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Functional metabolic diversity of the bacterial community in undisturbed resource island soils in the southern Sonoran Desert

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Abstract

Resource islands (RIs), a natural revegetation phenomenon in arid lands, consist of a single nurse tree or few large shrubs and numerous understory nurslings. We analyzed 18 individual mesquite RIs for plant diversity and richness, area, trunk diameter (reflecting age), soil characteristics, physiological functionality of microbial populations, and interactions among these variables. Nursing Capacity reflected the availability of habitat and was positively correlated to plant richness, but not to plant diversity. No relationship between plant diversity and bacterial diversity was found. The structure of the bacterial communities of RIs differed from the bacterial communities of bare areas, which showed greater richness and diversity compared with those of RIs. The Nursing Capacity of the RIs was related to plant richness and accompanied by variations in soil properties. A high correlation was found by substrate utilization analysis between metabolic parameters of bacteria and diversity and richness of plants in the RIs. RI bacterial communities were more metabolically active and could degrade different carbon sources than bare area communities. RI bacterial communities contained species with greater capability to metabolize diverse carbon substrates in soil with more organic matter. Bacteria from low, medium, and high plant diversity areas were cultured and found to belong to four bacterial families. This study demonstrates that numerous parameters interact, but not every parameter significantly affected bacterial activity in the RI.

KEYWORDS

arid soils, bacterial community, desert vegetation, mesquite, resource islands

1 | INTRODUCTION

Two natural microbial–floral phenomena dominate functionality in hot and cold desert ecosystems: (a) resource islands (RIs), which are characterized by a single anchor shrub or a few shrubs that significantly change their surroundings by accumulating plant resources under their canopy, thereby producing improved conditions for the establishment and growth of other plant species, and (b) biological soil crusts that establish and develop in open areas between islands of vegetation. Even though an individual area of either can be relatively small, these open areas occur on very large scales in many deserts, and both have integral microbial (bacteria, fungi, and arbuscular mycorrhizal [AM] fungi) communities. Without microbes, ecosystems cannot be created or function (Bashan & de Bashan, 2010; Makhalanyane et al., 2015). Over a relatively long period of time, desert RIs accumulate resources, thus stimulating microbial activity, and together, the RIs and the microbial activity lead to better growth of vegetation in nutrient-deficient areas (Flores & Jurado, 2003). The process of this type of 'habitat engineering' eases the initial establishment and growth of other plant species, whose survival often depends on the availability of a central and larger anchor nurse plant.

Several tree species are better builders of RIs in hot deserts than others. In the central Monte Desert of Argentina, the most common RI shrub is the mesquite *Prosopis flexuosa*, which supports numerous shrubs under its canopy (Rossi & Villagra, 2003). In the southern Sonoran Desert in the Baja California Peninsula of Mexico, over 20-year-old

nurse legumes, particularly mesquite amargo (*Prosopis articulata*) and palo fierro (*Olneya tesota*), support the largest number of nurslings under their respective canopies (Carrillo-Garcia, Leon de la Luz, Bashan, & Bethlenfalvay, 1999), whereas in the central Sonoran Desert in Arizona (USA), velvet mesquite trees (*Prosopis velutina*) serve the same purpose (Nobel, 1988; Schade & Hobbie, 2005). In the Tehuacán Desert and in Zapotitlán Salinas in Mexico, mesquite (*Prosopis laevigata*), palo verde (*Parkinsonia praecox*), and huizache (*Acacia tortuosa*) establish numerous RIs that dominate alluvial terraces (González-Ruiz, Rodríguez-Zaragoza, & Ferrera-Cerrato, 2008; Reyes-Reyes et al., 2002; Rodríguez-Zaragoza et al., 2008).

RIs characteristically have high water-holding capacity, lower evaporation rates, and accumulate nutrients via decomposition of organic matter. They have a higher pH, more nitrogen, and soil characteristics such as low bulk density, better aeration and finer texture, and a stable aggregate structure (Carrillo-Garcia et al., 1999; Cross & Schlesinger, 1999; Rango, Tartowski, Laliberte, Wainwright, & Parsons, 2006; Schade & Hobbie, 2005; Schlesinger, Raikes, Hartley, & Cross, 1996). Moreover, RIs have an established biological resource, namely, high mycorrhizal potential compared with the surrounding areas (Azcón-Aguilar et al., 2003; Bashan, Davis, Carrillo, & Linderman, 2000; Camargo-Ricalde & Dhillion, 2003; Ferrol, Calvente, Cano, Barea, & Azcón-Aguilar, 2004; He, Mouratov, & Steinberger, 2002). All resources, especially higher water content, facilitate desert plant growth (Bacilio, Vazquez, & Bashan, 2011; Carrillo-Garcia, Bashan, & Bethlenfalvay, 2000; Carrillo-Garcia, Bashan, Diaz-Rivera, & Bethlenfalvay, 2000; Muñoz, Squeo, León, Tracol, & Gutiérrez, 2008) and simultaneously accelerate the proliferation of heterotrophic bacteria in desert soils (Aguilera, Gutiérrez, & Meserve, 1999; González-Ruiz et al., 2008; Herman, Provencio, Herrera-Matos, & Torrez, 1995; Rodríguez-Zaragoza et al., 2008).

The water–soil attributes, which make the RIs an essential component of desert life, favor active communities of soil microorganisms that include plant growth-promoting bacteria such as *Rhizobium* sp., *Sinorhizobium* sp., *Azospirillum* sp., and AM fungi. All create additional changes in the soil and enhance its productivity. The microbes establish a network for nutrient exchange among plants and promote nutritional ion and cation solubilization, soil-to-plant transfer of mineral nutrients, and plant-to-soil transfer of organic compounds. Together, these factors lead to alterations in the composition of the vegetation (Bachar, Soares, & Gillor, 2012; Bashan et al., 2000; Carrillo-Garcia et al., 1999; Herman et al., 1995; Kaplan et al., 2013; Rango et al., 2006; Yu & Steinberger, 2011).

