated with the maximum likelihood estimation method and the structures for mixed model fitting were controlled. We also used the pairwise Tukey test at $p \leq 0.05$ level using "lsmeans" function to achieve the least-squares means and contrasts of measured soil features between the factors (Lenth, 2016). However, the huge volume of achieved least-squares means table prevented us from concisely presenting it. Since the effect size of slope position was higher than other factors, we assumed that the dominant impact of slope position might conceal the agronomic impacts. Therefore, to put aside the potent impact of topography and to simplify the presentation of the results, we additionally performed the analyses of agronomic practice impacts for each slope position individually. To avoid any confusion we assigned the linear mixed effect models on all occasions to the full data set, while the three-way ANOVA (strip-split plot layout) was conducted to evaluate the split data sets. This enabled us to evaluate the agronomic practice's impacts irrespective of topography and to present the results concisely. The impacts of various agricultural management practices on dependent variables relevant to each slope position were re-analyzed by three-way ANOVA with strip-split plot layout, applying the "agridat" package (Gomez and Gomez, 1984). A Duncan's new multiple range test (MRT) was used to detect mean differences between the three levels of N fertilizer treatments ($P < 0.05$), applying the "duncan.test" function in the "Agricolae" package. The pure effect of slope position on soil properties was further evaluated by a post hoc paired *t*-test. 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 effect models embedded in "lme4" package to assess the effects of the different treatments and their interactions on the z-scaling transformed microbial richness and alpha diversity indices by analogy with the soil edaphic properties analyses. Duncan's new multiple range test (MRT) as a post hoc test was applied to assess significant differences between the means of N fertilizer level ("agricolae" package in R language).

Variation in beta diversity was evaluated based on Hellinger-transformed Bray-Curtis dissimilarity matrices using "Vegan" and "ape" packages in R toolkit and visualized in Principal Coordinate Analysis (PCoA) plots, applying the "ggplot2" (Wickham, 2016). To statistically test for significant differences between groups of samples, adonis or permutational multivariate analysis of variance was conducted with 999 permutations based on the Bray-Curtis dissimilarity matrix in "Vegan". The interactive impacts of topography and agronomic practices (i.e., slope × tillage × rotation × N fertilizer) on prokaryotic community structure were also assessed through "adonis" function on Bray-Curtis dissimilarity matrices ("Vegan" package) (Oksanen, 2015). 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 assessed 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 similarities (1 – Bray-Curtis dissimilarity index) 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 "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 a 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 Hellinger-transformed Bray-Curtis distance matrix using the exponential decay model based on the log-linked Gaussian generalized linear model (GGLM). This was likewise done for the soil edaphic data and complemented by additional application of a best-fitted power model after comparing the respective AIC values. Except for soil edaphic data other data set showed the best fit with the exponential model with considerably lower AIC values. Hence, we selected the negative exponential model to fit with the elevational and spatial distances. The goodness of GGLM fit was computed as pseudo-R^2. GGLM Pseudo-R^2 values were used as the coefficient determination and *P* values were calculated applying the F test. Similarity decays were plotted using the "plot.decay" function of the "betapart" package (Nekola and McGill, 2014). The relationships were additionally tested by Mantel tests based on Spearman's correlation coefficient applying the Bray-Curtis similarity 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/elevational gradients) 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, applying 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_{adj}^2 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 a Venn diagram using the "varpart" function of the "Vegan" package.

3. Results

3.1. Implications of topography for soil physiochemical properties

Evaluation of slope position effects on soil physiochemical properties revealed that up-slope and foot-slope soils differed significantly in most analyzed parameters except for Fe, Mn, P, and silt contents (Table 1). Higher values for Ca, K, and Mg were observed in foot-slope soils. Likewise, pH (ranging from 5.7 to 6.2), 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. The percentages of total N% (MWN%) and C% (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 content was also significantly higher in the foot-slope soils, while sand content was higher among up-slope plots.

3.2. Implications of agronomic practices for soil physiochemical properties

The initial assessment of the impact of agronomic practices as the fixed and random factors on soil physicochemical properties was performed based on the full dataset using LMM, which unraveled the lower impact of agronomic practices as a function of soil edaphic variations compared to topography. The random factors' output, which is the estimate of the variances (standard deviation), was negligible in this study. Therefore, we did not report them. We found very few significant differences that were 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, NO_3^--N, P, MWC%, and MWN%. Besides, tillage × rotation × fertilizer interaction significantly changed soil K, Ca, and Mg contents and tillage × rotation was effective in shifting soil N_{min} and NO_3^--N (Table S1). Due to the prepotent impact of slope position, the impact of the agronomic practices was further assessed for each slope position independently.

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 post hoc paired *t*-tests with 95% confidence interval, P value correction was done by Benjamini-Hochberg method.

