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Microbial community shifts in pearl millet root zone soils with *Guiera senegalensis* intercropping along a rainfall and soil type gradient in the Sahel

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Abstract

The Sahel of West Africa has vulnerable agroecosystems that threatens food security. A potential solution is intercropping with the indigenous shrub, *Guiera senegalensis* J.F. Gmel. Previous research of the Optimized Shrub-intercropping System (OSS) (high density of ~1,500 shrubs ha^{-1} and coppiced residue incorporation) has been shown to dramatically improve pearl millet [*Pennisetum glaucum* (L.) R. Br.] yield, which is attributed to improved soil quality, nutrient and water availability, and harboring a distinct microbial community. Whether this response is consistent over a climate and soil type gradient in farmers' fields has not been investigated. Therefore, the objective was to determine the impact of *G. senegalenis* on soil chemistry, enzyme activity, microbiomes, and metabolic pathways of millet root zone soils in farmers' fields. The experiment was a three-by-two factorial with three rainfall and soil type sites along a north–south gradient in the Senegal Peanut Basin and two sampling locations (millet root zone soil within and outside the influence of the *G. senegalensis*). *Guiera senegalensis* shifted certain predicted bacterial metabolic pathways and enriched some bacterial and fungal genera. Notably, the increased crop growth due

Abbreviations: ITS, internal transcribed spacer; LDA, linear discriminant analysis; LEfSe, linear discriminant analysis size effect; MUB, modified universal buffer; NMDS, nonmetric multidimensional scaling; OSS, Optimized Shrub-intercropping System; OTU, operational taxonomic unit; PCR, polymerase chain reaction; PERMANOVA, permutational analysis of variance tests; ρNP, *p*-nitrophenol; rRNA, ribosomal RNA.

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to *G. senegalensis* positively correlated with the abundance of genera having plant growth promoting properties (e.g., *Enterobacter agglomerans* and *Paraburkholderia*). *Paucibacter*, a genera that has deleterious and/or pathogenic properties, was highly abundant in non-shrub soil but completely suppressed beneath the shrub. The results showed that *G. senegalensis* in farmers' fields even at typical, low densities, where coppiced residues are annually burned, still increased soil chemical and microbial properties, suggesting that a more important factor than litter is the presence of shrub roots that provide root turnover and exudates, and water inputs through hydraulic lift.

1 | INTRODUCTION

The Sahel is a semiarid, ecologically fragile region where the staple crop pearl millet [*Pennisetum glaucum* (L.) R. Br.] is grown with limited or no inorganic fertilizer and no irrigation (Belton & Taylor, 2002; FAO, 2015). This region is also under threat of soil degradation, desertification, and food insecurity, which will be exacerbated by climate change (Dai, 2013; World Food Programme, 2018). This increases the likelihood of conflict and mass migration from the region (Brown, 2008; Lambin et al., 2014; United Nations, 2016a). In Senegal, about 47% of the population is already food insecure (World Food Program, 2018), and the United Nations estimates a nearly 600% increase in population by the year 2100, potentially forcing this country to substantially rely on international aid to meet its food needs (United Nations, 2016).

To address these ecological, agronomic, and socioeconomic challenges, local and biologically based cropping systems are needed for the majority, subsistence farmers who grow food crops such as millet. Agroforestry where woody species are interplanted with crops, and sometimes referred to as "parkland agroforestry" in this region (Bayala et al., 2014), has potential to deliver services that can be used by rural communities in the Sahel. One such system is the Optimized Shrub-intercropping System (OSS). This system intercrops the native shrub, *Guiera senegalensis* J.F. Gmel at increased densities (three to four times the densities found in currently in farmer's fields: ~1,500 shrubs ha^{-1}) where coppiced biomass is annually incorporated into soils. Previous research on OSS has shown that this approach dramatically increases millet crop productivity (Bright et al., 2017, 2021; Dossa et al., 2012, 2013).

Guiera senegalensis is widely found in Senegal and throughout the Sahel, but at relatively low densities in farmers' fields (200–350 shrubs ha^{-1}) (Lufafa et al., 2008). The absence of mechanized agriculture enables these native plants to coexist with crops in the Sahel. *G. senegalensis* is well adapted to drought conditions and does not compete with millet for water (Kizito et al., 2006). Currently, farmers do not manage these shrubs except to coppice in the spring and unfortunately burn this residue, depriving soils of organic inputs (Diedhiou et al., 2009). The OSS is based on the ability of *G. senegalensis* to be a companion plant in cropped fields (Dossa et al., 2012, 2013). Extensive research has shown that OSS increases nutrient content and organic matter of soils and increases the microbial community diversity and activity (Debenport et al., 2015; Diedhiou-Sall et al., 2013; Dossa et al., 2009). The OSS has also been shown to increase crop biomass and yields and buffer against in-season drought (Bogie et al., 2018; Bright et al., 2017, 2021; Dossa et al., 2012, 2013).

In part, this resistance to drought can be attributed to the finding that *G. senegalensis* performs hydraulic lift (Kizito et al., 2012), which Bogie et al. (2018) found could "bio-irrigate" adjacent millet plants. However, the amount of water transferred to intercropped millet is relatively low. Nonetheless, yield responses to OSS with *G. senegalensis* over sole cropping have been nearly 900% (Bogie et al., 2018) to as high as 2,600% (Bright et al., 2021) in the absence of fertilizer application in long-term studies. This suggests that there are additional mechanisms of drought resilience conferred by shrubs. Given that there are microorganisms known to promote plant growth and drought resilience (Vurukonda et al., 2016), this could be another mechanism conferred by OSS but is entirely uninvestigated.

There is very little information on the influence of shrubs across soil types and climate moisture regimes within farmers' fields on soil microbial community dynamics. Therefore, the objective of this study was to determine shifts in millet root zone soil on microbiomes, predicted metabolic pathways, enzyme activities, and extractable nutrients in relation to millet growth, due to the presence or absence of the shrub, *G. senegalensis*, along a rainfall and soil type gradient of the Sahel, West Africa. Specifically, use of amplicon sequencing was done to determine whether shrubs harbor beneficial microorganisms known to promote plant growth as a further mechanism that contributes to the yield response of OSS.

2 | MATERIALS AND METHODS

2.1 | Site description and experimental design

The study was conducted in the Peanut Basin of Senegal, (14.70° N, 16.00° W) in a semiarid savannah with vegetation consisting primarily of shrubland with scattered trees, which is known as the Parkland system. The mean annual rainfall is 540 mm, with the majority of the rainfall occurring between August and October (Lufafa, 2008). Between 70 and 80% of the soils are sandy Ustipsamments classified as Dior (Rubic Arenosol with 95% sand) with <1% soil organic C. The remaining soils are generally the Deck soil (Vitrandic Haploxerolls), which is only found in depressional, low landscape positions (McClintock & Diop, 2005). Shrubs and trees are the dominant vegetation in this savanna. *G. senegalensis* is a dominates in the north, and *P. reticulatum* dominates the southern part of the Peanut Basin.

All sites were in fields under the management of separate farmers and have been managed in a peanut (*Arachis hypogea* L.)–pearl millet (*P. glaucum*) rotation for over 50 yr, as reported by collaborating farmers. The typical practice is that shrubs are coppiced in May and early June and burned. Prior to crop planting (around late June for southern sites to late July in northern sites), fields receive shallow (0–10 cm) sweep tillage and during the growing season are weeded with an in-row cultivator using animal traction and some hand weeding. Crops are planted with animal-drawn small planters with the onset of the rainy season. Regrowth of shrubs during the growing season is coppiced and laid between cropped rows. Little or no commercial fertilizer is used with small amounts of animal manure applied every few years (Badiane et al., 2001)

The experimental design was a three-by-two factorial with the following treatments: three rainfall and soil type gradient sites, two shrub sampling location treatments (inside and outside the influence of *G. senegalensis*), and five replicates. Within each rainfall and soil site, there were two spatially separated landscape-level replications. The three rainfall gradient sampling sites were chosen along a north–south rainfall gradient in the Peanut Basin of Senegal: (a) Louga (northern; 15.28° N, 15.53° W), (b) Theis (central; 14.78° N, 16.90° W), and (c) Kaolack (southern; 14.18° N, 16.25° W), which have average annual rainfall regimes of 450, 550, and 750 mm, respectively. The soils were sandy, being 95, 92, and 86% sand for northern, central, and southern sites, respectively. Each field site was on a different farm. The two soil sampling location treatments were (a) two millet plants within the influence of the *G. senegalensis* (<1 m from the center of the shrub), and (b) two millet plants outside *G. senegalensis* influence (>4 m from the shrub center) based on Dossa et al. (2010), who showed little or no influence of the shrub at 3 m.

