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Ureolytic biostimulation in aridisols - from microbiomes to MICP

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ABSTRACT

In arid regions, biocrusts create a 'living skin' that mediates most inputs, transfers, and losses across the soil surface. Landscape degradation due to anthropogenic overexploitation may adversely affect biodiversity, essential ecosystem services, and human well-being. MICP is considered an environmentally conscious ground improvement method, but the actual impacts of MICP on the microbial ecosystem are not widely addressed. Here, we present a study focusing on ureolytic biostimulation in aridisol of the Negev Desert (Israel). Our main goals were to characterize the native microbial community in the top 1 meter of soil, to establish the efficiency of biostimulation using native microbiomes, and to study the post-treatment microbial diversity. Ureolytic biostimulation induces a consistent shift in the composition of the microbial communities, leading to the enrichment of specific heterotrophs (*Firmicutes*) while suppressing autotrophs and other ecologically important groups. We found that in sites of low disturbance levels, soil depth outweighed horizontal heterogeneity in relation to the magnitude of influence on the microbial community and the ureolytic response. In contrast, in a high disturbance site, the ureolytic response was delayed at the soil surface and stronger in the deeper layers. Although most of the *Firmicutes* in our study sites were originally concentrated deeper in the soil, and their abundances and total microbial abundance increased similarly across the different depths following biostimulation, urea degradation rates were higher at the soil surface and decreased with depth. We propose that mass cell-mortality (*necromass*) at the surface might be an important factor that regulates the rate of ureolysis.

INTRODUCTION

Drylands encompass nearly half of the earth's terrestrial surface providing key ecosystem services to a third of the global human population (Lewin et al. 2024). Wind-induced soil erosion is one of the main adverse factors contributing to dryland desertification. It reduces biological diversity, causes loss of cultivated land, and environmental deterioration (Duniway et al. 2019). Landscape degradation due to anthropogenic overexploitation may entangle adverse implications for biodiversity, essential ecosystem services, and human well-being (Delgado-Baquerizo et al. 2014; Maestre et al. 2013; Rodriguez-Caballero et al. 2022). In arid regions, where plant cover is sparse,

biocrusts create a 'living skin' that mediates most inputs, transfers, and losses across the soil surface and stabilizes the soil (Weber et al. 2022).

Microbial-induced calcite Precipitation (MICP) is a biomineralization process intensively studied as a ground improvement for various environmental and engineering applications (DeJong et al. 2022). Recent studies have established the feasibility of applying MICP in aridisols by stimulating indigenous microorganisms (e.g., Gomez et al. 2018; Raveh-Amit et al. 2024). The treatment resulted in considerable reinforcement of the soil surface by decreasing desiccation cracking. Vertical heterogeneity may result in varying effectiveness of MICP since soil depth is one of the important drivers of microbial abundance and community structure (Fierer et al. 2003). Bacterial abundance tends to decrease with increasing depth (Fierer et al. 2003), while archaea become more abundant in deeper soil horizons (Sokol et al. 2022).

While MICP is considered an environment-friendly alternative to conventional ground improvement methods (e.g., grouting materials), the actual impacts of MICP implementation on the ecosystem and biodiversity are not widely addressed. MICP studies often under-characterize the microbial community on which the experimental system is based, which leads to missing crucial information required for successful implementation (Graddy et al. 2021). Studies that did address the environmental consequences of MICP application reported tangible alterations in the composition of the native microbial communities, releases of substantial amounts of ammonium, and changes in the pH of the treated medium (Gat et al. 2016; Gomez et al. 2017; Graddy et al. 2021; Ohan et al. 2020). Considering their roles in essential processes, such drastic alterations of the edaphic microbial diversity may negatively affect the ecosystem functions and services (Bahram et al. 2018). Nevertheless, the application of MICP is rapidly expanding to field-scale applications without considering the complexity of natural microbiomes or environmental effects. Here, we present a study focusing on ureolytic biostimulation in aridisol from the Negev Desert (Israel), where knowledge regarding the microbiology of MICP is particularly lacking. Our main goals were to characterize the native microbial community in depths that are relevant to the reinforcement of the top 1 meter of soil, to establish the efficiency of biostimulation using native microbiomes, and to study the post-treatment microbial diversity. We investigated possible relationships between the observed patterns in ureolysis and microbial diversity and suggested potential mechanisms that underlie these relationships