Soil physiochemical properties		Foot-slope	Up-slope	95% Confidence interval			
				Lower	Upper	T value	P_{adj} value
N_{min}[a]	g kg^{-1}	9.84 ± 0.47	5.54 ± 0.26	0.32	1.14	3.55	0.000***
NH_4^+-N	g kg^{-1}	4.61 ± 0.05	2.87 ± 0.04	0.21	1.12	2.96	0.005**
NO_3^--N	g kg^{-1}	5.20 ± 0.08	2.63 ± 0.06	0.20	0.97	3.07	0.003**
C/N[b]		13.39 ± 0.01	12.50 ± 0.02	0.38	1.19	3.87	0.000***
pH		6.19 ± 0.01	5.66 ± 0.01	0.34	1.07	3.89	0.000***
Ca	mg kg^{-1}	218.63 ± 0.88	37.15 ± 0.32	0.24	1.03	3.21	0.002**
K	mg kg^{-1}	14,812.12 ± 0.40	1179.12 ± 0.71	0.25	0.99	3.38	0.001***
Al	mg kg^{-1}	4779 ± 23	4389 ± 16	0.05	0.89	2.25	0.029*
Na	mg kg^{-1}	398 ± 0.95	303 ± 0.49	0.06	0.90	2.33	0.025*
Fe	mg kg^{-1}	7796 ± 0.56	8010 ± 0.35	−0.50	0.40	−0.22	0.825
Mn	mg kg^{-1}	150.68 ± 0.33	219.26 ± 0.54	−0.39	0.54	0.33	0.746
Mg	mg kg^{-1}	827.89 ± 0.52	454.60 ± 0.20	0.14	0.94	2.73	0.009**
P	mg kg^{-1}	117.59 ± 0.22	134.17 ± 0.22	−0.45	0.43	0.06	0.952
MWC[c]	%	0.65 ± 0.02	0.32 ± 0.01	0.41	1.22	4.06	0.000***
MWN[d]	%	0.05 ± 0.01	0.03 ± 0.00	0.35	1.16	3.77	0.000***
Clay	%	11.90 ± 0.11	6.99 ± 0.08	0.12	0.98	2.57	0.013*
Silt	%	8.54 ± 0.08	6.45 ± 0.08	−0.10	0.70	1.50	0.140
Sand	%	79.56 ± 0.06	86.58 ± 0.03	−1.00	−0.10	−2.45	0.018*
CEC[e]	cmol kg^{-1}	1032.80 ± 0.93	451.10 ± 0.73	0.07	0.97	2.30	0.03*
VWC[f]	%	0.021 ± 0.00	0.019 ± 0.00	0.18	1.05	2.83	0.007**
Temperature	°C	35.48 ± 0.06	34.53 ± 0.05	1.28	1.84	11.19	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 = total C %.
[d] MWN = total N %.
[e] CEC = cation exchange capacity.
[f] VWC = volumetric water content.

Individual management regimes had limited impact and were solely detected at the foot-slope position (Table 2). Three-way ANOVA accompanied with Duncan's new multiple range test (MRT) ascertained significant differences for clay content at zero N level in foot-slope soils (Table S2).

In addition to the individual effects, we noted a few interactive effects, which were related to altered soil physiochemical characteristics, especially at the foot-slope position (Table 2). This included the 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 within foot-slope soils. The 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 the significant impact of slope position on prokaryotic diversity with higher richness (t value = 7.99, $P < 0.001$), Chao1 (t value = 8.29, $P < 0.001$), ACE (t value = 8.72, $P < 0.001$), Shannon (t value = 6.22, $P < 0.001$), and evenness (t value = 5.83, $P < 0.001$) indices in foot-slope compared to up-slope soils (Table 3). Similarly, prokaryotic community composition was affected by topography as depicted in the PCoA plot (Fig. 2a), evidenced by distinct clustering of samples under slope position, whereby foot-slope samples depicted a broader variation compared to up-slope soils. The slope position potential in driving variation of prokaryotic community composition was statistically validated by adonis with an R^2-value of 0.110 ($P = 0.001$) (Table 4).

Overall, *Firmicutes*, *Actinobacteria*, *Proteobacteria*, *Acidobacteria*, *Bacteroidetes*, *Chloroflexi*, *Verrucomicrobia*, *Planctomycetes*, *Gemmatimonadetes*, and some unclassified phyla accounted for almost 98% of all

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 and rotation as well as $n = 16$ for each dosage of N fertilizer

Treatments	N_{min}[a]	C/N	K	Na	Fe	MWN[b]	MWC[c]	pH	NO_3^--N	NH_4^+-N	Temperature
	g kg^{-1}		mg kg^{-1}	mg kg^{-1}	mg kg^{-1}	%	%		g kg^{-1}	g kg^{-1}	°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	3.16	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	2.96	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	3.12
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	Al	Ca	Mg	P	CEC[d]	Clay	Silt	Sand	VWC[e]
	mg kg^{-1}	mg kg^{-1}	mg kg^{-1}	mg kg^{-1}	mg kg^{-1}	cmol kg^{-1}	%	%	%	%
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	**4.73***	3.40	0.15	2.05	**5.23***	0.93	1.86	0.11

Significance codes: $P < 0.05$ '*', $P < 0.01$ '**'; $P < 0.001$ '***'.
Significant elements were also highlighted with bold fonts in the table.
[a] N_{min} = mineral N.
[b] MWN = total N%.
[c] MWC = total C%.
[d] CEC = cation exchange capacity.
[e] VWC = volumetric water content.

Table 3
Comparison alpha diversity indices affected by slope position. Mean values (n = 48) and standard errors are given. Differences were assessed by paired *t*-tests (P_{adj} calculated by Benjamini-Hochberg method).

Richness and alpha diversity indices	Foot-slope	Up-slope	95% Confidence interval			
			Lower	Upper	T value	P_{adj} value
Richness	4826 ± 73	3913 ± 98	0.93	1.56	7.99	0.000***
Chao1	16,194 ± 27	12,895 ± 32	0.21	0.97	8.29	0.000***
ACE	18,275 ± 31	14,264 ± 36	0.20	1.02	8.72	0.000***
Evenness	0.70 ± 0.01	0.63 ± 0.01	0.38	0.63	5.83	0.000***
Shannon	5.20 ± 0.12	5.07 ± 0.07	0.34	0.69	6.22	0.000***

*** Significant with $P < 0.001$.

sequences in the samples (Fig. 3). At the family level, *Bacillaceae* (29%) and *Micrococcaceae* (25.9%) dominated prokaryotic community composition (Fig. S1). 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%).