Core Ideas

- *Guiera senegalensis*, a Sahelian shrub, increased enzyme activity and shifted microbial communities in millet root soil
- *Guiera senegalensis* had a greater abundance of microbial genera that have known plant growth properties and were positively correlated with millet biomass.
- *Paucibacter*, a deleterious/pathogenic genus, was suppressed to undetectable levels in presence of *G. senegalensis.*
- Positive shrub effects on soil properties were most evident at the northern site with low rainfall and low-organic-matter soils.

2.2 | Sampling

Soil samples were obtained for soil chemical analyses and extracellular enzyme activity assays in 2012 and 2013 and for microbial DNA extraction in 2012. Soils from two millet root-zone sampling locations, inside and outside the influence of *G. senegalensis*, were take over a 2-wk period from last week in August (southern site) through second week of September (central and northern sites) in both years. Both years, soil cores (0–20 cm by 2.54-cm diam.) were taken through the center of the millet root zone, stored in Ziploc bags, and transported on ice. In 2012, samples for microbial DNA extraction from the rhizosphere soil were placed in a plastic Ziploc bag and stored at −20 °C without sieving. All soil core samples for enzyme and nutrient analyses (2012 and 2013) were passed through a 2-mm sieve and gravimetric moisture content was measured prior to analysis.

Millet plants were harvested at the time of soil sampling both years. Notably, millet plants within the influence of *G. senegalensis* were consistently in late stages of tillering and early panicle initiation, whereas millet plants outside the influence of this shrub were in earlier stages of tillering. Two millet plants were harvested at each sampling location, and the aboveground fresh biomass was weighed and then averaged to give grams of biomass per plant.

2.3 | Soil chemistry

Soil pH was determined using a 1:2 soil/water slurry and a glass membrane electrode. Total C and N were measured using a Carlos Erba elemental analyzer. The nutrients PO_4–P, SO_4–S, K, Ca Mg, B, Zn, Fe, and Cu were measured on a Mehlich-3 extraction procedure on 2 g of air-dried soil as

described by Mehlich (1984), followed by inductively coupled plasma atomic emission spectrophotometry analysis.

The NH_4^+ and NO_3^- were determined colorimetrically by flow injection analysis as described by Mulvaney (1996). The NH_4^+ and NO_3^- analysis was done by extracting soil with 1 M KCl, passing extract through a glass fiber filter, and measuring it by the salicylate-nitroprusside and the hydrazine-sulfaniliamide colorimetric methods, respectively.

2.4 | Enzyme assays

Activities of acid phosphatase (EC 3.1.3.2 orthophosphoric-monoester phosphohydrolase), and β-glucosidase (EC 3.2.1.21 β-D-glucoside glucohydrolase) were determined as described by Tabatabai (1994) with the adaptations that follow. Acid phosphatase were determined with *p*-nitrophenyl phosphate as the substrate in a modified universal buffer (MUB) (pH 6.5) where the reaction was stopped with 0.5 M NaOH after a 1-h incubation. β-glucosidase activity used the substrate *p*-nitrophenyl β-D-glucose in a MUB (pH 6.0) and *Tris*-hydroxy aminomethane (THAM) (pH 12) was added to stop the hydrolysis reaction. N-acetyl-β-D-glucosaminidase (EC 3.2.1.30) (chitinase) activity was determined as described by Parham and Deng (2000) with the following modifications: 0.25 g field moist soil was added to *p*-nitrophenyl-N-acetyl-β-D-glucosaminide substrate in a acetate buffer (pH 5.5) solution, and the reaction was stopped with 0.5 M NaOH. No toluene was used in these assays because of the short incubation time. All assays were incubated at 37 ˚C for 1 h. Following incubation, after stopping the reaction, the solution was centrifuged for 5 min at 10,000 rpm, the supernatant was collected, the color was developed using the product *p*-nitrophenol (ρNP), and the color was measured using a spectrophotometer at 410 nm (Ultrospec 3000, Pharmacia-Biotech). Final concentrations of all above assays were determined in reference to a ρNP standards curve at 0, 5, 10, 15, 20, and 30 μg of ρNP. Controls were performed with each sample where the substrate was added after the incubation period was completed by killing the reaction, to account for color not derived from hydrolysis of substrate in the presence of soil. Enzyme activities are reported as micrograms ρNP per gram of dry soil per hour.

Urease (EC 3.5.1.5 urea amidohydrolase) activity was determined following the buffered procedure as modified by Kandeler and Gerber (1988). To account for color development not from the urease enzyme, controls were treated with 2.5 ml of 0.72 M urea solution after incubation. Enzyme activity was recorded as micrograms of N per gram of dry soil per hour.

Results of enzyme activities are reported on an oven-dry-weight basis, determined by drying soils for 24 h at 105 ˚C.

2.5 | Analysis of microbiomes

The overall data generation and analysis workflow flow of the 60 samples is summarized in Supplemental Figure S1. Bacterial and fungal DNA was extracted from 0.25 g millet rootzone soil via the MoBio PowerSoil DNA kit per the manufacturer's instructions. Agarose gel electrophoresis was used to confirm adequate genomic DNA, which was then used as a template for the polymerase chain reaction to amplify two gene regions: the 16S ribosomal RNA (rRNA) gene V3 region, for bacteria and archaea, and the internal transcribed spacer (ITS) 2 region, for fungi. Briefly, polymerase chain reaction (PCR) master mix was made of 5× GoTaq Flexi Buffer (Promega Corporation), 2 mM MgCl2, 2 mM deoxyribonucleotide triphosphates (dNTPs), PCR water, GoTaq Flexi Polymerase, RNAse ONE, Illumina forward and reverse primers + individual adapters for multiplexing (Supplemental Table S1), and 1 μl genomic DNA. The ITS2 and 16S rRNA gene V3 regions were amplified using Illumina F and R primers as follows: 16SrRNA gene primers 341F (5′-CCTACGGGAGGCAGCAG-3′) and 534R (5′-ATTACCGCGGCTGCTGG-3′), and ITS primers ITS3 (5′-GCATCGATGAAGAACGCAGC-3′) and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′). The 16S rRNA gene V3 region was amplified with the following thermocycler protocol: 95 ˚C for 5 min, followed by 20 cycles of 95 ˚C for 1 min, 50 ˚C for 1 min, and 72 ˚C for 1 min, with a final elongation protocol of 72 ˚C for 7 min. The ITS2 region was amplified with the following: 94 ˚C for 3 min, followed by 35 rounds of 94 ˚C for 45 s, 50 ˚C for 60 s, and 72 ˚C for 90 s, with a final elongation step at 72 ˚C for 10 min. Success of PCR was confirmed via 0.7% agarose gel electrophoresis visualization of amplicons. Amplicons were gel purified and sequenced on the Illumina GaIIx platform at the Molecular and Cellular Imaging Center at Ohio State University. Raw reads are available at the National Center for Biotechnology Information (NCBI) under Accession no. PRJNA856249.

2.6 | Bioinformatics

Raw reads were prepared for analysis using QIIME 2-2019.1 in 2019 (Bolyen et al., 2019), within which denoising was performed via Dada2. At the time of denoising, raw reads were split into 16S V3 reads and ITS reads based on alignment to the 99% SILVA.132 database. Quality control steps determined that forward reads were too degraded to provide much useful data, and so they were discarded, and reverse reads were used. Operational taxonomic unit (OTU) clustering was performed at 99%. Taxonomy was assigned via the 99% UNITE (fungal) and SILVA138.1 (bacterial and archaeal)

databases, and OTU and taxonomy tables were exported for further analysis.

The OTUs that were significantly enriched or depleted in either the presence or the absence of shrubs in at least one site were then determined via linear discriminant analysis size effect (LEfSe-1.1.2) (Segata et al., 2011). Within LEfSe, a factorial Kruskal–Wallis test determined differences in the presence and absence of shrubs across all sites site communities ($P < .05$), and a pairwise Wilcoxon signed-rank test was used to verify this enrichment in the northern, central, and southern sites respectively. The threshold linear discriminant analysis (LDA) score for discriminative OTUs was log(2). Using the SILVA138.1 16S database, OTU identity was confirmed to the genus level for all but two bacterial OTUs. The 99% OTU UNITE database and the SILVA138 18S database were used to determine further resolution of the fungal OTUs, but only one was identified beyond the phylum level (Quast et al., 2013).

