Tree-based green walls as a strategy for restoring soil functionality in semi-arid agave agroecosystems

Muros verdes como estrategia para restaurar la funcionalidad del suelo en agroecosistemas de agave semiáridos

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ABSTRACT. Agroforestry approaches, including green walls, have been proposed as promising alternatives for promoting restoration and long-term sustainability in arid and semi-arid agroecosystems; however, their impact on soil quality restoration remains insufficiently explored. This study aimed to evaluate the effect of *Acacia schaffneri* and *Neltuma laevigata* as green walls on soil carbon pools and the assembly of the soil microbiome in agave cropland within a semiarid region. Soil carbon stocks, including total soil organic carbon (TSOC), total soil inorganic carbon (TSIC) stocks, soil organic matter (SOM), carbonates, and labile carbon—were quantified. The bacterial community was characterized through 16S rRNA amplicon sequencing. Results demonstrated a clear gradient associated with proximity to the green walls. Areas near older trees (PA) showed the highest TSOC, SOM, and labile carbon, indicating improved soil quality under the influence of mature trees. In contrast, the middle of the agave cropland (PM) exhibited the lowest organic carbon levels and greater carbonate dominance, while areas near younger trees (PB) displayed intermediate conditions. β-diversity analyses revealed distinct microbial assemblages among zones, with PA harboring more diverse and structurally complex communities. Network analysis indicated a highly modular, non-random microbial organization dominated by Actinomycetota and Pseudomonadota. Overall, these findings highlight the strong potential of mature green walls composed of mesquite and huizache trees as an effective strategy for restoring soil functionality and resilience in semi-arid agave production systems.
Keywords: Huizache, mesquite, bacteriome, soil conservation, soil restoration.

RESUMEN. Los enfoques agroforestales, como los muros verdes, se han propuesto como alternativas prometedoras para promover la restauración y la sostenibilidad a largo plazo en agroecosistemas áridos y semiáridos; sin embargo, su impacto en la restauración de la calidad del suelo aún ha sido poco explorado. Este estudio tuvo como objetivo evaluar el efecto de *Acacia schaffneri* y *Neltuma laevigata* como muros verdes sobre los reservorios de carbono del suelo y el ensamblaje del microbioma edáfico en un cultivo de agave en una región semiárida. Se cuantificaron los reservorios de carbono del suelo, incluyendo almacenes de carbono orgánico (TSOC) e inorgánico (TSIC) total, materia orgánica del suelo (SOM), carbonatos y carbono lábil. La comunidad bacteriana se caracterizó mediante secuenciación del amplicón del gen 16S rRNA. Los resultados mostraron un gradiente claro asociado con la proximidad a los muros verdes. Las zonas cercanas a árboles mayores (PA) presentaron TSOC, SOM y carbono lábil más altos, lo que indica una mejora en la calidad del suelo bajo la influencia de árboles maduros. En contraste, el centro del cultivo de agave (PM) mostró los niveles más bajos de carbono orgánico y mayor dominancia de carbonatos, mientras que las áreas cercanas a árboles jóvenes (PB) exhibieron condiciones intermedias. El análisis de β-diversidad reveló ensamblajes microbianos distintos entre zonas, con PA albergando comunidades más diversas y estructuralmente complejas. En conjunto, estos hallazgos destacan el potencial de los muros verdes maduros para restaurar la funcionalidad y resiliencia del suelo en sistemas semiáridos de producción de agave.
Palabras clave: Huizache, mezquite, bacterioma, conservación de suelos, restauración del suelo.

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INTRODUCTION

Arid zones are particularly vulnerable to soil degradation driven by climate change. Moreover, anthropogenic activities, mainly agriculture and livestock activities, accelerate soil desertification, intensifying wind erosion and increasing the frequency of sand and dust storms (Sileshi *et al.* 2023). Wind erosion entails severe ecological processes, including intense rainfall events and wind-driven droughts, which affect ecosystem services at multiple spatial scales and threaten food security due to vegetation clearing for extensive agriculture (Pierre *et al.* 2022, Sun *et al.* 2024). In addition, the intensification of land use reduces soil quality and may further exacerbate wind erosion, potentially inducing regional degradation of agricultural fields (Iwasaki *et al*. 2024, Zhang *et al*. 2024). Thus, implementing soil conservation strategies is essential to promote restoration and long-term sustainability. Among these, agroforestry approaches such as green walls, continuous belts of trees established across dryland regions, have emerged as socioecological initiatives designed to curb desert expansion and protect the productivity of adjacent lands by stabilizing soils and enhancing ecosystem resilience (Turner *et al.* 2023). Agroforestry systems integrate crop production with the deliberate cultivation of trees, generating complementary interactions that benefit both agricultural productivity and the surrounding ecosystem. However, the effectiveness of green wall initiatives depends strongly on ecological suitability and species selection. Many dryland regions targeted for afforestation are naturally better suited to grasslands or steppe vegetation than to dense tree cover, and past reliance on exotic, water-demanding tree species has often resulted in poor establishment and limited benefits for local communities (Sop and Oldeland 2013, Wang *et al.* 2013, Niang *et al.* 2014, Turner *et al.* 2023). Consequently, recent approaches emphasize diversifying plantings to include native trees, shrubs, and grasses, and in some cases fruit trees adapted to local rainfall regimes.