The ground surface area of RIs in the southern Sonoran Desert—from a few m^2 to 50 m^2—depends on the shrub that anchors it. The RIs support a great variety and number of plant species as nurslings under the canopy of the main nurse tree (Carrillo-Garcia et al., 1999). However, very little information regarding the number and species of bacteria or their function in the RIs is known (Bachar et al., 2012; Ben-David, Zaady, Sher, & Nejidat, 2011; Kaplan et al., 2013). In this study, we analyzed relationships above and belowground in the RIs by correlating nurse characteristics, ecological attributes of the understory plants, and the structure and metabolic activity of bacterial soil communities. Two hypotheses were developed: (a) The increased diversity of plants in the RIs, the age of the RIs, and nutrient concentrations will have a positive impact on both bacterial diversity and metabolism; (b) bacterial inoculum potential in the RI is expressed only when favorable nutritional and environmental variables are locally presented to stimulate specific bacterial populations. To test these hypotheses, we chose 18 mesquite RIs from the same location. We studied the resources (ammonium, nitrate, organic matter, soluble P, and soil texture) supporting plant and bacteria growth, measured bacteria diversity by polymerase chain reaction-denaturing gradient gel electrophoresis (PCR-DGGE), and analyzed the metabolic profiles of soil microbial communities by measuring variable carbon source utilization.

2 | MATERIAL AND METHODS

2.1 | Study area and RI sampling and plant diversity

This study was conducted in an undisturbed, protected desert area (Estación Biológica 'Dra. Laura Arriaga Cabrera') located 17 km northeast of the city of La Paz, Baja California Sur, Mexico, at 24°07′N, 110°25′W (Figure S1a–c). The climate of the area is arid with an annual mean rainfall of 180 mm (Carrillo-Garcia et al., 1999). It is characterized by an extended drought period of 8 months, and extreme temperatures and solar irradiation during the summer (~40–45 °C at midday, up to 2,500 μmol photons·m^{-2} s^{-1}). Sampling was performed in November 2013, after the growing season of mostly perennials and herbs that took place in response to monsoon rains extending from July to October and contributing up to 81% of the annual precipitation (Figure S1d). Average temperatures during the sampling period were 22 °C with a dew point of 16 °C. The study area vegetation is composed of sarcocaulescent desert scrub (Carrillo-Garcia et al., 1999; León de la Luz, Pérez-Navarro, & Breceda, 2000). The soil is loamy fine sand, and plant water availability (%) is 2.9–3.9 (Bashan et al., 2000; Carrillo-Garcia et al., 1999). According to the model of Saxton, Rawls, Romberger, and Papendick (1986), the estimated field capacity of soil under the canopy of mesquite in these RIs varies to a small extent, 0.12 ± 0.03 cm^3 water·cm^{-3} soil and a drainage rate of 9.2 ± 3.5 cm hr^{-1} (Table S4). Eighteen RIs were defined as areas below the canopy of mesquite showing differences in soil color compared with surrounding soil and the presence of nursling plants below the canopy (Bashan & de Bashan, 2010, details in figure S1c). Two characteristics of the RI were considered: (a) the RI area, expressed as the canopy coverage calculated by the formula of an ellipse using two transverse lengths through the center of the RI, and (b) the trunk diameter 50 cm above soil, which was used as an indicator of mesquite maturity. Trunk diameter and RI area were combined in a factor designated as Nurse Capacity (NC), which indicated an increased likelihood of habitat availability for plants and microorganisms.

$$\mathrm{NC} = \text{Resource Island Area} \times \text{Trunk diameter}. \quad (1)$$

Therefore, the RIs were numbered in an increasing magnitude of Nursing Capacity. The total number of plants growing under the canopy of mesquite and their identity were recorded.

Plant richness (S) was expressed as the total number of observed species in each RI. Plant diversity was calculated using the Shannon index (Kent & Coker, 1992).

$$H' = -\Sigma p_i \ln(p_i). \quad (2)$$

Each RI was considered a plant community. Therefore, p_i is the relative abundance of each plant species in the community.

2.2 | Soil samplings

Four equidistant points (1 m) from the trunk in a cardinal direction were marked and chosen as representative of the RI. The top surface of the soil was carefully removed to avoid the potential interference of stones, dead leaves, and animal droppings. Soil samples from the first 0–10 cm (about 600 g per sample) were removed by shovel and mixed well in a plastic bag. Ten grams of the composite samples of soil were placed in a sterile 15-ml tube for bacterial community analysis (molecular biology and physiological profiles). Five bare soil samples, taken as for the RI samples (controls), were collected ≥3 m away from any plant. Samples were stored overnight at 4 °C for soil physical–chemical analyses and processed by standard procedures, and stored at −80 °C for molecular analyses. For bacterial physiological analysis, samples were processed immediately (within 2 hr).

2.3 | Soil analyses

Ammonia quantity was analyzed using a phenol-hypochlorite method (Solorzano, 1969). Nitrates were quantified by the Morris and Riley method with modifications (Strickland & Parsons, 1972). Organic matter was analyzed by estimation of the soil organic carbon using a chromic acid wet oxidation method (Walkley & Black, 1934). Soluble phosphorus was quantified by the Mehlich method with modifications (Jackson, 1958). Ammonia, nitrate, and soluble P samples were transferred to microplates and read in a Multiskan Ascent plate reader (Labsystems-Fisher, Vantaa, Finland). Soil texture was determined using a Laser Scattering Particle Size Distribution Analyzer (LA-950V2, Horiba, Japan).

