https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

The role of ecosystem engineers in shaping the diversity and function of arid soil bacterial communities

Capucine Baubin[1], Arielle M. Farrell[2], Adam Šťovíček[3], Lusine Ghazaryan[1], Itamar Giladi[2], Osnat Gillor[1]

[1]Zuckerberg Institute for Water Research, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Israel
[2]The Mitrani Department of Desert Ecology, Swiss Institute for Dryland Environmental and Energy Research, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Israel
[3]Department of Microbiology, Nutrition and Dietetics, Czech University of Life Sciences Prague, Kamycka 129, Prague 6, 16500, Czech Republic

Correspondence to:

Capucine Baubin, Zuckerberg Institute for Water Research, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Israel. Tel: 972-54-2944886; e-mail: baubin@post.bgu.ac.il

Osnat Gillor, Zuckerberg Institute for Water Research, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Israel. Tel: 972-8-6596986; e-mail: gilloro@bgu.ac.il

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

ABSTRACT

Ecosystem engineers (EEs) are present in every environment and are known to strongly influence ecological processes and thus shape the distribution of species and resources. In this study, we assessed the direct and indirect effect of two EEs (perennial shrubs and ant nests), individually and combined, on the composition and function of arid soil bacterial communities. To that end, topsoil samples were collected in the Negev Desert Highlands during the dry season from four patch types: (1) barren soil; (2) under shrubs; (3) near ant nests; or (4) near ant nests situated under shrubs. The bacterial community composition and potential functionality were evaluated in the soil samples (fourteen replicates per patch type) using 16S rRNA gene amplicon sequencing, together with physico-chemical measures of the soil. We have found that the EEs differently affected the community composition. Barren patches supported a soil microbiome, dominated by *Rubrobacter* and *Proteobacteria*, while in EE patches *Deinococcus-Thermus* dominated. The presence of the EEs similarly enhanced the abundance of phototrophic, nitrogen cycle and stress- related genes. In addition, the soil characteristics were altered only when both EEs were combined. Our results suggest that arid landscapes foster unique bacterial communities selected by patches created by each EE(s), solo or in combination. Although, the communities' composition differs, they support similar potential functions that may have a role in surviving harsh arid conditions. The combined effect of the EEs on soil microbial communities is a good example of hard to predict non-additive features of arid ecosystems that, therefore, merit further research.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

1. INTRODUCTION

Hot desert environments are characterized by long droughts interspersed by intermittent and unpredictable rain events. Water and nutrients in hot desert environments are scarce and unevenly distributed across the land, resulting in patches of contrasting productivities. High-productivity patches, also called resource islands, are defined by large concentrations of organic matter and nutrients (Ben-David et al., 2011; Schlesinger et al., 1996; West, 1981). These resource islands can be formed through the redistribution of nutrients and water by ecosystem engineers (EEs), such as perennial plants or invertebrates (Wilby et al., 2001; Wright et al., 2006). EEs are also known for impacting many components of a given environment, such as soil features, annual distribution, or community composition of microorganisms (De Graaff et al., 2015; Oren et al., 2007).

An EE is an organism that, directly or indirectly, modifies the availability of resources to other organisms by transforming the physical state of abiotic and/or biotic components of the ecosystem, *sensu* Jones et al. (1994). The impacts of EEs range from physical, through the creation of biogenic structures (e.g. tunnels) (Lavelle, 2002); to chemical, through the production of compounds that have physiological effects (e.g. root exudates) (Lavelle et al., 1992); to biological, through organisms behaviour (e.g. seed dispersal) (Lavelle et al., 2006). In drylands, resources, such as nutrients or water, are often concentrated around EEs, boosting the development of diverse populations of annual plants and invertebrates (Wright and Upadhyaya, 1996), as well as microbial communities (Bachar et al., 2012; Ginzburg et al., 2008; Saul-Tcherkas and Steinberger, 2011). The community's taxonomy is linked to its' potential function (Narayan et al., 2020), responding to the physico-chemical conditions. This implies that the variation in taxonomy by the presence of an EE would be associated with changes in potential function.

In desert ecosystems, ants are a notable example of an EE (Ginzburg et al., 2008). They redistribute resources by tilling the soil, bringing soil from the deep layers to the upper layers (bioturbation), and by gathering, storing, and ejecting food items, such as plant material, or dead invertebrates, in and around the nest (Filser et al., 2016; Folgarait, 1998; MacMahon et al., 2000). EEs in arid environments

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

also include perennial shrubs (Callaway, 1995; Schlesinger and Pilmanis, 1998; Segoli et al., 2012; Shachak et al., 2008; Walker et al., 2001). Their root systems create a soil mound that traps litter, and seeds, allowing for higher water infiltration. The root exudates increase the content of organic matter and the shrub canopies decrease evaporation, prolonging water availability following a rain event (Bachar et al., 2012). In addition, the presence of shrubs alters the course of water run-off (Oren et al., 2007), which impacts the locations of available water for soil microbial communities. In addition, root systems have their own microbiome, which interact with the soil microbial community (Steven et al., 2014).

The role of both ants and perennial shrubs as EEs were reported in various ecosystems (Facelli and Temby, 2002; Farji-Brener and Werenkraut, 2017; Frouz et al., 2003; Gosselin et al., 2016; Pariente, 2002; Schlesinger et al., 1996). However, we know little about their joint effect in arid ecosystems. We hypothesized that each EE would shape a unique soil bacterial community via changes in the soil physico-chemical properties. We further predicted that since shrubs canopy and ant nests may differently affect soil properties, their combined effect on the microbial community is non-additive and thus cannot be predicted by the contribution components. To test our hypotheses, we explored arid soil bacterial microbiomes and soil chemical features during the dry season of 2015. We sampled four different patches: under *Hammada scoparia* shrubs; near the nest openings of the harvester ant, *Messor ebeninus*; in combined patches of nests under shrubs; and in barren soil.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

2. MATERIALS AND METHODS

2.1. Sampling

The study was conducted in a long-term ecological research (LTER) site in the Central Negev Desert, Israel (Zin Plateau, 34°80'E, 30°86'N). It is characterised by a 90 mm annual rainfall and average monthly temperatures fluctuating from 13°C (January) to 35°C (August). Vegetation is scarce and dominated by the perennial shrubs *Hammada scoparia* and *Atriplex halimus* (Gilad et al., 2004).

Sampling was conducted as previously described (Baubin et al., 2019) with slight modifications, such as the inclusion of Shrub&Nest samples. To summarize, we sampled four distinct patch types: (1) barren soil (Barren); (2) under the canopy of *H. scoparia* (Shrub); (3) 20-30 cm from the main opening of the nest of *M. ebeninus* (Nest); and (4) 20-30 cm from ant nest's opening that was situated under a shrub canopy (Shrub&Nest). Samples were collected in October 2015, after an eight-month drought.

We sampled 14 random experimental blocks, from each of the four patches (4 patch types x 14 blocks = 56 samples). All samples were collected from the top 5 cm of the soil after removing crust and debris, then processed within 24 hours of collection. In the lab, the soil from two adjacent blocks was composited resulting in 28 samples that were further processed. Each sample was sieve-homogenized through a 2 mm mesh. 5 g of soil were stored in -80°C for molecular analysis, 20 g were used for water content analysis and the rest was dried at 65°C and used for physico-chemical analysis.

2.2. DNA extraction, amplification, and sequencing

Total nucleic acids were extracted from 0.5 g of soil as previously described (Angel, 2012), purified with the ExgeneTM Soil SV kit (GeneAll, Seoul, S. Korea) according to the manufacturer's instructions. The 16S rRNA encoding genes V3-V4 region was amplified using 341F and 806R primer (Klindworth et al., 2013). The PCR reaction consisted of 2.5 µL 10x standard buffer, 10 µM primers, 0.8 mM dNTPs, 0.4 µL DreamTaq DNA polymerase, 4 µL template, 1 mM bovine serum albumin (Takara, Kusatsu, Japan) and 12.6 µL Milli-Q water. Triplicate PCR reactions (95°C for 30 secs; 28 cycles of 95°C for 15 secs, 50°C for 30 secs, 68°C for 30 secs; 68°C for 5 min) were pooled and

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

amplicon concentration and purity were measured by electrophoresis, Nanodrop (ND-1000, Thermo Fisher Scientific, Waltham, MA, USA). The amplicon libraries were constructed and sequenced on the Illumina MiSeq platform (2x250 pair-end) at the Research Resources Centre at the University of Illinois.

2.3. Soil physico-chemical analysis

The physico-chemical parameters of the soil samples were assessed following the standard methods (SSSA, 1996). Water content was measured by gravimetry. Other parameters were measured as follows by the Gilat Hasade Services Laboratory (Moshav Gilat, Israel): organic matter (OM) content by dichromate oxidation; nitrate (NO_3^-) through aqueous extract; ammonium (NH_4^+) through KCl solution extract; phosphorus (P) by sodium bicarbonate extract; and pH in saturated soil extract. The soil parameters were plotted using a Principal Component Analysis (PCA) (stats package (R Core Team, 2016)) and the significance of difference between patches was evaluated using a non-parametric test: Kruskal-Wallis test and a post-hoc Dunn test (Dinno, 2017; Dunn, 1964; Kruskal and Wallis, 1952).

2.4. Community analysis

The results were analysed using QIIME2 (Bolyen et al., 2018) and Dada2 (Callahan et al., 2016), following the NeatSeq-Flow pipeline (Sklarz et al., 2018) and Amplicon Sequence Variants (ASVs) were created. The taxonomic assignment was done using Silva (version 132) (Quast et al., 2013), through QIIME2 and the statistical analysis was done using R (R Core Team, 2016). A NMDS plot was created using the Bray-Curtis dissimilarity and the significance of differences between patch types was analysed using ANOSIM (vegan package (Oksanen et al., 2014)). The taxonomy was plotted using a stacked bar plot and the significance of difference between patch types was assessed using a non-parametric test: Kruskal-Wallis test and a post-hoc Dunn test (Dinno, 2017; Dunn, 1964; Kruskal and Wallis, 1952). All sequences retrieved in this study were uploaded to BioProject (https://www.ncbi.nlm.nih.gov/bioproject) under the submission number PRJNA484096.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

2.5. Functional Prediction

The prediction of function of the 16S amplicons was done with Piphillin using the KEGG database (October 2018). Piphillin generates a genome abundance table that is normalized to the 16S rRNA copy number for each genome (Iwai et al., 2016; Narayan et al., 2020). To analyse the arid soil microbial functionality, we selected metabolisms and respective genes related to arid soil using groups and genes from the KEGG database (Kaneshisa and Goto, 2000). We selected steps in metabolic pathways for different methods of harvesting energy (organotrophy, lithotrophy and phototrophy) (Cordero et al., 2019; Greening et al., 2016; León-Sobrino et al., 2019; Tveit et al., 2019), for parts of the nitrogen cycle (Madigan et al., 2009), and for the survival of the individual during a drought (DNA conservation and repair, sporulation and Reactive Oxygen Species (ROS)-damage prevention) (Borisov et al., 2013; Hansen et al., 2007; Henrikus et al., 2018; Preiss, 1984; Preiss and Sivak, 1999; Rajeev et al., 2013; Repar et al., 2012; Slade and Radman, 2011). Then, we looked for each step in the KEGG database and picked out genes of interest to build our own database. The assignment of function to the KEGG numbers was done in R. The significance of the differences between patch types in predicted functionalities was evaluated using a non-parametric test: Kruskal-Wallis test and a post-hoc Dunn test (Dinno, 2017; Dunn, 1964; Kruskal and Wallis, 1952) and boxplots were created in R.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

3. RESULTS

3.1. Soil physico-chemical characteristics

The PCA (Figure 1) depict differences in the soil characteristics (listed in Table A1) between the Shrub&Nest and the other patches (barren, nest, and shrub). Therefore, we will present the average of these other patches compared to the Shrub&Nest average. The variance of the data is explained to 99.6% by the two first principal components. The difference between patches is driven by the high concentrations of NO_3 (4.7 mg/kg compared to 30 mg/kg, respectively) and P (22 mg/kg compared to 54 mg/kg, respectively). When verifying with a Kruskal-Wallis test and a Dunn test on the values of these soil variables (Table A2), we see that the differences between patch types are significant (Shrub&Nest vs all other patches, $p < 0.05$). Patches with two EE also have a significantly higher concentration of NH_4 (9.72 mg/kg) and OM (8.21%) compared to all other patches (NH_4 mean: 5.62 mg/kg, p-value <0.05; OM mean: 5.51%, $p \leq 0.05$). However, the water content and pH did not show significant differences between patches (Table A2).