METHODS

Soils from three sites in the Rotem Plateau (31.03◦N/35.09◦E), Negev Desert, Israel, were sampled. The region is arid, with an average annual rainfall of 70 mm. The sampling sites were located 3.5 to 4.5 km apart. A "non-disturbed" site that was located offroad, with limited access; a "low disturbance site" near the road, subjected to mild disturbances (mostly trampling); and a "high disturbance" site, in which the soil was subjected to mining about 20 years before this study. Within each site, soil was sampled from three depths: surface (topsoil), 50 cm below the surface, and 100 cm below the surface. These depths were sampled in duplicates within each site, with approximately 10 m separating between replicates (n = 6 for each sampling depth). Samples were stored refrigerated at 4◦C until the biostimulation experiments began. Mineralogical phase identification and particle size distribution are reported by Raveh-Amit and Tsesarsky (2020).

Biostimulation was performed by incubating 10.0 g of each soil sample in 100 mL of a stimulation medium containing 20 g/L (330 mM) urea and 1 g/L of yeast extract (YE) at ambient temperature with gentle shaking at 100 rpm for 10 days. The medium solution was filter-sterilized

by 0.22 μm Millex® syringe filters before adding YE. The stimulation medium was periodically sampled, and their pH and urea concentration (Knorst colorimetric method) were measured.

DNA from soil sampled from known depths in the non-disturbed and low-disturbance sites. DNA samples were extracted in triplicates at the end of the biostimulation experiment using the Powersoil Pro kit (Qiagen, Germany). DNA extracts were eluted in Tris-EDTA buffer (pH 8.0). Upon extraction, DNA samples were stored refrigerated. DNA concentrations were quantified by a NanoDrop 2000 (Thermo Scientific, MA) spectrophotometer. Library preparation and 16S amplicon sequencing were performed by Qiagen Genomic Services. Amplicons were sequenced on an Illumina MiSeq platform using reagent kits v3 with a minimum read depth of 50.000 reads per region. Operational Taxonomic Unit (OTU) assignment and clustering were carried out on the CLC Microbial Genomics module on the CLC Genomics Work Bench.

OTU and statistical analyses were performed on the v4v5 region using using RStudio (v2023.03.0) and Primer-E v7. The total abundance of each bacterial and archaeal taxon was calculated based on its relative abundance in the sample and DNA quantity according to the qPCR results. We used ANOVA and pairwise tests to compare the amount of DNA extracted from the different depths and the biostimulated and non-treated soils and to compare OTU diversity of the prokaryotic communities, beta diversity, and abundances of specific taxa. The data was log-transformed when the assumption of equal variances was not met. We conducted repeated-measures ANOVA to examine the changes in the pH and urea concentration of the soil samples during the experiment. Data was log-transformed to produce a heatmap representing the relative change in the main phyla found in the soil samples. We used Principal Component Analysis (PCA) to illustrate the distances between the communities of the compared soil samples. An Analysis of Similarities (ANOSIM) test was performed to determine the significance of differences between the composition of compared communities based on Bray-Curtis dissimilarities.

RESULTS

We present the following parameters: i) ureolytic activity rates in biostimulated soils; ii) the effect of biostimulation on total prokaryotic abundance and diversity; and iii) the taxonomical composition of the native microbial communities and how it is affected by biostimulation.
Ureolytic activity was successfully induced by the biostimulation treatment in soils from different depths (Fig. 1). The measured urea concentration significantly decreased during the days following the treatment. The ureolysis rate differed between soils from different depths with a site-related variation. At the soil surface, urea was completely depleted within approximately 5 days after treatment in the non-disturbed and low-disturbance sites. In the deeper soils, hydrolysis rates were milder than in the topsoil, and complete urea depletion was not achieved even after 18 days following the treatment (Fig. 1a, b).

