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Research Letter

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RESEARCH LETTER – Environmental Microbiology

Soil microbial composition and carbon mineralization are associated with vegetation type and temperature regime in mesocosms of a semiarid ecosystem

Morena Avitia[1], Alberto Barrón-Sandoval[1,6], Alejandra Hernández-Terán[1], Mariana Benítez[1,2], Greg A. Barron-Gafford[3], Katerina Dontsova[4], Mitchell A. Pavao-Zuckerman[5] and Ana E. Escalante[1,*,†]

[1]Laboratorio Nacional de Ciencias de la Sostenibilidad (LANCIS), Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad de México, 04510, Mexico, [2]C3, Universidad Nacional Autónoma de México, Ciudad de México, 04510, Mexico, [3]School of Geography and Development, University of Arizona, Tucson, AZ, 85721, USA, [4]Department of Environmental Science, University of Arizona, Tucson, AZ, 85721, USA, [5]Department of Environmental Science and Technology, University of Maryland, College Park, College Park, MD, 20742, USA and [6]Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, 92697, USA

*Corresponding author: Instituo de Ecologia, Universidad Nacional Autonoma de Mexico, A.P. 70-275 Circuito Exterior, Ciudad Universitaria, Coyoacan 04510, Ciudad de Mexico, Mexico. Tel: +52(55) 5623 7713; E-mail: aescalante@iecologia.unam.mx

One sentence summary: Relative role of plant type and temperature regime in soil microbial community assembly and associated functional dynamics in semiarid ecosystems.

Editor: Anne Cotton
†Ana E. Escalante, http://orcid.org/0000-0001-8147-4598

ABSTRACT

Transition from historic grasslands to woody plants in semiarid regions has led to questions about impacts on soil functioning, where microorganisms play a primary role. Understanding the relationship between microbes, plant diversity and soil functioning is relevant to assess such impacts. We evaluate the effect that plant type change in semiarid ecosystems has for microbial diversity and composition, and how this is related to carbon mineralization (C_{MIN}) as a proxy for soil functioning. We followed a mesocosm experiment during 2 years within the Biosphere 2 facility in Oracle, AZ, USA. Two temperature regimes were established with two types of plants (grass or mesquite). Soil samples were analyzed for physicochemical and functional parameters, as well as microbial community composition using 16S rRNA amplicon metagenomics (Illumina MiSeq). Our results show the combined role of plant type and temperature regime in C_{MIN}, where C_{MIN} in grass has lower values at elevated temperatures compared with the opposite trend in mesquite. We also found a strong correlation of microbial composition with plant type but not with temperature regime. Overall, we provide evidence of the major effect of plant type in the specific composition of microbial communities as a potential result of the shrub encroachment.

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Keywords: plant–soil–microbe interaction; carbon mineralization; microbial community assembly; Biosphere 2; shrub encroachment

INTRODUCTION

Shrub encroachment in the grasslands is a phenomenon that has been occurring for the past 100–200 years in different regions of the world, especially in arid and semiarid landscapes, and has been associated with altered climatic, fire and land-use regimes (Van Auken 2000; Stevens *et al.* 2017; Thomas *et al.* 2018; Xiang *et al.* 2018; Zhou *et al.* 2019). Vegetation changes from grass to woody plants result in increased soil heterogeneity associated with physical, biological and biogeochemical conditions (Cable *et al.* 2012; Xiang *et al.* 2018). Overall, implications of these changes include alterations of water and energy fluxes (Huxman *et al.* 2005; Scott *et al.* 2006, 2014; Yu and D'Odorico 2014), with direct impacts and feedbacks on local and global climate, particularly if we consider that arid and semiarid ecosystems correspond to 40% of Earth's land surface (Chandregowda, Murthy and Bagchi 2018).

Consequences of shrub encroachment on grasslands in terms of water and nutrient fluxes have been well documented (Cable *et al.* 2012; Bragazza *et al.* 2015; Xiang *et al.* 2018). However, no consensus exists on the direction of such fluxes associated with vegetation change (e.g. carbon dynamics associated with shrub encroachment) (Barron-Gafford *et al.* 2011, 2014; Eldridge *et al.* 2011; Chandregowda, Murthy and Bagchi 2018; Xiang *et al.* 2018). In contrast, there is consistent evidence for increased microbial activity and biomass associated with shrub encroachment (Yannarell, Menning and Beck 2014), but little information of the associated changes in soil microbial communities exists (Xiang *et al.* 2018). Microbial composition changes associated with shrub encroachment would help disentangle the effect of vegetation change on soil microbes and its concomitant influence on nutrient fluxes, particularly N and C, given their direct role as greenhouse gases and their contribution to climate change.