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, while only 92 genera were more prominent in up-slope soils. An enrichment of diverse genera in the orders of *Clostridiales*, *Bacillales*, *Rhizobiales*, and *Actinomycetales* (between 19 and 34 genera per order) was observed in foot-slope soils (Fig. S2). 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

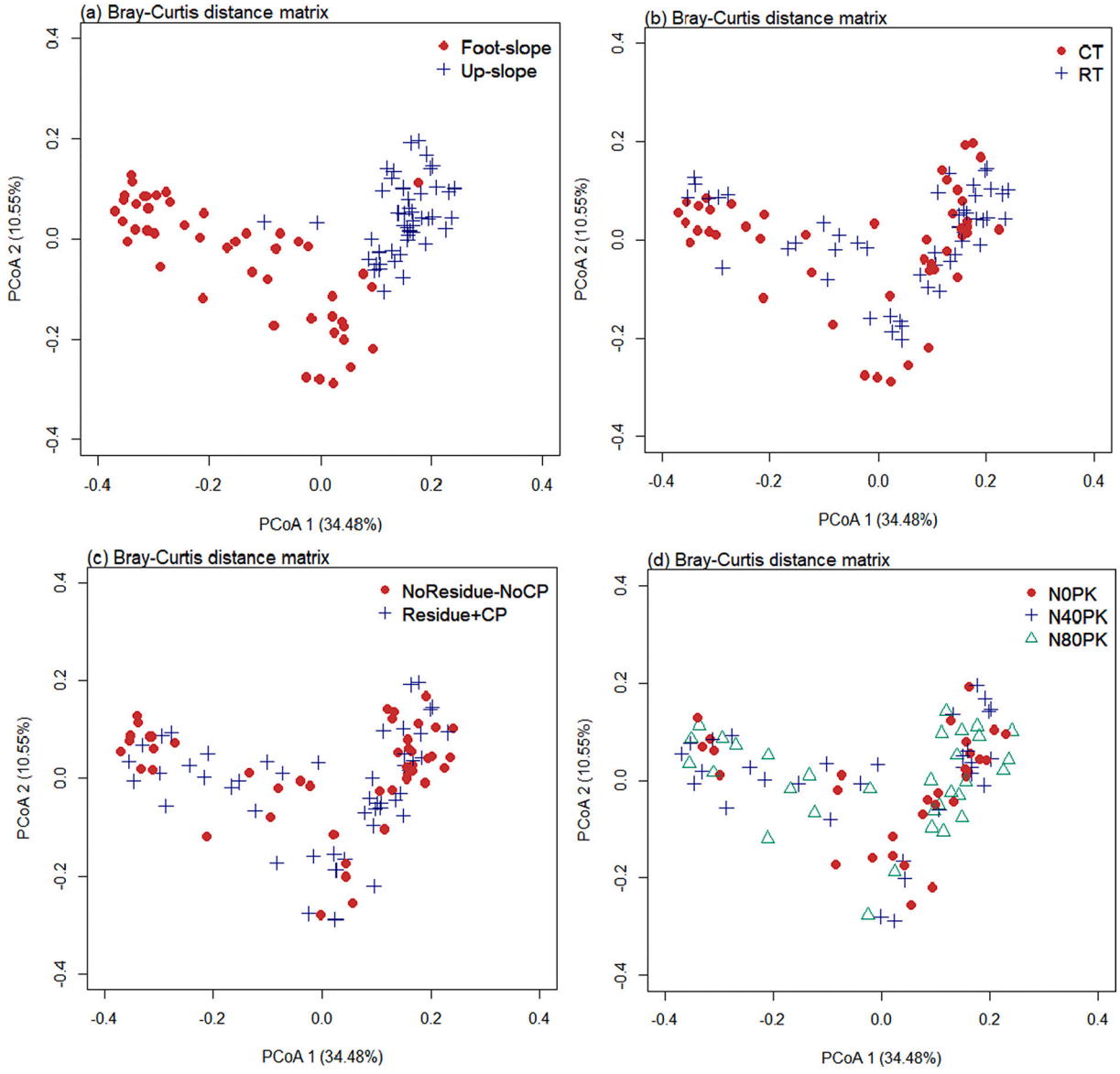

Fig. 2. Principal Coordinates Analysis (PCoA) plots to show variation in beta diversity. Color coding according to slope position (a) or management practices (b-d). Agronomic practices include different tillage practices (b), rotation practices (c), and fertilizers with different rates of nitrogen (d). Tillage: conventional tillage (CT), reduced tillage (RT), rotation practices: residual management including cover crop (Residue + CP) and no residual management and no cover crop retention (NoResidue-NoCP), fertilizers with different rates of nitrogen (N0PK, N40PK, and N80PK).