At the high disturbance site, the ureolytic response was delayed in comparison to the other sites, with complete urea depletion at the soil surface a week from the beginning of the experiment (Fig. 1c). Moreover, higher hydrolysis rates were recorded at the deeper soils at this site (46.64±10.39 mM urea measured after 18 days) in comparison to the non-disturbed and low disturbance sites (94.97±28.56 mM urea measured after 18 days). Lower hydrolysis rates at the surface, combined with higher rates at the deeper layers, might indicate that decades after the harsh disturbance, the amalgamation of soil layers is still reflected in the microbial community of the high-disturbance site. The functionally crucial surface community apparently has yet to be recovered. Indeed, biocrusts are known to be highly sensitive to disturbances and are characterized

by notoriously slow recovery rates (Belnap and Eldridge 2003). Although the ability to distinguish the effect of disturbance level from other influential factors is limited in environmental studies, our results provide evidence for functional consequences of mechanical disturbance to the soil microbiome.

The pH of the treated soils drastically increased during the experiment in accordance with urea hydrolysis (Fig. 1d-f), elevating from 7.9±0.1 to 8.9±0.3 after 48 hours and then stabilizing on pH 9.5±0.1 until experiment termination. Such changes in the chemical properties of MICP-treated soil pore fluids, even for a limited period of time, may have considerable environmental consequences. Specifically, soil pH is one of the most important factors shaping microbial communities (Fierer et al. 2003; Ratzke and Gore 2018).

Microbial DNA was extracted from the undisturbed and low-disturbance soils, and 16S amplicon sequencing was performed to assess the treatment's effect on prokaryotic abundance and diversity. The analysis yielded 877,848 reads, assigned to 8702 OTUs, belonging to 27 bacterial phyla and two archaeal phyla. Before the biostimulation, most of the DNA was recovered from the surface soil, decreasing, as expected, with depth. Following biostimulation, DNA concentrations sharply increased in all soils, from 10.54 ± 7.31 to 32.34 ± 14.24 ng DNA/g soil to a similar extent (one way ANOVA: $F_{2,8} = 1.77$, $P = 0.25$), despite the low initial abundance in some of the samples.