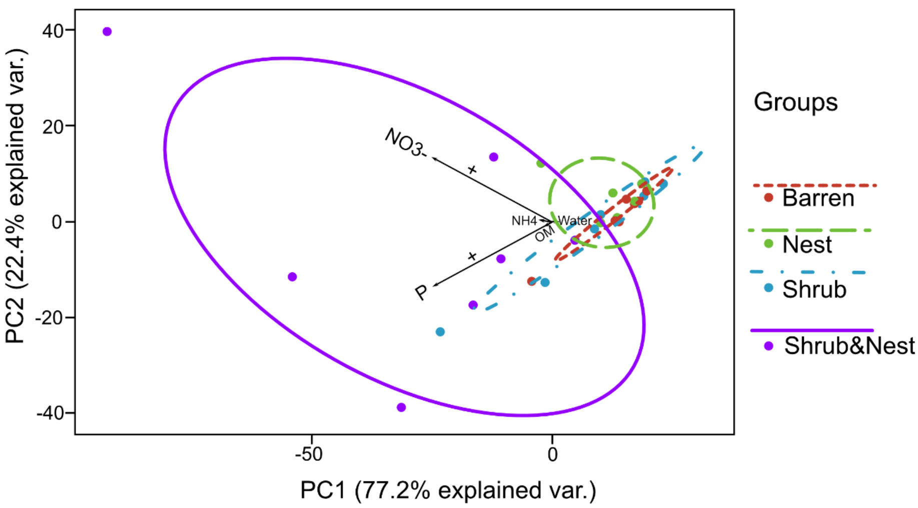

Figure 1. Principal Component Analysis of the soil parameters (NO3= Nitrate , P = Phosphorus, NH4 = Ammonium, OM = Organic Matter content, Water = Water content). The plus signs on the NO_3^- and the P vector show an increase in concentration in the Shrub&Nest patches.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

3.2. Beta diversity

The summary of the sequence analysis can be found in Table A4. DADA2 analysis yielded 2318 ASVs and the NMDS results (Figure 2) suggests that there are significant differences in the microbial community between patch types (ANOSIM, R= 0.28; p = 0.001). Most notably, the barren soil microbial communities (red circles) that were sampled in barren soil patches showed high similarities between blocks and were significantly different ($p < 0.05$, Table A3) from the communities of other patch types (high clustering of barren soil sampling points in the NMDS space). In contrast, the dissimilarities in community composition within the patch types that included shrubs (Shrub and Shrub&Nest) were high (large scatter of sampling points in the NMDS space).

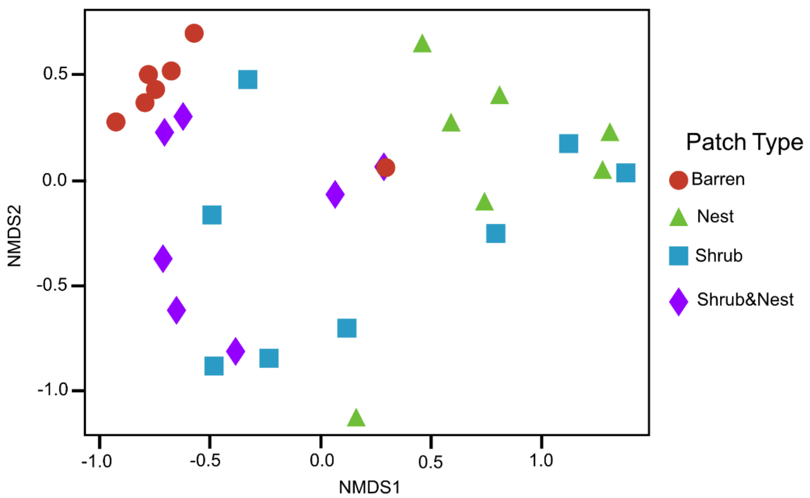

Figure 2. Non-Metric Multidimensional Scaling (NMDS) of the soil 16S microbial communities in the dry season under different patch types. The patch types are significantly different from each other (ANOSIM, R= 0.28247; p-value = 0.001)

3.3. **Community composition**

The community was mostly composed of *Actinobacteria, Proteobacteria, Deinococcus-Thermus, Bacteroidetes* and *Firmicutes* (Figure 3). The relative abundance for each phylum is detailed in Table A5. We focused on the results of the main three phyla: *Actinobacteria*, *Deinococcus-Thermus* and

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

Proteobacteria. Using pair-wise comparisons, we saw that shrub patches and nest patches had similar communities (no significant differences, p > 0.05) therefore, we considered them as single EE patches. For these patches, an average relative abundance of nest and shrub patches was used for statistical data. For the *Actinobacteria* phylum, patches with one EE had significantly lower relative abundance than barren patches (one EE: 9 % vs barren patch: 35% p < 0.005) or patches with two EEs (17%, p-value: 0.02). For the *Deinococcus-Thermus* phylum, barren patches had significantly lower relative abundance than patches with one or two EEs (Barren: 3%; vs one EE: 25%; vs two EEs: 9%, p < 0.05). A similar pattern was detected in the *Proteobacteria* phylum (Barren: 38%; vs one EE: 44%; vs two EEs: 39%, p < 0.05). All p-values can be found in Table A6.

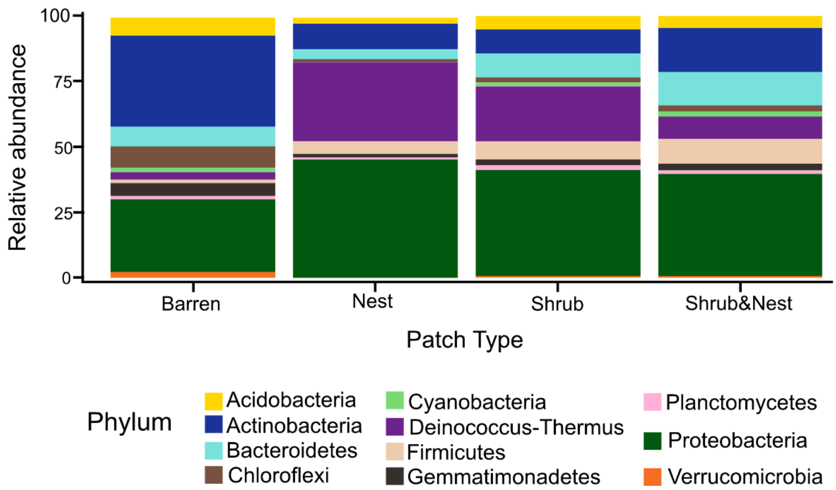

Figure 3. Barplot of the relative abundance (in %) of the most abundant phyla in the soil microbial community in the dry season under different patch types (phyla with a relative abundance > 0.05%). The relative abundance of *Deinococcus-Thermus* increases when one EE is present while the population of Actinobacteria decreases.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

3.4. Functional prediction

The abundance of each gene group has been normalized to the 16S rRNA copy number for each genome. The functional prediction results focus on eight distinct gene groups: Phototrophy, Lithotrophy, Organotrophy, DNA Conservation, DNA Repair, Nitrogen cycle, Sporulation and ROS-damage prevention (listed in Table A7). Figure 4 shows the pattern of the obtained functions. It shows higher abundances of the gene groups encoding for DNA conservation, DNA repair, nitrogen metabolism, ROS-damage prevention, sporulation, and phototrophy in patches associated with at least one EE compared to the barren patches (Table A8). Therefore, we analysed the results as barren vs average of the other three patch types that were not significantly different from one another (Table A9) and significant differences ($p < 0.04$) between barren and EE(s) patches were detected. The genes related to lithotrophy, only differed between patches with one EE and the barren patches ($p < 0.03$) but patches with two EEs were similar to the barren plots. Finally, for genes related to the organotrophy, there was no significant differences between the patches ($p > 0.05$).

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

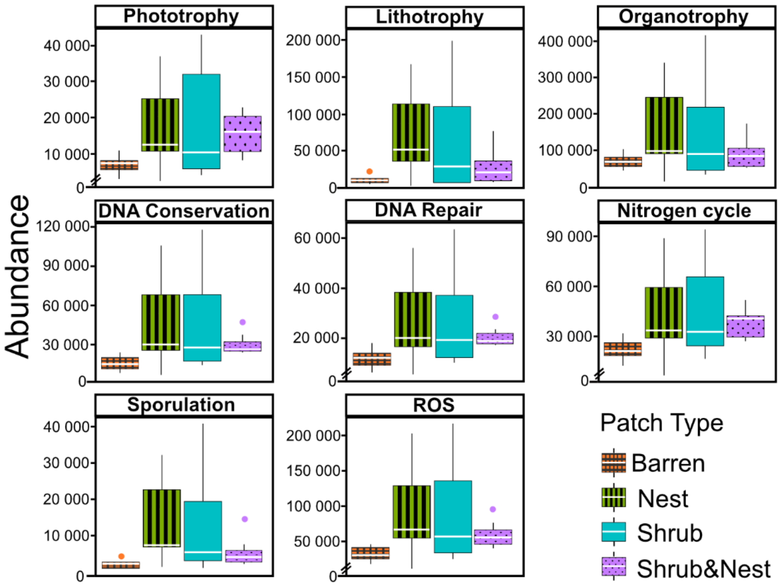

Figure 4.

Figure 4. Boxplots of the functional prediction of the 16S sequences. Each panel (Boxplot) represents a different group of genes associated with a certain functionality. The full list of genes can be found in Table A7. The patch types are represented by distinct colours and patterns. The y-axis is the abundance in copy number (CN) normalized to the 16S rRNA copy number for each genome.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

4. DISCUSSION

In desert environments, during the dry season, a large portion of the microbial community is dormant or showing reduced metabolic activity (Bay et al., 2018; Cordero et al., 2019; Lennon and Jones, 2011; Schulze-Makuch et al., 2018). However, the presence of EEs enhances the metabolic potential for metabolism-related and the survival-related functions (Figure 4). This implies that the soil microbial communities occupying EE patches are better adapted to confront stressful events (e.g., sudden rewetting or desiccation). However, these communities experience more habitable conditions due to the modulating effects of the EEs on the environmental conditions. The increase in the activity of gene groups can be explained by an increase in nutrients in the joint EEs patches (Table A1). However the physico-chemical measures, including soil water content, OM, nitrogen, P, and pH, did not match the changes observed in bacterial composition or function (Table A1, A2, A9 and Figure 1) as was previously reported (Angel et al., 2010; Bachar et al., 2012; Vonshak et al., 2018). Indeed, there was no significant link between the changes in the bacterial communities and the soil parameters (Table A10). We have previously proposed that the observed differences in communities could be mediated by microclimatic characteristics under shrub patches (Bachar et al., 2012). It has been reported that the desert dwarf shrubs affect the physical features of their immediate soil patch. Shrubs were shown to divert water flow and reduce evapotranspiration rates following rain events (Sarig and Steinberger, 1993; Segoli et al., 2008; Whitford and Duval, 2002) and reduce temperature and radiation year round (Kidron, 2009). Likewise, ants aerate the soil thus increasing infiltration during rain events (Berg and Steinberger, 2008) and mix the layers through bioturbation (Folgarait, 1998). Therefore, the prolonged water availability and altered physical conditions from the wet season may hold lasting effects on the community structure (Baubin et al., 2019), establishing the composition and functions observed here (Figure 3 and 4).

Both *Actinobacteria* and *Deinococcus-Thermus* were abundant in all patches, but their relative abundance was negatively correlated. Their two dominant genera are both well adapted to stress conditions: *Rubrobacter* dominated the barren soil, while *Deinococcus* dominated the EE patches (Figure 3 and Table A5). *Rubrobacter* are specialized in surviving strong desiccation and low nutrients

(Bull, 2011; Ferreira et al., 1999) showing high relative abundance in arid barren soils of the Negev highlands (Meier et al., 2021). *Deinococcus* are highly adapted to a wide range of extremes, such radiations, temperatures and, xerification. Some of these extreme conditions occur in the desert, while others are found in different environments, making *Deinococcus* versatile organisms (Chanal et al., 2006; Prieur, 2007; Slade and Radman, 2011). This versatility allows them to thrive in EE patches as they can better adapt to perturbations compared to *Rubrobacter*.

Only the combination of EEs resulted in significant changes (p-values: Table A2) of NO_3^-, P, and, to a lesser extent, NH_4^+, pH, and OM (values: Table A1). When located under a shrub, ants can increase their seed consumption, which enhances the amount of leftovers around the nest (Wagner, 1997), and increase the concentrations of NO_3^- and P. These macronutrients are important drivers of the biological processes, as they are often the limiting factors of microbial growth and activity in the terrestrial environments (Madigan et al., 2009). The EE patches analysed in this study share the same habitat and resources but their impacts are distinct (Passarelli et al., 2014), thus their joint impact is non-additive. The impact of an EE is defined by its lifetime, its population density, its spatial distribution, the time period of its presence on the site, the durability of its impact in the absence of other EEs, and the number, type, and magnitude of resource flows that are modified (Jones et al., 1994). The behaviour of each EE is important as it becomes a feature of the combined impact of both EEs (Alba-Lynn and Detling, 2008). However, the effect of both EEs together cannot be inferred from their individual environmental impact or from their mutual interaction (Gilad et al., 2004). Here, we investigated a sessile organism with a passive and slow impact (the perennial shrub) and compared it to a motile organism (the ants) with an active and transient impact. Ants have both a short-term impact through the seasonal accumulation of seeds and organic matter and a lasting impact due to the alternation of the nest mound which remains in the same place for decades (Wagner and Jones, 2004). Even though their impacts are clearly separated, they create favorable conditions increasing the activity of the subsoil bacterial communities (Figure 4). Indeed, they create havens of resources and water, which can be affiliated to the concept of resource islands (Schlesinger and Pilmanis, 1998). However, their individual, and combined, effects do not always lead to strong changes in the composition of the soil microbial community (Figure 3).