In this context, integrating green infrastructure (GI) into agricultural landscapes is increasingly recognized as a pathway to enhance soil health, biodiversity, and climate resilience (Ogwu and Kosoe 2025). Agroforestry-based GI, including green walls, can improve soil structure and fertility through organic matter inputs, enhance habitat availability for beneficial fauna, strengthen pest regulation and pollination, and increase carbon sequestration while reducing erosion (Fenster *et al.* 2021, Kenne and Kloot 2019). Evidence also indicates that tree–crop interactions can stimulate soil microbial diversity and biomass, key indicators of soil functionality, while improving water retention and nutrient cycling (Singh *et al.* 2023). Beyond ecological gains, such systems may diversify farm income through timber and non-timber products, reducing the economic risks of monoculture systems (Turner *et al.* 2021). However, tree establishment in arid and semiarid environments can generate complex and sometimes contrasting ecological effects. Potential benefits include reduced surface wind velocity, lower evaporation rates, dune stabilization, microclimate moderation, and increased soil organic matter deposition that may enhance fertility and biodiversity (Fenster *et al.* 2021, Ogwu and Kosoe 2025). Conversely, high tree densities may elevate transpiration, lower groundwater levels, reduce streamflow, and suppress native shrub and grass cover, processes that can ultimately intensify water stress and erosion (Khaouani *et al.* 2019, Wang *et al.* 2020, Zhang *et al.* 2021). Therefore, the net ecological outcomes of dryland afforestation remain context-dependent, underscoring the need for careful design and long-term monitoring of green wall interventions. Furthermore, significant research gaps remain regarding the soil-

mediated services of green infrastructure, particularly in dryland green wall systems. Processes such as nutrient cycling efficiency, metal immobilization, and broader soil-regulated ecosystem functions are still insufficiently characterized, and the role of the soil microbiome in mediating these benefits is especially underexplored. Therefore, this research aimed to evaluate the impact of green walls on soil microbiota and carbon stocks in degraded cropland within a semiarid region, contributing empirical evidence to support the optimization of green infrastructure design and management in dryland agroecosystems.

MATERIALS AND METHODS

Study site description

The study was conducted in an agricultural area located in Ejido Ignacio Allende, municipality of Guadalupe Victoria, Durango, Mexico. The site comprised a 4 ha field historically cultivated with common bean and subsequently converted to a cenizo agave (*Agave durangensis*) plantation, with an average slope of <5%. The area is located at 24.47° N and 103.95° W at an elevation of 1 981 masl. The native vegetation corresponds to shrubland and grassland typical of a temperate semiarid climate, with a mean annual precipitation of 522 mm and a mean annual temperature of 16.7 °C. Rainfed bean production is the predominant agricultural activity in the region. However, due to the extensive plains, croplands are highly susceptible to wind erosion. Under these conditions, fields are commonly bordered by linear remnants of native vegetation, primarily huizache (*Acacia schaffneri*) and mesquite (*Neltuma laevigata*), which function as natural windbreaks.

Three landscape positions were defined within the study area: upper slope outside the cropped field and near the tree drip line (PA), middle section of the agave plot (PM), and lower slope within the field but adjacent to the vegetation line (PB).

Soil sampling

Three soil samples (0–20 cm depth) were randomly collected from each treatment and combined to obtain one composite sample per treatment. Samples were air-dried and sieved through a 2.0 mm mesh prior to carbon analyses.

To assess the effectiveness of green walls for soil conservation and their influence on soil microbiota, soil samples were collected along the upslope gradient of the field, where the upper and lower positions were closest to the linear plantings. Four soil samples were randomly collected from each study zone at a depth of 20 cm. Samples were immediately placed into 2 mL BashingBead™ lysis microtubes containing 750 µL of Xpedition™ lysis/stabilization buffer (Zymo Research™) and homogenized using a TerraLyzer™ cell disruptor. Samples were subsequently stored at −20 °C until DNA extraction for metagenomic analysis.

Soil carbon analysis

Total carbonates were quantified using the Bernard calcimeter method (Rodríguez 1996), and total carbon (TC) was measured with an elemental analyzer. Total organic carbon (TOC) was calculated

by subtracting carbonate carbon from TC. Labile carbon was determined by permanganate-oxidizable carbon following Blair *et al.* (1995).

Total soil inorganic carbon (TSIC) and total soil organic carbon (TSOC) stocks (Mg C ha^{-1}) were calculated using the equation (Fan *et al.* 2014):

$$TSIC\ (TSOC)\ Stock = SIC(SOC) \times BD \times D \times 10$$

Where SIC and SOC are the inorganic and organic carbon concentrations (g C kg^{-1} soil), respectively; BD is bulk density (Mg m^{-3}); D is soil depth (0.2 m); and 10 is a unit conversion factor.

DNA extraction

Genomic DNA was extracted using the ZymoBIOMICS™ DNA MiniPrep kit (Zymo Research™) according to the manufacturer's instructions. Bacterial community profiling was performed by PCR amplification of the V3-V4 hypervariable regions of the 16S rRNA gene following Illumina protocols (Illumina 2017, 2023) with primers 341F and 806R.

