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Perennials but not slope aspect affect the diversity of soil bacterial communities in the northern Negev Desert, Israel

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Abstract. Underneath the canopy of perennials in arid regions, moderate soil temperature and evaporation, as well as plant litter create islands of higher fertility in the low-productivity landscape, known as 'resource islands'. The sparse distribution of these resource islands is mirrored by soil microbial communities, which mediate a large number of biogeochemical transformations underneath the plants. We explored the link between the bacterial community composition and two prevalent desert shrubs, *Zygophyllum dumosum* and *Artemisia herba-alba*, on northern- and southern-facing slopes in the northern highlands of the Negev Desert (Israel), at the end of a drought winter mild rainy season. We sequenced the bacterial community and analysed the physicochemical properties of the soil under the shrub canopies and from barren soil in replicate slopes. The soil bacterial diversity was independent of slope aspect, but differed according to shrub presence or type. Links between soil bacterial community composition and their associated desert shrubs were found, enabling us to link bacterial diversity with shrub type or barren soils. Our results suggest that plants and their associated bacterial communities are connected to survival and persistence under the harsh desert conditions.

Additional keywords: 16S rRNA, desert plants, next generation sequencing, ecosystem engineer, fertility island.

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Introduction

Arid landscapes are typified by barren soil punctuated by areas of sparse vegetation consisting of hardy perennials whose rhizospheres are dominated by microorganisms. These areas are called resource or fertility islands (Noy-Meir 1973; Schlesinger *et al.* 1996) typified by nutrient increase and moderated temperatures (Carrillo-Garcia *et al.* 2000a, 2000b). One parameter that significantly affects the composition, structure, and density of desert plant communities is slope aspect (the compass direction that the slope faces) due to the differences in solar radiation. In the northern hemisphere, vegetation abundance and structure increase significantly in north- compared with south-facing slopes despite the short distance separating them (Sternberg and Shoshany 2001; Drezner and Lazarus 2008). Bacterial dispersion was also shown to be influenced by slope aspect in a Mediterranean ecosystem (known as an evolution canyon), demonstrated by different genomic and physiological features exhibited by *Bacillus simplex* on the northern compared with southern slopes (Sikorski and Nevo 2005). Likewise, studies in the Colorado Plateau and Chihuahuan, Sonoran, and Mohave Deserts showed that north-facing slopes support more biomass and higher species numbers of arid soil biocrust and lichen

than comparable south-facing slopes (Iii *et al.* 1977; Bowker *et al.* 2006).

The distribution of arid soil microbial communities was correlated with the sparse shrub vegetation in numerous studies (reviewed in Bashan and de Bashan 2010). In the Negev (Saul-Tcherkas and Steinberger 2011; Yu and Steinberger 2011; Berg *et al.* 2015) and Chihuahuan (Herman *et al.* 1995) Deserts, bacterial diversities in barren and intra-canopy patches were significantly different. In the arid lands of Australia, plant-covered patches of soil exhibited an increase in the abundance and richness of protozoan communities (Robinson *et al.* 2002). Similarly, in the semiarid environments of Mexico (Camargo-Ricalde and Dhillion 2003) and Chile (Aguilera *et al.* 2016), one particular population of fungi was closely associated with the presence of plants, whereas another was detected in barren soil (Steven *et al.* 2014a).

Bacterial diversity may be governed not only by resource islands, but also by shrub species and seasonality. In arid-soil studies that compared bacterial diversity in barren soil and under the canopy of shrubs *Hammada scoparia* (Berg *et al.* 2015) or *Reaumuria negevensis* (Saul-Tcherkas and Steinberger 2011), the detected communities differed in accordance with patch type even though samples were collected in close proximity.