2.4 | DNA extraction and PCR-DGGE of non-cultivatible bacteria

The assessment of non-cultivatible bacteria aimed to characterize the bacterial communities in terms of structure, composition, and ecological attributes (richness and diversity). Approximately 0.5 g of soil samples were used to isolate total environmental DNA using a Fast DNA SPIN for soils kit (MP Biomedicals, Irvine, CA, USA). The binding matrix DNA complex was rinsed with 200 µl of guanidine thiocyanate (Fluka Sigma-Aldrich, Buchs, Switzerland) to remove humic acids (Lopez, Bashan, Trejo, & de-Bashan, 2013). For DNA quantification, a NanoDrop 2000c/2000 UV–Vis Spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA) was employed.

PCR was performed using 15 ng of total DNA. The highly variable V6–V8 regions of microbial 16S rDNA were amplified using the primer 984F containing a GC-clamp (5′-gc-AACGCGAAGAACCTTAC-3′) and 1378R primer (5′-CGGTGTGTACAAGGCCCGGGAACG-3′; Heuer, Krsek, Baker, Smalla, & Wellington, 1997). All PCR products were obtained using the GoTaq DNA Polymerase kit (Promega, Madison, WI, USA). For a 50-µl volume, 10 µl Promega GoTaq Buffer, 1 µl dNTP, and 2 µl oligonucleotides F984GC and R1378 (5 µM) were added. The PCR amplification conditions consisted of an initial denaturing step of 5 min at 95 °C, followed by 30 cycles of 1 min at 95 °C, 1 min of annealing at 55 °C, a 30-s extension at 72 °C, and a final extension step at 72 °C for 7 min. PCR products were visualized after electrophoresis on 1.5% agarose gels.

DGGE was done according to Lopez et al. (2013), but by modifying the 6% acrylamide gel preparation to include a 45–65% urea–formamide denaturing gradient. Supplementary material S2 gives the details of gel loading and electrophoresis. Gel images were analyzed in Quantity One 4.6.7 (Bio-Rad Laboratories) to generate densitometric profiles of bands, considering each band as an operational taxonomic unit (OTU).

The band profiles obtained from the gels were analyzed for similarity using the Dice coefficient, and a dendrogram was built from the unweighted pair group matching average. This dendrogram represented the average pattern of the four replicate gels. Bacterial richness considered each band as an individual OTU, obtained from the Band Type Report of the Quantity One 4.6.7 imaging software (Bio-Rad Laboratories), which provides the number of bands detected in the DGGE profiles. Bacterial diversity was calculated with Shannon's diversity index (Equation 2), where p is the relative intensity of each peak (corresponding to a defined band) divided by the total intensities of bands in the corresponding lane (Iwamoto et al., 2000).

2.5 | Community level physiological profiles (Eco-Microplates) of cultivatible bacteria

We used BIOLOG 96-well Eco-Microplates (Biolog, Hayward, CA, USA) to analyze metabolic profiles of soil microbial communities. These plates contain 31 different carbon sources and a negative control (water), with three replicates in each microplate. From each soil composite, a 3-g sample was mixed with 7 ml of saline (0.85% NaCl) and shaken at 230 rpm for 1 hr to remove bacteria from solid particles. The suspension was allowed to settle for 1 hr. The supernatant was used for further decimal serial dilutions in saline solution (0.85% NaCl; Hitzl, Rangger, Sharma, & Insam, 1997). One hundred and fifty microliters of soil suspension (bacterial density = 3.0×10^3–5.7×10^4 cfu ml^{-1}, determined by the plate count method in Tryptic Soy Agar [Difco, #236950], incubated at 35 ± 1 °C for 24 hr) were inoculated into each of the 96 wells and then incubated at 35 ± 1 °C, which was the soil temperature at sampling time. Autoclaved soil in sterile distilled water was used as a negative control.

Bacterial activity was measured as the average well color development (AWCD) at 590 nm every 24 hr until readings passed an absorbance of 2.0 (Weber & Legge, 2010). Readings from a single point of incubation were selected based on two criteria: (a) maximum variance among substrate responses and (b) absorbance readings within a linear absorbance range (Garland & Mills, 1991). AWCD was calculated as follows:

$$\mathrm{AWCD} = \Sigma(C-R)/31. \quad (3)$$

Where C is absorbance within each well (O.D. measurement) and R is the absorbance value of the control well (Garland & Mills, 1991). The

data were standardized to reduce any bias due to inoculum density difference between samples (Garland, 1997) and used to calculate functional diversity. Substrate diversity was calculated by Equation 2, where P_i was obtained by subtracting the control from each substrate absorbance and then dividing this value by the total absorbance for all substrates. The percentage of substrates utilized was calculated with absorbance values above 0.5. Multivariate analysis by principal component analysis (PCA) searched for trends in community level physiological profiles in the RIs according to substrate utilization of 31 carbon sources grouped in the five categories established by Weber and Legge (2010): (a) carbohydrates, (b) amines and amides, (c) carboxylic and ketonic acids, (d) polymers, and (e) amino acids (see Table S3). PCA was conducted in Multivariate Statistical Package version 3.22 (Kovach Computing Services, Anglesey, Wales, UK). Functional diversity index, the percentage of substrates, and PCA were based on 116-hr incubation readings.

2.6 | Identification of cultivatible bacteria representing the metabolic diversity of RI soils

This procedure was performed (a) to evaluate whether the Ecoplates had an internal bias towards pseudomonads as found previously (Kaplan et al., 2013) and (b) to identify the cultivatible bacteria representing the gradient of NC, richness, and diversity along the RIs. Three RIs (R5, R14, and R15) were used consistently as representative of the RI gradient, and five carbon sources (arginine, N-acetyl-glucosamine, glutamic acid, itaconic acid, and cyclodextrine) were selected as representative of the five biochemical categories described above.