Given the extension of land coverage of semiarid and arid ecosystems, their contribution to greenhouse gases and climate change through carbon mineralization (C_{MIN}; i.e. soil respiration) is of major importance (Cable *et al.* 2009). Microbes are largely responsible for soil respiration, and they may respond strongly to environmental changes, including increasing temperature or vegetation conversion (Reed and Martiny 2007; Allison and Martiny 2008; Strickland *et al.* 2009; Lauber *et al.* 2013; Tardy *et al.* 2015). However, a predictive understanding of how ecosystems will respond to environmental change is still in development (Grimm *et al.* 2016). An element of ecosystem response will be in how the heterogeneity of ecosystems (e.g. plant type, temperature, soil moisture and precipitation regimes) will impact soil processes that scale up to ecosystem level as the planet warms (Zhang, Drake and Wainwright 2004; Cable *et al.* 2012).

In the present study, we aim to specifically test for the influence of plant type (shrub vs grass) and temperature regime [ambient vs elevated (+4°C)] in both microbial community composition and the physicochemical properties of soil. We followed a mesocosm experimental approach with volcanic tephra as substrate, which allowed us to reduce the complexity found in natural environments and historical biogeochemical processes that could confound our results.

MATERIALS AND METHODS

Mesocosm design and incubation

This study was conducted at the Biosphere 2 facility in Oracle, AZ. A set of 1-m-deep mesocosms was constructed in 55-gallon plastic drums (0.59 m diameter) in 2011. The mesocosms were designed to complement the large-scale Landscape Evolution Observatory (LEO) experiment at Biosphere 2 (Huxman *et al.* 2009; Pangle *et al.* 2015) by imposing, for a 2-year period, the vegetation and temperature regime conditions. Due to the destructive nature of the sampling, we were able to collect soil cores only at the end of the experimental period in order to examine microbial community composition and soil physicochemical parameters.

Mesocosms were filled with basalt scoria (volcanic tephra) that was ground to a loamy sand texture and installed at a bulk density of ~1.5 g cm^{-3} to match the LEO experiment (Pangle *et al.* 2015; Haren *et al.* 2017). The basalt rock material was sourced from a 30-m-thick deposit of late Pleistocene airfall tephra from the Merriam Crater in northern Arizona. Mesocosms were planted with seedlings of either a shrub, velvet mesquite (*Prosopis velutina*), or a bunchgrass, sideoats grama (*Bouteloua curtipendula*). Three replicates of each plant type were maintained under ambient (at Oracle, AZ) or elevated (projected climate change, +4°C) air temperatures (Pachauri and Meyer 2014) for 2 years ($N = 12$). Temperature regimes were maintained in two independent sections of the Biosphere 2 facility: for ambient temperature, average daytime/nighttime air temperature was 25°C/21°C, and for elevated (+4°C) temperature, average daytime/nighttime temperature was 29°C/25°C. Rainfall was simulated with daily irrigation events of 5 mm for ~60 days, and then a 500 mm slow saturation irrigation was conducted to make sure that the moisture pulse was propagated through the entire 1-m-deep mesocosm. The temperature and precipitation regimes were maintained electronically by a control system that uses multiple independent air handlers to reach targeted set points (Zabel *et al.* 1999). The present study was conducted using samples collected at the end of the 2-year period through destructive sampling.

Soil sampling

Soil samples were triplicate cores collected from each mesocosm in the summer of 2013 (a total of 12 mesocosms were sampled) using a corer with a 2.54 cm × 95.89 cm plastic liner (AMS, Inc., American Falls, ID) attached to a power drill. The sampling device was unable to extract soil cores from deeper than 30 cm in all the mesocosms. The replicate cores were composited to make a single soil sample from each mesocosm.

Mesocosm soil samples were stored and transported on ice inside a cooler until processing. Once in the laboratory, samples were sieved (≤2 mm) and separated from root biomass. Root biomass was reserved, air dried and weighed. Samples were then divided into two subsamples: one for chemical analysis was stored at 4°C and one for DNA extraction was stored at −80°C.

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Laboratory procedures

Determination of soil physicochemical parameters

For the 12 mesocosms, determination of physicochemical parameters was performed twice (technical replicates). pH was determined using a benchtop pH meter on a 1:1 soil:water slurry. Gravimetric soil moisture content was determined by weighing soil samples before and after drying in a 105°C drying oven for 3 days. Soil organic matter (SOM) analysis was performed using loss-on-ignition ashing samples at 450°C for 4 h in a muffle furnace. Total C and N were determined via combustion using a CNS analyzer (Leco, Co., Saint Joseph, MI). Potential soil respiration (i.e. C_{MIN}) assays were used as an indicator of microbial activity. Soil samples were placed in a canning jar and brought to 60% water holding capacity and incubated for 24 h at 30°C. After this initial incubation period, C_{MIN} was measured by attaching canning jars to a benchtop infrared gas analyzer (LI-COR LI-7000, Lincoln, NE). CO_2 efflux from each jar was measured over a period of 90 s and respiration rates were calculated as μg CO_2-C per g dry soil per day. Values for physicochemical parameters are available in the Supporting Information.