Likewise, markedly different bacteria were isolated from under the canopies of *Atriplex halimus* and *Zygophyllum dumosum* although both perennials grew side by side in the sampling sites (Kaplan *et al.* 2013). The difference in bacterial groupings corresponded to the plant type where the soil was sampled and not to the abiotic conditions. A similar result was found for the soil bacterial community under the shrub *H. scoparia*, which differed from communities found under artificial shrubs (Berg *et al.* 2015). The observed changes in microbial communities could be related to root exudates (Steven *et al.* 2014b), but studies conducted thus far have been limited in scope. None has yet comprehensively analysed the diversity and community composition of bacteria in desert soil patches populated by various perennial species growing on different slope aspects.

In this study, we explored the impact of slope exposure and plant species on bacterial diversity of arid soils and the possible interactions between these two parameters. We hypothesised that the bacterial communities will change in accordance with slope as has been demonstrated for vegetation (Sternberg and Shoshany 2001). We also predicted that soil bacterial communities from the inter- and intra-shrub patches would significantly differ, yet the inter-shrub patches were predicted to have more in common with each other than with intra-shrub patches. To test our hypotheses, soil microbial diversity and abundance were studied at the end of a mild rainy season in the northern Negev Desert. Specifically, barren desert soils and soil under the canopies of two dominant perennials, *Z. dumosum* and *Artemisia herba-alba* (Asteraceae), were studied with the goal of assigning bacterial diversity and community composition in the different soil patches.

In the Negev Desert, typical of hot desert habitats, the slopes are dominated by communities of dwarf and semi-dwarf shrubs, among which sparse populations of annuals develop during the winter (Noy-Meir 1973). The perennials selected for this study, *Z. dumosum* and *A. herba-alba*, were both shown to dominate the rocky hills slopes of the northern and central Negev (Friedman 1971); although *Z. dumosum* was shown to dominate the south-facing slopes, *A. herba-alba* dominates the northern slopes (Friedman *et al.* 1977). *Z. dumosum* (Zygophyllaceae) is a Saharo-Arabian shrub forming a compact multi-branched canopy either ascending or spreading low to the ground (Granot *et al.* 2009). It was shown to possess a remarkable survival capacity under extremely dry habitats, with a cumulated amount of 11 mm of annual rain sufficient for growth resumption and bud emergence (Granot *et al.* 2009). *A. herba-alba*, commonly known as white wormwood, is a dwarf perennial shrub growing in semiarid and arid deserts of the Middle East. This plant has been widely used in folk medicine for the treatment of diabetes and hyperglycemia (Harlev *et al.* 2013).

Materials and methods

Site description and sample collection

To study plant-mediated changes in bacterial community composition, sampling was conducted in the northern Negev Desert (average annual precipitation, 90 mm). A hilly area (500–600 m above sea level) near the Sde Boker campus

(30°51'26.3"N, 34°46'01.6"E) was chosen because it featured similarly positioned northern and southern slopes in three consecutive rocky hills populated by *Z. dumosum* and *A. herba-alba*. Sampling was conducted at the end of the rainy season in April 2012 following a drought year (<65 mm annual rain).

For sampling, we placed 10 m × 10 m quadrants at approximately mid-hill for each of the six slopes (one quadrat per slope) and sampled three patch types: inter-shrub, intra-*Z. dumosum*, and intra-*A. herba-alba* soil. Eight randomly selected subsamples were taken from each patch type in each of the six quadrats. The eight subsamples from each patch type were combined to represent an average for that slope, resulting in a total of three composite soil samples per slope.

Approximately 100-g subsamples were collected after removing the crust and litter from the top 5 cm, placed into sterile plastic bags (Whirl-Pack, Nasco, Fort Atkinson, WI, USA), and stored at 4°C. All soil samples were transported to the laboratory and homogenised within 24 h of sampling. The subsamples were combined according to slope and patch type amounting to 18 samples (six slopes × three patch types). A 50-g subsample was stored at –80°C for molecular analysis and the remainder of the soil was used for physicochemical analysis.