Table 4
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**	**0.110**	**0.001*****
Tillage	**48**	**0.014**	**0.048***
Rotation	48	0.011	0.257
Fertilizer	32	0.019	0.412
Slope × tillage		0.013	0.109
Slope × rotation		0.010	0.303
Tillage × rotation		0.008	0.865
Slope × fertilizer		0.020	0.417
Tillage × fertilizer		0.017	0.841
Rotation × fertilizer		0.017	0.718
Slope × tillage × rotation		0.008	0.947
Slope × tillage × fertilizer		0.017	0.829
Slope × rotation × fertilizer		0.016	0.948
Tillage × rotation × fertilizer		0.017	0.769
Slope × tillage × rotation × fertilizer		0.017	0.801
Residuals		0.686	
Total		1.000	
Up-slope samples			
Tillage	24	0.019	0.864
Rotation	**24**	**0.041**	**0.049***
Fertilizer	16	0.040	0.697
Tillage × rotation		0.018	0.962
Tillage × fertilizer		0.038	0.940
Rotation × fertilizer		0.039	0.851
Tillage × rotation × fertilizer		0.043	0.424
Residuals		0.762	
Total		1.000	
Foot-slope samples			
Tillage	**24**	**0.031**	**0.011***
Rotation	24	0.020	0.861
Fertilizer	16	0.042	0.688
Tillage × rotation		0.019	0.954
Tillage × fertilizer		0.043	0.573
Rotation × fertilizer		0.040	0.864
Tillage × rotation × fertilizer		0.042	0.695
Residuals		0.765	
Total		1.000	

Significance codes: $P < 0.05$ '*', $P < 0.001$ '***'.
Significant factors were also highlighted by bold fonts.

methanotrophic genera (*Methylosinus*, *Methylocaldum*, *Methylomicrobium*). 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*). Additionally, 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 also enriched within foot-slope soils.

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 rather than the agronomic practices (Table S3). The impacts of the agronomic practices were also evaluated in detail within each slope position. The richness indices Chao1 and ACE responded significantly to the fertilizer application in up-slope soils (Table 5), with the highest dosage of N lending support to the 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.

Ordinating community similarities in PCoA plots (Fig. 2b–d) showed no manifested separation of samples according to agronomic practices, while adonis indicated a significant though weak effect of tillage ($R^2 = 0.01$, $P < 0.05$) in this regard (Table 4). Adonis performed for each slope position independently revealed that tillage affected beta diversity solely in the foot-slope samples ($R^2 = 0.03$, $P = 0.01$). Additionally, the prokaryotic community structure responded to the rotation treatment in up-slope soils ($R^2 = 0.04$, $P < 0.05$) (Table 4). No significant interactions between management practices were noticed through adonis.

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 diversity and structure were studied. The alpha diversity indices showed significant

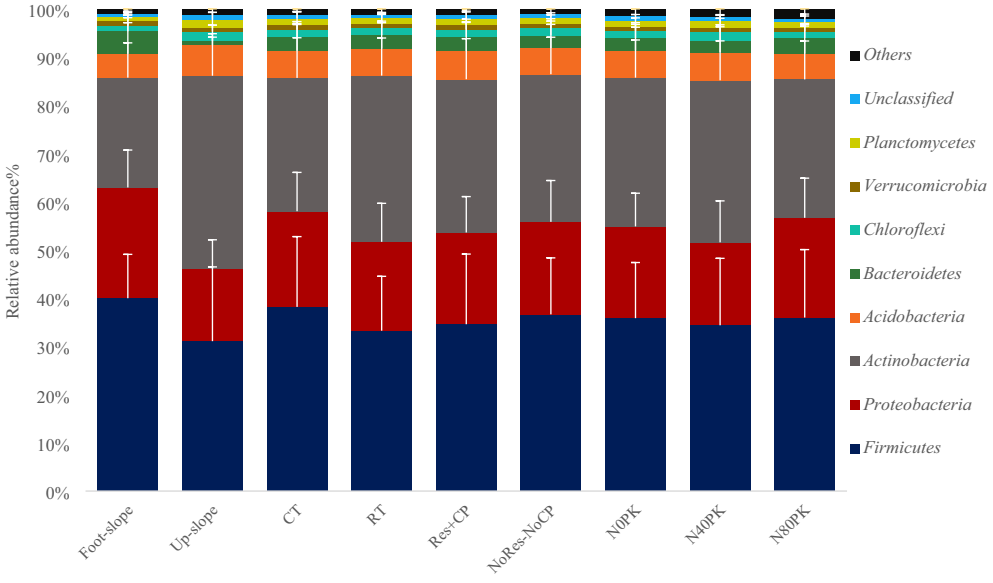

Fig. 3. Taxonomic distributions of the eight dominant phyla (>1%) in soil samples based on 16S rRNA gene sequence analysis. Data from the same samples are grouped by slope position (Foot-slope, Up-slope), tillage: conventional tillage (CT) and reduced tillage (RT), different crop rotation regimes: residual management including a cover crop (Res + CP) and no residual management with no cover crop retention (NoRes-NoCP), and fertilizer application with different levels of nitrogen (N0PK, N40PK and N80PK). Shown are mean values plus standard error. Phyla with ≤1% relative abundance are grouped as "Others".

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 indices were highlighted with bold fonts.
* Significant with $P < 0.05$.

positive correlations to several soil edaphic properties according to Spearman's rank correlation coefficient analysis (Fig. S3). 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. 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 Hellinger transformed OTU Bray-Curtis distance matrix. The significant negative slope of exponential decay (slope = −0.90, Pseudo $R^2 = 0.14$, $P < 0.001$, AIC = −11,780) and best-fitted power model (slope = −0.12, Pseudo $R^2 = 0.14$, $P < 0.001$, AIC = −11,760) based on GGLM explained the decay in prokaryotic community similarity with increasing soil edaphic heterogeneity (Fig. 4a). Redundancy analysis (RDA) was then 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" were comprised of 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). 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 (Fig. 5), 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. In the same manner, 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 (Fig. 5).