DNA extraction

Genomic DNA from each sample was extracted using PowerSoil DNA Isolation Kit (Mo Bio Laboratories, Solana Beach, CA, USA) according to the manufacturer's instructions with the following modifications: 0.5 g of sample instead of 0.25 g was used, incubation periods at 4°C were increased from 5 to 20 min and we added an incubation step at 55°C for 5 min prior to DNA elution (Rebollar *et al.* 2017).

Amplification and sequencing

The V1–V2 regions of the 16S ribosomal RNA (16S rRNA) gene were amplified and sequenced from the extracted DNA using Illumina MiSeq instrument (Illumina, Inc., San Diego, CA)1 at Research and Testing Laboratory (RTL) (Lubbock, TX, USA) using the primers 27F/388R [27F 5′-AGA GTT TGA TCC TGG CTC AG-3′ (Lane 1991) and 388R 5′-3TGC TGC CTC CCG TAG GAG T-3′ (RTL)].

Data processing and analyses

Statistical analyses of physicochemical data

Normal distribution of the data was verified by Shapiro test. Once normal or non-normal distribution of data was verified, statistical differences were evaluated through parametric or non-parametric tests. To evaluate the factors explaining observed differences among treatments, two-way ANOVAs (normal distributed variables) Mann–Whitney tests (non-normal distributed variables) were carried out. All statistical analyses of the soil physicochemical data were performed in R (R Core Team 2017) (version 3.4.3).

16S rDNA sequences analyses

Demultiplexing, filtering and chimera check

Illumina raw sequences were processed with QIIME v1.9.1 (Caporaso *et al.* 2010b). First, sequences were demultiplexed using local scripts. Next, reads were paired using join_paired_ends.py with default arguments. Joined sequences were filtered for quality based on two criteria: (i) sequences with 1 or more Ns were removed and (ii) sequences with overall 75% Phred quality scores >20 were kept. From the original number of reads (11 774 203), and after these steps, 16.3% were removed, leaving 9 855 008 total reads. The presence of chimeras was checked with the UCHIME2 (Edgar 2016) algorithm implemented in QIIME (Caporaso *et al.* 2010b). Chimeric sequences (4.1% of the total reads) were eliminated and the rest of the sequences were filtered by size keeping only the sequences with >320 bp in length. The raw data (paired end files) were deposited in the NCBI Sequence Read Archive with the accession number PRJNA549976.

OTU assignment

Demultiplexed and filtered sequences were clustered into operational taxonomic units (OTUs) using a *de novo* strategy with a sequence similarity threshold of 97% using the CD-HIT algorithm (Fu *et al.* 2012). Taxonomy for each OTU was assigned using the Ribosomal Database Project (RDP) classifier (Wang *et al.* 2007) and the Greengenes database (DeSantis *et al.* 2006). Representative sequences were aligned to the Greengenes database with PyNAST (Caporaso *et al.* 2010a), and a Maximum Likelihood phylogenetic tree was constructed using FastTree 2 v1.11 (Price, Dehal and Arkin 2010). The obtained OTU table was filtered using a minimum cluster size of 0.001% of the total number of reads, i.e. we kept OTUs with >92 reads (Bokulich *et al.* 2013).

Statistical analyses of molecular data

Diversity and statistical analyses

Alpha and beta diversity calculations, and relative abundance descriptions of the soil composition at the phylum level were performed on a rarefied OTU table at the depth of 21 712 sequences per sample using the R package 'phyloseq' (McMurdie and Holmes 2013). Hill numbers as alpha diversity metrics were calculated with OTU abundances using the 'hillR' package (Li 2018), with q equal to 0. To evaluate differences in alpha diversity (Hill numbers) across the experimental treatments, two-way ANOVAs (R Core Team 2017) were carried out. The differences of bacterial community composition among treatments (beta diversity calculated as weighted UniFrac distance; Lozupone and Knight 2005) were visualized by non-metric multidimensional scaling (NMDS), with corresponding soil properties fitted using 'envfit' in 'vegan' package (Oksanen *et al.* 2018) (version 2.5-1). Confidence ellipses were calculated with the 'dataEllipse' function of the 'car' package (Fox and Weisberg 2019). Permutational analysis of variance (PERMANOVA) based on 1000 permutations was carried out to test for statistical significant differences in microbial community composition across treatments with the 'adonis' function in 'vegan' package. Identification of bacterial taxa that differed significantly among treatments was performed using linear discriminant analysis (LDA) effect size (LEfSe) (Segata *et al.* 2011) with the web-based tool 'Microbiome-Analyst' (Dhariwal *et al.* 2017). Mantel tests were used to evaluate the correlation between community similarity and environmental similarity by comparing UniFrac distance matrix with a standardized (z-score transformed values) Euclidean matrix for all variables and an unstandardized Euclidean matrix for each soil physiochemical variable, with 9999 permutations and using the Pearson's correlation coefficient (Martiny *et al.* 2006). All statistical analyses were conducted in R (R Core Team 2017) (version 3.4.3).