Soil physicochemical parameters

About 500 g of the collected samples were chemically analysed as previously described (Bachar *et al.* 2012) to assess changes in important soil parameters, such as pH, electrical conductivity (EC), soil total organic matter, and ammonium, nitrate, phosphorus, potassium, and chloride ions. Values of pH and EC were measured in a saturated soil paste extract. Phosphorus ions were extracted from the soil by the Olsen and Watanabe (1957) extraction method (with 0.5 mol L⁻¹ NaHCO₃) and analysed colourimetrically with an autoanalyser (ASX-520 series, Quickchem 8500 series 2, Lachat instruments, Milwaukee, WI, USA). Potassium, extracted by CaCl₂, was measured by flame atomic absorption spectrophotometry (Flame photometer M410; Sherwood Scientific, Cambridge, UK). Chloride was measured in saturated soil paste extract with a chloride meter (Chloride analyzer 926; Sherwood Scientific, Cambridge, UK). Soil organic matter content was estimated by the weight loss on ignition method.

DNA extraction

Total nucleic acids were extracted from the soil samples according to a previously described method (Angel and Conrad 2009) and the extract was purified using a DNA Purification Kit (Bioneer, Seoul, South Korea). The DNA samples were stored at –80°C for further analysis.

Quantitative PCR

In order to estimate the number of 16S rRNA units in the soil samples, a calibration curve of a known number of rRNA gene copies was constructed as follows. Environmental DNA was amplified using the S-D-Bact-0341-b-S-17/S-D-Bact-0515-a-A-19 bacterial universal primer set (Klindworth *et al.* 2013). This primer set was evaluated in the Silva database (<https://www.arb-silva.de/>) and found to cover 91.2% of

known sequences within total bacteria and 0% for archaea and fungi (Klindworth *et al.* 2013). Standards were generated from amplicons of *Escherichia coli* using the bacterial universal primer set cloned in a high copy-number plasmid. Each qPCR reaction contained the following mixture: 10 μ L of SYBR Absolute Blue qPCR Rox Mix (Thermo-Fisher, Waltham, MA, USA), 400 nmolL⁻¹ of each primer (Metabion, Munich, Germany), 5 μ L of template cDNA, and 3 μ L of molecular grade water (HyLab, Rehovet, Israel). The qPCR assay was performed under the following conditions: 95°C for 15 min, followed by 35 cycles of 95°C for 10 s, 60°C for 15 s, and 72°C for 30 s of extension.

Amplification of 16S rRNA genes, and library generation

The genomic DNA was amplified using the 16S rRNA gene V4, V5 regions primer set (S*-Univ-0515-a-S-19/S-D-Arch-0786-a-A-20), adapted for MiSeq (Illumina, San Diego, CA, USA) sequencing by adding nine extra bases that included the Illumina flow cell adaptor sequences. The reverse amplification primer also contained a 12-base barcode sequence that supports pooling of up to 2167 different samples in each lane (Caporaso *et al.* 2011, 2012). The PCR amplification reaction contained 12 μ L of PCR Water (MoBio, Carlsbad, CA, USA), 10 μ L of HotMasterMix (5Prime, Hilden, Germany), 2 μ L primers (each at 200 pmol final concentration), and 1 μ L of template DNA. The conditions for PCR were as follows: 94°C for 3 min, 35 cycles at 94°C for 45 s, 50°C for 60 s, and 72°C for 90 s, and a final extension of 10 min at 72°C. PCR amplifications were done in triplicate, pooled, and quantified using PicoGreen (Life Technologies, Carlsbad, CA, USA) according to the manufacturer's instructions. After quantification, different volumes of each amplicon were pooled together such that each amplicon was equally represented. The pool was then cleaned up using UltraClean[®] PCR Clean-Up Kit (MoBio), quantified using the Qubit (Life Technologies) method, and diluted to 2 nM, denatured, and diluted to a final concentration of 4 pmol with a 30% PhiX spike for loading on the MiSeq sequencer. Amplicons were then sequenced in a 251 bp \times 12 bp \times 251 bp MiSeq run using custom sequencing primers and procedures previously described (Caporaso *et al.* 2012).