Bioinformatic analysis

Sequence data were processed in R using DADA2 v1.18 (Callahan *et al.* 2016). Paired-end reads were quality filtered, truncated to 250 bp (both forward and reverse), merged, and screened for chimeras to generate an amplicon sequence variant (ASV) table. Sequences shorter than 250 bp were discarted. Quality filtering criteria were set at zero ambiguous bases (maxN = 0) and a maximum of 3 and 5 expected errors (EE) for forward and reverse reads, respectively. Reads were truncated at the first instance of a quality score (Q) less than 2. Additionally, contaminant sequences matching the genome were removed using the isPhiX algorithm. Importantly, archaeal sequences were retained in the dataset.

Taxonomic assignment was performed with the DECIPHER classifier (Wright 2016) against the SILVA SSU v138 reference database. Sequences lacking classification above the order level, as well as those identified as chloroplast or mitochondrial in origin, were removed, representing 9.8% of the total reads. Sequences were submitted to GenBank, NCBI database (PRJNA1429442).

Alpha diversity was estimated using ASV richness, Shannon diversity, and Simpson dominance indices implemented in vegan v2.6-10 (Oksanen *et al.* 2001). Differences in community structure were evaluated by non-metric multidimensional scaling (NMDS) with Bray-curtis using the same package. For downstream analyses, ASVs were aggregated at the genus level. Differentially abundant taxa were identified using Linear Discriminant Analysis Effect Size (LEfSe) with the lefser package v1.21.7 (Segata *et al.* 2011). Statistical significance was determined using a p-value < 0.05, and only taxa meeting a Linear Discriminant Analysis (LDA) score threshold of > 2.5 were considered differentially abundant.

Core microbiota and Venn diagrams

To visualize the distribution of shared and unique taxa among sites, Venn diagrams were constructed. For this analysis, only ASVs present in at least two samples per site with a relative abundance > 0.01% were considered. This filtering step was applied to ensure the inclusion of

representative and stable microbial members while reducing noise from rare or transient sequences.

Community network analysis

To identify stable microbial interaction patterns across soil conditions, pairwise correlations among genera were inferred using the SparCC (Sparse Correlations for Compositional Data) algorithm implemented in SpiecEasi v1.1.1 (Kurtz *et al.* 2015). This approach was chosen to account for the compositional nature of the 16S rRNA dataset (12 samples from three locations). Only associations with an absolute SparCC correlation coefficient (r) > 0.70 and a significance level of $p < 0.05$, after adjustment for the False Discovery Rate (FDR), were retained to construct an undirected weighted network. Network modules were subsequently detected by maximizing modularity through the Louvain algorithm implemented in igraph v2.1.4 (Csárdi *et al.* 2025).

Statistical analysis

Data of soil parameters normality was verified using the Shapiro-Wilk test with a 95% confidence level, while homogeneity of variance was assessed via Levene's test using RStudio. Non-normal data were transformed using a $\log_{10}$ function. Subsequently, a one-way analysis of variance (ANOVA) was performed at a 95% confidence level. When significant differences were detected, pairwise comparisons were performed using Fisher's Least Significant Difference (LSD) as a post hoc test. The resulting p-values were adjusted using the Bonferroni correction with the agricolae package v1.3-7.

To evaluate the associations between microbial counts and soil physicochemical characteristics, Spearman's rank correlation was employed. P-values were corrected using the False Discovery Rate (FDR) method; only associations with an adjusted $p < 0.05$ were considered significant. All statistical analyses were conducted using R software (R Core Team 2025).

RESULTS

Soil carbon fractions showed a clear spatial gradient associated with proximity to green walls, where the mature green walls seem to promote organic carbon sequestration (with highest values of TSOC, SOM, and labile C) that improve soil quality, while younger structures generate transitional effects (Figure 1). A total of 232 different taxa were found, most of them belonged to the Acidobacteria, Bacteroidota, Gemmatimonadota, Pseudomonadota, Actinomycetota, Chloroflexota, Nitrospirota, and Thermoproteota phyla (Figure 2a).

Alpha diversity was not significantly different among studied zones in the landscape (Figure 2b), but the NMDS ordination revealed a clear separation among PA, PB, and PM communities (Figure 2d). The Venn diagram, on the other hand, reveals both a shared core microbiome across sites and location-specific taxa (n = 185), indicating that proximity to mature green walls promotes microbial differentiation while maintaining a common baseline community in the agave agroecosystem, probably due to the improvement of soil quality by the increase of soil organic carbon stocks (Figure 2c).