Cultures from the wells representing RI and carbon sources were collected from three Ecoplates and pooled for DNA isolation-DGGE of cultivatible bacteria. DNA extraction was performed using the Wizard Genomic DNA Purification Kit (Promega) following the manufacturer's instructions. PCR-DGGE was performed as described earlier for non-cultivatible bacteria. Bands at different positions along the lane were defined as representative bands, excised from DGGE, and purified in successive PCR-DGGE gels. PCR products with verified purity were used for a second amplification using the same primers, but the forward primer (984F) was used without a GC clamp. The PCR conditions were the same. The products were purified with the Wizard SV Gel and PCR Clean-Up System (Promega) kit and sent for commercial sequencing using both primers (GENEWIZ, South Plainfield, NJ, USA). The sequences were analyzed for chimeras using DECIPHER software (Wright, Yilmaz, & Noguera, 2012), and sequences (~400-bp length) were assembled using the sense and antisense sequences in BioEdit software (Hall, 1999). The sequences were Basic Local Alignment Search Tool (BLAST)-assisted with the National Center for Biotechnology Information (NCBI) database (https://www.ncbi.nlm.nih.gov/), and the two closest matches of each sequence were used to build the topology trees using Molecular Evolutionary Genetics Analysis version 6 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013).

To confirm the presumptive occurrence of nitrogen-fixing bacteria, soils from three RIs were collected in the summer of 2014 and used to culture bacteria on a medium commonly used for rhizobial cultivation (CR-YMA: congo red-yeast, mannitol agar, Kneen & La Rue, 1983) and for azospirilla (modified OAB (Okon, Albrecht, Burris) medium, Bashan & de-Bashan LE., 2015). Morphotypes were isolated and identified by sequencing the 16S rDNA as described in Lopez, Tinoco-Ojanguren, Bacilio, Mendoza, and Bashan (2012).

2.7 | Statistical analysis

Pearson correlations were performed to determine linear relationships between ecological attributes of the understory plants and bacteria, and metabolic activity with soil properties. Pearson coefficients were calculated using Statistica v. 8.0 (Statsoft, Tulsa, OK, USA). Patterns in RIs associated with edaphic properties, NC, and abundance of understory plants were searched by canonical correspondence analysis (CCA) simultaneously using the environmental data and the abundance of species. CCA was performed using a Multivariate Statistical Package v. 3.22 (Kovach Computing Services).

Bacterial richness and diversity were calculated independently for each of the four replicate gels and analyzed for differences between bare soils and RIs by comparing the single datum of the composite sample from the bare soils and the mean of the sample from the RIs (Sokal & Rohlf, 1995).

3 | RESULTS

3.1 | Characteristics of RI

The numbers of individual plant species in 18 mesquite RIs with different numbers of understory plants are shown in Table S2. In total, 21 different plant species belonging to 11 botanical families, mainly cacti (*Mammillaria dioica* and *Pachycereus pringlei*), were detected.

Table 1 shows that the plant diversity H′ significantly varied from as low as 0.693 to almost threefold higher (2.046) with a concomitant increase in plant richness S (from 2 to 9). The RI area varied significantly, from 5.18 to 40.31 m^2, and was significantly correlated with the trunk collar diameter ($r = .74$, $p = .0001$, $N = 18$), thus confirming that this trait is a reliable indicator of NC of the RI. In addition, NC was highly correlated with plant richness ($r = .62$, $p = .005$, $N = 18$), but not to plant diversity ($r = .0.4$, $p > .05$, $N = 18$). We followed the guideline classification of Carrillo-Garcia et al. (1999) where trunks thicker than 20 cm in diameter are considered mature trees for forming an RI in this area of the desert. In our study, all trees, except for five, were mature, but even immature trees (11–16-cm trunk diameter) had nursling plants even though they had lower NC and plant diversity and richness.

3.2 | Patterns of correlation between Nursing Capacity, soil properties, and plant abundance

CCA indicated that the ordination of RIs was determined primarily by the NC of the RI and secondarily by the following soil properties: percentage of sand, field capacity, percentage of silt, and soluble phosphorus (correlation to first axis: .816, −.678, .673, .658, and .612, respectively, Table 2). In Figure 1, the species-environment biplot shows that RIs of greater NC (i.e., R18, R17, R16, R14, and R12) were associated with soils with higher field capacity, a higher percentage of silt, and an abundance of plant species such as cacti

TABLE 1 Attributes of resource islands. Diversity and richness of plants growing under the canopy of mesquite, area of the resource islands, and Nursing Capacity of mesquite. RIs were numbered in an increasing magnitude of Nursing Capacity

Resource island ID	Resource island area (m^2)	Diameter of trunk at 50 cm from soil (m)	Nursing Capacity[a]	Plant richness (S)	Shannon diversity index (H′)
R1	5.18	0.1337	0.69	3	1.10
R2	5.28	0.1496	0.79	4	1.31
R3	8.95	0.1146	1.03	3	1.10
R4	7.07	0.2228	1.58	3	1.06
R5	10.41	0.1687	1.76	2	0.69
R6	7.70	0.2546	1.96	5	1.68
R7	9.30	0.2387	2.22	5	1.01
R8	17.28	0.1592	2.75	3	1.17
R9	15.9	0.3119	4.96	4	0.97
R10	18.09	0.3247	5.87	4	1.06
R11	21.65	0.3501	7.58	4	1.31
R12	23.17	0.4043	9.37	7	1.34
R13	27.89	0.3438	9.59	7	1.46
R14	17.34	0.6048	10.49	9	2.05
R15	29.47	0.382	11.26	4	1.17
R16	29.81	0.3979	11.86	9	2.00
R17	27.33	0.6366	17.40	8	1.64
R18	40.31	0.5348	21.56	5	1.19

[a]Nursing Capacity is defined as the capacity of the resource island to concentrate resources and therefore habitat availability to plants and microorganisms. Nursing Capacity = resource island area (m^2) and trunk diameter at 50 cm from soil (m).