Sequencing analysis

Of the total number of sequences, ~32% mismatched their barcode with the sample barcodes, 8% were less than 75 bp in length, and 0.05% consisted of ambiguous bases. Sequences that passed these filters were de-multiplexed based on exact matches to the barcode sequences. The QIIME suite was used for the analysis of the samples. The sequences were clustered into 97% identity operational taxonomic units (OTUs) with the UCLUST reference-based method (Edgar 2010) and by comparison against the greengenes core set of aligned sequences (DeSantis *et al.* 2006). One representative from each OTU was selected for further analysis. Sequences were aligned using PyNAST (Caporaso *et al.* 2010) and chimeric sequences were removed with ChimeraSlayer (Haas *et al.* 2011). OTUs were classified taxonomically with the Mothur classifier (Schloss *et al.* 2009) using RDP v9 (<http://rdp.cme.msu.edu/>). All QIIME scripts were from the 1.7.0 release (Kuczynski *et al.* 2012) and run using default parameters unless otherwise stated. Plots were produced in the R environment based on the QIIME results. Diversity in the samples was estimated using the unweighted UniFrac method (Lozupone *et al.* 2011) on a subset of the sequences (containing 66 137 sequences each) to yield similar coverage (see Fig. S1 available as Supplementary Material to this paper). Principal component analysis was generated based on the distances between the samples as determined by UniFrac (Lozupone *et al.* 2011). ANOSIM tests were performed with the QIIME using `categories.py` script. A heatmap was created in QIIME using `make_otu_heatmap.py`. For technical reasons, we did not use all the barren soil samples.

Results

Physicochemical parameters

We found no significant differences between the soil physicochemical parameters of the northern compared with the southern slopes ($P > 0.05$), except for ammonium ($t_{(12)} = 2.17$, $P = 0.01$) (Table 1). The physicochemical characteristics of the soil samples taken from under the *Z. dumosum* canopy at the end of the rainy season were distinct from the samples taken

Table 1. Physicochemical analysis of soil samples collected under the canopies of *Zygophyllum dumosum* and *Artemisia herba-alba* and in barren soil. Values represent average \pm standard deviation. EC = Electric conductivity; OM = organic matter; WC = water content; *Statistical analysis of the differences between patches was performed with one-way ANOVA; **Statistical analysis between slopes was performed using two-tailed *t*-test assuming unequal variance

Soil parameters	Units	Plant type						Among patches*	Between slopes**	
		<i>Zygophyllum dumosum</i>		<i>Artemisia herba-alba</i>		Northern (n=3)	Southern (n=3)			
		Northern (n=3)	Southern (n=3)	Northern (n=3)	Southern (n=3)					
Ammonium-N	mg kg ⁻¹	17 \pm 1.5	14.8 \pm 1.6	15.7 \pm 1.1	15.2 \pm 2.7	16.7 \pm 1.7	12.1 \pm 1.9	0.825	0.45	0.01
Nitrate-N	mg kg ⁻¹	75.5 \pm 4.5	74.2 \pm 25.0	40.8 \pm 13.2	29.5 \pm 29.6	11.9 \pm 19.4	23.9 \pm 16.2	8.37	0.005	0.88
Phosphorus	mg kg ⁻¹	15.2 \pm 1.0	17.5 \pm 4.5	12.6 \pm 3.5	12.8 \pm 2.9	14.5 \pm 3.2	6.9 \pm 1.9	4.54	0.02	0.56
Potassium	mg kg ⁻¹	289.8 \pm 52.2	230.4 \pm 32.2	257.9 \pm 14.3	206.1 \pm 26.2	138.4 \pm 34.2	91.9 \pm 28.3	25.02	<0.001	0.14
Chloride	mg kg ⁻¹	1333.3 \pm 292.8	1133.3 \pm 344.9	377.3 \pm 470	123.3 \pm 108.0	57 \pm 78.0	129 \pm 96.0	31.25	<0.001	0.68
EC	dS m ⁻¹	4.4 \pm 0.8	3.3 \pm 0.6	1.8 \pm 1.3	1.1 \pm 0.6	0.6 \pm 0.7	1 \pm 0.9	11.14	0.001	0.58
pH		7.7 \pm 0.1	7.8 \pm 0.1	8 \pm 0.1	8 \pm 0.1	8 \pm 0.1	7.9 \pm 0.1	11.14	0.001	0.72
OM	%	4.4 \pm 0.5	3.6 \pm 1.5	2.8 \pm 0.7	2.3 \pm 0.6	2.1 \pm 0.8	2.3 \pm 1.1	10.76	0.001	0.51
WC	%	2.6 \pm 0.6	2 \pm 0.4	2.3 \pm 0.2	2 \pm 0.5	2.5 \pm 1.2	3.3 \pm 0.6	1.98	0.17	0.92