The PICRUSt2 pipeline was then used to predict the functional profile of the bacterial and archaeal community based on the reverse complement 16S rRNA gene amplicon profiles generated by seqtk1.3 (Li & Wu, 2018). The PICRUSt2 pipeline uses phylogenetic context relative to physiologically known references to predict metabolic gene-family copy numbers (Douglas et al., 2020). Predictions were classified by the Kyoto Encyclopedia of Genes and Genomes (KEGG) Orthologs (KO) database, Enzyme Commission numbers, and MetaCyc (Langille et al., 2013; Douglas et al., 2020). The resulting list of predicted metabolic pathways associated with each community was then analyzed via LEfSe-1.1.2 as above for enrichment by region or by shrub presence, and discriminant pathways were further defined using the MetaCyc reference database.

2.7 | Statistics

R version 4.0.2 was used for all statistical analyses. Wilcox signed rank tests were used to determine the effect of site and soil sampling location on millet growth. Tukey's honest significant difference was used to means separation of site and sampling location on millet growth response, relative abundance of taxa, and enzyme activities. Preprocessing of OTU and taxonomy tables was performed using the Phyloseq package. Reads were rarefied to an even depth prior to calculating Shannon's diversity and species richness. Nonrarefied data were then square root transformed, and nonmetric multidimensional scaling (NMDS) and permutational analysis of variance tests (PERMANOVA) were performed to determine differences in the compositions of the microbial and fungal communities and potential drivers of these differences. Spearman's correlations were used to determine relationships among OTUs, millet health characteristics, and site descriptors (Supplemental Figure S1).

3 | RESULTS

3.1 | Millet response

At time of sampling, millet had significantly greater fresh biomass in the presence of shrubs at all sites ($P < .05$). Millet grown in the presence of shrubs had an average fresh biomass of 463 g plant^{-1}, whereas millet plants grown outside shrub influence averaged 115 g plant^{-1}. The shrub effect on millet biomass was highest at the northern and central sites. Conversely, there was no significant difference on millet biomass in the absence of the shrub treatment across the gradient sites (Figure 1a).

3.2 | Soil chemistry and enzyme activities

Total N and C increased north to south along the rainfall gradient in both the presence and absence of the shrub, and NH_4^+–N was highest in the central sites and lowest in the southern sites (Table 1). There was a consistent shrub effect on total C and N across ($P < .05$) (Table 1). There was no significant effect for the northern and central sites on soil pH, but there was at the southern site (Table 1).

Table 1 shows soil chemical properties averaged over 2012 and 2013, where the presence of *G. senegalensis* significantly ($P < .05$) increased total C, total N, NH_4^+–N, and Zn but had no significant effect on Ca, Cu, Fe, K, Mg, SO_4–S, PO_4^-– P, or NO_3^-–N (Table 1). The Mehlich extractable nutrients (excludes total N and C), NO_3^-–N, and NH_4^+-N varied between years, except for Zn and K, which were similar between 2012 and 2013 (data not shown). There was also some variation for the ranking of extractable nutrients between sites that varied between years—the northern site had the lowest levels in 2013, whereas during 2012, Ca, SO_4, and Cu were at the highest levels in the northern region and the lowest in the southern region (data not shown).

All enzyme activities averaged over 2012 and 2013, were lower at the northern sites compared with the southern and central sites, but not always significantly between sites at $P < .05$ (Figure 2). The northern site consistently had a significant shrub effect for all enzyme activities, whereas at the central site, this effect was shown for β-glucosidase and β-glucosaminidase (chitinase), but not urease (Figure 2). Figure 2 shows that the most consistent impact ($P < .05$) of *G. senegalensis* was on β-glucosaminidase and β-glucosidase activities at the Northern and Central sites. For the most part these averaged results were the same between years, except for the northern site in 2012 for acid phosphatase and

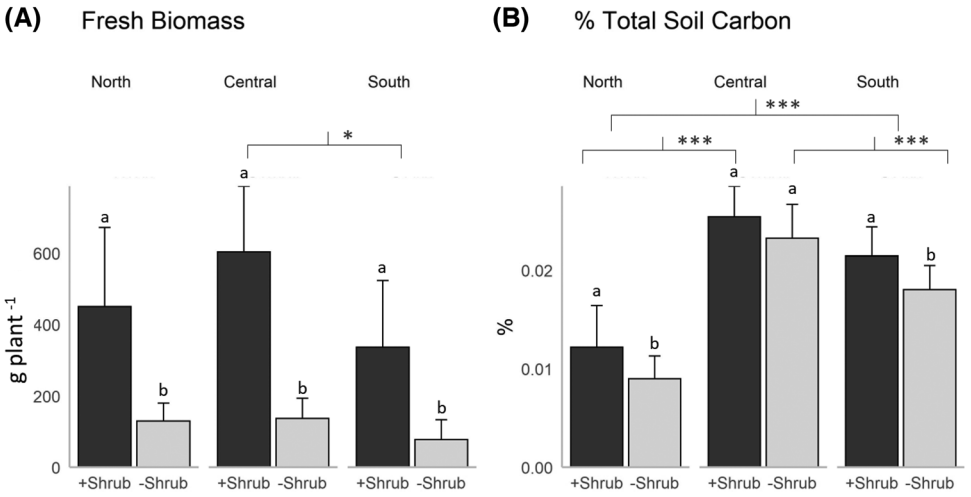

FIGURE 1 (A) Fresh millet biomass (g plant^{-1}), at time of sampling, averaged over 2012 and 2013. Pairs of +shrub and −shrub values within a site followed by the same letter are not significantly different at Wilcox $P \leq .05$. Brackets indicate a significant difference of fresh millet biomass between sites in the presence of shrubs at $^{*}P < .05$ or $^{**}P < .01$ (ANOVA). (B) Percentage total soil C at time of sampling, averaged for 2012 and 2013. Pairs of +shrub and −shrub values within a site followed by the same letter are not significantly different wit at Wilcox $P \leq .05$. Brackets indicate a significant difference ($^{***}P < .001$, ANOVA) in total C between sites in both +shrub and −shrub samples

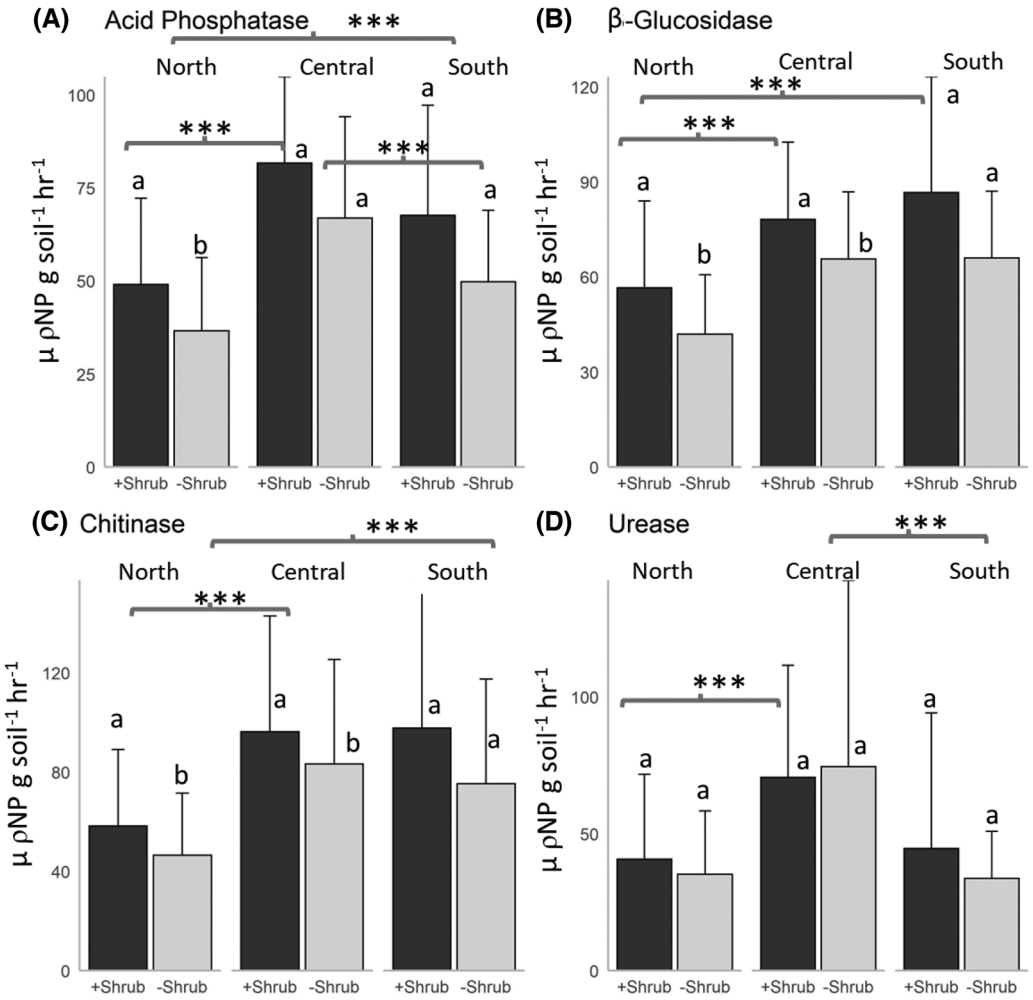

FIGURE 2 Extracellular enzyme activities averaged over 2012 and 2013 sampling seasons. Pairs of +shrub and −shrub values followed by the same letter are not significantly different within site at $P \leq .05$ (Welch's T test). Brackets indicate a significant difference ($^{***}P < .001$, ANOVA) in enzyme activity between sites in both +shrub and −shrub samples. ρNP, *p*-nitrophenol