Lastly, the relationship between the relative abundance of dominant families to the variation of soil physiochemical properties was investigated by Spearman's correlations (Fig. 6). 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 the aforementioned soil edaphic properties. The *Micrococcaceae* showed negative correlations to several of these soil traits including MWN%, MWC%, Mg, Ca, pH, K, NO_3^--N, N_{min}, and temperature. Such negative correlations were also seen for *Koribacteraceae* and *Intrasporangiaceae* (Fig. 6). 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 (Fig. 4b & c). Mantel tests revealed significant findings with $R = -0.22$ ($P < 0.01$) for the correlation of community compositional differences with spatial distance, and $R = -0.33$ ($P < 0.01$) with elevation, which reflects topography. Plots displaying taxanomic similarity versus geographic or elevational distances revealed negative relationships in both cases. The exponential model of GGLM confirmed the slightly negative slope for spatial distance (slope = −0.46, Pseudo $R^2 = 0.08$, $P < 0.001$, AIC = −11,500) and a stronger significant negative relationship with elevational gradients (slope = −0.03, Pseudo $R^2 = 0.16$, $P < 0.001$, AIC = −11,800).

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 (Fig. 7). To this end, the six selected significant PCNM vectors, the eight most relevant soil edaphic properties as presented in RDA biplot, 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 (Fig. 7). The highest co-variation (9.2%) was seen between soil physicochemical traits and slope position.

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 site (Table 1) suggests that surface erosion is likely to have occurred. Translocation and deposition of basic elements into foot-slope sediments have been reported previously (Seibert et al., 2007; Lal and 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 edaphic 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. The erosion/deposition processes reduce the physical protection of SOC at eroding sites and simultaneously accumulate higher C and N contents at the depositional foot-slope sites (Gómez et al., 2020; Shi et al., 2019). This can explain the higher MWC% and MWN% values determined at our foot-slope plots

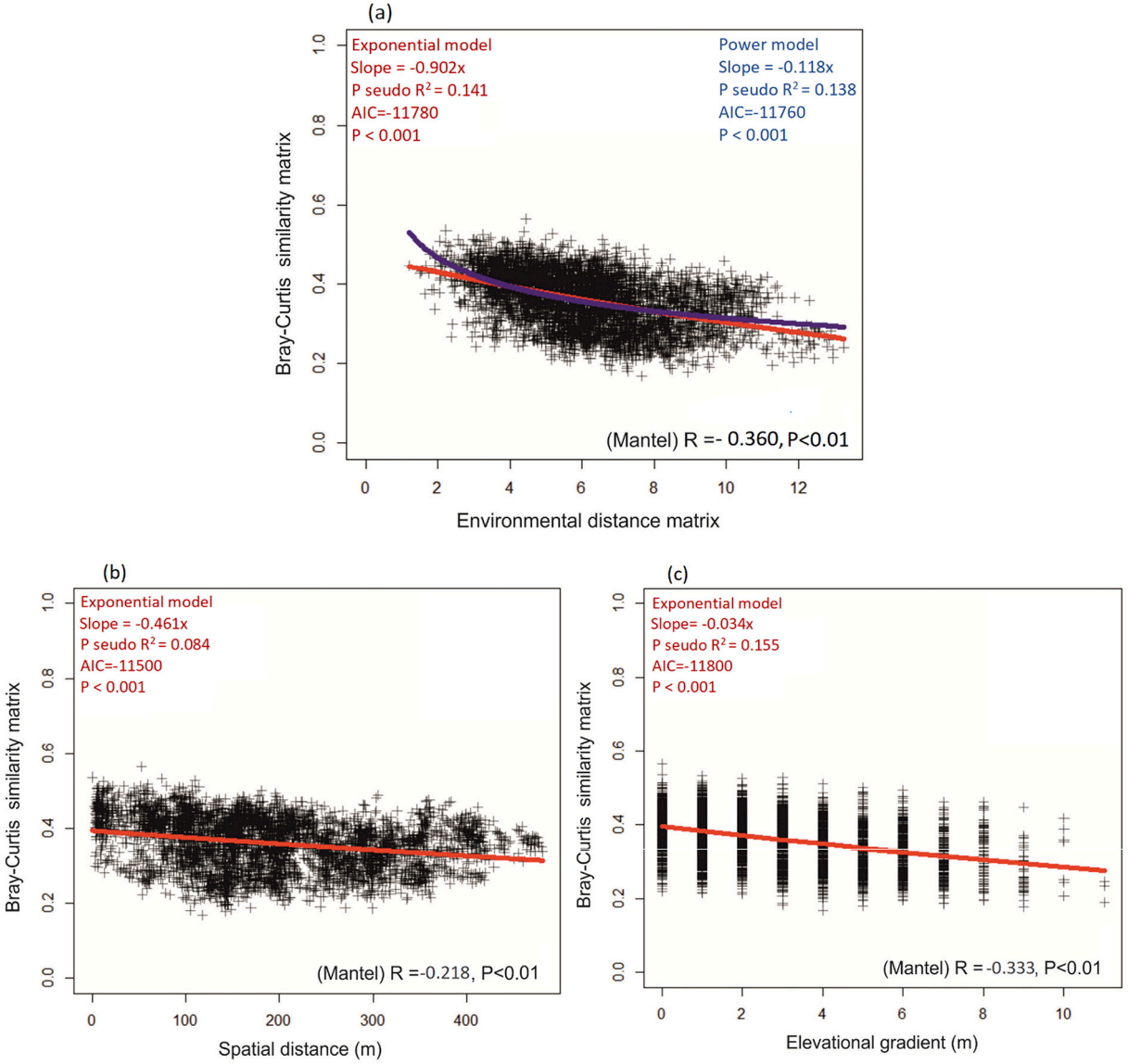

Fig. 4. Distance-decay curves showing the relationship between bacterial community similarities (based on comparisons of OTU profiles using the Bray-Curtis similarity index (1-Bray-Curtis dissimilarity index)) against distance matrices reflecting soil physiochemical properties (a), spatial distances between plots of sampling (b), and slope positions defined by the elevational gradient (c). Distance-decay curves were calculated based on the negative exponential model (red) and for soil properties additionally based on the best-fitted power model (blue). The regression slopes of the linear relationships based on the log-linked Gaussian generalized linear model (GGLM) 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 similarity matrix, were additionally performed.