RESULTS

The experimental design of the study allowed us to test explicitly the relative role and interaction of two principal factors, temperature regime and plant type, on microbial composition and C_{MIN}. Overall, results show that (i) temperature regime has no effect on microbial composition, (ii) plant type has a strong effect on microbial composition and (iii) the interactive effect of temperature regime and plant type explains changes in C_{MIN}.

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Effect of temperature regime and plant type on soil physicochemical and functional parameters

Values of soil physicochemical parameters across samples (Table 1) showed significant differences only for the plant type treatment in the case of soil moisture, being higher for grasses in both temperature regimes (Mann–Whitney: $W = 144$, $P = <0.001$) and C:N, and being higher for grasses in both temperature regimes (Mann–Whitney: $W = 118$, $P = <0.05$). For pH, none of the experimental factors nor their interaction explains the observed variance. For the rest of the analyzed soil physicochemical variables, given their non-normal distribution, it was not possible to test for the contribution of the interaction of factors in explaining the observed variance. Graphical representation for all soil physicochemical values means and corresponding standard error (SE; non-normal distribution) or standard deviation (SD; normal distribution) are shown in Fig. 1. Overall, there is no consistency for how different variables responded to the treatments (Table 2; Fig. 1A–F).

Two-way analysis of variance focused on the plant type/temperature regime treatment showed that for C_{MIN} the interaction of both experimental factors (plant type and temperature regime; Table 2) statistically explains the differences in treatments (Fig. 1F; two-way ANOVA: $F = 21.38$, $P < 0.001$), shrubs being the treatment with higher values of C_{MIN} in both temperature regimes.

Effect of temperature regime and plant type on bacterial diversity and composition

Alpha diversity

A total of 9629 OTUs were identified from the 12 soil samples. Regarding diversity, and according to Hill numbers, no significant differences in alpha diversity were found across treatments (Fig. 2A).

Beta diversity

When looking at bacterial composition, or beta diversity, differences across treatments can be observed in the relative abundance of bacterial phyla (Fig. 2B). Temperature regime was not a statistically significant factor explaining differences in microbial composition (weighted UniFrac distances). In contrast, plant type resulted as the main experimental factor explaining microbial community composition differences evidenced by the NMDS analysis (PERMANOVA: $F = 5.977$, $P < 0.0009$; Fig. 3).

Dominant bacterial groups per plant type

LEfSe analysis allowed the identification of bacterial taxa that were differentially abundant between grass and mesquite treatments. Specifically, in grass mesocosms, the most abundant phyla were Proteobacteria, Cyanobacteria and Chloroflexi, while in mesquite mesocosms Actinobacteria was the most abundant phyla (Figure S1, Supporting Information). When looking at the relative abundance of specific genera, in the case of grass *Rhodobacter*, *Pseudomonas* and *Pedomicrobium* were the most abundant genera, while in the case of mesquite *Streptomyces*, *Sinorhizobium* and *Arthrobacter* were the most frequent genera (Fig. 4).

Correlation of bacterial community structure and physicochemical parameters

Mantel tests for differences in bacterial composition (beta diversity as UniFrac distance) and differences in soil physicochemical parameters (Table 3) showed a significant correlation for soil moisture ($r = 0.77$; $P < 0.0001$).

DISCUSSION

Our results provide evidence of the influence of the plant type and temperature regime in different aspects of the soil ecosystem, from the physicochemical characteristics of soil and microbial community composition, to C_{MIN} as an emergent property of the soil–plant–microbe interaction.

Role of plant type and temperature regime in the physicochemical properties of soil