In our ecosystem, shrubs and ants are not the only two EEs and further studies should also consider the impact of other EEs. For example, the soil crust and the cyanobacteria living in it are recognized as an important EE in arid ecosystems (Eldridge et al., 2010; Gilad et al., 2004; Jones et al., 1994; West, 1990). Furthermore, the soil crust in our system is often disturbed by the action of the other two EEs (Li et al., 2014; Oren et al., 2007). Thus, this third type of EE is not only important for its potential impact on the microbial community composition and soil physico-chemical properties (Schulz et al., 2016), but its distribution is also dependent on those of the other two EEs. Such complicated relationships may explain some of the discrepancies presented in our study.

5. CONCLUSIONS

In conclusion, the main stress-resistant phyla (Actinobacteria and Deinococcus-Thermus) react differently to the presence of EEs. The presences of these EEs also lead to a higher potential activity in the microbial communities. However, even though they have similar impacts, when together, EEs have non-additive effects.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

ACKOWLEDGMENTS

This study was supported by the Koshland Foundation to Itamar Giladi and Osnat Gillor.

DATA AVAILABILITY

The data (raw reads) are available in Bioproject under the submission number PRJNA484096.

COMPETING INTERESTS

The authors declare that they have no conflict of interest.

AUTHORS CONTRIBUTIONS

IG, OG and AMF conceptualized and designed the methodology; AMF and AS collected the samples and metadata; LG and AMF did the laboratory work and sequencing; CB did the formal analysis, visualization, data curation and wrote the manuscript; IG, OS and CB did the reviewing and editing of the manuscript.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

REFERENCES

Alba-Lynn, C. and Detling, J. K.: Interactive disturbance effects of two disparate ecosystem engineers in North American shortgrass steppe, Oecologia, 157(2), 269–278, doi:10.1007/s00442-008-1068-0, 2008.

Angel, R.: Total Nucleic Acid Extraction from Soil, [online] Available from: http://dx.doi.org/10.1038/protex.2012.046, 2012.

Angel, R., Soares, M. I. M., Ungar, E. D. and Gillor, O.: Biogeography of soil archaea and bacteria along a steep precipitation gradient, ISME J., 4(4), 553–563, doi:10.1038/ismej.2009.136, 2010.

Bachar, A., Soares, M. I. M. and Gillor, O.: The effect of resource islands on abundance and diversity of bacteria in arid soils, Microb. Ecol., 63(3), 694–700, doi:10.1007/s00248-011-9957-x, 2012.

Baubin, C., Farrell, A. M., Šťovíček, A., Ghazaryan, L., Giladi, I. and Gillor, O.: Seasonal and spatial variability in total and active bacterial communities from desert soil, Pedobiologia (Jena)., 74(September 2018), 7–14, doi:10.1016/j.pedobi.2019.02.001, 2019.

Bay, S., Ferrari, B. and Greening, C.: Life without water: How do bacteria generate biomass in desert ecosystems?, Microbiol. Aust., 39(1), 28–32, doi:10.1071/MA18008, 2018.

Ben-David, E. A., Zaady, E., Sher, Y. and Nejidat, A.: Assessment of the spatial distribution of soil microbial communities in patchy arid and semi-arid landscapes of the Negev Desert using combined PLFA and DGGE analyses, FEMS Microbiol. Ecol., 76(3), 492–503, doi:10.1111/j.1574-6941.2011.01075.x, 2011.

Berg, N. and Steinberger, Y.: Role of perennial plants in determining the activity of the microbial community in the Negev Desert ecosystem, Soil Biol. Biochem., doi:10.1016/j.soilbio.2008.07.019, 2008.

Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C., Al-Ghalith, G. A., Alexander, H., Alm, E. J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J. E., Bittinger, K., Brejnrod, A., Brislawn, C. J., Brown, C. T., Callahan, B. J., Caraballo-Rodríguez, A. M., Chase, J., Cope, E., Da Silva, R., Dorrestein, P. C., Douglas, G. M., Durall, D. M., Duvallet, C., Edwardson, C. F., Ernst, M., Estaki, M., Fouquier, J., Gauglitz, J. M., Gibson, D. L., Gonzalez, A., Gorlick, K., Guo, J., Hillmann, B., Holmes, S., Holste, H., Huttenhower, C., Huttley, G., Janssen, S., Jarmusch, A. K., Jiang, L., Kaehler, B., Kang, K. Bin, Keefe, C. R., Keim, P., Kelley, S. T., Knights, D., Koester, I., Kosciolek, T., Kreps, J., Langille, M. G. I., Lee, J., Ley, R., Liu, Y.-X., Loftfield, E., Lozupone, C., Maher, M., Marotz, C., Martin, B. D., McDonald, D., McIver, L. J., Melnik, A. V, Metcalf, J. L., Morgan, S. C., Morton, J., Naimey, A. T., Navas-Molina, J. A., Nothias, L. F., Orchanian, S. B., Pearson, T., Peoples, S. L., Petras, D., Preuss, M. L., Pruesse, E., Rasmussen, L. B., Rivers, A., Robeson Michael S, I. I., Rosenthal, P., Segata, N., Shaffer, M., Shiffer, A., Sinha, R., Song, S. J., Spear, J. R., Swafford, A. D., Thompson, L. R., Torres, P. J., Trinh, P., Tripathi, A., Turnbaugh, P. J., Ul-Hasan, S., van der Hooft, J. J. J., Vargas, F., Vázquez-Baeza, Y., Vogtmann, E., von Hippel, M., Walters, W., Wan, Y., et al.: QIIME 2: Reproducible, interactive, scalable, and extensible microbiome data science, PeerJ Prepr., 6, e27295v2, doi:10.7287/peerj.preprints.27295v2, 2018.

Borisov, V. B., Forte, E., Davletshin, A., Mastronicola, D., Sarti, P. and Giuffrè, A.: Cytochrome bd oxidase from Escherichia coli displays high catalase activity: An additional defense against oxidative stress, FEBS Lett., 587(14), 2214–2218, doi:10.1016/j.febslet.2013.05.047, 2013.

Bull, A. T.: Actinobacteria of the Extremobiosphere, in Extremophiles Handbook, edited by K. Horikoshi, pp. 1203–1240, Springer Japan, Tokyo., 2011.

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A. and Holmes, S. P.: DADA2: High-resolution sample inference from Illumina amplicon data, Nat. Methods, 13(7), 581–583, doi:10.1038/nmeth.3869, 2016.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

SOIL Discussions Open Access EGU

Callaway, R. M.: Positive interactions among plants, Bot. Rev., 61(4), 306–349, 1995.

Chanal, A., Chapon, V., Benzerara, K., Barakat, M., Christen, R., Achouak, W., Barras, F. and Heulin, T.: The desert of Tataouine: An extreme environment that hosts a wide diversity of microorganisms and radiotolerant bacteria, Environ. Microbiol., 8(3), 514–525, doi:10.1111/j.1462-2920.2005.00921.x, 2006.

Cordero, P. R. F., Bayly, K., Man Leung, P., Huang, C., Islam, Z. F., Schittenhelm, R. B., King, G. M. and Greening, C.: Atmospheric carbon monoxide oxidation is a widespread mechanism supporting microbial survival, ISME J., 13(11), 2868–2881, doi:10.1038/s41396-019-0479-8, 2019.

Dinno, A.: Package ‘dunn.test,’ CRAN Repos., 1–7 [online] Available from: https://cran.r-project.org/web/packages/dunn.test/dunn.test.pdf, 2017.

Dunn, O. J.: Multiple Comparisons Using Rank Sums, Technometrics, 6(3), 241–252, 1964.

Eldridge, D. J., Bowker, M. A., Maestre, F. T., Alonso, P., Mau, R. L., Papadopoulos, J. and Escudero, A.: Interactive effects of three ecosystem engineers on infiltration in a semi-arid Mediterranean grassland, Ecosystems, 13(4), 499–510, doi:10.1007/s10021-010-9335-4, 2010.

Facelli, J. M. and Temby, A. M.: Multiple effects of shrubs on annual plant communities in arid lands of South Australia, Austral Ecol., 27(4), 422–432, doi:10.1046/j.1442-9993.2002.01196.x, 2002.

Farji-Brener, A. G. and Werenkraut, V.: The effects of ant nests on soil fertility and plant performance: a meta-analysis, J. Anim. Ecol., 86(4), 866–877, doi:10.1111/1365-2656.12672, 2017.

Ferreira, A. C., Nobre, M. F., Moore, E., Rainey, F. A., Battista, J. R. and Da Costa, M. S.: Characterization and radiation resistance of new isolates of Rubrobacter radiotolerans and Rubrobacter xylanophilus, Extremophiles, 3(4), 235–238, doi:10.1007/s007920050121, 1999.

Filser, J., Faber, J. H., Tiunov, A. V., Brussaard, L., Frouz, J., De Deyn, G., Uvarov, A. V., Berg, M. P., Lavelle, P., Loreau, M., Wall, D. H., Querner, P., Eijsackers, H. and Jiménez, J. J.: Soil fauna: Key to new carbon models, Soil, 2(4), 565–582, doi:10.5194/soil-2-565-2016, 2016.

Folgarait, P.: Ant biodiversity to ecosystem functioning: a review, Biodivers. Conserv., 7, 1121–1244, doi:10.1023/A:1008891901953, 1998.

Frouz, J., Holec, M. and Kalčík, J.: The effect of Lasius niger (Hymenoptera, Formicidae) ant nest on selected soil chemical properties, Pedobiologia (Jena)., 47(3), 205–212, doi:10.1078/0031-4056-00184, 2003.

Gilad, E., von Hardenberg, J., Provenzale, A., Shachak, M. and Meron, E.: Ecosystem Engineers: From Pattern Formation to Habitat Creation, Phys. Rev. Lett., 93(9), 098105, doi:10.1103/PhysRevLett.93.098105, 2004.

Ginzburg, O., Whitford, W. G. and Steinberger, Y.: Effects of harvester ant (Messor spp.) activity on soil properties and microbial communities in a Negev Desert ecosystem, Biol. Fertil. Soils, 45(2), 165–173, doi:10.1007/s00374-008-0309-z, 2008.

Gosselin, E. N., Holbrook, J. D., Huggler, K., Brown, E., Vierling, K. T., Arkle, R. S. and Pilliod, D. S.: Ecosystem engineering of harvester ants: effects on vegetation in a sagebrush-steppe ecosystem, West. North Am. Nat., 76(1), 82–89, doi:http://dx.doi.org/10.3398/064.076.0109, 2016.

De Graaff, M. A., Adkins, J., Kardol, P. and Throop, H. L.: A meta-analysis of soil biodiversity impacts on the carbon cycle, Soil, 1(1), 257–271, doi:10.5194/soil-1-257-2015, 2015.

Greening, C., Biswas, A., Carere, C. R., Jackson, C. J., Taylor, M. C., Stott, M. B., Cook, G. M. and Morales, S. E.: Genomic and metagenomic surveys of hydrogenase distribution indicate H 2 is a widely utilised energy source for microbial growth and survival, ISME J., 10(3), 761–777, doi:10.1038/ismej.2015.153, 2016.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

Hansen, B. B., Henriksen, S., Aanes, R. and Sæther, B. E.: Ungulate impact on vegetation in a two-level trophic system, Polar Biol., 30(5), 549–558, doi:10.1007/s00300-006-0212-8, 2007.

Henrikus, S. S., Wood, E. A., McDonald, J. P., Cox, M. M., Woodgate, R., Goodman, M. F., van Oijen, A. M. and Robinson, A.: DNA polymerase IV primarily operates outside of DNA replication forks in Escherichia coli, PLoS Genet., 14(1), 1–29, doi:10.1371/journal.pgen.1007161, 2018.

Iwai, S., Weinmaier, T., Schmidt, B. L., Albertson, D. G., Poloso, N. J., Dabbagh, K. and DeSantis, T. Z.: Piphillin: Improved prediction of metagenomic content by direct inference from human microbiomes, PLoS One, 11(11), 1–18, doi:10.1371/journal.pone.0166104, 2016.

Jones, C. G., Lawton, J. H. and Shachak, M.: Organisms as Ecosystem Engineers, Oikos, 69(3), 373–386, 1994.

Kaneshisa, M. and Goto, S.: KEGG: Kyoto Encyclopedia of Genes and Genomes, Nucleic Acids Res., 28(1), 27–30, doi:10.3892/ol.2020.11439, 2000.

Kidron, G. J.: The effect of shrub canopy upon surface temperatures and evaporation in the Negev Desert, Earth Surf. Process. Landforms, 34, 123–132, 2009.