(Table 1).

It is widely known that erosion adversely impacts soil microbial diversity, primarily due to the redistribution of sediments, organic matter, and soil nutrients along the slope (Du et al., 2020; Huang et al., 2013; Liu et al., 2018). We noticed higher prokaryotic richness and diversity at our depositional site (Table 3), which was closely associated with the accrual of soil nutrients at the foot-slope position (Fig. S3). 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 reinforce 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, is 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 leads to the development of a more diverse bacterial community at the depositional sites (Pett-Ridge and Firestone, 2005).

Slope position also appeared to be the chief underlying force behind shifts in prokaryotic community structure at our field scale, evidenced by PCoA plots and adonis results (Table 4 and Fig. 2a). 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 well 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 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 capable of

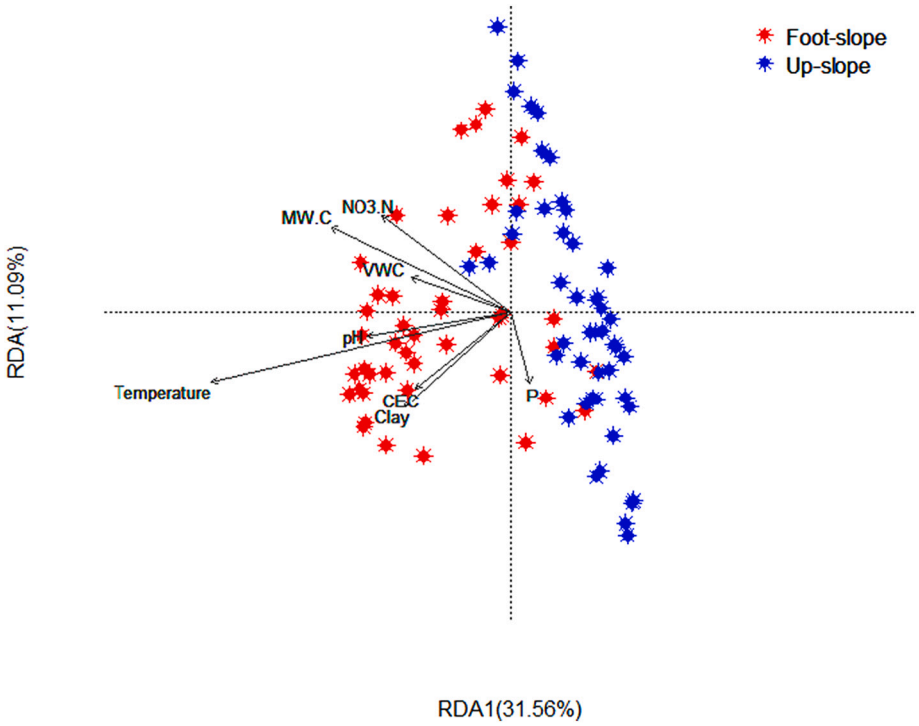

Fig. 5. Redundancy analysis (RDA) of prokaryotic community composition constrained by soil physiochemical properties. Red dots represent the foot-slope and blue dots the up-slope sites. Relevant soil properties were chosen based on the "ordiR2step" function and are shown as arrows. They represent quantitative explanatory variables with arrowheads indicating the direction of increasing "bp" scores. MW·C = mean mass of C%, NO3·N = NO_3^--N, CEC = cation exchange capacity, VWC = volumetric water content, and P = phosphorus.

surviving under growth-limiting, extremely 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 N cycling prokaryotes at the foot-slope position in tandem with higher availability of NH_4^+-N and NO_3^--N. This may be accompanied with higher nitrification and denitrification rates within the foot-slope plots (Pett-Ridge and Firestone, 2005; Xu et al., 2021), which potentially indicates frequent anoxic conditions and accelerated N cycling in foot-slope soils. Microbial denitrification and chemodenitrification in anoxic conditions can incite the emission of N_2O (Wang et al., 2019). Methanotrophic genera that are known to rely on the activities and byproducts of strictly anaerobic methanogens (Knief, 2019) were detected at foot-slope (Fig. S2). Further taxa which are specific to anoxic environments including *Syntrophobacteraceae* affiliated genera, is known as an indicator of early-stage wetland degradation (Gu et al., 2018) as well as *Desulfovibrionaceae* and *Desulfobulbaceae* families, are involved in the reduction of sulfate to sulfide (Karnachuk et al., 2021), were also seen in foot-slope soils. These shifts in prokaryotic communities due to anoxic conditions can enhance gaseous loss of C and N through emissions of NO, N_2O, CO_2, and CH_4 in foot-slope plots. Anoxic conditions are tightly linked to higher soil water contents (Pett-Ridge and 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 only did 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 (slope positions) 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 accessibility.