Our experimental design allowed us to specifically test for the influence of plant type (grass vs shrub) and temperature regime (ambient vs elevated) on the physicochemical properties of the soil. An expectation based on previous studies (Cable *et al.* 2009, 2012) was that C_{MIN} (as an integrative parameter of both physical and biological aspects of the soil ecosystem) would be higher in shrub mesocosms and under higher temperatures, given improved litter quality and better thermodynamic conditions (increased temperature for increased metabolic rates in microbes). Nonetheless, our results do not show higher C_{MIN} in shrubs compared with grass in general, and increased temperature for each plant type did not result in increased metabolism (Table 2; Fig. 1F). Potential explanations for these observations could be, for C_{MIN} differences, that the shrubs in our mesocosms were still in early stages of development, or seedlings, with limited contribution of litter to C into the soils at the moment of our sampling, which might not be the case for grasses (Cable *et al.* 2009, 2012). These differences in developmental stages and contribution of litter to C into soils can also be seen in C:N ratio, which is significantly lower in mesquite than in grass (Table 1). Root anatomy differences could explain the contrasting correlations that we observe regarding soil moisture (Table 1; Fig. 1A), since root anatomy for grasses and shrubs could substantially differ (Gregory 2006). Moreover, root anatomy can have a major role in the development of soil structure, inducing the formation of aggregates, which influence a range of soil characteristics, including aeration, infiltration, erodability, physicochemical properties and weathering (Gregory 2006; Puga-Freitas and Blouin 2015; Centenaro *et al.* 2018; Saleem *et al.* 2018). Moreover, we can see that although less strong than plant type, temperature regime seems to influence C_{MIN}, but in combination with the plant, higher C_{MIN} values are observed in specific plant–temperature pairs (i.e. mesquite–elevated; grass–ambient). This correspondence of higher C_{MIN} with specific plant–temperature pairs in the present study can lead to the hypothesis of selection of specific microbial assemblages to specific environmental and host conditions that could lead to optimal metabolic functioning in such combinations (Strickland *et al.* 2009; Garcia-Pichel *et al.* 2013). Thus, in order to understand the impact that environmental change can have on soil, it is important to consider the combined role of biological and environmental factors.

Microbial community composition is strongly associated with plant type

In the context of the microbially mediated biogeochemical processes, our results show evidence that bacterial composition is strongly correlated with plant type, suggesting plant-driven mechanisms selecting for specific bacterial groups from a common pool (Figs 3 and 4). For instance, in the case of mesquite, microbial communities are dominated by Actinobacteria, while in grass, the numerically dominant group is Proteobacteria (Fig. 4; Figure S1, Supporting Information). More specifically, in

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Table 1. Soil physicochemical variables. Data are presented as mean ± SD.

	Ambient		Elevated (+4°C)	
	Grass	Mesquite	Grass	Mesquite
pH	8.87 ±0.14	9.15 ±0.54	8.70 ±0.18	8.75 ±0.38
Soil moisture(g water/g dry soil)	0.14 ±0.01	0.01 ±0.01	0.15 ±0.01	0.07 ±0.02
SOM (%)	0.12 ±0.06	0.42 ±0.79	0.11±0.01	0.13±0.02
Root volume(g/cm^3)	1.22e+01 ±9.54e+00	1.27e+01±8.09e+00	1.63e+01 ±4.18e+00	8.83e+00 ±4.71e+00
C:N	22.17 ±9.59	16.75 ±6.34	26.75 ±8.04	15.16 ±4.57
C_{MIN}(μg CO_2-C/g dry soil/day)	559.49 ±174.53	336.35 ±221.90	208.00 ±82.87	598.37 ±137.76