TABLE 1 Chemical properties averaged over 2012 and 2013 in millet root zone soil in the presence or absence of *G. senegalensis* across a north–south rainfall and soil type gradient in Senegal

		Rainfall gradient site			
Property	**Shrub**	**North**	**Central**	**South**	**Mean**
pH	+Shrub	5.73a[a]	5.89a	5.63a	5.64a
	−Shrub	5.70a	5.99a	5.76b	5.81b
Total C, %	+Shrub	0.131a	0.241a	0.301a	0.224a
	−Shrub	0.103b	0.215a	0.251b	0.190b
Total N, %	+Shrub	0.011a	0.027a	0.022a	0.020a
	−Shrub	0.008b	0.024b	0.018b	0.017b
$N\text{-}NH_4^+$, mg kg^{-1}	+Shrub	5.47a	7.21a	6.17a	6.28a
	−Shrub	5.28a	6.64a	5.65a	5.86a
$N\text{-}NO_3^-$, mg kg^{-1}	+Shrub	1.38a	1.91a	1.52a	1.60a
	−Shrub	1.035a	1.33a	1.06a	1.14a
P, mg kg^{-1}	+Shrub	9.39a	9.79a	9.81a	9.67a
	−Shrub	9.49a	8.57a	8.42b	8.83b
Ca, mg kg^{-1}	+Shrub	118.5a	244.2a	204.8a	189.2a
	−Shrub	108.5a	310.1a	159.8a	192.72a
Cu, mg kg^{-1}	+Shrub	0.243a	0.296a	0.227a	0.255a
	−Shrub	0.229a	0.316a	0.225a	0.256a
Fe, mg kg^{-1}	+Shrub	23.9a	30.5a	30.8a	28.4a
	−Shrub	23.6a	31.3a	30.6b	28.5b
K, mg kg^{-1}	+Shrub	27.3a	38.7a	25.9a	30.6a
	−Shrub	21.6b	38.9a	19.2b	26.5b
Mg, mg kg^{-1}	+Shrub	31.2a	53.3a	46.5a	43.7a
	−Shrub	28.6a	59.6a	38.7b	42.3a
S, mg kg^{-1}	+Shrub	2.23a	2.85a	3.74a	2.95a
	−Shrub	1.90b	2.85a	3.47a	2.83a
Zn, mg kg^{-1}	+Shrub	0.593a	1.22a	0.421a	0.473a
	−Shrub	0.473a	0.792b	0.371b	0.542b

[a]Pairs of +shrub and −shrub values followed by the same letter are not significantly different within a site at $P \leq .05$.

β-glucosaminidase activities and in 2013 for β-glucosidase activity were significantly ($P < .05$) affected by the presence of *G. senegalensis* (data not shown).

3.3 | Alpha diversity and microbial community composition

Deep amplicon sequencing resulted in a per-sample average of 589,981 post-quality controlreads. These produced 8,020 bacterial + archaeal 99% OTUs across 60 samples, 871 of which could be identified to the genus level, and 1,093 fungal OTUs, with 114 identified to the genus level. Lineage accumulation curves suggest that 99% OTU diversity was saturated at this high per-sample sequencing depth (Supplemental Figure S2), and for diversity metrics, the data were rarefied to a depth of 250,000 and 45,000 reads per sample for bacterial + archaeal and fungal sequences, respectively. No statistically significant differences were observed in species richness or Shannon's diversity with shrub presence across all sites, although fungal diversity increased with shrub presence in the southern site and fungal richness increased with shrub presence in the northern site (Supplemental Figure S3).

3.4 | Differentially enriched OTUs

Ten bacterial and four fungal OTUs were found to be significantly enriched in the presence or absence of the shrub. Thirteen OTUs (four fungal and nine bacterial) were significantly ($P < .05$) enriched by at least two log-fold in either the presence or absence of shrubs (Figure 3). One bacterial OTU and zero fungal OTUs were enriched in the absence of shrubs in at least one site. On average, the enriched OTUs comprised a very small proportion of the total community. The most abundant of these was an uncultured member of the

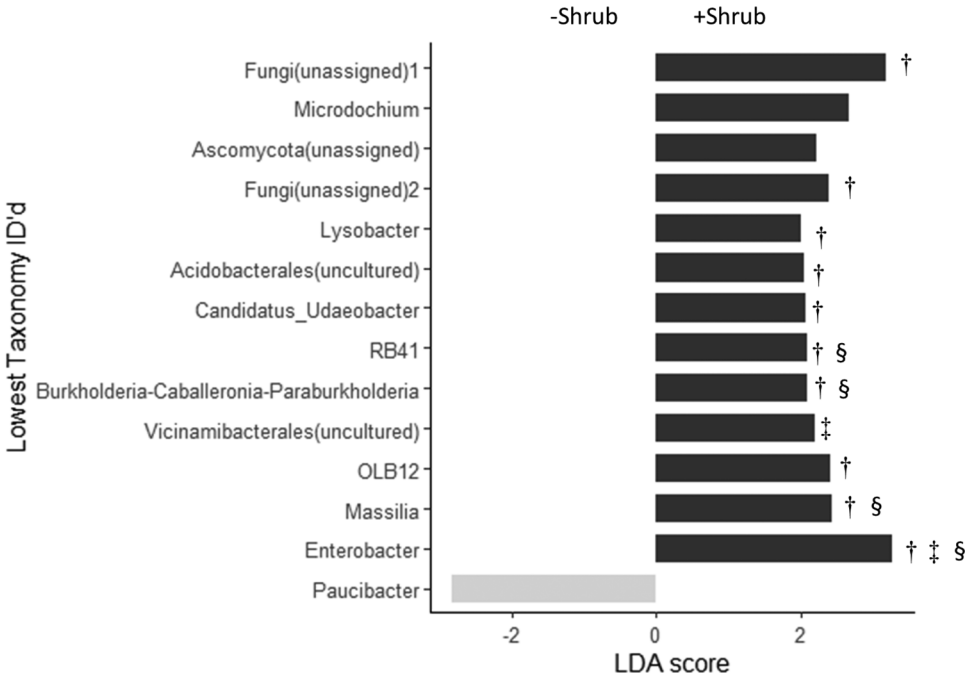

FIGURE 3 The effect of presence or absence of *G. senegalenis* on log-fold operational taxonomic unit (OTU) enrichment of 16S or internal transcribed spacer (ITS) soil communities as determined via linear discriminant analysis size effect (LEfSe). Differentially enriched OTUs were identified to the lowest possible taxonomy via SILVA NGS 138.1, and all are at least two log-fold enriched in either the presence or absence of shrubs across all sites. LDA, linear discriminant analysis

bacterial order Vicinamibacterales (0.0700%), and *Burkholderia–Caballeronia–Paraburkholderia* (0.0003%) was the least abundant overall. In a simplified community composed of only the enriched OTUs, bacterial genus *Enterobacter* comprised a large part of the community (39.9%), and an unknown member of the fungal phylum Ascomycota was the least abundant (0.348%). Although there were differences in the relative abundances or log-fold enrichments of certain OTUs, all enriched OTUs are found at all three sites.

It was also observed that, similar to the pattern observed in both the fungal and bacterial communities, landscape sampling site was responsible for the most variation in community composition across all sites (R^2 = .13), followed by shrub presence (R^2 = .06) (P < .05) (Figure 4). The strongest relationship between shrub presence and community composition was in the southern site (R^2 = .111), with the relationship between shrub presence and community composition in the northern and central site trailing behind (R^2 = .098 and .094, respectively), although the only site with significant enrichment with or without shrub was the southern site (P < .05).