from under *A. herba-alba* and from barren soil in terms of organic matter, nitrate, potassium, and chloride concentrations, and EC and pH (Table 1). In contrast, ammonium, phosphorus, and water content showed no differences among the patches. Potassium concentrations exhibited a unique pattern in that its levels in all plant-covered soils were elevated compared with the barren soils (Table 1).

Bacteria 16S rRNA gene abundance

The *Z. dumosum* supported a higher number of rRNA gene copies in the soil under its canopy, compared with the barren soil and the soil collected under *A. herba-alba* (Fig. 1 and Table 1). These differences in gene copies were significant ($F_{(2, 15)} = 6.84$, $P = 0.01$). In contrast, slope aspect did not affect bacterial abundance supporting $4.4 \times 10^{10} \pm 3.3 \times 10^{10}$ and $3.8 \times 10^{10} \pm 1.3 \times 10^{10}$ rRNA gene copies per gram of soil taken from the southern and northern slopes, respectively ($t_{(16)} = 2.11$, $P = 0.6$).

Bacterial diversity

We extracted the DNA from the soil samples and estimated the number of 16S rRNA gene copies under the different shrub canopies and barren soil. The sequencing effort yielded 16 samples (two samples taken from barren soil failed) and 1 600 729 quality sequences were obtained (see Materials and methods). When grouped at 97% similarity level, these clustered into 84 470 OTUs. Of these OTUs, 10 244 (or 12.1%) were earmarked as chimeric and the remaining OTU sequences were divided unevenly between the samples, ranging from 66 137 to 229 480 sequences per sample (see Table S1 available as Supplementary Material to this paper). Of the 74 226 OTUs obtained, 889 were unclassified, 296 were classified as archaea, and 73 041 as bacteria. Of the 73 337 OTUs classified as archaea or bacteria, 14 551 could not be classified to known phyla. Fifty percent of the OTUs were represented by a single sequence in the entire dataset and

64% of the OTUs were found in a single soil sample. At the sampling depth used in this study, the coverage did not quite reach saturation (Fig. S1).