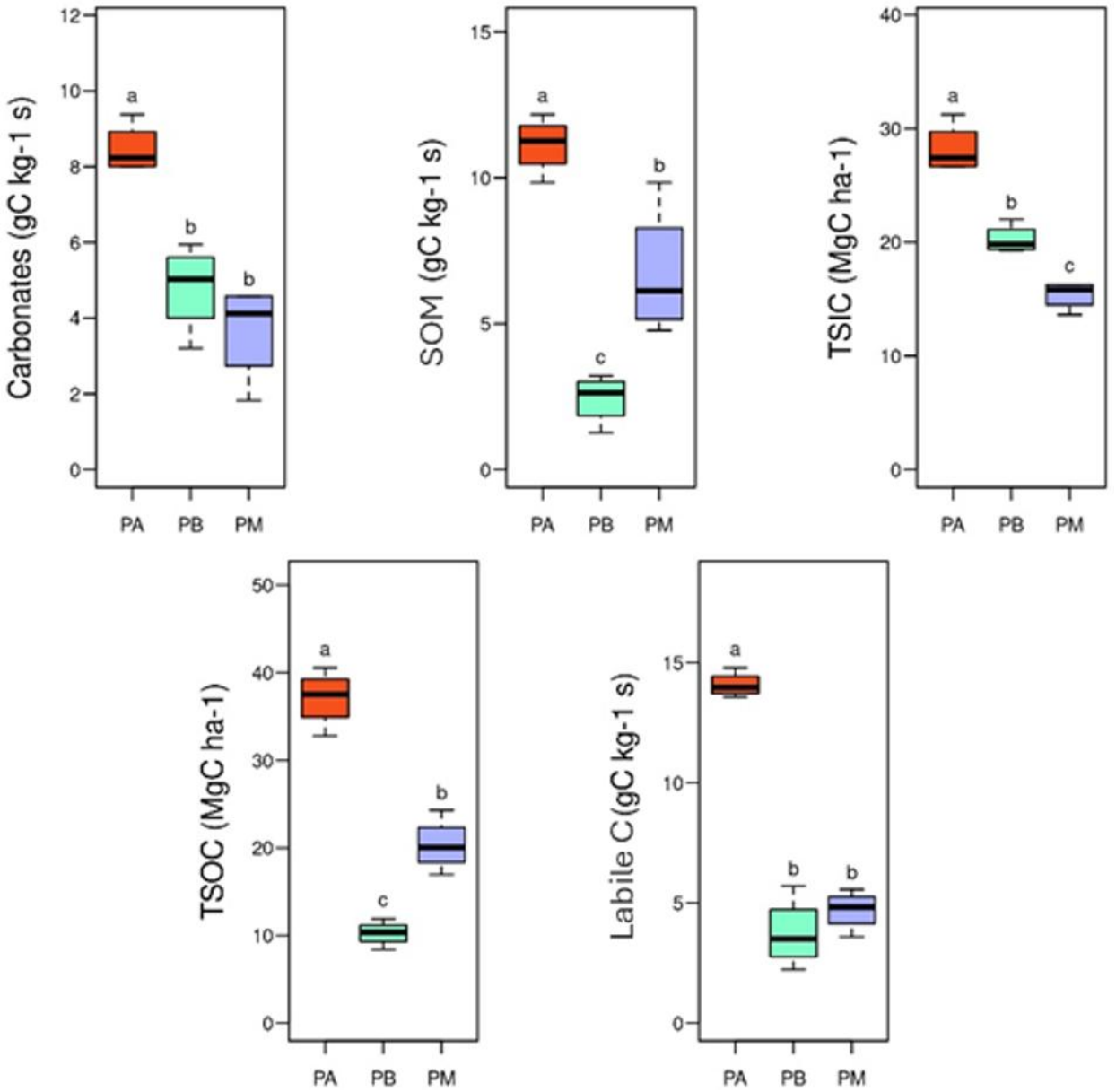

Figure 1. Carbon stocks in different landscape analyzed positions within the study area: upper slope outside the cropped field and near the mature tree drip line (PA), middle section of the agave plot (PM), and lower slope within the field but adjacent to young vegetation line (PB). Different letters indicate significant differences between group means of measured parameters by Tukey. SOM - soil organic matter; TSIC –total inorganic carbon stock; TSOC – total organic carbon stock; Labil C – labil carbon.

Furthermore, LEfSe analysis identifies distinct taxonomic biomarkers for each zone (Figure 3), with the highest number of biomarkers in PM. Moreover, the correlation heatmap showing the relationships between the discriminant microbial genera and the measured soil carbon stocks indicated that shifts in soil carbon pools near green walls are not only quantitative but also selectively shape microbial community composition, reinforcing the role of organic matter enrichment in structuring the soil microbiome (Figure 4).

A co-occurrence network was inferred using SparCC correlations to explore microbial interaction patterns. After retaining only strong associations ($r \geq 0.75$), the network comprised 119 ASVs connected by 154 edges, of which 40% were negative (n = 44) (Figure 5A). The relatively high proportion of negative links suggests the coexistence of both cooperative and potentially competitive interactions within the soil microbiome. Most taxa in the network belonged to the phyla Actinomycetota (40 taxa) and Pseudomonadota (30 taxa), indicating that these groups play central roles in structuring microbial associations in the studied soils (Figure 5B).