Many of the shrub-enriched OTUs (three of the four fungal, and eight of the nine bacterial) were significantly and positively correlated with fresh millet biomass in at least one site (Table 2). It was more common for bacterial OTUs to positively correlate with millet fresh biomass in the Southern site (four of nine OTUs) and for fungal OTUs to correlate with millet fresh biomass at the central site (all four OTUs) (Figure 3). One bacterial OTU, *Paucibacter*, was correlated with reduced millet biomass across all sites, and this correlation was the strongest and most negative at the Central and Southern sites (ρ = −.50 & −.60, respectively) (Table 2). The strength of the correlations between each differentially enriched OTU and millet fresh biomass varied across samples and sites. There were no significant differences in the average strength of these relationships across the landscape (Supplemental Table S4).

3.5 | Beta diversity and drivers of community variation

In the total bacterial and fungal communities, NMDS with Bray Curtis distances resulted in clustering by landscape region first, and then by shrub sampling location in both the bacterial and fungal communities (P < .05). Therefore, the drivers of the overall bacterial and archaeal community were observed to be landscape sampling site (R^2 = .193), followed by shrub presence (R^2 = .050) (Figure 5). The drivers of the overall fungal community followed a similar trend; region and shrub presence accounted for 10.8 and 2.7% of the variation in community composition. Percentage total C was also the main driver in differences in fungal community composition

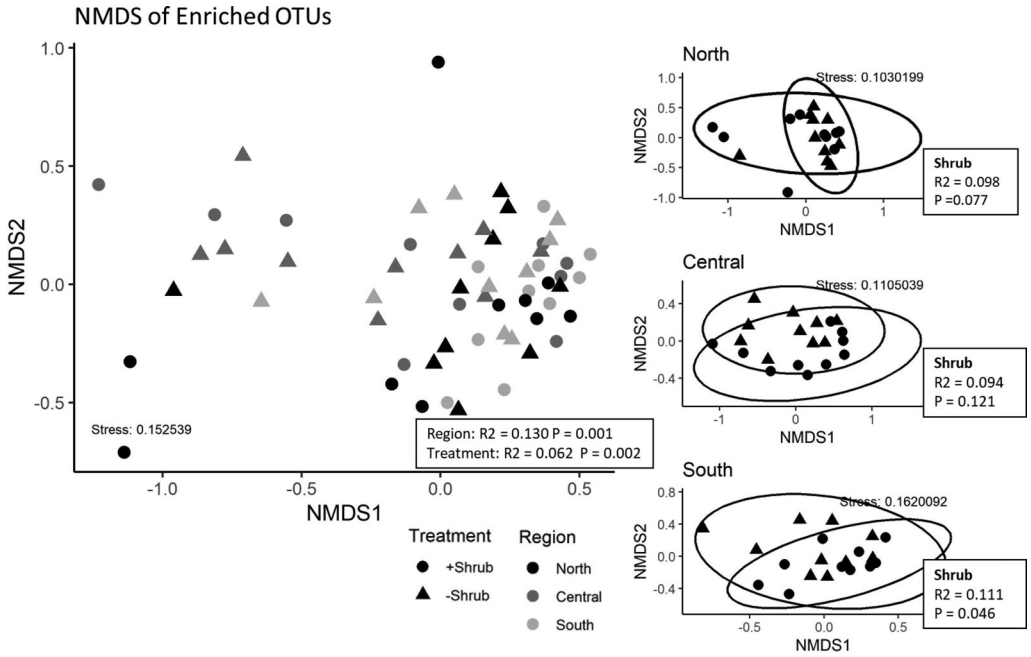

FIGURE 4 Nonmetric multidimensional scaling (NMDS) of a simplified microbial community generated from the differentially enriched operational taxonomic units (OTUs) determined via linear discriminant analysis size effect (LEfSe). The LEfSe is shown across the community and within each site. *P* and R^2 values included on the plots refer to the influence of the presence or absence of shrub on the composition of the microbial community at each site ($P < .17$ with Bonferroni's correction, permutational ANOVA [PERMANOVA])

TABLE 2 Spearman's correlation results and significance between discriminant operational taxonomic units (OTUs) and millet fresh biomass (averaged over 2012 and 2013)

	Rainfall gradient site			
Lowest taxonomic rank identified	**Overall**	**North**	**Central**	**South**
Acidobacterales (uncultured)	.303[a]	.393	.550[a]	.723[a]
Burkholderia–Caballeronia–Paraburkholderia	.299[a]	.118	.295	.506[a]
Candidatus Udaeobacter	.289[a]	.232	.350	.775[a]
Enterobacter	.354[a]	.029	.411	.538[a]
Lysobacter	.423[a]	.191	.503[a]	.331
Massilia	.358[a]	.032	.545[a]	.451
OLB12	.272[a]	−.112	.269	.405
Paucibacter	−.174	−.113	−.502[a]	−.609[a]
RB41	.353[a]	.207	.353	.318
Vicinamibacterales (uncultured)	.058	.096	−.244	.413
Ascomycota (unassigned)	.192	.006	.467[a]	.239
Fungi (unassigned) 1	.502[a]	.192	.630[a]	.506[a]
Fungi (unassigned) 2	.500[a]	.191	.712[a]	.810[a]
Microdochium	.170	.042	.595[a]	.343

[a]Values followed significantly correlated with millet fresh biomass at $P \leq .05$.

across all sites ($R^2 = .11$), followed by region ($R^2 = .108$), shrub presence ($R^2 = .027$), and the interaction between total C and shrub presence ($R^2 = .024$) ($P < .05$, Figure 6).

Members of the bacterial + archaeal community significantly clustered by shrub presence within each site (Figure 5). Within the northern site, 15.5% of the variation within the community could be explained by proximity to the shrub, and in the central and southern sites, shrub presence accounted for 8.6 and 4.6%, respectively. Congruent with the clustering of enriched OTUs at the southern site, the variation

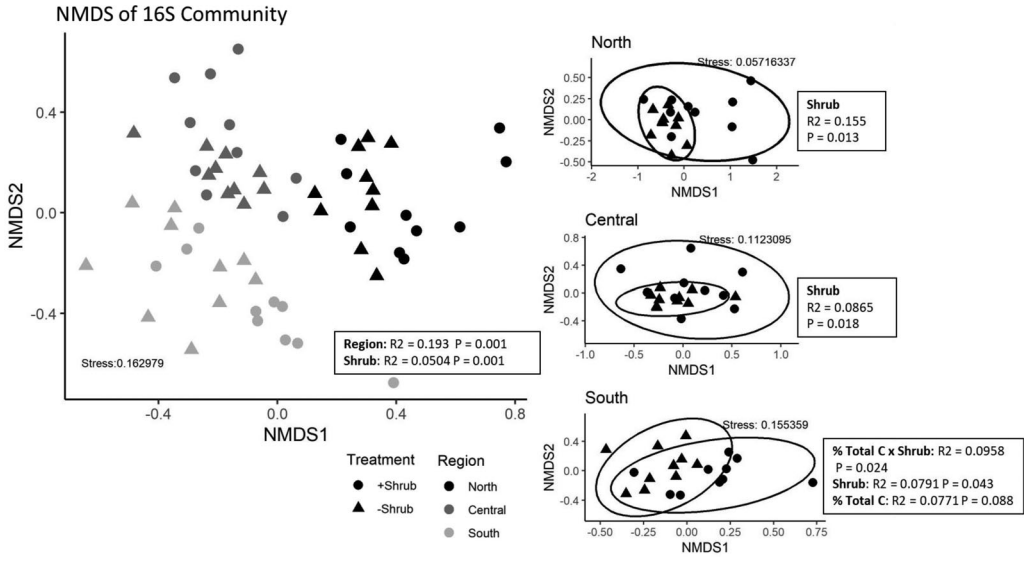

FIGURE 5 Nonmetric multidimensional scaling (NMDS) of bacterial communities at each site. Unless otherwise indicated, P and R^2 values included on the plots refer to the influence of the presence or absence of shrub on the composition of the microbial community at each site ($P < .017$ with Bonferroni's correction, permutational ANOVA [PERMANOVA])