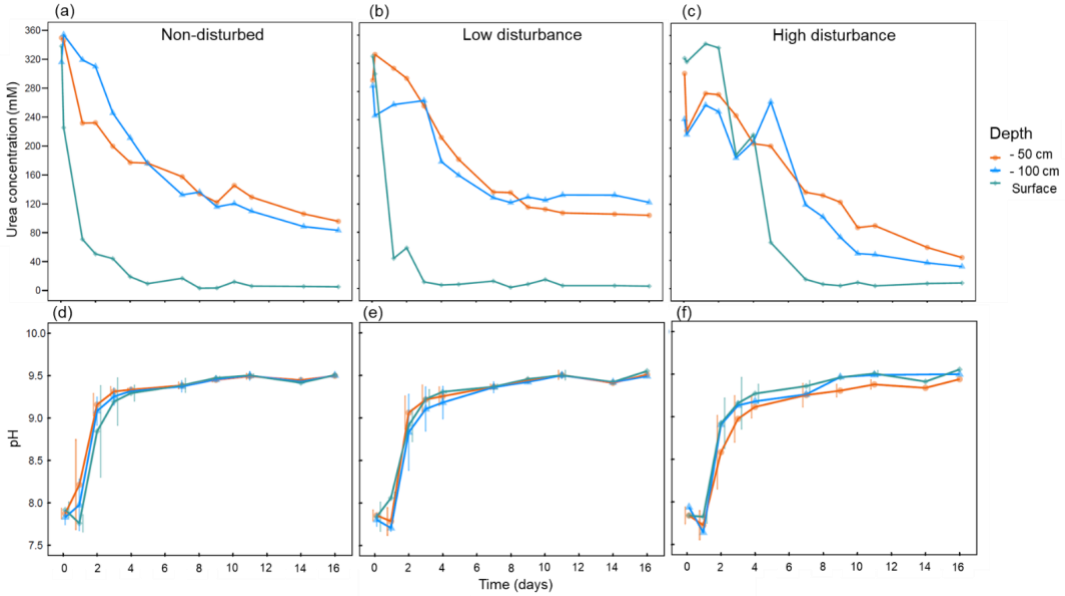


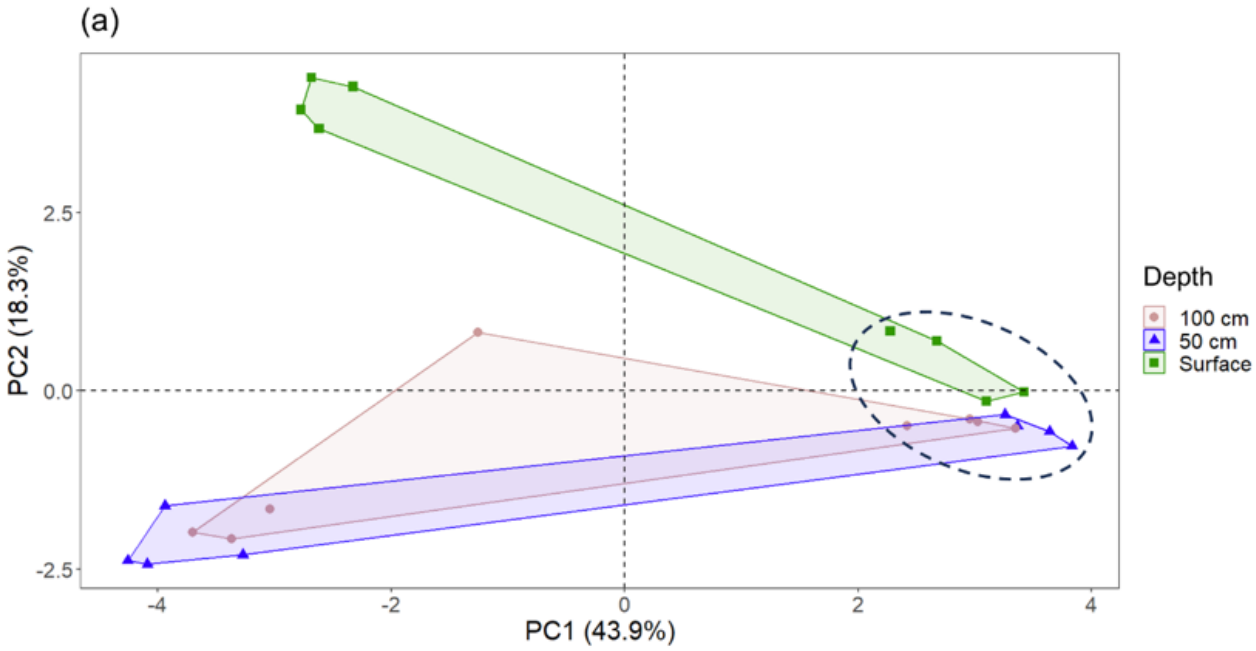
Figure 1. Ureolytic activity profiles and pH changes in three soil layers at sites with varying levels of mechanical disturbance: (a, d) a non-disturbed site, (b, e) a low disturbance site and (c, f) a high disturbance site.

The native soil was populated by distinct communities at different depths, dominated by the rigid-walled, mostly chemoorganotrophic *Actinobacteria* (50 ± 11% of total reads). Most of the bacterial phyla were detected at the surface, with higher abundances of *Proteobacteria*, *Cyanobacteria*, *Bacteroidetes*, and *Chloroflexi* in comparison to the deeper layers, while containing a small amount of *Firmicutes* (Fig. 2b). The communities of the deeper soils were richer in *Firmicutes* than the topsoil. Following biostimulation, loss of biodiversity was mainly derived from a drastic increase in the abundance of the endospore-forming *Firmicutes* at the expense of many other taxa (Fig. 3b). Biostimulation homogenized the communities, which no longer differed between depths (and were

all dominated solely by this phylum (80± 21 % of all reads in treated soils in comparison to 11 ± 10 % in untreated soils).