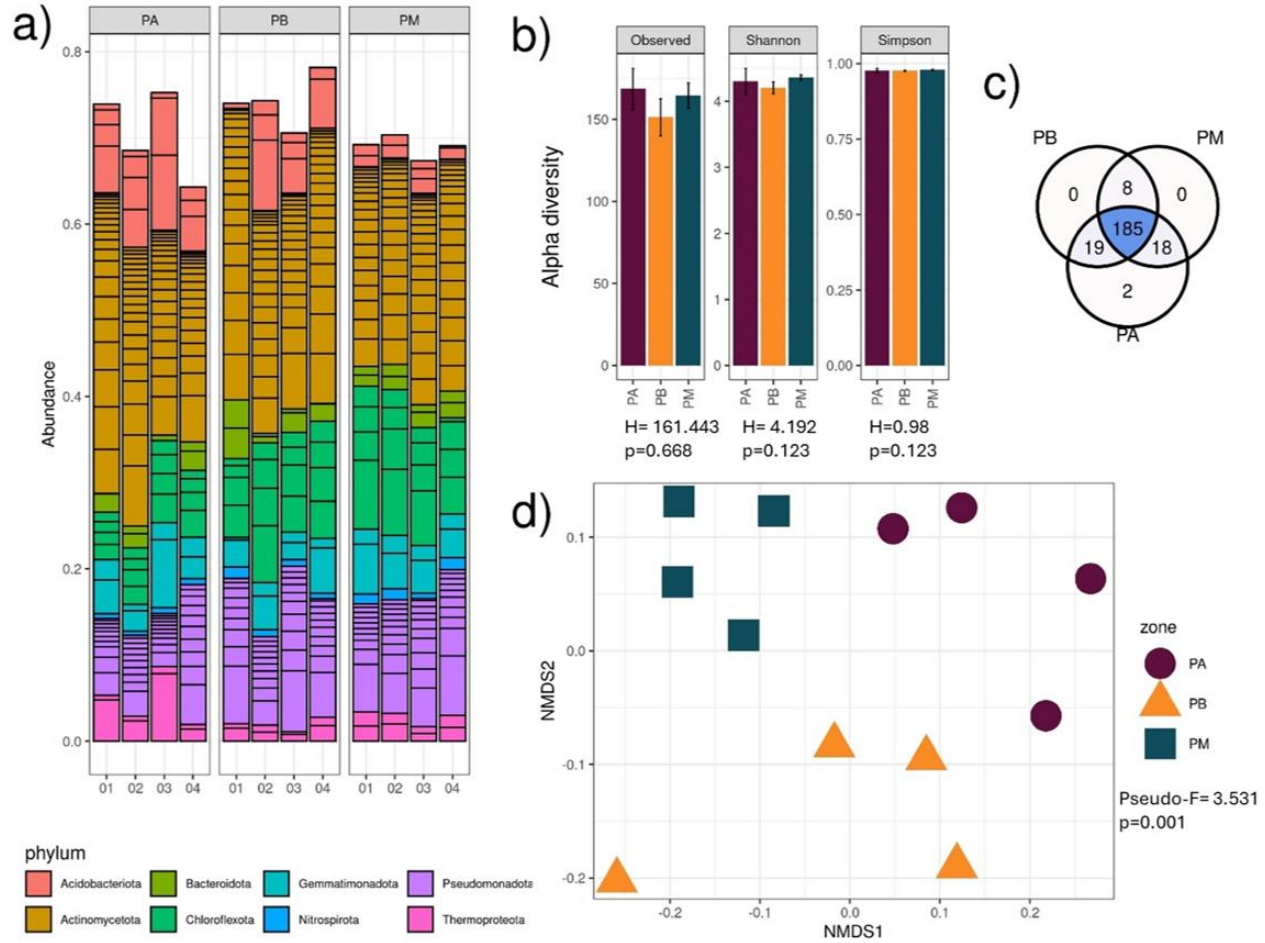

Figure 2. Diversity and taxonomic composition of soil bacterial communities in the studied areas: a) Relative abundance of dominant bacterial phyla across individual samples from the three study zones: PA (near older green walls), PB (near younger green walls), and PM (center of the agave field); b) α-diversity indices of the bacterial communities, including Observed ASVs (richness), Shannon diversity, and Simpson diversity, comparing the three zones. Bars represent mean values with their corresponding variation among samples; c) Venn diagram showing the number of shared and unique ASVs among the three zones (PA, PB, and PM), highlighting the core and zone-specific bacterial taxa; d) Non-metric multidimensional scaling (NMDS) ordination based on community composition, illustrating differences in bacterial community structure among zones. Each point represents a sample, and symbols/colors indicate the sampling zone.