Klindworth, A., Pruesse, E., Schweer, T., Peplies, J., Quast, C., Horn, M., Glöckner, F. O. and Glockner, F. O.: Evaluation of general 16S ribosomal RNA gene PCR primers for classical and next-generation sequencing-based diversity studies, Nucleic Acids Res., 41(1), 1–11, doi:10.1093/nar/gks808, 2013.

Kruskal, W. H. and Wallis, W. A.: Use of Ranks in One-Criterion Variance Analysis, J. Am. Stat. Assoc., 47(260), 583–621, doi:10.1080/01621459.1952.10483441, 1952.

Lavelle, P.: Functional domains in soils, Ecol. Res., 17(4), 441–450, doi:10.1046/j.1440-1703.2002.00509.x, 2002.

Lavelle, P., Blanchart, E., Martin, A., Spain, A. V. and Martin, S.: Impact of Soil Fauna on the Properties of Soils in the Humid Tropics, Soil Sci. Soc. Am., (29), doi:10.2136/sssaspecpub29.c9, 1992.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P. and Rossi, J. P.: Soil invertebrates and ecosystem services, Eur. J. Soil Biol., 42(SUPPL. 1), doi:10.1016/j.ejsobi.2006.10.002, 2006.

Lennon, J. T. and Jones, S. E.: Microbial seed banks: the ecological and evolutionary implications of dormancy, Nat Rev Micro, 9(2), 119–130 [online] Available from: http://dx.doi.org/10.1038/nrmicro2504, 2011.

León-Sobrino, C., Ramond, J. B., Maggs-Kölling, G. and Cowan, D. A.: Nutrient acquisition, rather than stress response over diel cycles, drives microbial transcription in a hyper-arid Namib desert soil, Front. Microbiol., 10(MAY), 1–11, doi:10.3389/fmicb.2019.01054, 2019.

Li, X. R., Gao, Y. H., Su, J. Q., Jia, R. L. and Zhang, Z. S.: Ants mediate soil water in arid desert ecosystems: Mitigating rainfall interception induced by biological soil crusts?, Appl. Soil Ecol., 78, 57–64, doi:10.1016/j.apsoil.2014.02.009, 2014.

MacMahon, J. A., Mull, J. F. and Crist, T. O.: Harvester ants (Pogonomyrmex spp.): their community and ecosystem influences, Annu. Rev. Ecol. Syst., 31(1), 265–291, doi:10.1146/annurev.ecolsys.31.1.265, 2000.

Madigan, M. T., Martinko, J. M., Dunlap, P. V and Clark, D. P.: Brock Biology of microoragnisms., 2009.

Meier, D. V., Imminger, S., Gillor, O. and Woebken, D.: Distribution of Mixotrophy and Desiccation Survival Mechanisms across Microbial Genomes in an Arid Biological Soil Crust Community, mSystems, 6(1), 1–20, doi:10.1128/msystems.00786-20, 2021.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

Narayan, N. R., Weinmaier, T., Laserna-Mendieta, E. J., Claesson, M. J., Shanahan, F., Dabbagh, K., Iwai, S. and Desantis, T. Z.: Piphillin predicts metagenomic composition and dynamics from DADA2-corrected 16S rDNA sequences, BMC Genomics, 21(56), 1–12, doi:10.1186/s12864-020-6537-9, 2020.

Oksanen, J., Blanchet, F. G., Kindt, R., Legen-, P., Minchin, P. R., Hara, R. B. O., Simpson, G. L., Solymos, P. and Stevens, M. H. H.: Package ‘ vegan ,’ , doi:ISBN 0-387-95457-0, 2014.

Oren, Y., Perevolotsky, A., Brand, S. and Shachak, M.: Livestock and engineering network in the Israeli Negev: Implications for ecosystem management, in Ecosystem Engineers, vol. 4, pp. 323–342, Elsevier Inc., 2007.

Pariente, S.: Spatial patterns of soil moisture as affected by shrubs, in different climatic conditions, Environ. Monit. Assess., 73(3), 237–251, doi:10.1023/A:1013119405441, 2002.

Passarelli, C., Olivier, F., Paterson, D. M., Meziane, T. and Hubas, C.: Organisms as cooperative ecosystem engineers in intertidal flats, J. Sea Res., 92, 92–101, doi:10.1016/j.seares.2013.07.010, 2014.

Preiss, J.: Bacterial glycogen synthesis and its regulation, Annu. Rev. Microbiol., 38, 419–458, 1984.

Preiss, J. and Sivak, M.: 3.14 - Starch and Glycogen Biosynthesis, edited by S. D. Barton, K. Nakanishi, and O. B. T.-C. N. P. C. Meth-Cohn, pp. 441–495, Pergamon, Oxford., 1999.

Prieur, D.: An Extreme Environment on Earth: Deep-Sea Hydrothermal Vents. Lessons for Exploration of Mars and Europa, in Lectures in Astrobiology: Volume II, edited by M. Gargaud, H. Martin, and P. Claeys, pp. 319–345, Springer Berlin Heidelberg, Berlin, Heidelberg., 2007.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J. and Glöckner, F. O.: The SILVA ribosomal RNA gene database project: improved data processing and web-based tools, Nucleic Acids Res., 41(D1), D590–D596, doi:10.1093/nar/gks1219, 2013.

R Core Team, I.: R: A language and environment for statistical computing, R Found. Stat. Comput. [online] Available from: http://www.r-project.org, 2016.

Rajeev, L., Da Rocha, U. N., Klitgord, N., Luning, E. G., Fortney, J., Axen, S. D., Shih, P. M., Bouskill, N. J., Bowen, B. P., Kerfeld, C. A., Garcia-Pichel, F., Brodie, E. L., Northen, T. R. and Mukhopadhyay, A.: Dynamic cyanobacterial response to hydration and dehydration in a desert biological soil crust, ISME J., 7(11), 2178–2191, doi:10.1038/ismej.2013.83, 2013.

Repar, J., Briski, N., Buljubašić, M., Zahradka, K. and Zahradka, D.: Exonuclease VII is involved in “reckless” DNA degradation in UV-irradiated Escherichia coli, Mutat. Res., 750, doi:10.1016/j.mrgentox.2012.10.005, 2012.

Sarig, S. and Steinberger, Y.: Microbial pools of N and P under desert halophyte shrubs: Response to soil salinity, Beyond biomass Compos. Funct. Anal. soil Microb. communities, 1993.

Saul-Tcherkas, V. and Steinberger, Y.: Soil microbial diversity in the vicinity of a Negev desert shrub-Reaumuria negevensis, Microb. Ecol., 61(1), 64–81, doi:10.1007/s00248-010-9763-x, 2011.

Schlesinger, W. H. and Pilmanis, A. M.: Plant-soil Interactions in Deserts, Biogeochemistry, 42(1), 169–187, doi:10.1023/A:1005939924434, 1998.

Schlesinger, W. H., Raikks, J. A., Hartley, A. E. and Cross, A. F.: On the spatial pattern of soil nutrients in desert ecosystems, Ecology, 77(2), 364–374, doi:10.2307/2265615, 1996.

Schulz, K., Mikhailyuk, T., Dreßler, M., Leinweber, P. and Karsten, U.: Biological Soil Crusts from Coastal Dunes at the Baltic Sea: Cyanobacterial and Algal Biodiversity and Related Soil Properties, Microb. Ecol., 71(1), 178–193, doi:10.1007/s00248-015-0691-7, 2016.

Schulze-Makuch, D., Wagner, D., Kounaves, S. P., Mangelsdorf, K., Devine, K. G., de Vera, J.-P.,

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

Schmitt-Kopplin, P., Grossart, H.-P., Parro, V., Kaupenjohann, M., Galy, A., Schneider, B., Airo, A., Frösler, J., Davila, A. F., Arens, F. L., Cáceres, L., Cornejo, F. S., Carrizo, D., Dartnell, L., DiRuggiero, J., Flury, M., Ganzert, L., Gessner, M. O., Grathwohl, P., Guan, L., Heinz, J., Hess, M., Keppler, F., Maus, D., McKay, C. P., Meckenstock, R. U., Montgomery, W., Oberlin, E. A., Probst, A. J., Sáenz, J. S., Sattler, T., Schirmack, J., Sephton, M. A., Schloter, M., Uhl, J., Valenzuela, B., Vestergaard, G., Wörmer, L. and Zamorano, P.: Transitory microbial habitat in the hyperarid Atacama Desert, Proc. Natl. Acad. Sci., 115(11), 2670–2675, doi:10.1073/pnas.1714341115, 2018.

Segoli, M., Ungar, E. D. and Shachak, M.: Shrubs enhance resilience of a semi-arid ecosystem by engineering and regrowth, Ecohydrology, 1, 330–339, doi:10.1002/eco, 2008.

Segoli, M., Ungar, E. D., Giladi, I., Arnon, A. and Shachak, M.: Untangling the positive and negative effects of shrubs on herbaceous vegetation in drylands, Landsc. Ecol., 27(6), 899–910, doi:10.1007/s10980-012-9736-1, 2012.

Shachak, M., Boeken, B., Groner, E., Kadmon, R., Lubin, Y., Meron, E., Ne'eman, G., Perevolotsky, A., Shkedy, Y. and Ungar, E. D.: Woody species as landscape modulators and their effect on biodiversity patterns, Bioscience, 58(3), 209–221, doi:10.1641/B580307, 2008.

Sklarz, M. Y., Levin, L., Gordon, M. and Chalifa-Caspi, V.: NeatSeq-Flow: A Lightweight High Throughput Sequencing Workflow Platform for Non-Programmers and Programmers alike, bioRxiv, 173005, doi:10.1101/173005, 2018.

Slade, D. and Radman, M.: Oxidative Stress Resistance in Deinococcus radiodurans., 2011.

SSSA, S. S. S. of A.: Methods of Soil Analysis: Part 3 Chemical methods, 5.3, edited by D. L. Sparks, A. L. Page, H. P. A, R. H. Loeppert, P. N. Soltanpour, M. A. Tabatabai, C. T. Johnson, and S. M. E., 1996.

Steven, B., Gallegos-Graves, L. V., Yeager, C., Belnap, J. and Kuske, C. R.: Common and distinguishing features of the bacterial and fungal communities in biological soil crusts and shrub root zone soils, Soil Biol. Biochem., 69, 302–312, doi:10.1016/j.soilbio.2013.11.008, 2014.

Tveit, A. T., Hestnes, A. G., Robinson, S. L., Schintlmeister, A., Dedysh, S. N., Jehmlich, N., Von Bergen, M., Herbold, C., Wagner, M., Richter, A. and Svenning, M. M.: Widespread soil bacterium that oxidizes atmospheric methane, Proc. Natl. Acad. Sci. U. S. A., 116(17), 8515–8524, doi:10.1073/pnas.1817812116, 2019.

Vonshak, A., Sklarz, M. Y., Hirsch, A. M. and Gillor, O.: Perennials but not slope aspect affect the diversity of soil bacterial communities in the northern Negev Desert, Israel, Soil Res., 56(2), 123–128, doi:10.1071/SR17010, 2018.

Wagner, D.: The Influence of Ant Nests on Acacia Seed Production, Herbivory and Soil Nutrients, J. Ecol., 85(1), 83–93, doi:10.2307/2960629, 1997.

Wagner, D. and Jones, J. B.: The Contribution of Harvester Ant Nests, Pogonomyrmex rugosus (Hymenoptera, Formicidae), to Soil Nutrient Stocks and Microbial Biomass in the Mojave Desert, Environ. Entomol., 33(3), 599–607, doi:10.1603/0046-225X-33.3.599, 2004.

Walker, L. R., Thompson, D. B. and Landau, F. H.: Experimental manipulations of fertile islands and nurse plant effects in the Mojave Desert, USA, West. North Am. Nat., 61(1), 25–35, 2001.

West, N. E.: Nutrient cycling in desert ecosystems, in Arid land ecosystems: Volume 2, Structure, functioning and management, pp. 301–324., 1981.

West, N. E.: Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions, Adv. Ecol. Res., doi:10.1016/S0065-2504(08)60055-0, 1990.

Whitford, W. G. and Duval, B. D.: Ecology of Desert Systems., 2002.

Wilby, A., Shachak, M. and Boeken, B.: Integration of ecosystem engineering and trophic effects of

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

herbivores, Oikos, 92(3), 436–444, doi:10.1034/j.1600-0706.2001.920305.x, 2001.

Wright, J. P., Jones, C. G., Boeken, B. and Shachak, M.: Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales: *Shrub mound effects on annual plant diversity*, J. Ecol., 94(4), 815–824, doi:10.1111/j.1365-2745.2006.01132.x, 2006.

Wright, S. F. and Upadhyaya, A.: Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi, Soil Sci., 161(9) [online] Available from: http://doi.org/10.1097/00010694-199609000-00003, 1996.

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

549 **APPENDICE A**

550 Table A1. Soil characteristics data. $NH_4^+$and P show the highest discrepancy between Shrub&Nest
551 patches and the other three types.