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 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). Many 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 microbiota. 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 up-slope, characterized by nutritional deficiency, rather than to the foot-slope soils. Furthermore, an impact of crop rotation management was seen in the prokaryotic community composition within up-slope soils (Tables 4 and S4). 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 agronomic practices on the prokaryotic community structure were primarily seen in response to tillage (Table 4). Although soil properties were not responsive to the individual tillage practice in these soils, the tillage × rotation interaction affected MWC%, MWN%, N_{min}, and NO_3^--N as well as VWC (Table 2) and

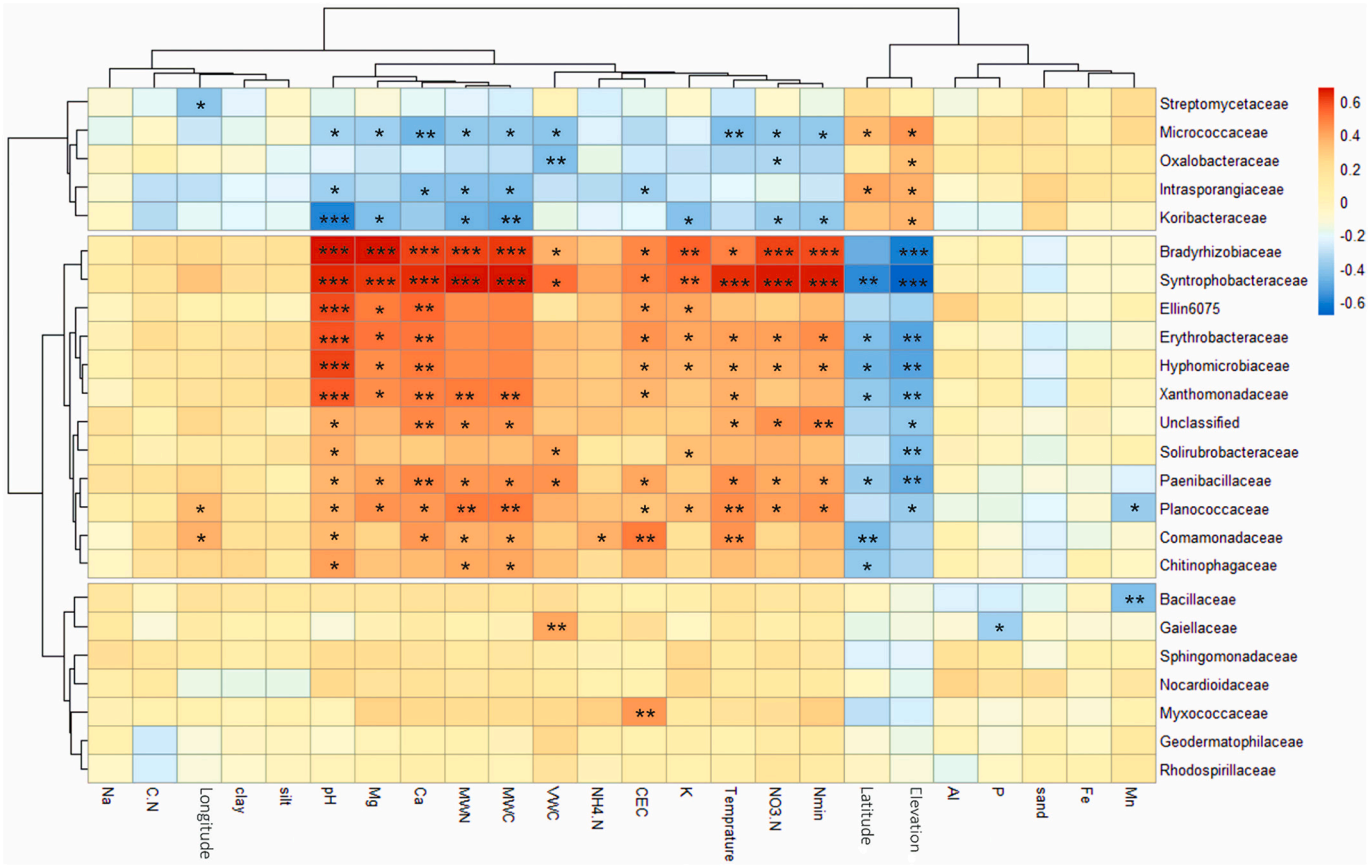

Fig. 6. Heatmap showing the correlation of the abundant (>1% relative abundance) prokaryotic families with environmental factors applying Spearman correlation analysis. Values of Spearman correlation coefficients are indicated from red (positive) to blue (negative). Slope positions are defined by elevation. Dendrograms show the grouping of families with similar response patterns to the environmental parameters. Likewise, environmental parameters with similar correlation patterns to prokaryotic 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.
Significance codes: $P < 0.05$ '*', $P < 0.01$ '**'; $P < 0.001$ '***'