TABLE 2 Canonical correspondence analysis of species, soil properties, and Nursing Capacity of resource islands. Correlation of ordination axes with variables, eigenvalues, and percentage variances explained

Variable	Axis 1	Axis 2
Organic matter	0.440	0.509
Soluble phosphorus	**0.612**	−0.091
Nitrates	−0.128	0.657
Ammonium	−0.036	0.677
% Clay	0.193	−0.306
% Sand	**−0.678**	−0.027
% Silt	**0.658**	0.073
Field capacity	**0.673**	−0.064
Drainage rate	−0.101	−0.057
Nursing Capacity	**0.816**	0.448
Eigenvalue	0.472	0.338
Cumulative percentage of variance explained	51	64

and perennial herbs (*Stenocereus gummosus* Engl. and *Ruellia californica* I.M.Johnst.). In contrast, the RIs with lower NC (R1, R3, R4, R6, R7, R9, and R10) were characterized by sandy soils with a higher drainage rate and were occupied by plants usually in open areas (*Jatropha* spp, *P. articulata* S. Watson).

3.3 | Structure of soil bacterial communities

On the basis of the presence/absence of OTUs in four replicate DGGE gels, cluster analysis indicated that all the RIs have a similar structure of bacterial communities (87% of Dice similarity) and lower similarity to the bare soils reference sample (without plants; ~70% of Dice similarity). Thus, the RIs have a similar bacterial composition based on the clustering shown (Figure 2). The same pattern was found in four replicate gels and with five different samples of bare soil. Unexpectedly, bacterial richness and diversity showed significant differences (bacterial richness: $t_{(17)} = 2.34$, $p < .05$; H′: $t_{(17)} = 2.54$, $p < .05$) between RI and bare soils, with higher values in samples of bare soils (S = 13; H′ = 1.02) compared with RI (S = 11 ± 0.97; H′ = 0.92 ± 0.06).

The structure and diversity of plant communities under the RI did not correlate with bacterial structure and diversity (Table 3).

3.4 | Substrate utilization analysis

When analyzing microbial metabolic parameters, the overall metabolic activity, percentage of utilized substrates, and substrate diversity were positively correlated with plant richness and diversity (Table 4). A correlation was also found between bacterial diversity and organic matter ($r = .81$, $p < .01$, $N = 18$). A PCA plot of RIs on the basis of utilization patterns of each substrate group is shown in Figure 3. It should be considered that this PCA plots the RI according to bacterial substrate utilization and not necessarily has to fit to the RI's NC pattern. The first two principal components account for 80% of the explained variance. The carbon source types that contributed more to PC1 were the amines and amides (0.717) and carbohydrates (−0.463). Thus, the former showed an increasing utilization among the RIs. Bacterial substrate utilization demonstrated that most of the RIs were associated with a particular carbon source whereas the bare soils activity was not correlated with any particular substrate (Figure 3).

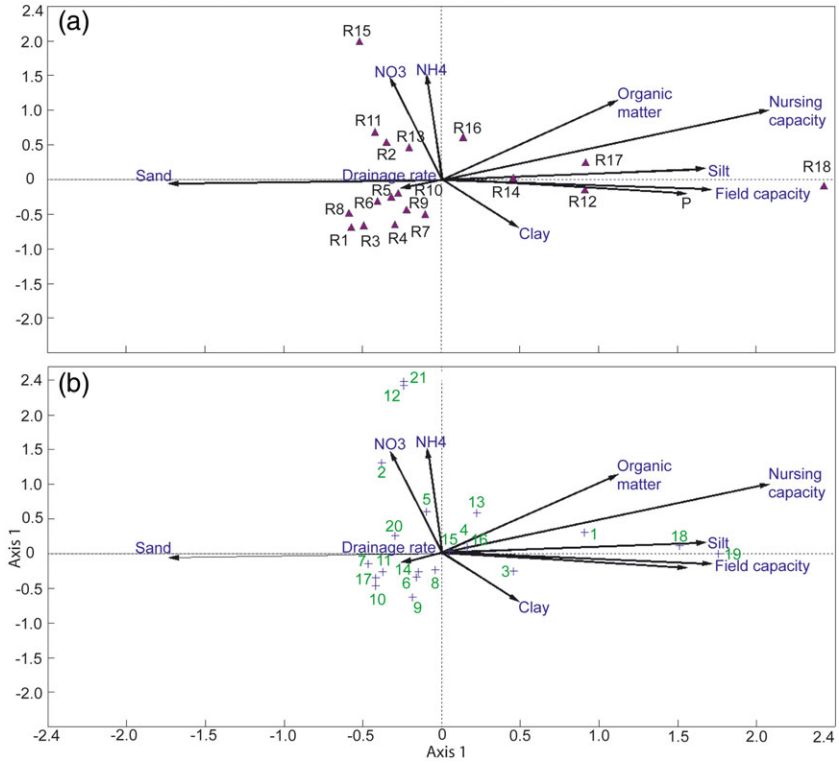

FIGURE 1 Canonical correspondence analysis of resource islands of mesquite associated to edaphic variables and abundance of the understory plants. Resource islands/environment biplot (a) and species/environment (b). Nursing Capacity is included as covariable on the *x* axis. R1 to R18 = resource islands in increasing order of Nursing Capacity (1) *Agave datylio*, (2) *Atriplex canescens*, (3) *Bursera epinnata*, (4) *Bursera hindsiana*, (5) *Capparis atamisquea*, (6) *Cylindropuntia cholla*, (7) *Cylindropuntia lindsayi*, (8) *Euphorbia eriantha*, (9) *Jatropha cinerea*, (10) *Jatropha cuneata*, (11) *Krameria* sp., (12) *Lophocereus schottii*, (13) *Lycium californicum*, (14) *Mammillaria dioica*, (15) *Pachycereus pringlei*, (16) *Parkinsonia florida*, (17) *Prosopis articulata*, (18) *Ruellia californica*, (19) *Stenocereus gummosus*, (20) *Stenocereus thurberi*, (21) *Ziziphus obtusifolia* [Colour figure can be viewed at wileyonlinelibrary.com]