ID	pH	NH_4^+ (mg/kg)	NO_3^- (mg/kg)	Water content (%)	Organic Matter (%)	P (mg/kg)
Barren	7.9	6.2	6.0	1.5	1.5	42.1
Barren	8.1	6.9	1.8	1.8	0.3	20.3
Barren	8.3	4.6	2.7	1.5	0.4	20.8
Barren	8.1	4.1	2.0	1.6	0.5	14.6
Barren	8.0	6.7	3.9	1.6	0.5	15.9
Barren	8.1	7.2	2.0	1.5	0.5	11.7
Barren	8.3	3.8	2.4	1.5	0.3	15.4
Nest	8.2	8.4	4.2	2.0	0.4	23.0
Nest	7.7	10.2	2.9	1.9	0.6	31.1
Nest	7.8	5.4	21.9	1.7	0.6	23.2
Nest	8.0	7.1	2.4	1.6	0.5	15.0
Nest	7.8	6.0	4.0	1.5	0.6	11.4
Nest	8.0	5.4	6.9	1.5	0.4	17.1
Nest	8.2	2.3	3.0	1.5	0.3	20.3
Shrub	8.2	5.2	4.5	1.7	0.6	25.0
Shrub	8.2	6.0	3.8	1.7	0.8	40.2
Shrub	8.2	6.6	12.3	1.3	0.6	62.8
Shrub	8.4	4.3	1.9	1.6	0.7	13.0
Shrub	8.3	3.4	0.9	1.4	0.6	8.4
Shrub	8.3	4.4	3.8	1.5	0.4	10.7
Shrub	8.1	4.0	5.7	1.7	0.7	22.2
Shrub&Nest	8.0	7.6	6.9	1.4	0.6	79.9
Shrub&Nest	7.7	9.5	5.3	1.5	0.8	29.4
Shrub&Nest	7.7	11.6	42.0	1.5	0.7	76.3
Shrub&Nest	7.7	8.5	11.0	1.6	0.9	54.0
Shrub&Nest	7.8	9.6	29.8	1.4	0.9	29.0
Shrub&Nest	7.7	14.3	105.2	1.5	0.8	66.9
Shrub&Nest	7.9	7.0	13.8	1.4	1.0	43.2
Chi2	16.5	13.9	13.1	4.7	13.3	11.5

552

553

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

Table A2. P-values of the Dunn Test between patch types on the soil characteristics variables. Bold numbers are significant (<0.05)

Comparisons	**Water**	**pH**	**NO_3^-**	**NH_4^+**	**P**	**OM**
Barren - Nest	0.218	0.103	0.084	0.279	0.385	0.500
Barren - Shrub	0.448	0.119	0.194	0.190	0.354	0.067
Nest - Shrub	0.181	**0.007**	0.301	0.072	0.468	0.067
Barren - Shrub&Nest	0.086	**0.004**	**0.0003**	**0.004**	**0.001**	**0.001**
Nest - Shrub&Nest	**0.016**	0.079	0.018	**0.017**	**0.004**	**0.001**
Shrub - Shrub&Nest	0.108	**0.000**	**0.004**	**0.000**	**0.005**	**0.050**

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

558 Table A3. Results of the pairwise adonis test between patch types done on the NMDS data. Bold
559 numbers are significant (<0.05).

560

Comparison	**R2**	**P value**
Control vs Nest	0.38473901	**0.012**
Control vs Shrub	0.25759869	**0.006**
Control vs Shrub&Nest	0.21665172	**0.048**
Nest vs Shrub	0.08725184	1.000
Nest vs Shrub&Nest	0.21988027	0.054
Shrub vs Shrub&Nest	0.08914105	1.000

561

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

562 Table A4. Number of reads before and after the trimming stage, and during the dada2 stage.

		Number of reads				
Sample	**Patch Type**	**Raw**	**trimmed**	**filtered**	**denoised**	**non-chimeric**
Samples_AD1	Barren	42089	41265	36421	33675	33141
Samples_AD2	Barren	28759	28008	24434	21984	21507
Samples_AD3	Barren	30166	29410	25782	23285	22830
Samples_AD4	Barren	27024	26664	23906	21545	21171
Samples_AD5	Barren	48612	47548	41813	38854	38352
Samples_AD6	Barren	23816	23120	20084	18008	17857
Samples_AD7	Barren	21806	19454	16803	15532	15482
Samples_AD8	Nest	22559	20965	18485	17118	17118
Samples_AD9	Nest	28231	26041	22688	21213	21088
Samples_AD10	Nest	24428	22266	19719	18340	18161
Samples_AD11	Nest	39081	37713	33573	31772	31124
Samples_AD12	Nest	18426	17446	15756	14567	14494
Samples_AD13	Nest	22881	13779	10573	9234	9151
Samples_AD14	Nest	47080	44925	39700	37254	36423
Samples_AD15	Shrub	51183	48988	43764	41558	40506
Samples_AD16	Shrub	51519	37941	30791	28403	27721
Samples_AD17	Shrub	35494	33858	29858	27875	27349
Samples_AD18	Shrub	29615	27956	24841	22947	22847
Samples_AD19	Shrub	39011	37117	32622	30293	29544
Samples_AD20	Shrub	50894	38156	30901	28515	28169
Samples_AD21	Shrub	35365	32529	28933	27200	27033
Samples_AD22	Shrub	41660	27359	21466	19924	19629
Samples_AD23	Shrub&Nest	37107	35185	31099	28722	28201
Samples_AD24	Shrub&Nest	55386	34724	27058	24657	24136
Samples_AD25	Shrub&Nest	58632	42065	34139	31435	30693
Samples_AD26	Shrub&Nest	67273	47135	37618	33503	33089
Samples_AD27	Shrub&Nest	35493	31891	27756	26086	25915
Samples_AD28	Shrub&Nest	34645	29939	26141	24533	24297
Samples_AD29	Shrub&Nest	76888	53655	42659	38753	38044

563

564

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

565 Table A5. Relative abundance (%) of the taxonomic community per patch type.

Phylum	Patch Type	Relative Abundance
Acidobacteria	Control	7.02
Acidobacteria	Nest	2.33
Acidobacteria	Shrub	5.10
Acidobacteria	Shrub&Nest	4.52
Actinobacteria	Control	34.72
Actinobacteria	Nest	9.79
Actinobacteria	Shrub	9.13
Actinobacteria	Shrub&Nest	16.83
Bacteroidetes	Control	7.41
Bacteroidetes	Nest	3.86
Bacteroidetes	Shrub	9.24
Bacteroidetes	Shrub&Nest	12.42
Chloroflexi	Control	8.15
Chloroflexi	Nest	1.01
Chloroflexi	Shrub	1.75
Chloroflexi	Shrub&Nest	2.24
Cyanobacteria	Control	1.59
Cyanobacteria	Shrub	1.48
Cyanobacteria	Shrub&Nest	1.95
Deinococcus-Thermus	Control	2.77
Deinococcus-Thermus	Nest	30.19
Deinococcus-Thermus	Shrub	20.85
Deinococcus-Thermus	Shrub&Nest	8.69
Firmicutes	Control	1.20
Firmicutes	Nest	4.89
Firmicutes	Shrub	6.93
Firmicutes	Shrub&Nest	9.12
Gemmatimonadetes	Control	4.93
Gemmatimonadetes	Nest	1.13
Gemmatimonadetes	Shrub	2.40
Gemmatimonadetes	Shrub&Nest	2.78
Planctomycetes	Control	1.29
Planctomycetes	Nest	0.55
Planctomycetes	Shrub	1.39
Planctomycetes	Shrub&Nest	1.20
Proteobacteria	Control	27.67
Proteobacteria	Nest	45.32
Proteobacteria	Shrub	40.44
Proteobacteria	Shrub&Nest	38.77

566

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

Table A6. P-values of the Dunn tests between patch types on the relative abundance of the five most abundant phyla. Bold numbers are significant (<0.05).

Comparisons	**Actinobacteria**	**Bacteroidetes**	**Deinococcus-Thermus**	**Firmicutes**	**Proteobacteria**
Barren - Nest	**0.0004**	**0.0129**	**0.0003**	0.3768	**0.0394**
Barren - Shrub	**0.0004**	0.4774	**0.0009**	0.0718	**0.0120**
Nest - Shrub	0.4661	**0.0124**	0.3352	0.1274	0.3294
Barren - Shrub&Nest	**0.0991**	**0.0836**	**0.0320**	**0.0129**	**0.0042**
Nest - Shrub&Nest	**0.0207**	**0.0002**	0.0583	**0.0278**	0.1897
Shrub - Shrub&Nest	**0.0216**	0.0690	0.1160	**0.200**8	0.3206

Table A7. List of the genes used for function prediction ordered by groups and subgroups.

Group	Metabolic Trait	KEGG ID	Function
DNA conservation	Putative DNA-binding protein	K02524	K10; DNA binding protein (fs(1)K10, female sterile(1)K10)
	Putative DNA-binding protein	K03111	ssb; single-strand DNA-binding protein
	Putative DNA-binding protein	K03530	hupB; DNA-binding protein HU-beta
	Putative DNA-binding protein	K03622	ssh10b; archaea-specific DNA-binding protein
	Putative DNA-binding protein	K03746	hns; DNA-binding protein H-NS
	Putative DNA-binding protein	K04047	dps; starvation-inducible DNA-binding protein
	Putative DNA-binding protein	K04494	CHD8, HELSNF1; chromodomain helicase DNA binding protein 8 [EC:3.6.4.12]
	Putative DNA-binding protein	K04680	ID1; DNA-binding protein inhibitor ID1
	Putative DNA-binding protein	K05516	cbpA; curved DNA-binding protein
	Putative DNA-binding protein	K05732	ARHGAP35, GRLF1; glucocorticoid receptor DNA-binding factor 1
	Putative DNA-binding protein	K05787	hupA; DNA-binding protein HU-alpha
	Putative DNA-binding protein	K09061	GCF, C2orf3; GC-rich sequence DNA-binding factor
	Putative DNA-binding protein	K09423	BAA; Myb-like DNA-binding protein BAA
	Putative DNA-binding protein	K09424	REB1; Myb-like DNA-binding protein REB1
	Putative DNA-binding protein	K09425	K09425; Myb-like DNA-binding protein FlbD
	Putative DNA-binding protein	K09426	RAP1; Myb-like DNA-binding protein RAP1
	Putative DNA-binding protein	K10140	DDB2; DNA damage-binding protein 2
	Putative DNA-binding protein	K10610	DDB1; DNA damage-binding protein 1
	Putative DNA-binding protein	K10728	TOPBP1; topoisomerase (DNA) II binding protein 1

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

	Putative DNA-binding protein	K10748	tus, tau; DNA replication terminus site-binding protein
	Histone-like protein	K10752	RBBP4, HAT2, CAF1, MIA6; histone-binding protein RBBP4
	Putative DNA-binding protein	K10979	ku; DNA end-binding protein Ku
	Putative DNA-binding protein	K11367	CHD1; chromodomain-helicase-DNA-binding protein 1 [EC:3.6.4.12]
	Histone-like protein	K11495	CENPA; histone H3-like centromeric protein A
	Putative DNA-binding protein	K11574	CBF2, CBF3A, CTF14; centromere DNA-binding protein complex CBF3 subunit A
	Putative DNA-binding protein	K11575	CEP3, CBF3B; centromere DNA-binding protein complex CBF3 subunit B
	Putative DNA-binding protein	K11576	CTF13, CBF3C; centromere DNA-binding protein complex CBF3 subunit C
	Putative DNA-binding protein	K11642	CHD3, MI2A; chromodomain-helicase-DNA-binding protein 3 [EC:3.6.4.12]
	Putative DNA-binding protein	K11643	CHD4, MI2B; chromodomain-helicase-DNA-binding protein 4 [EC:3.6.4.12]
	Histone-like protein	K11659	RBBP7; histone-binding protein RBBP7
	Putative DNA-binding protein	K11685	stpA; DNA-binding protein StpA
	Putative DNA-binding protein	K12965	ZBP1, DAI; Z-DNA binding protein 1
	Putative DNA-binding protein	K13102	KIN; DNA/RNA-binding protein KIN17
	Putative DNA-binding protein	K13211	GCFC; GC-rich sequence DNA-binding factor
	Putative DNA-binding protein	K14435	CHD5; chromodomain-helicase-DNA-binding protein 5 [EC:3.6.4.12]
	Putative DNA-binding protein	K14436	CHD6; chromodomain-helicase-DNA-binding protein 6 [EC:3.6.4.12]
	Putative DNA-binding protein	K14437	CHD7; chromodomain-helicase-DNA-binding protein 7 [EC:3.6.4.12]
	Putative DNA-binding protein	K14438	CHD9; chromodomain-helicase-DNA-binding protein 9 [EC:3.6.4.12]
	Putative DNA-binding protein	K14507	ORCA2_3; AP2-domain DNA-binding protein ORCA2/3
	Histone-like protein	K15719	NCOAT, MGEA5; protein O-GlcNAcase / histone acetyltransferase [EC:3.2.1.169 2.3.1.48]
	Putative DNA-binding protein	K16640	ssh7; DNA-binding protein 7 [EC:3.1.27.-]
	Putative DNA-binding protein	K17693	ID2; DNA-binding protein inhibitor ID2
	Putative DNA-binding protein	K17694	ID3; DNA-binding protein inhibitor ID3
	Putative DNA-binding protein	K17695	ID4; DNA-binding protein inhibitor ID4
	Putative DNA-binding protein	K17696	EMC; DNA-binding protein inhibitor ID, other
	Histone-like protein	K18710	SLBP; histone RNA hairpin-binding protein