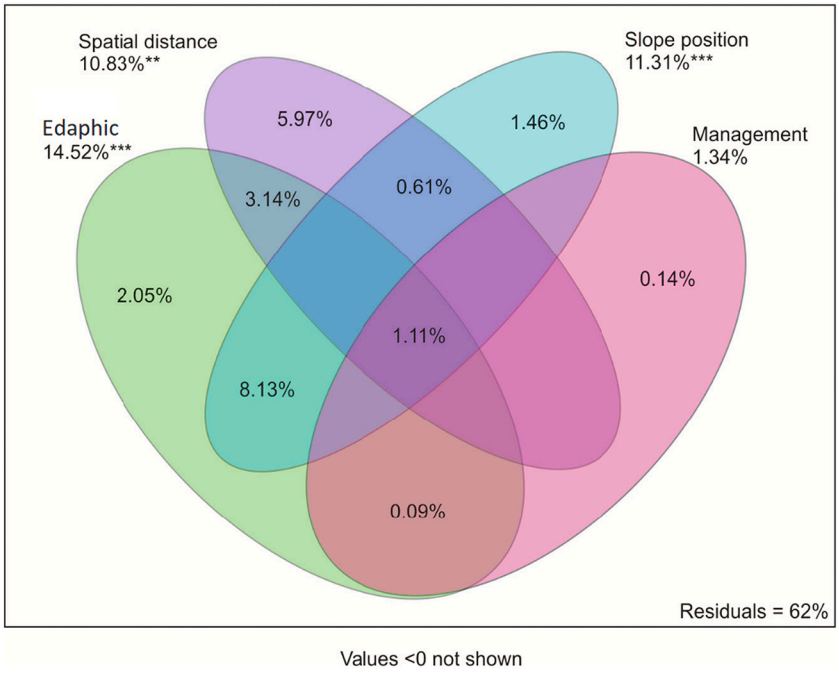

Fig. 7. Venn diagram representing the contribution of soil edaphic properties (significant chemical and physical properties including MWC%, temperature, P, pH, NO_3^--N, VWC, CEC, and clay content), management practices, spatial distance (6 significant PCNM vectors), and slope position on the variation of prokaryotic 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 of each contributor according to ANOVA ($P < 0.01$ '**'; $P < 0.001$ '***').

modulated the soil nutrient and possibly the oxygen status at the foot-slope position. It is known that tillage 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 and Paul, 2015; Zhao et al., 2020b). Moreover, tillage causes closer contact between unprotected organic matter and the consumers in soil (Horwath, 2007; Horwath and Paul, 2015). 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 shifts (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 up-slope 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; 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 manifested that the effects of the agronomic practices were largely slope-dependent, as hypothesized. This is reflected in different interactive responses of the soil physiochemical properties. Among the interactive effects slope × tillage and slope × rotation interactions effectively altered soil physiochemical characteristics (Table S1). This was in part reflected in the soil prokaryotic community structure, which was solely responsive to tillage at the foot-slope position and to rotation at up-slope (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 3-year-period the field experiment was ongoing before sample collection and the fact that samples were taken six months after the latest maize and cowpea residues were incorporated into the soil. Returned residue may have left a detectable footprint on the prokaryotic community structure as one kind of legacy effect, but it may not yet have induced long-lasting shifts in soil edaphic properties.

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 the homogenizing nature of agronomic practices (Rodrigues et al., 2013). In addition, spatial heterogeneity at the study site, which explained 11% of the variation in community composition (Fig. 7), might have modulated the effects of other factors. Moreover, heterogeneous cropping regimes prior to initiating our experiment may have also modified responses in individual plots, resulting in plot-specific and thus heterogeneous responses. Lastly, the period of three 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 sloping study field. The distance decay relationship was significant (Fig. 4b) and spatial distance explained 10.8% of the variation in prokaryotic community composition (Fig. 7). 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 existence of microbial biogeographical patterns in farmlands. Soil edaphic heterogeneity at both the microsite and pedon scale is a common issue affecting our and other findings, being more influential than other underlying processes in driving microbial biogeographical pattern. We also observed a high overlap of soil edaphic properties with slope position (9.2%) (Fig. 7), which agrees with the clear effects of topography on soil physiochemical properties, and the presence of tight bonds between soil physiochemical properties and prokaryotic community composition (Fig. 6). Mentioned outcome underlines the relevance of geomorphic patterns in distributing prokaryotic community composition in sloping farmlands, which shapes soil microbiota primarily by modifying soil edaphic properties.

Among soil physiochemical properties, soil pH, clay content, temperature, MWC%, VWC, CEC, and NO_3^--N were the key elements in shaping prokaryotic community composition and diversity (Figs. 5, 6, and S3). 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., 2016a, 2016b), 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). The aforementioned 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 (Fig. 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 factor in affecting 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*), and have been reported for their oligotrophic life strategy and adaption to harsh environments (Delgado-Baquerizo et al., 2018; Fierer et al., 2007; Zhang et al., 2016a, 2016b). This correlative analysis at the family level confirms our conclusions on selective mechanisms resulting in topographic-induced variations of prokaryotic community composition. However, these correlations are not necessarily the result of specific adaptations. Therefore, this aspect deserves further appraisal in future studies.

5. Conclusions

Topography was found to be the predominant influence over soil physiochemical heterogeneity and thus prokaryotic community structure. The extent of agronomic management impacts was contingent upon topography for the soil physiochemical 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 schemes were also 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 the 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 recurrently 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 observed a geomorphic pattern of distribution for prokaryotic communities at our field scale with soil physiochemical properties such as soil pH, clay content, temperature, MWC%, VWC, CEC, and NO_3^--N as the

most relevant underlying factor of this systematic distribution. Evidently, soil microbiota was in a tight relationship with soil edaphic properties. Nutrient deficiency at up-slope was compensated through the application of N fertilizer and rotation × N fertilizer which to some extent favored prokaryotic diversity. However, at fortified foot-slope solely tillage structured prokaryotic community significantly by disturbing soil aggregates and increasing nutrient availability for soil microbiota. Thus, the appropriate agronomic scheme for hilly farmland does not follow a fixed scheme but should be selected corresponding to exogenic movement and geomorphic pattern of distribution for soil edaphic properties and microbiota. We propose further investigation of the taxonomic and functional core microbiome stability in hilly farmland that might provide better support to inform the management of sloping farmlands.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2022.104446.

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