The proliferation of *Firmicutes* following ureolytic stimulation has been reported in several previous studies on MICP (Gat et al. 2016; Graddy et al. 2021; Ohan et al. 2020) and agricultural-related nitrogen amendments (Kaminsky et al. 2021) This might be attributed to their physiological abilities to cope with the applied selection pressure (i.e., urea addition and the rapid increase in pH following ureolysis) and even utilize the new niche, with reduced competition, to flourish. Our results support the findings of (Graddy et al. 2021), showing a clear convergence of bacterial communities in biostimulation and augmentation experiments. MICP in both forms has a deterministic and consistent effect on the microbial communities, regardless of preexisting structural differences. This further emphasizes the robustness of MICP, as substantial and rapid urea hydrolysis can be obtained using distinct microbiomes from different soil depths.

Firmicutes overtake following biostimulation has been demonstrated before. However, the fate of other populations remains largely unaddressed. Our results show that many of the native residents almost or entirely disappeared following the treatment, leaving only 13 of the 29 phyla that were originally detected. Ureolythic biostimulation dramatically decreased the abundance of autotrophs (e.g., *Cyanobacteria*, *Chloroflexi*), which are extremely important to the formation and function of biocrusts (Maier et al. 2018). Even though some of the disappearing taxa belong to the rare biosphere, this could result in the loss of functionally important groups. For example, *Thaumarchaeota*, an archaea phylum contributing to ammonia-oxidation (Marusenko et al. 2014) that was found in the native soils, was indeed not detected again in treated soil (Fig. 2b).



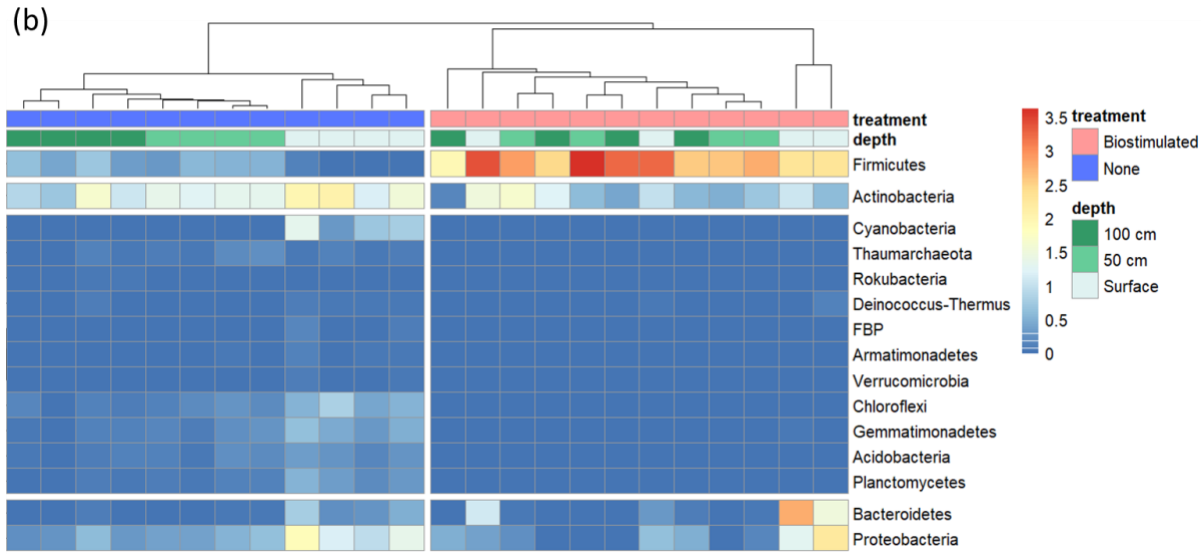


Figure 2. (a) PCA based on OTU abundance at the different soil samples. The biostimulated soils are circled by a dashed black line. (b) A heatmap of the relative changes in the abundances of main prokaryotic phyla (log-transformed) between the studied soil samples (columns). The phylogenetic tree represents the similarity between the composition of sample communities based on Euclidean distances.