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

	Putative DNA-binding protein	K18946	gp32, ssb; single-stranded DNA-binding protein
	Putative DNA-binding protein	K19442	ICP8, DBP, UL29; Simplexvirus major DNA-binding protein
	Histone-like protein	K19799	RPH1; DNA damage-responsive transcriptional repressor / [histone H3]-trimethyl-L-lysine36 demethylase [EC:1.14.11.69]
	Putative DNA-binding protein	K20091	CHD2; chromodomain-helicase-DNA-binding protein 2 [EC:3.6.4.12]
	Putative DNA-binding protein	K20092	CHD1L; chromodomain-helicase-DNA-binding protein 1-like [EC:3.6.4.12]
	Putative DNA-binding protein	K22592	AHDC1; AT-hook DNA-binding motif-containing protein 1
	Putative DNA-binding protein	K23225	SATB1; DNA-binding protein SATB1
	Putative DNA-binding protein	K23226	SATB2; DNA-binding protein SATB2
	Putative DNA-binding protein	K23600	TARDBP, TDP43; TAR DNA-binding protein 43
DNA repair	DNA polymerase PolA (COG0258)	K02320	POLA1; DNA polymerase alpha subunit A [EC:2.7.7.7]
	DNA polymerase PolA (COG0258)	K02321	POLA2; DNA polymerase alpha subunit B
	DNA polymerase PolA (COG0258)	K02335	polA; DNA polymerase I [EC:2.7.7.7]
	DNA polymerase IV	K02346	dinB; DNA polymerase IV [EC:2.7.7.7]
	Exodeoxyribonuclease VII	K03601	xseA; exodeoxyribonuclease VII large subunit [EC:3.1.11.6]
	Exodeoxyribonuclease VII	K03602	xseB; exodeoxyribonuclease VII small subunit [EC:3.1.11.6]
	DNA polymerase IV	K04479	dbh; DNA polymerase IV (archaeal DinB-like DNA polymerase) [EC:2.7.7.7]
	Exodeoxyribonuclease VII	K10906	recE; exodeoxyribonuclease VIII [EC:3.1.11.-]
	DNA polymerase IV	K10981	POL4; DNA polymerase IV [EC:2.7.7.7]
	DNA polymerase IV	K16250	NRPD1; DNA-directed RNA polymerase IV subunit 1 [EC:2.7.7.6]
	DNA polymerase IV	K16252	NRPD2, NRPE2; DNA-directed RNA polymerase IV and V subunit 2 [EC:2.7.7.6]
	DNA polymerase IV	K16253	NRPD7, NRPE7; DNA-directed RNA polymerase IV and V subunit 7
Lithotrophy	NiFe hydrogenase	K00437	hydB; [NiFe] hydrogenase large subunit [EC:1.12.2.1]
	NiFe hydrogenase	K02587	nifE; nitrogenase molybdenum-cofactor synthesis protein NifE
	CO-dehydrogenase CoxM & CoxS	K03518	coxS; aerobic carbon-monoxide dehydrogenase small subunit [EC:1.2.5.3]
	CO-dehydrogenase CoxM & CoxS	K03519	coxM, cutM; aerobic carbon-monoxide dehydrogenase medium subunit [EC:1.2.5.3]
	CO-dehydrogenase large subunit (coxL) Form I	K03520	coxL, cutL; aerobic carbon-monoxide dehydrogenase large subunit [EC:1.2.5.3]

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

	NiFe hydrogenase	K05586	hoxE; bidirectional [NiFe] hydrogenase diaphorase subunit [EC:7.1.1.2]
	NiFe hydrogenase	K05587	hoxF; bidirectional [NiFe] hydrogenase diaphorase subunit [EC:7.1.1.2]
	NiFe hydrogenase	K05588	hoxU; bidirectional [NiFe] hydrogenase diaphorase subunit [EC:7.1.1.2]
	SOX sulfur-oxidation system	K17218	sqr; sulfide:quinone oxidoreductase [EC:1.8.5.4]
	SOX sulfur-oxidation system	K17222	soxA; L-cysteine S-thiosulfotransferase [EC:2.8.5.2]
	SOX sulfur-oxidation system	K17223	soxX; L-cysteine S-thiosulfotransferase [EC:2.8.5.2]
	SOX sulfur-oxidation system	K17224	soxB; S-sulfosulfanyl-L-cysteine sulfohydrolase [EC:3.1.6.20]
	SOX sulfur-oxidation system	K17225	soxC; sulfane dehydrogenase subunit SoxC
	SOX sulfur-oxidation system	K17226	soxY; sulfur-oxidizing protein SoxY
	SOX sulfur-oxidation system	K17227	soxZ; sulfur-oxidizing protein SoxZ
	NiFe hydrogenase	K18005	hoxF; [NiFe] hydrogenase diaphorase moiety large subunit [EC:1.12.1.2]
	NiFe hydrogenase	K18006	hoxU; [NiFe] hydrogenase diaphorase moiety small subunit [EC:1.12.1.2]
	NiFe hydrogenase	K18008	hydA; [NiFe] hydrogenase small subunit [EC:1.12.2.1]
	Propane monooxygenase (soluble)	K18223	prmA; propane 2-monooxygenase large subunit [EC:1.14.13.227]
	Propane monooxygenase (soluble)	K18224	prmC; propane 2-monooxygenase small subunit [EC:1.14.13.227]
	Propane monooxygenase (soluble)	K18225	prmB; propane monooxygenase reductase component [EC:1.18.1.-]
	Propane monooxygenase (soluble)	K18226	prmD; propane monooxygenase coupling protein
	SOX sulfur-oxidation system	K22622	soxD; S-disulfanyl-L-cysteine oxidoreductase SoxD [EC:1.8.2.6]
	SOX sulfur-oxidation system	K24007	soxD; cytochrome aa3-type oxidase subunit SoxD
	SOX sulfur-oxidation system	K24008	soxC; cytochrome aa3-type oxidase subunit III
	SOX sulfur-oxidation system	K24009	soxB; cytochrome aa3-type oxidase subunit I [EC:7.1.1.4]
	SOX sulfur-oxidation system	K24010	soxA; cytochrome aa3-type oxidase subunit II [EC:7.1.1.4]
	SOX sulfur-oxidation system	K24011	soxM; cytochrome aa3-type oxidase subunit I/III [EC:7.1.1.4]
Organotrophy	ABC sugar transporters	K02025	ABC.MS.P; multiple sugar transport system permease protein
	ABC sugar transporters	K02026	ABC.MS.P1; multiple sugar transport system permease protein
	ABC sugar transporters	K02027	ABC.MS.S; multiple sugar transport system substrate-binding protein
	ABC sugar transporters	K02056	ABC.SS.A; simple sugar transport system ATP-binding protein [EC:7.5.2.-]
	ABC sugar transporters	K02057	ABC.SS.P; simple sugar transport system permease protein

	ABC sugar transporters	K02058	ABC.SS.S; simple sugar transport system substrate-binding protein
	PTS sugar importers	K02777	crr; sugar PTS system EIIA component [EC:2.7.1.-]
	Amino acid transporter	K03293	TC.AAT; amino acid transporter, AAT family
	Peptide transporter	K03305	TC.POT; proton-dependent oligopeptide transporter, POT family
	Amino acid transporter	K03311	TC.LIVCS; branched-chain amino acid:cation transporter, LIVCS family
	Carboxylate transporters	K03326	TC.DCUC, dcuC, dcuD; C4-dicarboxylate transporter, DcuC family
	Amino acid transporter	K03450	SLC7A; solute carrier family 7 (L-type amino acid transporter), other
	Glycosyl hydrolases	K04844	ycjT; hypothetical glycosyl hydrolase [EC:3.2.1.-]
	Amino acid transporter	K05048	SLC6A15S; solute carrier family 6 (neurotransmitter transporter, amino acid/orphan) member 15/16/17/18/20
	Amino acid transporter	K05615	SLC1A4, SATT; solute carrier family 1 (neutral amino acid transporter), member 4
	Amino acid transporter	K05616	SLC1A5; solute carrier family 1 (neutral amino acid transporter), member 5
	Amino acid transporter	K07084	yuiF; putative amino acid transporter
	Carboxylate transporters	K07791	dcuA; anaerobic C4-dicarboxylate transporter DcuA
	Carboxylate transporters	K07792	dcuB; anaerobic C4-dicarboxylate transporter DcuB
	ABC sugar transporters	K10546	ABC.GGU.S, chvE; putative multiple sugar transport system substrate-binding protein
	ABC sugar transporters	K10547	ABC.GGU.P, gguB; putative multiple sugar transport system permease protein
	ABC sugar transporters	K10548	ABC.GGU.A, gguA; putative multiple sugar transport system ATP-binding protein [EC:7.5.2.-]
	Carboxylate transporters	K11689	dctQ; C4-dicarboxylate transporter, DctQ subunit
	Carboxylate transporters	K11690	dctM; C4-dicarboxylate transporter, DctM subunit
	Amino acid transporter	K13576	SLC38A3, SNAT3; solute carrier family 38 (sodium-coupled neutral amino acid transporter), member 3
	Carboxylate transporters	K13577	SLC25A10, DIC; solute carrier family 25 (mitochondrial dicarboxylate transporter), member 10
	Amino acid transporter	K13780	SLC7A5, LAT1; solute carrier family 7 (L-type amino acid transporter), member 5
	Amino acid transporter	K13781	SLC7A8, LAT2; solute carrier family 7 (L-type amino acid transporter), member 8
	Amino acid transporter	K13782	SLC7A10, ASC1; solute carrier family 7 (L-type amino acid transporter), member 10

	Amino acid transporter	K13863	SLC7A1, ATRC1; solute carrier family 7 (cationic amino acid transporter), member 1
	Amino acid transporter	K13864	SLC7A2, ATRC2; solute carrier family 7 (cationic amino acid transporter), member 2
	Amino acid transporter	K13865	SLC7A3, ATRC3; solute carrier family 7 (cationic amino acid transporter), member 3
	Amino acid transporter	K13866	SLC7A4; solute carrier family 7 (cationic amino acid transporter), member 4
	Amino acid transporter	K13867	SLC7A7; solute carrier family 7 (L-type amino acid transporter), member 7
	Amino acid transporter	K13868	SLC7A9, BAT1; solute carrier family 7 (L-type amino acid transporter), member 9
	Amino acid transporter	K13869	SLC7A11; solute carrier family 7 (L-type amino acid transporter), member 11
	Amino acid transporter	K13870	SLC7A13, AGT1; solute carrier family 7 (L-type amino acid transporter), member 13
	Amino acid transporter	K13871	SLC7A14; solute carrier family 7 (cationic amino acid transporter), member 14
	Amino acid transporter	K13872	SLC7A6; solute carrier family 7 (L-type amino acid transporter), member 6
	Peptide transporter	K14206	SLC15A1, PEPT1; solute carrier family 15 (oligopeptide transporter), member 1
	Amino acid transporter	K14207	SLC38A2, SNAT2; solute carrier family 38 (sodium-coupled neutral amino acid transporter), member 2
	Amino acid transporter	K14209	SLC36A, PAT; solute carrier family 36 (proton-coupled amino acid transporter)
	Amino acid transporter	K14210	SLC3A1, RBAT; solute carrier family 3 (neutral and basic amino acid transporter), member 1
	Carboxylate transporters	K14388	SLC5A8_12, SMCT; solute carrier family 5 (sodium-coupled monocarboxylate transporter), member 8/12
	Carboxylate transporters	K14445	SLC13A2_3_5; solute carrier family 13 (sodium-dependent dicarboxylate transporter), member 2/3/5
	Peptide transporter	K14637	SLC15A2, PEPT2; solute carrier family 15 (oligopeptide transporter), member 2
	Peptide transporter	K14638	SLC15A3_4, PHT; solute carrier family 15 (peptide/histidine transporter), member 3/4
	Amino acid transporter	K14990	SLC38A1, SNAT1, GLNT; solute carrier family 38 (sodium-coupled neutral amino acid transporter), member 1