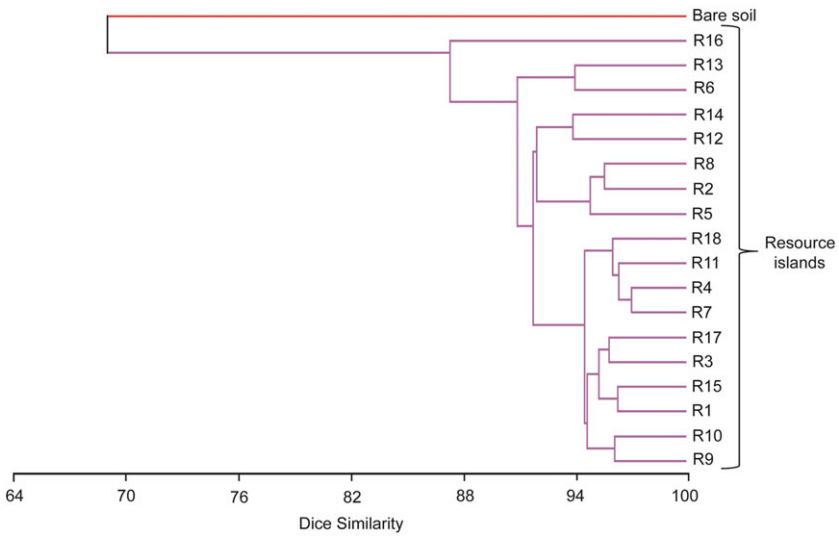

FIGURE 2 Bacterial soil community structure in mesquite resource islands compared with a composite sample from bare soil. Clustering of resource islands by Dice coefficient and unweighted pair group method with arithmetic mean of denaturing gradient gel electrophoresis bands. The resource islands are in purple, and the bare soil is in red. Differences in the structure were determined at 70% of similarity. Gel representatives from of four replicates with the same pattern of clustering are shown [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Pearson correlation between bacterial and plant diversity

Attribute	Bacterial richness (OTUs)		Bacterial diversity (H′)	
	r	*p*	*r*	*p*
Plant richness (S)	.056	NS	.126	NS
Plant diversity (H′)	.126	NS	.217	NS

Note. S = number of species; OTUs = operational taxonomic units; *r* = Pearson correlation coefficient; NS = no statistical significance; $p \leq .05$. $N = 18$.

TABLE 4 Correlation between metabolic parameters and plant diversity and richness of the plants in the resource islands

Metabolic parameter	Plant diversity (H′)		Plant richness (S)	
	r	*p*	*r*	*p*
Metabolic activity	.675	**	.706	**
Carbon sources utilized (%)	.608	**	.658	**
Substrate diversity utilization (H′)	.557	*	.576	*

Note. *r* = Pearson correlation coefficient. $N = 18$.

*$p \leq .05$. **$p \leq .01$.

It was observed that the RIs with the lowest organic matter content (R3 and R4) metabolized carbohydrates and carboxylic-keto acids. In addition, to determine whether a correlation between the physicochemical soil characteristics and bacterial metabolic activity exists (AWCD at 116 hr), the Pearson correlation coefficient indicated that organic matter has the highest correlation with metabolic activity ($r = .81$, $p < .01$), followed by NC ($r = .64$, $p < .01$) and sand ($r = -.52$, $p < .01$; Table 5). All the other parameters, soluble phosphate, nitrates, ammonium, and clay content, field capacity, and drainage rate lacked statistical significance.

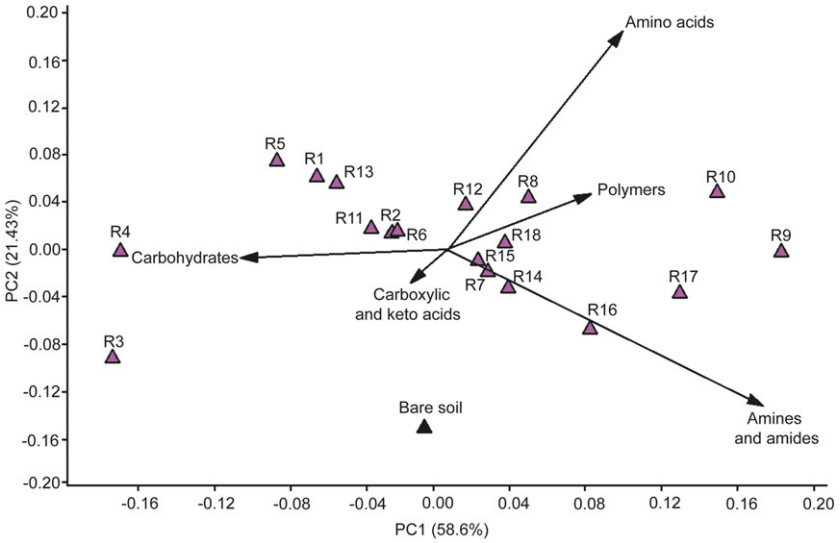

FIGURE 3 Principal component analysis of carbon sources utilization by microbial community in the mesquite resource islands and bare soil. The importance of each variable is displayed by the biplot method using the variable eigenvectors scores. Vectors indicate the direction in which the carbon sources utilization increases [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 5 Physicochemical parameters in relation to metabolic activity

Physicochemical parameter	*r*	*p* value
Organic matter	.8054	**
% Sand	−.5265	*
% Silt	.5222	*
Soluble phosphorus	.1978	NS
Nitrates	.2966	NS
Ammonium	.4318	NS
% Clay	.4045	NS
Field capacity	.3619	NS
Drainage rate	−.0204	NS
Nursing Capacity	.6438	**

Note. NS = no statistical significance.