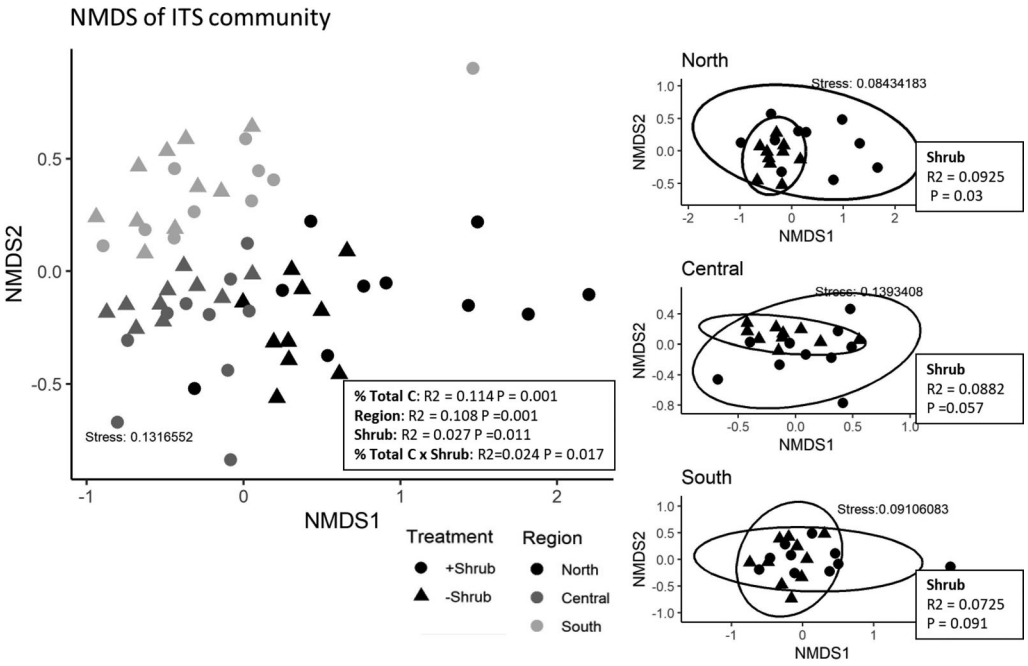

FIGURE 6 Nonmetric multidimensional scaling (NMDS) of fungal communities at each site. Unless otherwise indicated, P and R^2 values included on the plots refer to the influence of the presence or absence of shrub on the composition of the microbial community at each site ($P < .017$ with Bonferroni's correction, permutational ANOVA [PERMANOVA]). ITS, internal transcribed spacer

observed in the bacterial + archaeal community was significantly driven by total C ($R^2 = .078$) and the interaction between total C and shrub presence ($R^2 = .096$) ($P < .05$). A similar trend was observed in the fungal community with shrub presence accounting for 9.3, 8.8, and 7.3% along the northern, central, and southern sites, respectively ($P < .05$) (Figure 6).

3.6 | Predicted function

PICRUSt2 was used to predict metabolic pathways present in the community inferred by phylogeny. The composition of the pathways clustered by rainfall regime, which accounted for 7.4% of their variance (PERMANOVA, $P < .05$), and were significant drivers of community structure (Figure 7). Shrub

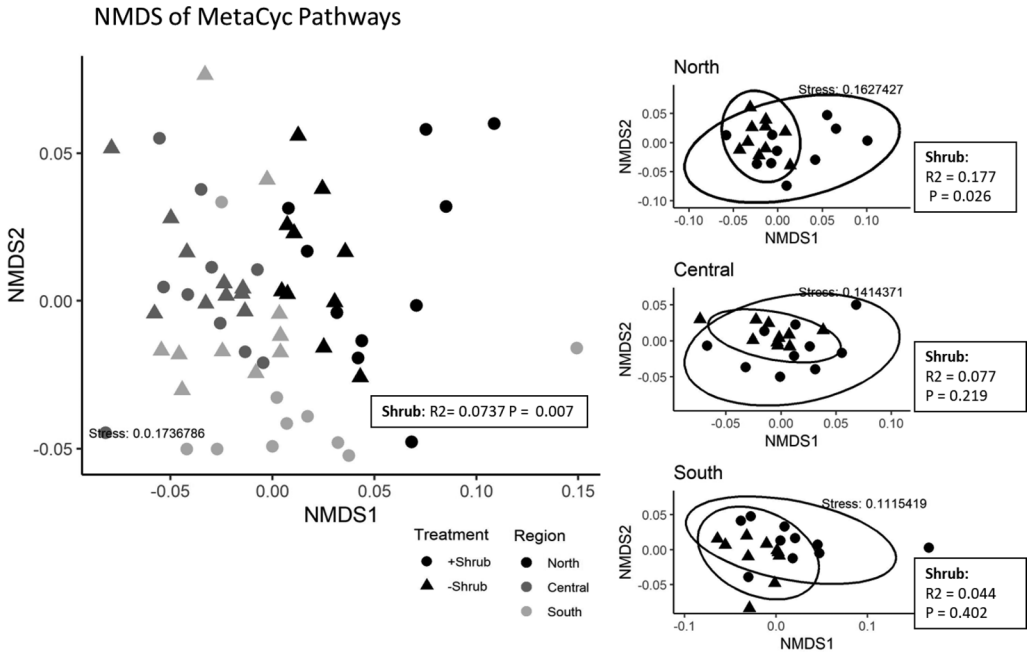

FIGURE 7 Nonmetric multidimensional scaling (NMDS) of microbial metabolic pathways at each site. Unless otherwise indicated, P and R^2 values included on the plots refer to the influence of the presence or absence of shrub on the composition of the microbial community at each site ($P < .017$ with Bonferroni's correction, permutational ANOVA [PERMANOVA])

presence did not influence the composition of community metabolic pathways in the dataset overall or at any site.

Despite not influencing the composition of metabolic pathways in the overall community, the presence of the shrub enriched 74 specific predicted metabolisms across regions related to biosynthesis and cell growth [$P > .05$, LDA > log(2)]. At the northern site, 38 pathways were enriched with shrub, and 42 pathways were enriched without shrub. Twenty-six pathways enriched in the presence of shrub at the northern site were related to biosynthesis or growth, many of which were related to fatty acid biosynthesis. There were 21 related to biosynthesis that were enriched in the absence of shrubs. Eight related to the degradation of compounds in the soil and their subsequent assimilation were enriched without shrub, and 14 were enriched with shrub. At the southern site, 33 pathways were enriched in the presence of shrubs, and 24 pathways were enriched in their absence. In both the presence, 12 enriched pathways were related to biosynthesis of cellular compounds and cellular growth, whereas in the absence of shrubs, 16 pathways were related to biosynthesis (Supplemental Figure S4; Supplemental Table S4).

4 | DISCUSSION

4.1 | Nutrient dynamics

The effect on extractable macro- and micronutrients across the landscape gradient varied over 2012 and 2013. Calcium levels were much higher in 2012 than 2013. Copper, Fe, K, Mg, and SO_4 levels were higher during 2012 for at least one of the sampling regions. This could be due to variations in rainfall, as 2013 was a drier year, which would reduce microbial activity and in turn mineralization of nutrients from organic sources.

Research in arid and semiarid regions has documented that woody species such as shrubs accumulate nutrients and organic matter, which is referred to as "islands of fertility" or "resource islands." These distinct soil ecosystems have higher soil C and N, and improved microclimate and water availability (Kieft et al., 1998; Schlesinger et al., 1996; Van Miegroet et al., 2000). This is largely accomplished by roots exploring soil horizontally and vertically for nutrients and water, which are then redistributed in soil beneath woody species through litter input, root turnover, and root exudates (Gathumbi et al., 2003).

However, the "island of fertility" effect of the shrubs in this study was not reflected in extractable nutrient levels, as a majority were not significantly elevated in millet root zone soils in the presence of *G. senegalensis*. This can be attributed to tillage homogenization and burning of coppiced residues that occurred in these fields under farmer management (Dossa et al., 2012; Lufafa et al., 2008). In the case of PO_4–P, our results are contrary to Dossa et al. (2008, 2009, 2012), who found a significant shrub effect, likely because those studies were done at the long-term experimental site of Keur Matar, Senegal, where optimized shrub management had coppiced residue incorporated from shrubs at a much higher density

(~1,500 shrubs ha^{-1}) (Dossa et al., 2012) than in farmer's fields (200–400 shrubs ha^{-1}) (Lufafa et al., 2008). Further, it should be noted that the nutrients (except for inorganic N forms) in our study were extracted with the Mehlich-3 extractant, which captures plant available nutrient forms (Mehlich, 1984). Since the sampling was done during the growing season and from soil in millet root zone, it is likely all the nutrients were taken up by the millet plants, masking the shrub effect.

Nonetheless, there was an "island of fertility" effect reflected in extractable Zn and total N and C, which in 2012 were at elevated levels across all regions in soils beneath *G. senegalensis*. Total N and C contents were elevated across a soil type and climate gradient in farmers' fields provides evidence that *G. senegalensis* forms resource islands because these properties are more stable and change slowly.

The elevated level of total N, and NH_4^+–N in the soils beneath *G. senegalensis* could be due to the stimulation of free-living N fixers. For example, a likely mechanism is that this shrub promotes diazotrophs, which is supported by observations that this shrub stimulates microbial biomass, diversity, and activity (as shown in the current study and by Debenport et al., 2015).