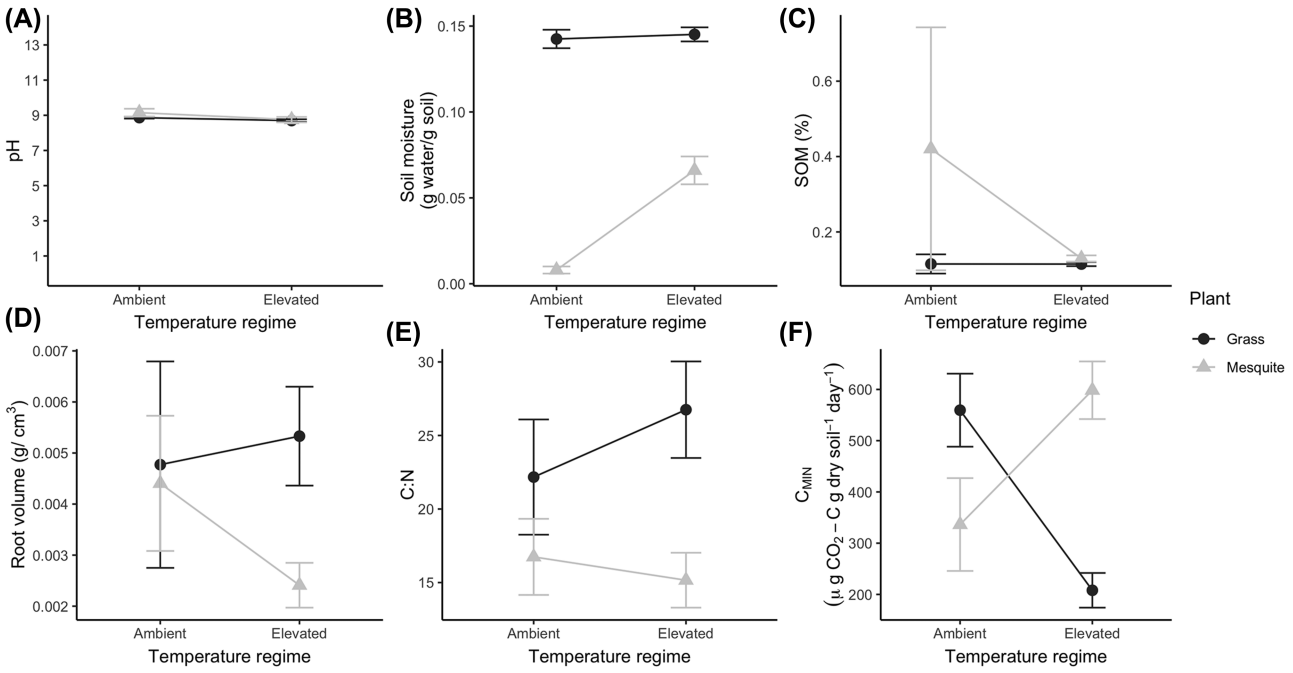

Figure 1. Interaction plots for soil physicochemical variables. Data correspond to mean values ± SE for **(B)** soil moisture, **(C)** SOM, **(D)** root volume and **(E)** carbon to nitrogen ratio (C:N), or mean values ± SD for **(A)** pH and **(F)** C_{MIN}. Dark circles correspond to grass treatments and light triangles correspond to mesquite treatments. See Table 2 for the two-way ANOVA test statistical parameter summary.

Table 2. Statistical tests to evaluate the effect of the environment and plant on soil physicochemical variables.

Variable	Factor	F_1/W	P
pH	Temperature regime	3.94	0.06
	Plant	1.34	0.25
	Temperature regime × plant	0.67	0.42
C_{MIN}	Temperature regime	0.45	0.51
	Plant	1.59	0.22
	Temperature regime × plant	21.38	**<0.001**
Soil moisture[a]	Temperature regime	51	0.23
	Plant	144	**<0.001**
SOM[a]	Temperature regime	58.5	0.45
	Plant	58.5	0.45
Root volume[a]	Temperature regime	97	0.97
	Plant	93	0.24
C:N[a]	Temperature regime	63	0.62
	Plant	118	**<0.05**

Two-way ANOVAs and Mann–Whitney test results are shown. *F* values for two-way ANOVAs and *W* values for Mann–Whitney tests.
[a]Variables with non-normal distribution for which non-parametrical tests were performed. Significant *P*-values (<0.05) are shown in bold.

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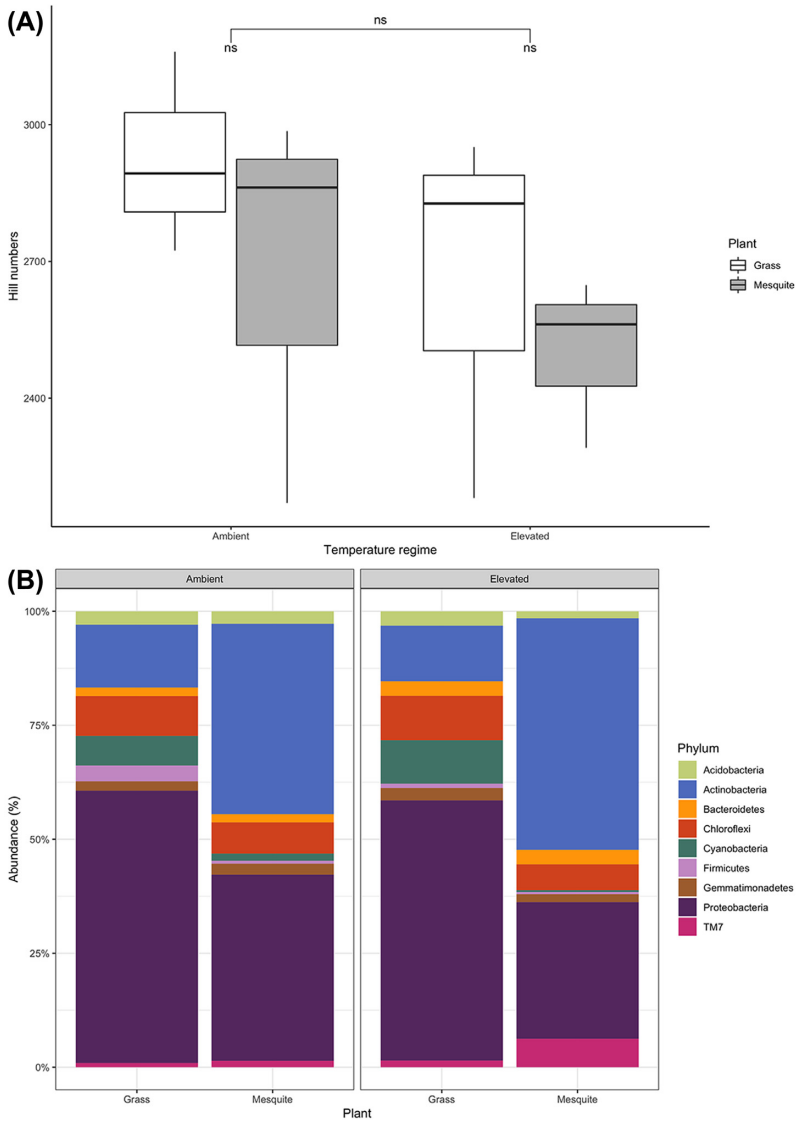