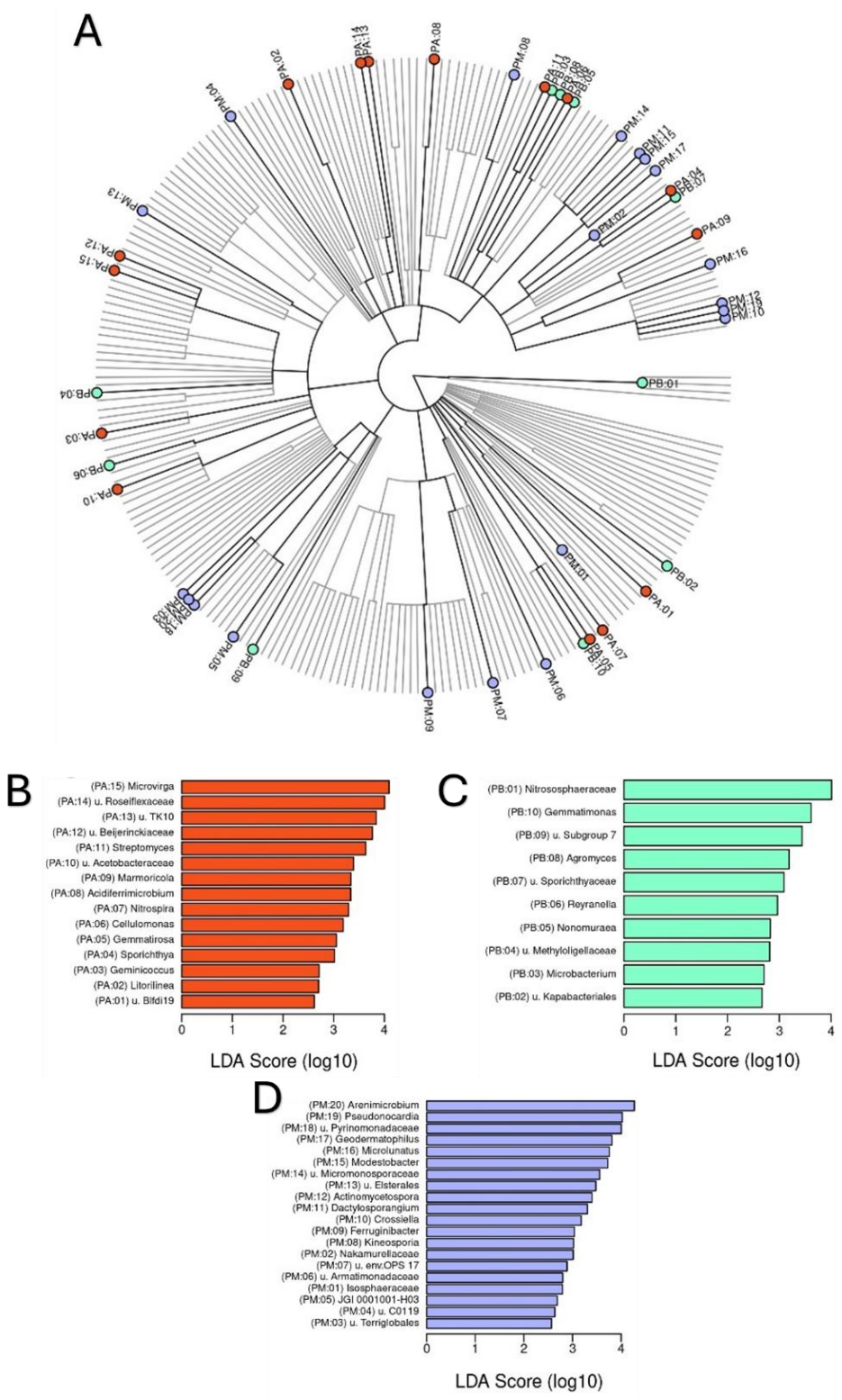

Figure 3. Microbial community responses across the three study zones located along the green wall gradient: PA (adjacent to large and old green walls), PB (adjacent to small green walls), and PM (center of the agave field). A) Cladogram showing differentially abundant taxa identified by LEfSe; B–D) LDA scores highlighting taxonomic biomarkers for each site (PA, PB, and PM).

Community modularity analysis using the Louvain algorithm identified 19 clusters, revealing a highly modular network organization. Collectively, the ASVs included in the network accounted for more than 65% of the total relative abundance across samples, indicating that the inferred interactions represent the dominant fraction of the community. The most represented modules were Cluster 5 (10.55% ± 1.98% relative abundance) and Cluster 8 (10.75% ± 4.41%) (Figure 5B). Cluster 5 comprised 11 genera distributed across four phyla, whereas Cluster 8 included 9 genera belonging to two phyla, suggesting differences in phylogenetic breadth and potential functional complementarity between modules. Furthermore, different relative abundance of each cluster was shown in different zones of study (Figure 5c), providing evidence of a structured and non-random community.