4.2 | Enzyme activities

All enzyme activities were lower at the northern sites than at the southern and central sites, which can be attributed to lower production and stabilization of these enzymes in the soil matrix. This corresponds to the lower rainfall and sandy soils of the northern region. Sandy soils generally have low soil organic content and cation exchange capacity, as do soils at our northern site (Table 1). Furthermore, sandy soils have high nutrient leaching rates (Pieri, 1992; Sanchez & Logan, 1992). This was the case for the northern site that had the lowest nutrient levels and total C (Table 1).

Extracellular enzymes are largely of microbial origin, with some enzymes having a significant fraction stabilized on soil colloids while remaining catalytic over long periods (Burns, 1982; Knight & Dick, 2004; Nannipieri et al., 1996). The activity of ß-glucosidase in soils, for example, is largely associated with this stabilized fraction (50% [Busto & Perez-Mateos, 1995] to as much as 75% [Knight & Dick, 2004]). A key factor for stabilizing enzymes is clay and organic matter content, and as the clay and organic matter content decrease, there is less ability for extracellular enzymes to be protected in soils. Thus, given the sandy and low organic matter soils of the northern region, it would be expected to have less potential to stabilize enzymes in the soil matrix, allowing for the decreased activities at this site.

In most cases, the presence of *G. senegalensis* in millet fields across the main cropping region of Senegal promoted enzyme activities. In both sampling years, the activities of β-glucosidase, acid phosphatase, and β-glucosaminidase were highest (but not always at $P < .05$, see below) in soils within the influence of the shrub and lowest in the millet root zone soils, far from the shrub. This enzyme response corresponded to the higher total C and N levels in soil beneath shrub canopies compared with outside the shrub, as discussed in the previous section. The presence of shrubs provides litter inputs, root exudates, and root turnover, which are C and nutrient substrates that stimulate microorganisms to produce hydrolytic enzymes to degrade these compounds. In addition, the ability of *G. senegalensis* to perform hydraulic lift or redistribution could be another factor. Redistribution occurs at night when stomata close, which allows water to move through roots along a water potential gradient, from the wet subsurface to the dry soil surface (Kizito et al., 2012; Scholz et al., 2002). This mechanism contributes to greater microbial biomass and greater production of enzymes, by maintaining some level of moisture in the rhizosphere of *G. senegalensis*, even over the 9-mo dry period in Senegal (Diedhiou-Sall et al., 2013, 2021).

There was a consistent shrub effect for β-glucosaminidase and β-glucosidase activities at the northern and central sites, and only for the northern site for acid phosphatase ($P > .05$), but no significant effects on urease activity (Figure 2). The overall positive *G. senegalensis* effect on enzyme supports previous findings by Diedhiou-Sall et al. (2013, 2021) but is more nuanced. This is likely due to a couple factors. One is that the previous research compared the OSS with a treatment with no shrubs, whereas the OSS had high shrub density (1,200–1,500 ha^{-1}) and coppiced biomass was annually incorporated. In contrast, the current study was done in farmers' fields where coppiced biomass was burned and soils were deprived of organic inputs. Secondly, the previous studies were done on soil samples collected beneath shrubs in the absence of any crop plants, whereas the current study took soil samples through the millet root zone where dense mass of roots could confound or influence microbial enzyme production by root exudates and root turnover.

Urease, however, exhibited a different pattern than the other enzymes in both sampling seasons (data not shown), being slightly higher in soil outside the influence *G. senegalensis*, with the central site having the highest activity. This corresponded to higher levels of NH_4 and NO_3 at these same locations, which could drive suppression of urease. This is because urease releases NH_3, which is quickly converted to NH_4 in soil (Bremner & Mulvaney, 1978). Thus, if NH_4, the end product of urease, is present, microorganisms suppress urease production due to feedback inhibition (Dick et al., 1988). However, a more likely reason is that the presence of shrubs would not contribute to or affect the distribution of urea, the substrate of urease.

4.3 | Microbial community composition

The PERMANOVA analysis showed that the composition of each community was greatly affected by shrub presence, second only to the rainfall gradient effect (Figures 5 and 6). Shannon's diversity analysis was similar in the presence and absence of shrubs for both the fungal and bacterial communities, except for the fungal community at the South site. However, overall species richness of the fungal community tended to decrease with shrub presence; but was significantly increased with shrub presence only at the northern site ($P < .05$, Supplemental Figure S3).

Studies in general have shown that plant roots promote high microbial activity and diversity, which in turn drive plant–microbial–soil interactions and their functions (Baudoin et al., 2001; Jones et al., 2019; Li & Wu, 2018; Reinhold-Hurek et al., 2015; Schmidt et al., 2019). However, in the current study, there was no significant shrub effect on microbial diversity. This stands in contrast with Diedhiou-Sall et al. (2009, 2021), where diversity was affected by OSS. There are potentially several reasons for this. First OSS has high shrub density (~1,500 ha^{-1}) and all coppiced residues were incorporated. Conversely, the current study was done in farmers' fields where shrub densities are low (<200 to ~350 shrubs ha^{-1}), which reduces the potential for organic inputs and most importantly farmers typically burn coppiced shrub residues, thus depriving soils of C inputs to stimulate the microbial community. Furthermore, the soil was sampled from the millet root zone and thus the millet root effects (exudates and root turnover) may have overridden the shrub effect.

However, diversity by itself does not necessarily indicate an improved microbiome for delivering agroecosystem services. Rather, shifts in subpopulations with beneficial or detrimental properties or functionality are potential mechanisms for improved or inhibited plant growth in the presence of shrubs. Indeed, the sections below discuss potentially positive functional traits and stimulation of beneficial microorganisms due to the presence of *G. senegalensis*.

4.4 | Differentially enriched OTUs

Although dominant taxonomic groups did not change in relative abundance in the presence of shrubs, some rare OTUs were found to be significantly enriched by shrub presence at all sites. It was determined that 12 bacterial OTUs and four fungal OTUs were enriched by shrub presence (Table 2). Several of these bacterial OTUs were from the Burkholderieaceae family, which was also observed as shrub-enriched by Debenport et al. (2015) at the OSS experimental site. The relative abundance of the genera *RB41*, a member of the order Xanthomondales, was found to be enriched in the presence of shrubs in this study and in rhizosphere soils of maize in other studies (Meier et al., 2021; Schmidt et al., 2019). *Burkholderia–Caballeronia–Paraburkholderia* is another common rhizosphere genus, and *Massilia* is a genus common to the rooting zones of plants in arid- and semiarid soils (Ofek et al., 2012; Ren et al., 2018).

Several taxa enriched in the presence of shrubs are known to have plant growth promoting properties. For example, *Enterobacter agglomerans* is capable of PO_4^{3-} solubilization and hydrolysis of organic P for plant growth via acid phosphatase production and is stimulated by organic matter amendments (Kim et al., 1998), which is consistent with *G. senegalensis* increasing total C. Another group, *Paraburkholderia*, have beneficial properties, including the production of chitinase and other hydrolytic enzymes which promote fungal and plant residue decomposition (Eberl & Vandamme, 2016; Tapia-García et al., 2020). This is supported in that both *Paraburkholderia* and chitinase activity increased in the presence of *G. senegalensis*. *Burkholderia–Caballeronia–Paraburkholderia* also correlated with millet biomass production. This could be due to its suppression of fungal pathogens, as chitinase activity is a pathogenic antagonist and that other members of Burkholderiaceae can reduce fungal pathogens (Benítez & McSpadden-Gardener, 2009). Furthermore, these organisms promote plant growth by fixing N_2 gas and providing N inputs (Estrada de los Santos et al., 2001), and by producing the beneficial plant hormones gibberellin and auxin (Poupin et al., 2013).

In addition to the enrichment of beneficial microorganisms by *G. senegalensis*, an OTU of the genus *Paucibacter* was found to be enriched in soils of the millet root zone taken outside the influence of *G. senegalensis* (Table 2). Some *Paucibacter* species have been recently found to inhabit the rhizosphere soils of diseased plants (Liao et al., 2021), and others have been found to produce antimicrobials (Mullis et al., 2019), suggesting a relationship between this genus and plant disease. Further, in our study, this genus was negatively correlated with millet fresh biomass. It is potentially an important observation because if *Paucibacter* has species that are deleterious or pathogenic, this would provide a previously unrecognized mechanism for low millet yields in degraded soils throughout the Sahel. Historically, low productivity has been attributed to soils having low organic matter and poor structure where, even with the addition of inorganic fertilizer, there is little yield response (Badiane et al., 2001). However, it may well be that the lack of organic inputs and/or absence of shrubs also promotes pathogenic and/or deleterious microorganisms such as *Paucibacter*. More research is needed to determine the species-level identity of *Paucibacter* and confirm that it has negative effects on millet growth.