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

	Amino acid transporter	K14991	SLC38A4, SNAT4; solute carrier family 38 (sodium-coupled neutral amino acid transporter), member 4
	Amino acid transporter	K14992	SLC38A5, SNAT5; solute carrier family 38 (sodium-coupled neutral amino acid transporter), member 5
	Amino acid transporter	K14993	SLC38A6, SNAT6; solute carrier family 38 (sodium-coupled neutral amino acid transporter), member 6
	Amino acid transporter	K14994	SLC38A7_8; solute carrier family 38 (sodium-coupled neutral amino acid transporter), member 7/8
	Amino acid transporter	K14995	SLC38A9; solute carrier family 38 (sodium-coupled neutral amino acid transporter), member 9
	Amino acid transporter	K14996	SLC38A10; solute carrier family 38 (sodium-coupled neutral amino acid transporter), member 10
	Amino acid transporter	K14997	SLC38A11; solute carrier family 38 (sodium-coupled neutral amino acid transporter), member 11
	Amino acid transporter	K15015	SLC32A, VGAT; solute carrier family 32 (vesicular inhibitory amino acid transporter)
	Carboxylate transporters	K15110	SLC25A21, ODC; solute carrier family 25 (mitochondrial 2-oxodicarboxylate transporter), member 21
	Amino acid transporter	K16261	YAT; yeast amino acid transporter
	Amino acid transporter	K16263	yjeH; amino acid efflux transporter
	Peptide transporter	K17938	sbmA, bacA; peptide/bleomycin uptake transporter
Phototrophy	RuBisCO	K01601	rbcL; ribulose-bisphosphate carboxylase large chain [EC:4.1.1.39]
	Chlorophyll synthesis	K01669	phrB; deoxyribodipyrimidine photo-lyase [EC:4.1.99.3]
	Chlorophyll synthesis	K02689	psaA; photosystem I P700 chlorophyll a apoprotein A1
	Chlorophyll synthesis	K02690	psaB; photosystem I P700 chlorophyll a apoprotein A2
	Chlorophyll synthesis	K02691	psaC; photosystem I subunit VII
	Chlorophyll synthesis	K02692	psaD; photosystem I subunit II
	Chlorophyll synthesis	K02693	psaE; photosystem I subunit IV
	Chlorophyll synthesis	K02694	psaF; photosystem I subunit III
	Chlorophyll synthesis	K02695	psaH; photosystem I subunit VI
	Chlorophyll synthesis	K02696	psaI; photosystem I subunit VIII
	Chlorophyll synthesis	K02697	psaJ; photosystem I subunit IX
	Chlorophyll synthesis	K02698	psaK; photosystem I subunit X
	Chlorophyll synthesis	K02699	psaL; photosystem I subunit XI
	Chlorophyll synthesis	K02700	psaM; photosystem I subunit XII
	Chlorophyll synthesis	K02701	psaN; photosystem I subunit PsaN
	Chlorophyll synthesis	K02702	psaX; photosystem I 4.8kDa protein
	Chlorophyll synthesis	K02703	psbA; photosystem II P680 reaction center D1 protein [EC:1.10.3.9]
	Chlorophyll synthesis	K02704	psbB; photosystem II CP47 chlorophyll apoprotein

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

	Chlorophyll synthesis	K02705	psbC; photosystem II CP43 chlorophyll apoprotein
	Chlorophyll synthesis	K02706	psbD; photosystem II P680 reaction center D2 protein [EC:1.10.3.9]
	Chlorophyll synthesis	K02707	psbE; photosystem II cytochrome b559 subunit alpha
	Chlorophyll synthesis	K02708	psbF; photosystem II cytochrome b559 subunit beta
	Chlorophyll synthesis	K02709	psbH; photosystem II PsbH protein
	Chlorophyll synthesis	K02710	psbI; photosystem II PsbI protein
	Chlorophyll synthesis	K02711	psbJ; photosystem II PsbJ protein
	Chlorophyll synthesis	K02712	psbK; photosystem II PsbK protein
	Chlorophyll synthesis	K02713	psbL; photosystem II PsbL protein
	Chlorophyll synthesis	K02714	psbM; photosystem II PsbM protein
	Chlorophyll synthesis	K02716	psbO; photosystem II oxygen-evolving enhancer protein 1
	Chlorophyll synthesis	K02717	psbP; photosystem II oxygen-evolving enhancer protein 2
	Chlorophyll synthesis	K02718	psbT; photosystem II PsbT protein
	Chlorophyll synthesis	K02719	psbU; photosystem II PsbU protein
	Chlorophyll synthesis	K02720	psbV; photosystem II cytochrome c550
	Chlorophyll synthesis	K02721	psbW; photosystem II PsbW protein
	Chlorophyll synthesis	K02722	psbX; photosystem II PsbX protein
	Chlorophyll synthesis	K02723	psbY; photosystem II PsbY protein
	Chlorophyll synthesis	K02724	psbZ; photosystem II PsbZ protein
	Chlorophyll synthesis	K03157	LTB, TNFC; lymphotoxin beta (TNF superfamily, member 3)
	Chlorophyll synthesis	K03159	TNFRSF3, LTBR; lymphotoxin beta receptor TNFR superfamily member 3
	Chlorophyll synthesis	K03541	psbR; photosystem II 10kDa protein
	Chlorophyll synthesis	K03542	psbS; photosystem II 22kDa protein
	Chlorophyll synthesis	K03716	splB; spore photoproduct lyase [EC:4.1.99.14]
	Chlorophyll synthesis	K05468	LTA, TNFB; lymphotoxin alpha (TNF superfamily, member 1)
	Chlorophyll synthesis	K06315	splA; transcriptional regulator of the spore photoproduct lyase operon
	Chlorophyll synthesis	K06876	K06876; deoxyribodipyrimidine photolyase-related protein
	Chlorophyll synthesis	K08901	psbQ; photosystem II oxygen-evolving enhancer protein 3
	Chlorophyll synthesis	K08902	psb27; photosystem II Psb27 protein
	Chlorophyll synthesis	K08903	psb28; photosystem II 13kDa protein
	Chlorophyll synthesis	K08904	psb28-2; photosystem II Psb28-2 protein
	Chlorophyll synthesis	K08905	psaG; photosystem I subunit V
	Chlorophyll synthesis	K08928	pufL; photosynthetic reaction center L subunit
	Chlorophyll synthesis	K08929	pufM; photosynthetic reaction center M subunit
	Chlorophyll synthesis	K08940	pscA; photosystem P840 reaction center large subunit
	Chlorophyll synthesis	K08941	pscB; photosystem P840 reaction center iron-sulfur protein

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

	Chlorophyll synthesis	K08942	pscC; photosystem P840 reaction center cytochrome c551
	Chlorophyll synthesis	K08943	pscD; photosystem P840 reaction center protein PscD
	Chlorophyll synthesis	K11524	pixI; positive phototaxis protein PixI
	Chlorophyll synthesis	K13991	puhA; photosynthetic reaction center H subunit
	Chlorophyll synthesis	K13992	pufC; photosynthetic reaction center cytochrome c subunit
	Chlorophyll synthesis	K13994	pufX; photosynthetic reaction center PufX protein
	Chlorophyll synthesis	K14332	psaO; photosystem I subunit PsaO
	Chlorophyll synthesis	K19016	IMPG1, SPACR; interphotoreceptor matrix proteoglycan 1
	Chlorophyll synthesis	K19017	IMPG2, SPACRCAN; interphotoreceptor matrix proteoglycan 2
	Chlorophyll synthesis	K20715	PHOT; phototropin [EC:2.7.11.1]
	Chlorophyll synthesis	K22464	FAP; fatty acid photodecarboxylase [EC:4.1.1.106]
	Chlorophyll synthesis	K22619	Aequorin; calcium-regulated photoprotein [EC:1.13.12.24]
	Chlorophyll synthesis	K24165	PCARE; photoreceptor cilium actin regulator
ROS-damage prevention	Cytochrome C oxidase	K00404	ccoN; cytochrome c oxidase cbb3-type subunit I [EC:7.1.1.9]
	Cytochrome C oxidase	K00405	ccoO; cytochrome c oxidase cbb3-type subunit II
	Cytochrome C oxidase	K00406	ccoP; cytochrome c oxidase cbb3-type subunit III
	Cytochrome C oxidase	K00407	ccoQ; cytochrome c oxidase cbb3-type subunit IV
	Cytochrome bd ubiquinol oxidase	K00424	cydX; cytochrome bd-I ubiquinol oxidase subunit X [EC:7.1.1.7]
	Cytochrome C oxidase	K00424	cydX; cytochrome bd-I ubiquinol oxidase subunit X [EC:7.1.1.7]
	Cytochrome bd ubiquinol oxidase	K00425	cydA; cytochrome bd ubiquinol oxidase subunit I [EC:7.1.1.7]
	Cytochrome C oxidase	K00425	cydA; cytochrome bd ubiquinol oxidase subunit I [EC:7.1.1.7]
	Cytochrome bd ubiquinol oxidase	K00426	cydB; cytochrome bd ubiquinol oxidase subunit II [EC:7.1.1.7]
	Cytochrome C oxidase	K00426	cydB; cytochrome bd ubiquinol oxidase subunit II [EC:7.1.1.7]
	Cytochrome C oxidase	K00428	E1.11.1.5; cytochrome c peroxidase [EC:1.11.1.5]
	Cytochrome C oxidase	K02256	COX1; cytochrome c oxidase subunit 1 [EC:7.1.1.9]
	Cytochrome C oxidase	K02258	COX11, ctaG; cytochrome c oxidase assembly protein subunit 11
	Cytochrome C oxidase	K02259	COX15, ctaA; cytochrome c oxidase assembly protein subunit 15
	Cytochrome C oxidase	K02260	COX17; cytochrome c oxidase assembly protein subunit 17
	Cytochrome C oxidase	K02261	COX2; cytochrome c oxidase subunit 2
	Cytochrome C oxidase	K02262	COX3; cytochrome c oxidase subunit 3

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

	Cytochrome C oxidase	K02263	COX4; cytochrome c oxidase subunit 4
	Cytochrome C oxidase	K02264	COX5A; cytochrome c oxidase subunit 5a
	Cytochrome C oxidase	K02265	COX5B; cytochrome c oxidase subunit 5b
	Cytochrome C oxidase	K02266	COX6A; cytochrome c oxidase subunit 6a
	Cytochrome C oxidase	K02267	COX6B; cytochrome c oxidase subunit 6b
	Cytochrome C oxidase	K02268	COX6C; cytochrome c oxidase subunit 6c
	Cytochrome C oxidase	K02269	COX7; cytochrome c oxidase subunit 7
	Cytochrome C oxidase	K02270	COX7A; cytochrome c oxidase subunit 7a
	Cytochrome C oxidase	K02271	COX7B; cytochrome c oxidase subunit 7b
	Cytochrome C oxidase	K02272	COX7C; cytochrome c oxidase subunit 7c
	Cytochrome C oxidase	K02273	COX8; cytochrome c oxidase subunit 8
	Cytochrome C oxidase	K02274	coxA, ctaD; cytochrome c oxidase subunit I [EC:7.1.1.9]
	Cytochrome C oxidase	K02275	coxB, ctaC; cytochrome c oxidase subunit II [EC:7.1.1.9]
	Cytochrome C oxidase	K02276	coxC, ctaE; cytochrome c oxidase subunit III [EC:7.1.1.9]
	Cytochrome C oxidase	K02277	coxD, ctaF; cytochrome c oxidase subunit IV [EC:7.1.1.9]
	Cytochrome C oxidase	K02297	cyoA; cytochrome o ubiquinol oxidase subunit II [EC:7.1.1.3]
	Cytochrome C oxidase	K02298	cyoB; cytochrome o ubiquinol oxidase subunit I [EC:7.1.1.3]
	Cytochrome C oxidase	K02299	cyoC; cytochrome o ubiquinol oxidase subunit III
	Cytochrome C oxidase	K02300	cyoD; cytochrome o ubiquinol oxidase subunit IV
	Cytochrome C oxidase	K02826	qoxA; cytochrome aa3-600 menaquinol oxidase subunit II [EC:7.1.1.5]
	Cytochrome C oxidase	K02827	qoxB; cytochrome aa3-600 menaquinol oxidase subunit I [EC:7.1.1.5]
	Cytochrome C oxidase	K02828	qoxC; cytochrome aa3-600 menaquinol oxidase subunit III [EC:7.1.1.5]
	Cytochrome C oxidase	K02829	qoxD; cytochrome aa3-600 menaquinol oxidase subunit IV [EC:7.1.1.5]
	Mn2+ catalase	K07217	K07217; Mn-containing catalase
	Cytochrome C oxidase	K15408	coxAC; cytochrome c oxidase subunit I+III [EC:7.1.1.9]
	Cytochrome C oxidase	K15862	ccoNO; cytochrome c oxidase cbb3-type subunit I/II [EC:7.1.1.9]
	Cytochrome C oxidase	K18173	COA1; cytochrome c oxidase assembly factor 1
	Cytochrome C oxidase	K18174	COA2; cytochrome c oxidase assembly factor 2