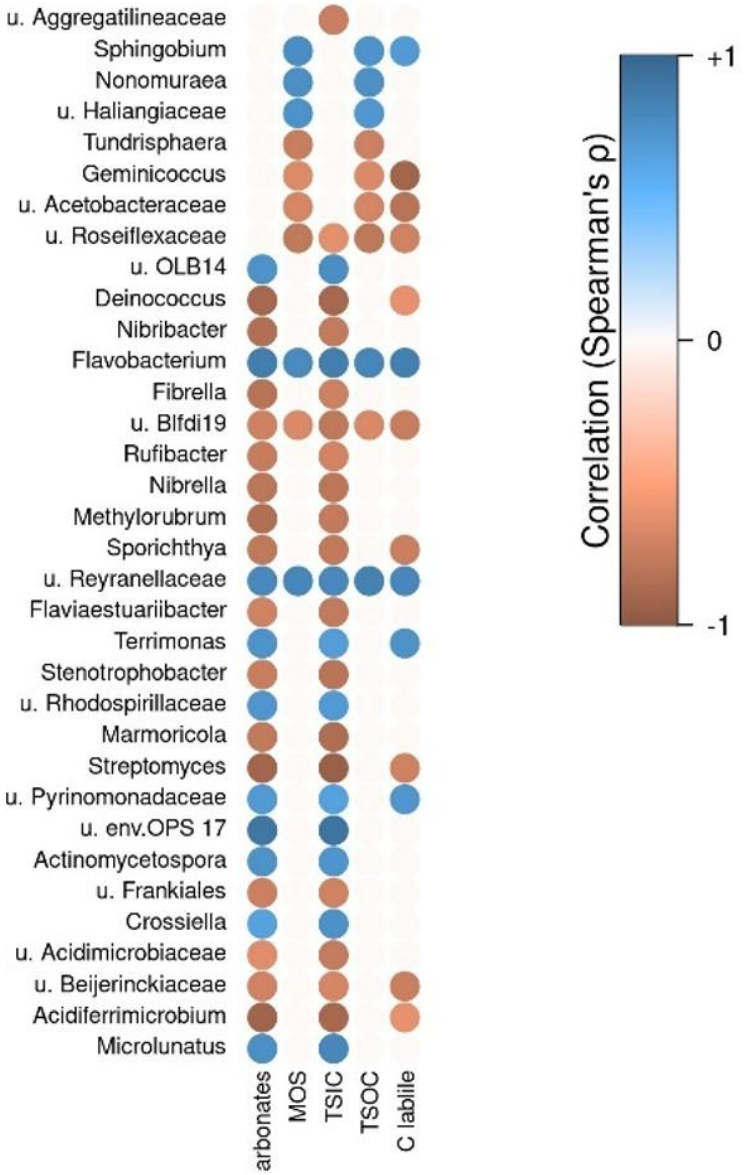

Figure 4. Correlation heatmap between discriminant genera and soil variables, including total soil organic carbon stock (TSOC), total soil inorganic carbon stock (TSIC), soil organic matter (SOM), carbonates, and labile carbon.

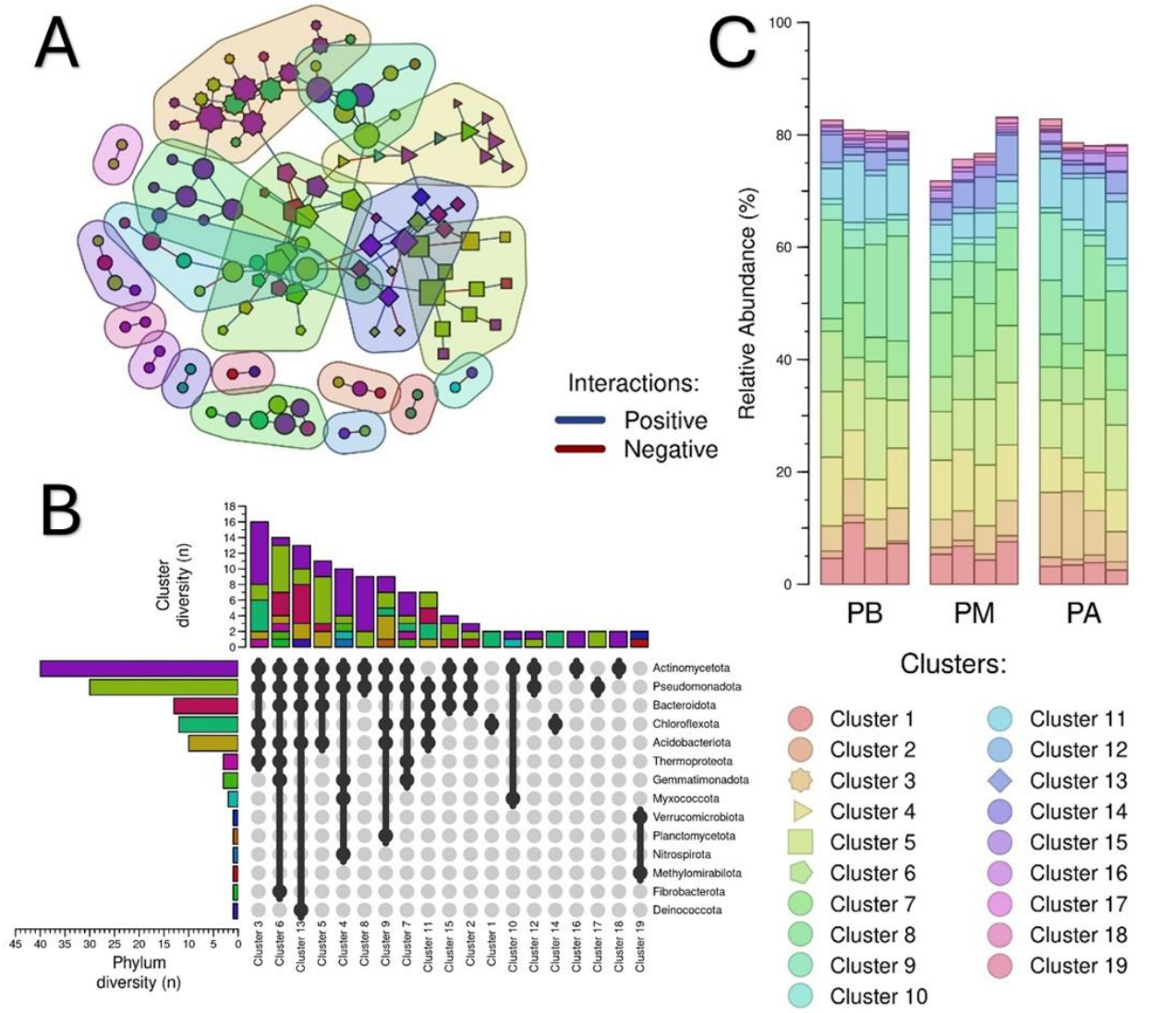

Figure 5. Microbial co-occurrence network inferred using SparCC based on genus-level abundances across the three study zones. A) Undirected weighted network showing significant correlations (r ≥ 0.75) among ASVs; edge colors indicate positive and negative associations, and node size reflects relative abundance; B) Taxonomic composition and relative contribution of the main network clusters identified using the Louvain modularity algorithm; C) Relative distribution of the main network modules (clusters) across the samples or study zones.