Biostimulation also alters the within-phylum composition (Fig. 3). Before treating the soils, some differences were noted in the order composition of *Actinobacteria* between depths (Fig. 3a). Following the treatment, the majority (98.2 ± 4.0%) of *Actinobacteria*, found in all samples, belonged to the order *Micrococcales*, which composed only up to 42.2 % of Actinobacterial orders in non-treated samples. The Firmicutes maintained a larger proportion of their original diversity following the treatment (Fig. 3b). In the untreated soils, the main *Firmicute* families were *Paenibacillaceae* and *Bacillaceae*, the treated soils were dominated by *Planococcaceae*, and specifically by the genus *Sporosarcina*, which increased from 2.5 ± 3.5% of the reads in native soils in comparison to 44.5 ± 24.4 % in treated ones. A single OTU, annotated as *Sporosarcina sp*., was attributed with 17.6% of the variance between the composition of treated and non-treated communities (SIMPER analysis). Other bacteria that seem to have survived the treatment are some *Bacteroidetes* at the soil surface (Fig. 3b), and particularly the strictly aerobic, chemoorganotrophic genus *Pontibacter*, which possesses the ability to hydrolyze DNA (Nedashkovskaya and Kim 2015). The strong selective pressure that is induced by the treatment seems to grant opportunistic heterotrophs an advantage over nitrogen-fixing autotrophs and others. The bacteria that survive the treatment and succeed in coexisting alongside the *Firmicutes* may actively contribute to the ureolytic response. For example, *Micrococcaceae*, the main *Actinobacteria* that were found in treated soils, is known as ureolytic (Varaldo and Satta 1978).

DISCUSSION

Our findings support the notion that environmental heterogeneity is an influential variable that should be considered in MICP experiments and applications. In sites under low disturbance levels, soil depth outweighed horizontal heterogeneity in relation to the magnitude of influence on the microbial community, and hence on the ureolytic response. In contrast, when the disturbance level was high, we found it had a more prominent influence on the ureolytic response, which was

delayed at the soil surface and stronger in the deeper layers compared to the other sites. Hence, environmental variability affects the efficiency of MICP. Regardless of preexisting differences between the communities, the application of biostimulation had a detrimental impact on the native microbiome.

The consistent proliferation of *Firmicutes* in MICP studies reasonably leads to the assumption that *Firmicutes*, and particularly highly ureolytic species such as *S. pasteurii*, are the engine behind the ureolytic response. Our results support this notion, yet interestingly indicate that the process involves greater complexity. Although most of the *Firmicutes* and *Sporosarcina* members in our study sites were originally concentrated in the deeper layers of soil (as they are facultative anaerobes) and although their abundances and total microbial abundance increased similarly across the different depths following biostimulation (Fig. 2a-c), the ureolytic response was not uniform. Urea degradation rates were higher at the soil surface and decreased in deeper soils (Fig. 1a-c). The stronger response at the surface was documented despite being measured at identical laboratory conditions of light, temperature, available oxygen, etc. Furthermore, our results suggest that a large proportion of the microbial community does not survive the treatment (Fig. 2a). Therefore, massive cell mortality might be an important factor that regulates the rate of ureolysis. This dead biomass (necromass) may turn to an additional carbon source (Sokol et al. 2022), which fuels the more rapid response at the surface. This hypothesis might also explain the between-site variation in ureolytic response. The distinct response profile of the high disturbance site (Fig. 1c) compared to the other sites (Fig. 1a, b) might originate from a severe die-off that contributed microbial necromass to the organic matter pool of the soil. The dependence of the necromass hypothesis on oxygen availability in the soil should be further tested.