Bacterial community composition

Our results suggest that the bacterial community in soil samples taken from under *Z. dumosum* plants clustered separately from soil taken from under *A. herba-alba* and from barren soil ($r = 0.77$, $P = 0.001$) (Fig. 2a), but was independent of the slope aspect ($r = -0.44$, $P = 0.62$) (Fig. 2b). To elucidate the contribution of the perennials to the soil bacterial taxa, we clustered the samples in a heatmap (Fig. 3), which showed that the relative abundance of Acidobacteria, Betaproteobacteria, Cyanobacteria, Deltaproteobacteria, and Verrucomicrobia increased in soils collected under *A. herba-alba* and in barren soil, whereas Alphaproteobacteria, Bacteroidetes, Gammaproteobacteria, and Firmicutes were more prevalent in soils under the *Z. dumosum* canopy (Fig. 3). We further determined which group had the highest influence on the uniqueness of the *Z. dumosum* sample communities. To that end, we performed non-metric multidimensional scaling (NMDS) on the OTU table and assigned taxa (normalised to the sum of sequences per sample, so that the total count per sample equalled 1) (Fig. 3). The pattern whereby soil communities under the canopy of *Z. dumosum* clustered separately was constant, and could be attributed to the changes in the abundance of Firmicutes and Alpha-proteobacteria (Fig. 3). Other groups, such as Gamma-proteobacteria and Bacteroidetes, were also more abundant under the *Z. dumosum* canopy (Table S2).

Discussion

The results indicated that the slope aspect did not determine the subterranean bacterial community (Fig. 2b) in contrast to studies suggesting that radiation and increased evaporation in south-facing slopes yielded decreased in the microbial communities compared with northern slopes (Iii *et al.* 1977;

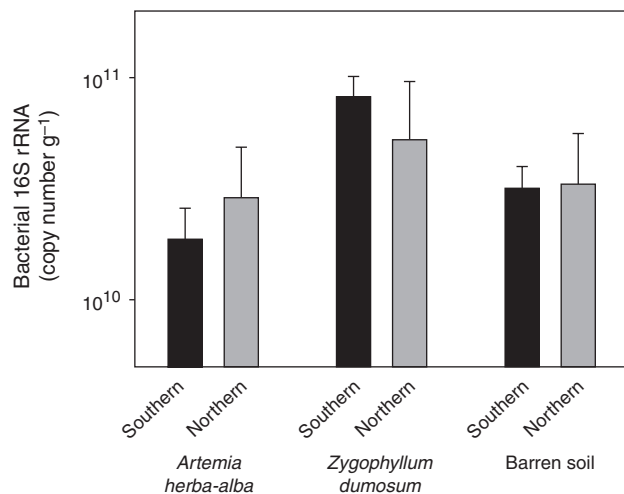


Fig. 1. Bacterial copy numbers in arid soil samples. Spatial distribution of the abundance of total bacteria 16S rRNA copy numbers under the canopies of *Zygophyllum dumosum* and *Artemisia herba-alba* and in barren soil. The bars are average of duplicate measurements of triplicate samples at each time point \pm standard deviation.

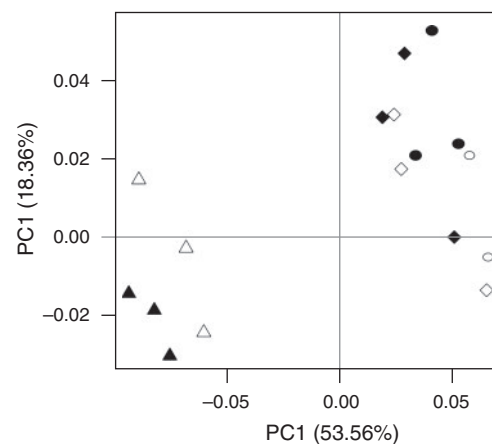


Fig. 2. Cluster analysis of the soil bacterial community based on UniFrac. Differences are depicted by patch type including barren soil (circles), *Zygophyllum dumosum* (triangles), and *Artemisia herba-alba* (diamond), as well as slope direction including northern (open symbols) and southern slopes (closed symbols). Of the variance, 53.6% was explained by principal component 1 (PC1) and 18.4% by PC2.