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

	Cytochrome C oxidase	K18175	CCDC56, COA3; cytochrome c oxidase assembly factor 3, animal type
	Cytochrome C oxidase	K18176	COA3; cytochrome c oxidase assembly factor 3, fungi type
	Cytochrome C oxidase	K18177	COA4; cytochrome c oxidase assembly factor 4
	Cytochrome C oxidase	K18178	COA5, PET191; cytochrome c oxidase assembly factor 5
	Cytochrome C oxidase	K18179	COA6; cytochrome c oxidase assembly factor 6
	Cytochrome C oxidase	K18180	COA7, SELRC1, RESA1; cytochrome c oxidase assembly factor 7
	Cytochrome C oxidase	K18181	COX14; cytochrome c oxidase assembly factor 14
	Cytochrome C oxidase	K18182	COX16; cytochrome c oxidase assembly protein subunit 16
	Cytochrome C oxidase	K18183	COX19; cytochrome c oxidase assembly protein subunit 19
	Cytochrome C oxidase	K18184	COX20; cytochrome c oxidase assembly protein subunit 20
	Cytochrome C oxidase	K18185	COX23; cytochrome c oxidase assembly protein subunit 23
	Cytochrome C oxidase	K18189	TACO1; translational activator of cytochrome c oxidase 1
	Cytochrome bd ubiquinol oxidase	K22501	appX; cytochrome bd-II ubiquinol oxidase subunit AppX [EC:7.1.1.7]
	Cytochrome C oxidase	K22501	appX; cytochrome bd-II ubiquinol oxidase subunit AppX [EC:7.1.1.7]
	Cytochrome C oxidase	K24007	soxD; cytochrome aa3-type oxidase subunit SoxD
	Cytochrome C oxidase	K24008	soxC; cytochrome aa3-type oxidase subunit III
	Cytochrome C oxidase	K24009	soxB; cytochrome aa3-type oxidase subunit I [EC:7.1.1.4]
	Cytochrome C oxidase	K24010	soxA; cytochrome aa3-type oxidase subunit II [EC:7.1.1.4]
	Cytochrome C oxidase	K24011	soxM; cytochrome aa3-type oxidase subunit I/III [EC:7.1.1.4]
Sporulation	Glycogen synthesis	K00693	GYS; glycogen synthase [EC:2.4.1.11]
	Sporulation (Actinobacteria)	K02490	spo0F; two-component system, response regulator, stage 0 sporulation protein F
	Sporulation (Actinobacteria)	K02491	kinA; two-component system, sporulation sensor kinase A [EC:2.7.13.3]
	Glycogen synthesis	K03083	GSK3B; glycogen synthase kinase 3 beta [EC:2.7.11.26]
	Sporulation (Actinobacteria)	K03091	sigH; RNA polymerase sporulation-specific sigma factor
	Sporulation (Actinobacteria)	K04769	spoVT; AbrB family transcriptional regulator, stage V sporulation protein T
	Sporulation (Actinobacteria)	K06283	spoIIID; putative DeoR family transcriptional regulator, stage III sporulation protein D
	Sporulation (Actinobacteria)	K06348	kapD; sporulation inhibitor KapD
	Sporulation (Actinobacteria)	K06359	rapA, spo0L; response regulator aspartate phosphatase A (stage 0 sporulation protein L) [EC:3.1.-.-]

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

	Sporulation (Actinobacteria)	K06371	sda; developmental checkpoint coupling sporulation initiation to replication initiation
	Sporulation (Actinobacteria)	K06375	spo0B; stage 0 sporulation protein B (sporulation initiation phosphotransferase) [EC:2.7.-.-]
	Sporulation (Actinobacteria)	K06376	spo0E; stage 0 sporulation regulatory protein
	Sporulation (Actinobacteria)	K06377	spo0M; sporulation-barren protein
	Sporulation (Actinobacteria)	K06378	spoIIAA; stage II sporulation protein AA (anti-sigma F factor antagonist)
	Sporulation (Actinobacteria)	K06379	spoIIAB; stage II sporulation protein AB (anti-sigma F factor) [EC:2.7.11.1]
	Sporulation (Actinobacteria)	K06380	spoIIB; stage II sporulation protein B
	Sporulation (Actinobacteria)	K06381	spoIID; stage II sporulation protein D
	Sporulation (Actinobacteria)	K06382	spoIIE; stage II sporulation protein E [EC:3.1.3.16]
	Sporulation (Actinobacteria)	K06383	spoIIGA; stage II sporulation protein GA (sporulation sigma-E factor processing peptidase) [EC:3.4.23.-]
	Sporulation (Actinobacteria)	K06384	spoIIM; stage II sporulation protein M
	Sporulation (Actinobacteria)	K06385	spoIIP; stage II sporulation protein P
	Sporulation (Actinobacteria)	K06386	spoIIQ; stage II sporulation protein Q
	Sporulation (Actinobacteria)	K06387	spoIIR; stage II sporulation protein R
	Sporulation (Actinobacteria)	K06388	spoIISA; stage II sporulation protein SA
	Sporulation (Actinobacteria)	K06389	spoIISB; stage II sporulation protein SB
	Sporulation (Actinobacteria)	K06390	spoIIIAA; stage III sporulation protein AA
	Sporulation (Actinobacteria)	K06391	spoIIIAB; stage III sporulation protein AB
	Sporulation (Actinobacteria)	K06392	spoIIIAC; stage III sporulation protein AC
	Sporulation (Actinobacteria)	K06393	spoIIIAD; stage III sporulation protein AD
	Sporulation (Actinobacteria)	K06394	spoIIIAE; stage III sporulation protein AE
	Sporulation (Actinobacteria)	K06395	spoIIIAF; stage III sporulation protein AF
	Sporulation (Actinobacteria)	K06396	spoIIIAG; stage III sporulation protein AG
	Sporulation (Actinobacteria)	K06397	spoIIIAH; stage III sporulation protein AH
	Sporulation (Actinobacteria)	K06398	spoIVA; stage IV sporulation protein A
	Sporulation (Actinobacteria)	K06399	spoIVB; stage IV sporulation protein B [EC:3.4.21.116]
	Sporulation (Actinobacteria)	K06401	spoIVFA; stage IV sporulation protein FA
	Sporulation (Actinobacteria)	K06402	spoIVFB; stage IV sporulation protein FB [EC:3.4.24.-]
	Sporulation (Actinobacteria)	K06403	spoVAA; stage V sporulation protein AA
	Sporulation (Actinobacteria)	K06404	spoVAB; stage V sporulation protein AB

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

SOIL Discussions Open Access EGU

	Sporulation (Actinobacteria)	K06405	spoVAC; stage V sporulation protein AC
	Sporulation (Actinobacteria)	K06406	spoVAD; stage V sporulation protein AD
	Sporulation (Actinobacteria)	K06407	spoVAE; stage V sporulation protein AE
	Sporulation (Actinobacteria)	K06408	spoVAF; stage V sporulation protein AF
	Sporulation (Actinobacteria)	K06409	spoVB; stage V sporulation protein B
	Sporulation (Actinobacteria)	K06412	spoVG; stage V sporulation protein G
	Sporulation (Actinobacteria)	K06413	spoVK; stage V sporulation protein K
	Sporulation (Actinobacteria)	K06414	spoVM; stage V sporulation protein M
	Sporulation (Actinobacteria)	K06415	spoVR; stage V sporulation protein R
	Sporulation (Actinobacteria)	K06416	spoVS; stage V sporulation protein S
	Sporulation (Actinobacteria)	K06417	spoVID; stage VI sporulation protein D
	Sporulation (Actinobacteria)	K06437	yknT; sigma-E barrenled sporulation protein
	Sporulation (Actinobacteria)	K06438	yqfD; similar to stage IV sporulation protein
	Sporulation (Actinobacteria)	K07697	kinB; two-component system, sporulation sensor kinase B [EC:2.7.13.3]
	Sporulation (Actinobacteria)	K07698	kinC; two-component system, sporulation sensor kinase C [EC:2.7.13.3]
	Sporulation (Actinobacteria)	K07699	spo0A; two-component system, response regulator, stage 0 sporulation protein A
	Sporulation (Actinobacteria)	K08293	SMK1; sporulation-specific mitogen-activated protein kinase SMK1 [EC:2.7.11.24]
	Sporulation (Actinobacteria)	K08384	spoVD; stage V sporulation protein D (sporulation-specific penicillin-binding protein)
	Glycogen synthesis	K08822	GSK3A; glycogen synthase kinase 3 alpha [EC:2.7.11.26]
	Sporulation (Actinobacteria)	K12576	SPO12; sporulation-specific protein 12
	Sporulation (Actinobacteria)	K12771	SPA; sporulation-specific protein 1 [EC:2.7.11.1]
	Sporulation (Actinobacteria)	K12772	SPD; sporulation-specific protein 4
	Sporulation (Actinobacteria)	K12773	SPR3; sporulation-regulated protein 3
	Sporulation (Actinobacteria)	K12783	SSP1; sporulation-specific protein 1
	Sporulation (Actinobacteria)	K13532	kinD; two-component system, sporulation sensor kinase D [EC:2.7.13.3]
	Sporulation (Actinobacteria)	K13533	kinE; two-component system, sporulation sensor kinase E [EC:2.7.13.3]
	Glycogen synthesis	K16150	K16150; glycogen synthase [EC:2.4.1.11]
	Exopolysaccharide synthesis	K16566	exoY; exopolysaccharide production protein ExoY
	Exopolysaccharide synthesis	K16567	exoQ; exopolysaccharide production protein ExoQ
	Exopolysaccharide synthesis	K16568	exoZ; exopolysaccharide production protein ExoZ

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

	Sporulation (Actinobacteria)	K16947	SPR28; sporulation-regulated protein 28
	Glycogen synthesis	K20812	glgA; glycogen synthase [EC:2.4.1.242]

572

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

573 Table A8. Abundance (in copy number (CN)) of each patch type within each group of gene.

Group	Patch Type	Abundance (in CN)
DNA conservation	Barren	16,153.38
DNA conservation	Nest	47,287.31
DNA conservation	Shrub	46,252.92
DNA conservation	Shrub&Nest	30,860.48
DNA repair and degradation	Barren	12,091.56
DNA repair and degradation	Nest	27,516.74
DNA repair and degradation	Shrub	27,102.20
DNA repair and degradation	Shrub&Nest	20,810.48
Lithotrophs	Barren	11,856.26
Lithotrophs	Nest	73,242.15
Lithotrophs	Shrub	65,602.91
Lithotrophs	Shrub&Nest	29,183.05
Nitrogen	Barren	14,971.68
Nitrogen	Nest	29,265.84
Nitrogen	Shrub	30,326.47
Nitrogen	Shrub&Nest	25,184.32
Organotrophs	Barren	69,296.86
Organotrophs	Nest	16,1271.21
Organotrophs	Shrub	15,0159.89
Organotrophs	Shrub&Nest	90,170.34
Phototrophy	Barren	6,949.817
Phototrophy	Nest	17,722.912
Phototrophy	Shrub	19,736.83
Phototrophy	Shrub&Nest	15,555.43
ROS-damage prevention	Barren	33,660.03
ROS-damage prevention	Nest	93,064.68
ROS-damage prevention	Shrub	88,543.76
ROS-damage prevention	Shrub&Nest	60,566.25
Sporulation capsule & C-storage	Barren	2,129.44
Sporulation capsule & C-storage	Nest	14,338.20
Sporulation capsule & C-storage	Shrub	12,904.33
Sporulation capsule & C-storage	Shrub&Nest	5,514.04

574

575

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

576 Table A9. Chi-square values and p-values of the Dunn tests between patches done on the functional
577 prediction results. Bold numbers are significant (< 0.05)

Comparisons	Nitrogen	ROS-damage	Sporulation	Phototrophy
Control - Nest	**0.0278**	**0.0046**	**0.0014**	**0.0207**
Control - Shrub	**0.0271**	**0.0212**	**0.0073**	**0.0235**
Nest - Shrub	0.4790	0.2545	0.2623	0.4516
Control - Shrub&Nest	**0.0140**	**0.0207**	**0.0421**	**0.0164**
Nest - Shrub&Nest	0.3888	0.2860	0.1046	0.4625
Shrub - Shrub&Nest	0.3653	0.4693	0.2545	0.4134
Chi-square	6.1179803	7.80073892	10.0155172	6.28472906

Comparisons	Organotrophy	DNA Conservation	DNA Repair	Lithotrophy
Control - Nest	0.0513	**0.0038**	**0.0110**	**0.0066**
Control - Shrub	0.2267	**0.0121**	**0.0227**	**0.0320**
Nest - Shrub	0.1746	0.3077	0.3577	0.2391
Control - Shrub&Nest	0.2549	**0.0060**	**0.0085**	0.1165
Nest - Shrub&Nest	0.1653	0.4376	0.4625	0.0991
Shrub - Shrub&Nest	0.4725	0.3668	0.3221	0.2676
Chi-square	2.69926108	9.30837438	7.53793103	6.68743842

https://doi.org/10.5194/soil-2021-29
Preprint. Discussion started: 15 April 2021

Table A10. Results of the adonis analysis of the impact of soil parameters on the bacterial community.

Soil parameter	R2	P-value
NH_4^+	0.03383	0.451
pH	0.01542	0.948
NO_3^-	0.03141	0.512
OM	0.04244	0.263
Water	0.03851	0.355
P	0.03863	0.343