*$p < .05$. **$p < .01$.

3.5 | Phylogenetic relationship among bacterial OTUs recovered from BIOLOG Ecoplates

3.5.1 | Cultivatible bacteria representing the metabolic diversity of RI soils

Cultures from the BIOLOG Ecoplates were processed for 16S rDNA PCR-DGGE analysis. Similarities in the bacterial structure analyzed by DGGE were confirmed when bands from three different RIs were sequenced. Among the OTUs appeared expected families such as *Pseudomonaceae* and *Enterobacteriaceae*. Interestingly, the putative occurrence of nitrogen-fixing bacteria from *Rhizobiaceae* and *Rhodospirillaceae* was detected. These OTUs were preliminarily identified as *Rhizobium* sp., *Sinorhizobium* sp., and *Azospirillum* sp. (in Figure 4, Sequences S2, S3, and S6).

3.5.2 | Isolation and identification of putative plant-growth promoting bacteria

In the summer of 2014, fresh soil of three representative RIs (R5, R14, and R15) was collected for isolating nitrogen-fixing bacteria. Nine morphotypes were isolated on medium commonly used for rhizobial cultivation and also for azospirilla. Six morphotypes were common to the three RIs sampled (in Figure 5: M1 to M5, NFX1), and three were found only in one of the three selected RIs. After sequencing the complete 16S rDNA gene, NFX1 was identified as *Sinorhizobium*, the other six morphotypes belonged to *Bacillus* spp., two morphotypes were identified as *Sphingomonas* sp., but a morphotype that clustered with *Azospirillum* was not found.

4 | DISCUSSION

Few species of desert plants reduce the impact of hostile arid conditions by modifying their habitats to allow natural vegetation and by serving as nurse plants. Our study focused on the potential relationships among the nursling vegetation of mesquite trees in the RIs, the soil characteristics of their habitat, RI age and size, which suggests the potential of the RI to concentrate resources, and the functional metabolic diversity of the bacterial community residing in the RIs. Finally, we examined the potential presence of plant growth-promoting bacteria in these environments.

The interactions of the flora with soil components, weather, and nutrients in the RIs has been studied before (Carrillo-Garcia et al., 1999; Reyes-Reyes et al., 2002; Reynolds, Virginia, Kemp, de Soyza, & Tremmel, 1999; Schade & Hobbie, 2005; Schlesinger et al., 1996), and the dominant influence was the accumulation of organic matter under the canopy of the tree, which this study also shows. Although the mechanisms whereby the flora interacts with the microbial community have been examined (Bachar et al., 2012; Berg, Unc, & Steinberger, 2015; Ewing, Southard, Macalady, Hartshorn, & Johnson, 2007; Herman et al., 1995; Jia, Liu, Wang, & Zhang, 2010; Saul-Tcherkas & Steinberger, 2011; Yu & Steinberger, 2011), the functional aspects of these interactions have not been evaluated in extensive detail. This study explored these interactions.

Our main findings are (a) no relationship was found between plant diversity in the RI and the bacterial diversity residing there; (b) the NC of mesquite was accompanied by variations in soil

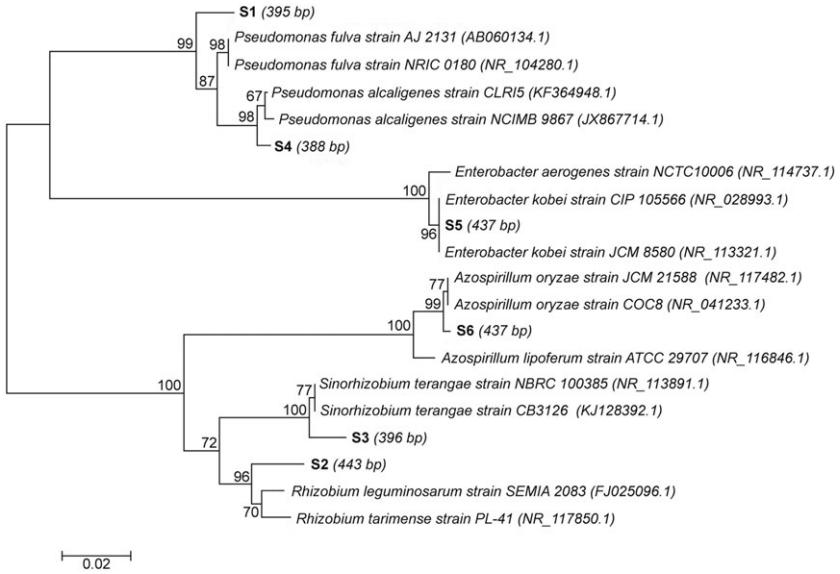

FIGURE 4 Tree topology of the representative bacterial groups (marked by the letter S in bold) after the BIOLOG culture and 16S rDNA polymerase chain reaction-denaturing gradient gel electrophoresis band purification. Tree topology built by neighbor-joining method in Molecular Evolutionary Genetics Analysis version 6 (Tamura et al., 2013). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1,000 replicates) is shown next to the branches. GenBank accession numbers are indicated in parentheses after the taxon names