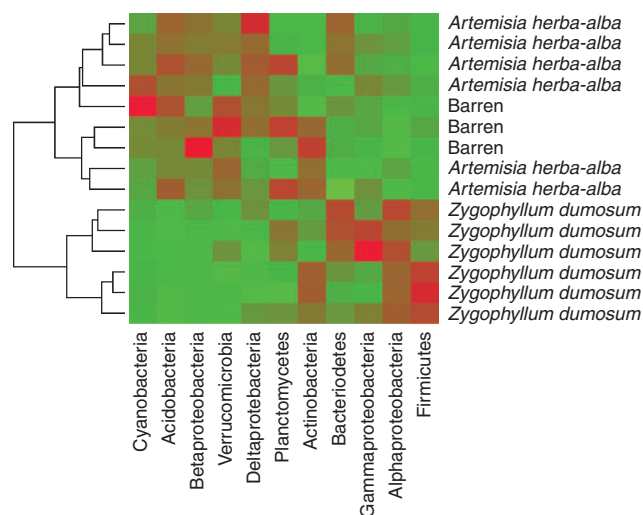


Fig. 3. Heatmap linking bacterial groups with patch type. Rows refer to the sample origin and columns to the affiliated bacterial phylum or class. The clustering of the samples (rows) is based on the Manhattan distance measure, but was stable when using other distance measures. The colour depicts the relative abundance of OTUs per phylum or class normalised between samples. The colour scale range between rare (green) and abundant (red) though the numbers used are bacterial group dependent and thus arbitrary. The ordering of the bacterial phylum/class is based on the NMDS analysis.

Sikorski and Nevo 2005; Bowker *et al.* 2006). We hypothesise that microorganisms residing in the soil surfaces would be directly exposed to the differences in solar radiation, temperature, and precipitation resulting from the slope aspect (Noy-Meir 1974). Reports have shown that biocrust and lichen increase in diversity and abundance in the north-facing slopes that are less exposed to radiation (Iii *et al.* 1977; Bowker *et al.* 2006). In contrast, the top soil (collected after the removal of the crust and litter) under the canopy of *Z. dumosum* and *A. herba-alba* did not differ in physicochemical parameters, bacterial abundance, diversity, and community composition (Figs 1–3).

Soil was sampled at the end of a drought winter season with 30% less rain than the annual average, which has been shown to result in a decrease in annuals' biomass and limited growth resumption and bud emergence for annuals (Reynolds *et al.* 1999). These stressful conditions are predicted to lessen the biotic and abiotic effects of resource islands (Bachar *et al.* 2012). The results suggest that the soil bacterial community composition detected under *A. herba-alba* and barren soil overlapped (Figs 2, 3) similar to the diversity patterns depicted at the end of the dry season (Martirosyan *et al.* 2016). The results suggest that this annual no longer served as a resource island to its soil-associated communities. In contrast, the soil diversity under *Z. dumosum* differed from the other patches. The canopy of *Z. dumosum* is larger than that of *A. herba-alba* and the foliage more pronounced (Friedman 1971); moreover, this annual was shown to be highly resistant to drought conditions (Granot *et al.* 2009), indicating that despite the drought, *Z. dumosum* was able to maintain its ecosystem function.

The observations presented here are in agreement with previous studies (Saul-Tcherkas and Steinberger 2011; Yu and Steinberger 2011; Bachar *et al.* 2012; Berg *et al.* 2015) showing

that in hot deserts the perennial canopy creates a 'resource island' whereby plant spatial heterogeneity is mirrored by subterranean microbial diversity, abundance, and productivity. We propose that resource islands are plant-dependent: the microbial communities under plants that are less tolerant to desiccation, such as *A. herba-alba* (Friedman *et al.* 1977), are unable to support their unique community and end up sharing the majority of their communities with the barren soil. In contrast, desiccation resistant annuals, such as *Z. dumosum* (Granot *et al.* 2009), maintain their community even under severe drought. Finally, plant-associated resource islands are the major contributors to arid soil bacterial composition whereas slope exposure, although significant to plant dispersal and diversity (Sternberg and Shoshany 2001; Sikorski and Nevo 2005), could not be linked to the bacterial diversity or community composition.

Conflicts of interest

The authors declare no conflicts of interest.

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