Figure 2. Soil microbial community diversity per treatment. **(A)** Box plot of alpha diversity estimates (Hill numbers); *t*-test significance values are indicated above pairs of samples (ns = non-significant). **(B)** Mean relative abundance of the 12 most abundant (>1%) bacterial phyla.

Table 3. Mantel test results. Correlation between microbial composition differences (UniFrac distance) and physicochemical differences (Euclidean distance).

Variable	*r*	*P*
All variables	0.34	**<0.05**
C_{MIN}	0.04	0.33
C:N	0.10	0.24
Soil moisture	0.71	**<0.001**
Root volume	0.07	0.21
SOM	0.08	0.36
pH	0.00	0.49

the case of the dominant Proteobacteria in grass, we found *Rhodobacter*, *Pseudomonas* and *Pedomicrobium* as highly abundant.

Moreover, as mentioned before, in addition to plant type, temperature regime seems to influence C_{MIN}; higher C_{MIN} values are observed in specific plant–temperature pairs (i.e. mesquite–elevated; grass–ambient). This correspondence of higher C_{MIN} with specific plant–temperature pairs can lead to speculation on selection of specific microbial groups to specific environmental and host conditions (Strickland *et al.* 2009; Garcia-Pichel *et al.* 2013). For instance, the increased frequency of Actinobacteria in the mesquite treatment would be consistent with increased C_{MIN} in the mesquite–elevated temperature treatment as various studies have reported Actinobacteria as important organic matter decomposers (Strap 2011). Potentially, this would explain increased fertility in soils subject to shrub encroachment as they are enriched in Actinobacteria (Hibbard *et al.* 2001; Peng *et al.* 2013). Nonetheless, given our results, it is hard to attribute a specific function to the differentially abundant microbial groups between grass and mesquite and temperature treatments, especially since we did not find significant differences in SOM.

The presence in high abundance of *Sinorhizobium* (Proteobacteria) is consistent with the fact that mesquites are leguminous plants, frequently associated with these nitrogen-fixing bacteria (Long 1989). Given this, it would be important to direct future efforts to investigate the effect of plant type in soil fertility in terms of N forms.

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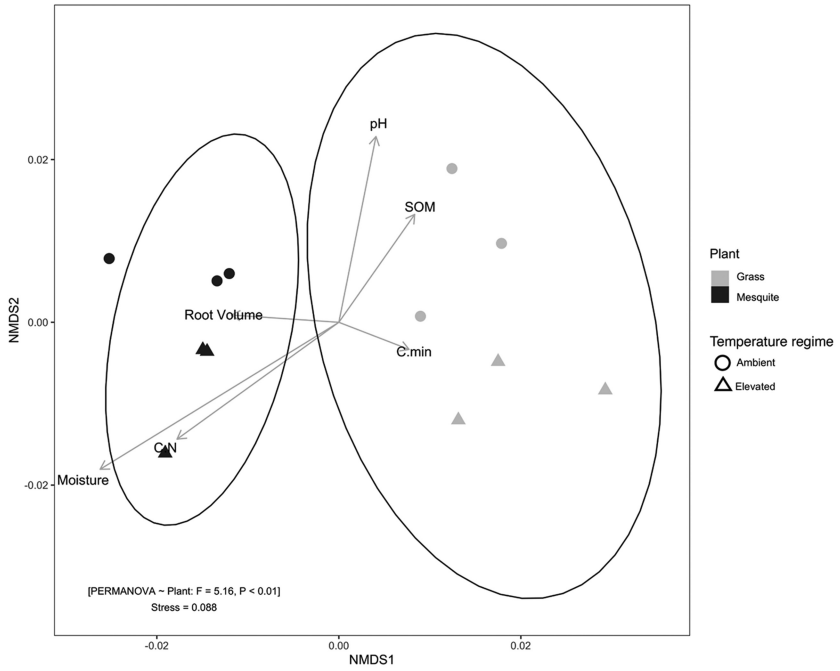

Figure 3. NMDS plot for bacterial community composition distance across samples. Distance was estimated as weighted UniFrac metric with soil physicochemical parameter vectors fitted using 'envfit' function in 'vegan' package. Dark shapes correspond to grass treatments and light shapes correspond to mesquite treatments. Circles correspond to ambient temperature regime and triangles correspond to elevated temperature regimes. Confidence ellipses were calculated with the 'dataEllipse' function of the 'car' package in R.