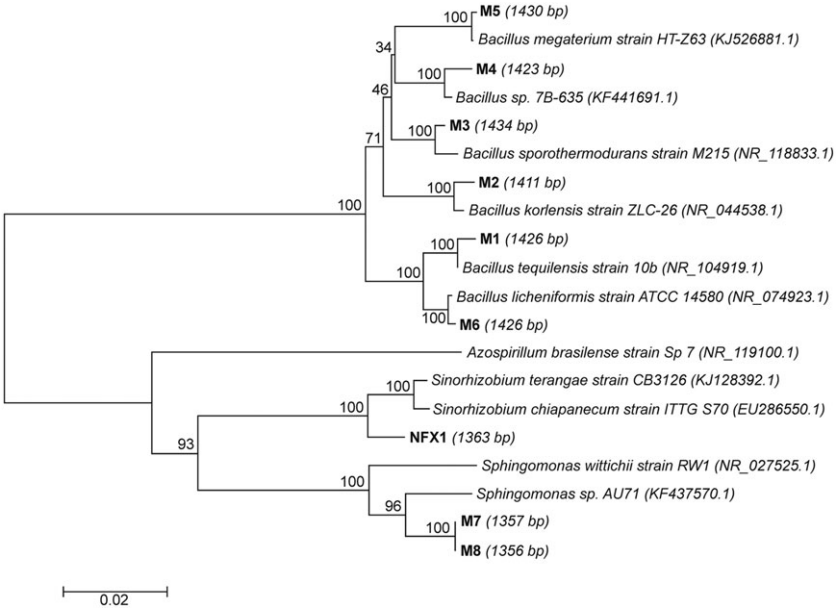

FIGURE 5 Tree topology of the cultivable bacteria recovered from resource island soils. The tree was built by the neighbor-joining method in Molecular Evolutionary Genetics Analysis version 6 (Tamura et al., 2013). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1,000 replicates) is shown next to the branches. GenBank accession numbers are indicated in parentheses after the taxon names. All morphotypes (M1 to M6 and NFX1 to NFX3) were isolated from OAB-modified medium. Note that only NFX1, NFX2, and NFX were confirmed as potential nitrogen-fixing bacteria

properties; (c) richness of bacterial communities of RIs is significantly different from those of bare areas, with higher values in the bare soils samples; (d) the bacterial community is similar among the RIs, but (e) the RIs' metabolic functionality differs depending on other specific edaphic/nutritional parameters that exist in a specific RI. These findings support our hypothesis that the bacterial inoculum potential of the RI under the mesquite nurse tree in the southern Sonoran Desert is probably always present. It is expressed, however, only when other favorable nutritional/environmental variables exist, which stimulate the establishment of specific bacterial populations. The pattern of a potential inoculum waiting for a proliferation stimulus was shown previously for AM fungi in RIs (Bashan et al., 2000) and for endophytic bacteria permanently residing in the seeds of cacti that depend on their endophytes for survival because they grow in soil-less rocks (Lopez, Bashan, & Bacilio, 2011; Lopez et al., 2012; Puente, Li, & Bashan, 2009a, 2009b).

In spite of the lack of correspondence between the structure–diversity of the plant communities in the RI and the same attributes of bacterial communities, metabolic activity increased in RIs with higher plant richness and was accompanied by variations in soil properties. Therefore, the RI capacity not only represents increased habitat availability for plants and microorganisms but also results in concentrating resources and modifying the environment (Binkley & Menyailo, 2006).

We employed common molecular PCR-DGGE community fingerprints for determining bacterial community composition (Berg et al., 2015). A different fingerprinting method (Bachar et al., 2012; Ewing et al., 2007), phospholipid fatty acid analysis (Ben-David et al., 2011), and sequencing of clones (Saul-Tcherkas & Steinberger, 2011) were used for studying arid environments. Plate count methods using different media have also been performed (Herman et al., 1995). The community profiles among all these studies differed because a unique

but variable environmental condition exists in each RI. However, the primary factor was RI soil versus bare area soil as found in this study in the Sonoran Desert. Alternatively, different plant species in each RI could develop their own special ecophysiological adaptations to a desert environment, resulting in perennial shrubs with unequal microbial diversity (Yu & Steinberger, 2011). However, this alternative is not supported by this study where most of the RIs in the Sonoran Desert consist of similar plants.

Even though the bacterial diversity was similar among the RIs, we pursued a Biolog Ecoplate study to analyze the metabolic capacities of these populations (Garland & Mills, 1991; Weber & Legge, 2010). A recent study employed a similar technique to measure respiration of the bacterial population, MicroResp™ plates (Yu & Steinberger, 2011). Our finding of the high correlation between metabolic activity of the bacteria and diversity and richness of plants, but not bacterial diversity in the RIs, suggests a constant input of organic matter around the mesquites trees. This supply could enhance bacterial metabolic capacity to degrade different substrates. Therefore, we conclude that soil bacterial communities in the RI not only have more metabolic activity but also have more capacity to degrade different carbon sources.

Furthermore, the observation that the RIs with the lowest organic matter content preferentially metabolized simple carbohydrates and carboxylic-keto acids more than more complex metabolic groups (amines/amides, polymers) indicates that the whole bacterial community has a greater capability to metabolize different carbon substrates in soils with more organic matter.

A previous Biolog Ecoplate analysis in a small RI produced by perennial plants (~3 m^2) in the Negev Desert in Israel indicated a potential bias of this analytical system towards pseudomonads (Kaplan et al., 2013). Our study analyzing far larger RIs (averaging 18 m^2) in the Sonoran Desert in Mexico has not shown such a bias. The difference may result from precipitation levels in the two deserts; the central Negev Desert is far drier (average of 90 vs. 180 mm annually). This explanation was also supported by Bachar et al. (2012) who, using other methods, found variability in bacterial phyla in the Negev Desert, proposed that the abundance of each phylum was affected by precipitation.

In conclusion, our study demonstrates that numerous parameters work together and affect the microbial community structure of RIs, but not every factor significantly affects bacterial metabolic activity in the community. Although bacterial diversity may be similar in all RIs and it is likely that plant diversity does not affect bacterial diversity, the functionality of these bacterial populations significantly varied according to local edaphic and nutritional conditions in each RI.

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AUTHOR'S CONTRIBUTION

D. E. G. acquired samples, performed analyses, and data presentation. B. R. L. helped in analyzing the data, data presentation, and writing the paper. L. E. d.-B. helped in all data analyses and interpretations and writing the paper. A. M. H. and M. M. advised during the project and revised the manuscript. Y. B. managed the entire project and wrote most of the paper including the final version.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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