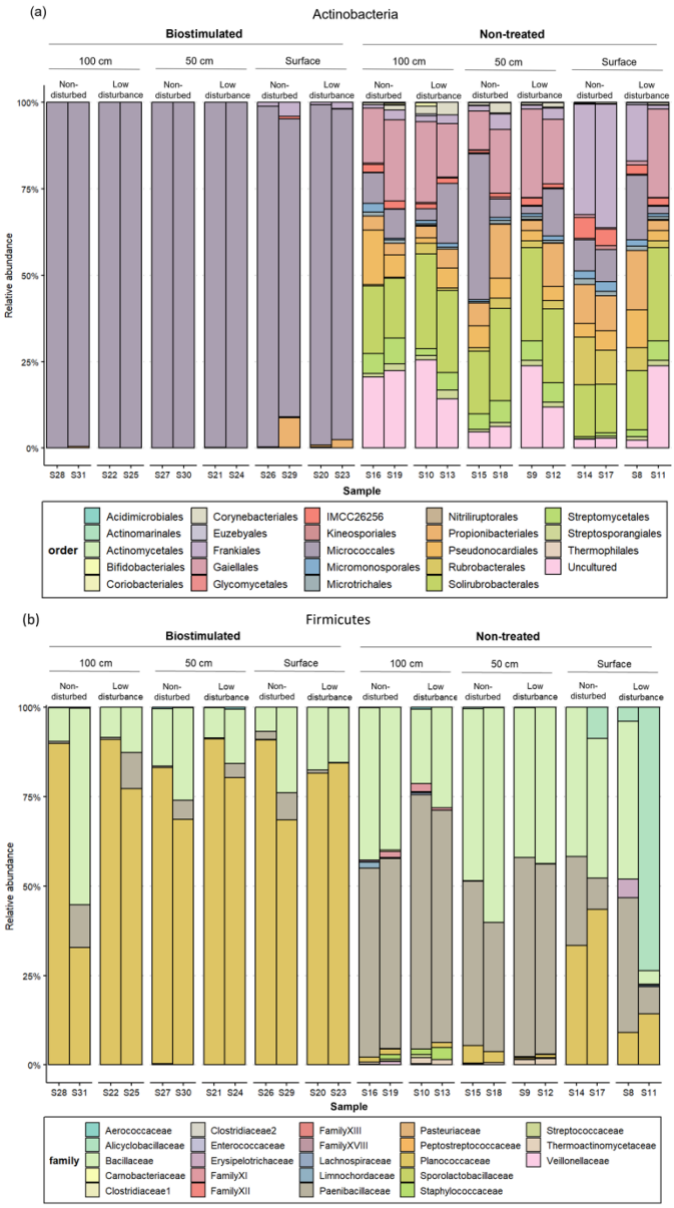


Figure 3. The family and order composition of the dominant phyla (a) Actinobacteria and (b) Firmicutes in studied soil depths, before and after ureolytic biostimulation.

Our necromass hypothesis is supported by the known necessity for a carbon source to successfully induce an effective ureolytic response (Gat et al. 2016). Further support comes from a study demonstrating a stronger ureolytic response of *S. pasteurii* when co-cultured with the non-ureolytic bacterium *Bacillus subtilis* (Gat et al. 2014). In the latter, the authors postulated that their observation might derive from elevated release levels of enzymes by *S. pasteurii* due to predation by the cannibalistic *B. subtilis* or due to more rapid nutrient depletion in the co-culture. While the mechanism behind these observations is still unknown, it appears that cell mortality might be a regulator of the ureolytic response. This might explain the survival of the DNA-hydrolyzing bacterial genus *Pontibacter* in the treated soils. In future research, monitoring changes in live and dead microbial biomass would be imperative to test the necromass hypothesis.

CONCLUSIONS

Ureolytic biostimulation for MICP can be used to stabilize the soil surface in arid environments. However, the treatment induces a consistent shift in the composition of the microbial communities, leading to the enrichment of specific taxa while suppressing autotrophs and other ecologically important groups. Considering the important functions of the upper layer of soil in arid environments and its vulnerability, our findings call for taking precautions when considering the application of MICP in arid habitats.

Our results capture a short-term time frame of the treatment's effects. Kaminsky et al. (2021) have reported similar impacts of urea amendments on microbial diversity, yet they also found some recovery trends seven weeks after the treatment. To our knowledge, the succession of the microbial community over time following MICP was not monitored in previous studies. Considering the central functions of microbiomes in biogeochemical cycles and the evidence of functional effects, this issue should be addressed in future studies.

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