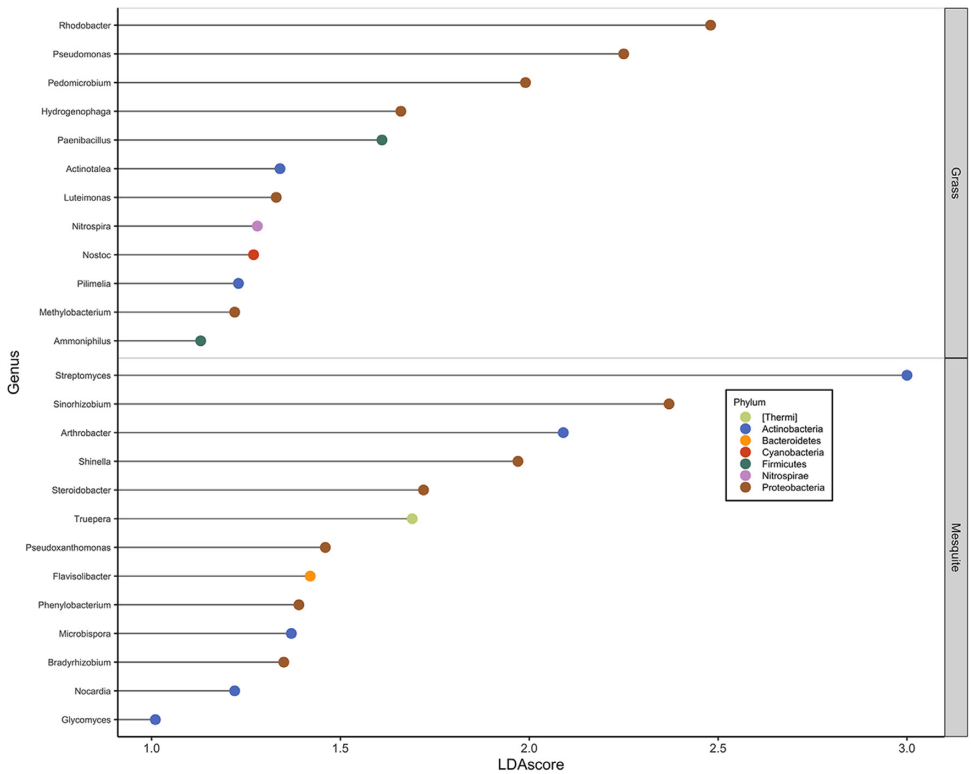

Figure 4. LEfSe analysis of soil bacterial genera associated with plant type. Bars indicate LDA values. Colors indicate genera corresponding phyla. Plant types are indicated on the right-hand side.

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Although the grain of our classification is coarse, it gives us hints on the divergent nature of community assembly for the different plant types, and in turn of potentially divergent biogeochemical/metabolic dynamics regarding nutrient cycling processes such as C_{MIN}. Previous studies have documented various mechanisms through which plants influence microbial community assembly in soil and rhizosphere (Berg and Smalla 2009; Aira *et al.* 2010; Philippot *et al.* 2013). A very well established mechanism is the chemical nature of the root exudates of plants, which can vary phylogenetically and even at the genotype level of the same plant species (Miethling *et al.* 2000; Bais *et al.* 2006; Huang *et al.* 2014; Lakshmanan, Selvaraj and Bais 2014). Another well-documented mechanism of selective community assembly of microbes in rhizosphere is root anatomy that influences the environmental conditions of soil and selects for different types of microbial communities (DeAngelis *et al.* 2009; Pérez-Jaramillo *et al.* 2017; Centenaro *et al.* 2018). Nonetheless, in the present study, without information on root anatomy it is not possible to associate this factor with microbial community composition in the different plant phylogenetic groups.

Overall, looking at both the physicochemical parameters and microbial composition of the experimental mesocosms of the present study, we can reflect on the major influence of environmental conditions and host species on microbial community assembly and the consequences on microbially mediated ecosystem processes (Strickland *et al.* 2009). Further studies looking at the specific mechanisms behind host/environmental selection of functional groups within microbial communities are needed for a better understanding and predictions of ecosystem function in the context of terrestrial ecosystem management under climate change.

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SUPPLEMENTARY DATA

Supplementary data are available at *FEMSLE* online.

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