DISCUSSION

The higher carbon stocks observed in PA, particularly TSOC, SOM, and labile C, reflect the positive influence of mature mesquite and huizache trees on soil quality and carbon sequestration. This enhancement is likely driven by greater inputs of litter and root exudates from older trees, reduced wind erosion, and improved microclimatic conditions near well-developed green walls. Similar trends have been reported in arid ecosystems, where increased soil carbon sequestration under mesquite canopy has been documented (Ansari and Sadeghi 2021). Likewise, Hosseinzadeh *et al.* (2025) demonstrated that high-density mesquite afforestation in desert environments improves soil

quality and enhances vegetative growth and productivity, with effects becoming more pronounced as stands mature. Comparable responses have been observed in *Acacia* systems; plantations of *Acacia senegal* have been associated with significant increases in SOC, particularly in the topsoil (Abaker *et al.* 2018), closely linked to higher soil nutrient availability (N, P, and K). The progressive accumulation of SOM and SOC with plantation age has been attributed to sustained litter deposition, root turnover, and nutrient uplift from deeper soil layers. Moreover, Camelo *et al.* (2021) found an increase in TSOC level in a forage cactus and tree legumes agroforestry system, after seven years of implementation. Collectively, these findings underscore the key role of tree-based systems in promoting carbon sequestration and restoring soil fertility in degraded semi-arid landscapes (Pan *et al.* 2025).

In soil bacterial communities' analysis, the β-diversity index indicates that bacterial assemblages differ significantly among zones, where environmental filtering driven by soil carbon status and green wall influence was evident. Bacteriome of PA was compositionally distinct from PM, with PB occupying an intermediate position, which indicates that green wall proximity not only affects microbial abundance but reshapes community composition, demonstrating that agroforestry systems shape microbial communities through labile carbon content. Thus, the proximity to mature green walls is a key driver of bacterial community turnover in this arid agroforestry system, as well as tree maturity.

Furthermore, the shift in bacterial composition along the PA > PB > PM gradient reflects a transition in ecological strategies, likely driven by the quality and availability of carbon pools. These findings are consistent with recent agroforestry research demonstrating that soil organic carbon fractions, particularly labile SOC, play a dominant role in governing bacterial community assembly and functional potential (Wang *et al.* 2026). Moreover, previous work has shown that transitions toward tree-based systems can increase stochasticity and network complexity in microbial communities (Li *et al.* 2023, Shi *et al.* 2025, Wang *et al.* 2026). In PA, the higher concentration of labile C suggests an environment that favors copiotrophic or *r-strategist* microorganisms, such as *Marmoricola* and *Acidiferrimicrobium* (Araujo *et al.* 2023, Yang *et al.* 2023). These taxa are characterized by rapid growth and high metabolic activity in nutrient-rich conditions, facilitating accelerated organic matter turnover. Conversely, the dominance of *Geodermatophilus* and *Arenimicrobium* in the PM zone (center of the crop field) indicates a shift toward oligotrophic or *K-strategists* (Wüst *et al.* 2016, Castro *et al.* 2018, Karray *et al.* 2020). These taxa are specialized in resource scarcity and environmental stress (e.g., high carbonates and low SOC), employing high-affinity transport systems and slow growth rates to persist in degraded semi-arid soils. This ecological filtering demonstrates that green walls do not just increase biomass, but redefine the metabolic lifestyle of the soil microbiome. Collectively, these results indicate that mature green wall systems function similarly to agroforestry configurations by increasing labile SOC, which in turn drives microbial community reassembly and potentially enhances soil functional capacity in semi-arid agave systems, potentially enhances soil functional capacity in semi-arid agave agroecosystems, providing a biological foundation for sustainable productivity under increasing environmental stress.

Finally, the presence of well-defined modules and numerous strong correlations indicates a non-random and structured microbial network. The dominance of Actinomycetota and

Pseudomonadota, together with the substantial contribution of a few key clusters, suggests the existence of core interaction hubs that may contribute to community stability and carbon processing in these arid soils. These patterns are consistent with the observed gradients in soil carbon pools, supporting the idea that improved organic matter conditions near green walls promote more complex and potentially resilient microbial interaction networks (Feng *et al.* 2025).

CONCLUSIONS

Our findings demonstrate that mesquite and huizache green walls function as a primary driver of functional restoration in agave agroecosystems by significantly enhancing soil organic carbon pools, particularly TSOC and labile fractions. This resource enrichment does not merely increase microbial abundance but fundamentally reshapes soil microbial ecology, shifting from stress-constrained oligotrophic communities toward more complex, structured, and potentially resilient bacterial networks. The intensification of these effects with tree age underscores that soil functional recovery is a cumulative, time-dependent process. Overall, this study highlights the strategic potential of mature tree-based barriers as an effective nature-based solution to mitigate soil degradation and enhance the long-term sustainability and resilience of semiarid agave production systems.

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COMPETING INTERESTS

The authors declare that they have no competing interests.

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