Enriched taxa may also colonize unique niches provided by the association between millet and shrubs or to take advantage of other emergent properties of the system. One such taxa may be *Candidatus Udaeobacter*. This group is abundant

in soil but poorly described in literature and may use nutrients released when other microbes are lysed via antimicrobial compounds produced by other community members (Willms et al., 2020). As described in Diedhiou-Sall et al. (2009), community diversity tended to increase in the presence of shrubs, and *Ca. Udaeobacter* may be highly competitive for limited nutrients in densely populated rhizosphere, while being resistant to multiple antibiotics.

In the low-C soil, low-rainfall northern site, it could be expected that intercropping with shrubs may have a stronger effect on composition and diversity of predicted function, but this was not the case. However, as discussed above, there were shifts in abundance of subpopulations due to the presence of *G. senegalensis* within each region, and significant changes in community composition at the southern, high-C site. This indicates that *G. senegalensis* affected microbial metabolic processes more in regions with greater soil C content and higher rainfall, compared with drier, low-C regions, as determined via NMDS. Similar to the community overall, enriched OTUs clustered by region first and secondly by shrub presence. However, when split by region, only the southern, site shows significant clustering with shrub presence (Figure 4). The significant clustering may be linked to the increased total C content in the southern site, implying that there may exist a threshold for total soil C, past which it has a significant impact on the microbial community and function. Such a phenomena have been observed by Hao et al. (2021) and Reischke et al. (2015), adding a layer of complexity to the relationship among shrubs, the microbial community, and C storage in arid soils under climate change. For future research, predicted or potential functions of the microbial community may be of more interest for determining the role of *G. senegalensis* in drought resilience in millet (Langille, 2018).

Finally, there was no significant difference in the average strength of relationship across sites between each differentially enriched OTU and the fresh biomass of millet (Supplemental Table S4). This indicates that, although *G. senegalensis* enriches for distinct OTUs with the potential to influence the growth of millet, there was no one organism that could be linked to millet growth across landscape sites; the increased millet growth was at least, in part, an emergent property of the entire microbial community, the assembly of which was driven by intercropping with *G. senegalensis*.

4.5 | Predicted function of the bacterial community

Previous studies have also shown that shrub presence increases enzyme activities and microbial properties, possibly due to the increase in shrub residues, root exudates, and fine root turn over (Debenport et al., 2015; Diakhate et al., 2016; Diedhiou et al., 2020, 2021; Diedhiou-Sall et al., 2013). Specifically, the availability of energy sources, particularly labile C and other rhizodeposits, affects community composition or capabilities (Baudoin et al., 2001; Hester et al., 2019; Schmidt et al., 2019). A greater diversity of substrates tends to reduce metabolic overlap and higher diversity of metabolic pathways, decoupled from the taxonomic diversity or species richness (Hester et al., 2019), as could be surmised from the current study; soils at the southern site are richer in C and on average receive more rainfall, increasing the availability of substrates.

Further, although there is no consistently significant pathway enrichment across all sites, it does appear that in samples with shrub at the northern site, there are a greater number of biosynthesis pathways related to fatty acid synthesis (Supplemental Table S4). This is notable because there has previously been observed a significant increase in phospholipid fatty acids in soils with shrub, which has been linked to increased microbial activity and diversity (Diedhiou-Sall et al., 2009). Significantly increased fungal diversity and increased acid phosphatase, β-glucosidase, and β-glucosaminidase were also observed at this site (Figure 3; Supplemental Figure S3), further suggesting that the shrub promotes the growth of certain microbial clades that are highly active in the more degraded and low-quality soils at the northern, more arid site.

4.6 | Millet response to *G. senegalensis*

Millet biomass increased in the presence of shrubs at each site; notably, this increase was greater in the northern site with low soil quality and rainfall than at the southern site with higher soil quality and rainfall. This is the first report across a landscape gradient on the impact of *G. senegalensis* on millet growth under farmer management. This highlights the unusual ability of *G. senegalensis* to promote a favorable growth environment for millet, even at low plant densities where farmers use little or no external inputs, and coppiced shrub residue is annually burned.

These growth responses to shrub intercropping are consistent with long-term studies of the OSS (elevated plant densities) and annual incorporation of coppiced residues. For *G. senegalensis* in long-term experiments as a companion plant, Dossa et al. (2013) and Bright et al. (2021) showed dramatic yield responses (groundnut [*A. hypogaea*] and millet), even in years with low rainfall in the northern Peanut Basin (same region as our northern site). Another shrub species found in farmers' fields of the Sahel, *Piliostigma reticulatum* (DC.) Hochst., has also improved crop yields in Burkina Faso (sorghum [*Sorghum bicolor* (L.) Moench]) (Félix et al., 2018) and in Senegal (groundnut and millet) (Bright et al., 2017). Furthermore, Félix et al. (2018) reported that *P. reticulatum* promoted sorghum yields under low rainfall and naturally low fertility soils, similar to the northern site in the current

study. Similar to Debenport et al. (2015), our study had a crop growth response to shrubs that corresponded to a shift in microbial subpopulations known to have plant growth promoting properties and/or suppress deleterious or pathogenic microorganisms.

It is common in West Africa for farmers to have trees in cropped fields, which is known as the Parkland system. Parkland management is promoted as a means to increase sustainability of dryland cropping systems (Garrity et al., 2010; Mbow et al., 2014; Takimoto et al., 2008). Although trees provide landscape stability and reduce wind erosion, the tree species typically found in the Sahelian Parkland agroforestry systems, except for *Faidherbia albida* (Delile) A.Chev. (Garrity et al., 2010), do not increase crop yields, largely due to shading (Bayala et al., 2012; Kessler & Breman, 1991; Sinare & Gordon, 2015). The presence of shrubs in the intra-tree space would synergestically improve tree based systems, by increasing crop productivity and remediating degraded soils.

5 | CONCLUSIONS

The presence of *G. senegalensis* at low densities typically found in Senegalese farmers' fields increased aboveground millet fresh biomass and enriched certain bacterial and fungal genera, some of which are known to have plant-growth-promoting properties. It was found that site location and the presence of *G. senegalensis* drive shifts in structure of bacterial and fungal communities and some of the bacterial community's predicted metabolic pathways. These positive shrub effects were most evident at the northern site of the major cropping region of Senegal, which has low rainfall and soils with low organic matter. Total soil C content across all sites was also a factor for controlling predicted metabolic pathways.

The results showed that when *G. senegalensis* is in farmers' fields that are at low densities and where coppiced residues are annually burned, it still increases soil enzyme activities and shifts microbial communities, which corresponds to enhanced millet productivity. These results are similar to the OSS that has high shrub densities and incorporation of coppiced shrub residues in the long-term researcher managed experiments of Dossa et al. (2012), Diedhiou-Sall et al. (2009), Debenport et al. (2015), and Bright et al. (2021). However, in the current study, because the research sites were under farmer management where coppiced shrub residue was burned, the amount of litter inputs was greatly diminished. This suggests that an important factor over litter inputs in driving shrub-induced crop response is the presence of shrub roots that provides organic inputs through root turnover and exudates, and water inputs through hydraulic lift.

These mechanisms would not only benefit crops directly but also cause a shift to a microbiome that has plant growth promoting subpopulations. This can be inferred from the positive correlation crop growth due to *G. senegalensis* with the abundance of genera known for having plant growth properties. Furthermore, the presence of this shrub completely suppressed to undetectable levels the genera *Paucibacter* that has deleterious and/or pathogenic properties. Although more research is needed to connect shifts in microbiome with beneficial plant responses due to the presence of *G. senegalensis*, the current results provide support for farmers to conserve and increase *G. senegalensis* density to improve soil quality and crop productivity to reduce food insecurity.

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AUTHOR CONTRIBUTIONS

Laura Mason: Data curation; Formal analysis; Investigation; Validation; Writing – original draft; Writing – review & editing. Chelsea DeLay: Data curation; Formal analysis; Investigation; Writing – original draft. Spencer Debenport: Data curation; Investigation; Validation; Writing – review & editing. Ibrahima Diedhiou: Data curation; Investigation; Methodology; Project administration; Resources; Validation; Writing – review & editing. Brian B. McSpadden Gardener: Data curation; Investigation; Supervision; Writing – review & editing. Komi B. Assigbetse: Data curation; Investigation; Writing – review & editing. Virginia Rich: Data curation; Formal analysis; Investigation; Supervision; Validation; Writing – original draft; Writing – review & editing. Richard P. Dick: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Supervision; Validation; Writing – review & editing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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