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Resilience of microbial communities in Mediterranean soil after induced drought and manipulated UV radiation

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Abstract

Enhanced UV radiation levels and decreased rainfall in Mediterranean terrestrial ecosystems due to climate change might impact soil bacterial communities, significantly altering their structure and affecting biogeochemical cycles. The aim of this study was to evaluate the effect of UV-B and UV-A radiation on soil bacterial richness, abundance and community composition in a Typic Dystroxerept of Mediterranean shrubland and to determine whether these effects depend on reduced rainfall and/or soil physicochemical properties. Soils were subjected to long-term UV conditions: UV-A + UV-B exclusion (UV0 plots), UV-B exclusion (UVA plots), or ambient UV-A + UV-B exposure (UVAB plots), and combined with two rainfall regimes, natural (NR) and reduced (RR) rainfall. Barcoded amplicon 16S rRNA gene sequencing was used to analyse changes in microbial diversity. UV radiation did not affect bacterial richness and diversity indexes and only minor differences in species composition were observed. Unidentified species of the *Longimicrobiaceae* appeared to be in greater abundance in the UV0 plots than in the UVA and UVAB, especially under natural rainfall, whereas members of the *Pyrinomonadaceae* and *Ktedonobacteraceae* were more abundant in UVAB. Rainfall reduction resulted in lower bacterial abundance but higher diversity (Shannon–Weiner and InvSimpson indexes) under UV exclusion. The results pointed to a combined response of soil bacterial communities to UV radiation and rainfall treatments. However, the small changes observed suggest a high resilience of the Mediterranean shrubland soil microbiome to the projected changes in UV and rainfall conditions.

Highlights

- Microbial abundance and diversity were analysed in Mediterranean soils exposed to contrasted UV radiation and rainfall treatments
- Reduced rainfall exerted a greater effect on soil bacteria than UV radiation exposure.

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- Limited effects of UV and rainfall changes support a high resilience of soil bacterial communities.

KEYWORDS

bacterial diversity, rainfall, shrubland, soil microbiome, UV-A radiation, UV-B radiation

1 | INTRODUCTION

According to climatic models, a reduction in cloudiness in the Mediterranean Basin (Sanchez-Lorenzo et al., 2017) is expected, which will result in increased aridity and a concomitant increment in ultraviolet (UV) radiation fluxes, both UV-B (280–315 nm) and UV-A (315–400 nm), that reach the soil surface (Bornman et al., 2011). Specifically, the application of climate models for the Mediterranean area predicts an increase in solar radiation (10%–15%) and a modification of the rainfall regime with longer dry periods (Calbó, 2010; Stocker et al., 2013). Other components of global change in the Mediterranean Region, such as land abandonment and higher forest fire frequency (IPCC, 2012), will eventually propitiate the spread of shrublands and the decline of forests and/or grasslands (Acácio et al., 2009). The alteration of UV radiation and precipitation regimes, mainly in the summer season, along with shifts to a more sclerophyllous (and/or with higher C:N ratio) vegetation, can directly impact soil structure and functionality (i.e., carbon fluxes) (Darenova et al., 2017) and trigger changes in soil bacterial communities (Bornman et al., 2019; Caldwell et al., 2007; Johnson, 2003). Soil microorganisms are essential not only for litter decomposition and nutrient cycling (Hättenschwiler et al., 2005) but also for soil formation and plant and animal health (Van Der Heijden et al., 2008). Despite this, current knowledge about UV (UV-B and UV-A) radiation effects on the structure and functioning of soil bacterial communities is scarce (Bornman et al., 2019; Harborne, 1976), especially in semiarid Mediterranean ecosystems (Baker & Allison, 2015; Sardans & Peñuelas, 2013). Studies on the interactive effects between UV-B and/or UV-A radiation and soil moisture are even less represented in the literature.

UV radiation effects on soil bacteria are multifaceted. UV-B radiation has a low penetration capacity and thus it can only directly affect microbes living at the soil surface (Johnson, 2003). In fact, UV-B radiation can damage DNA and produce reactive oxygen species (ROS), inhibiting soil microbial activity and altering the bacterial community composition (Harborne, 1976). Soil surface bacterial communities rely on UV-B tolerance abilities (Caldwell et al., 2007; Wang et al., 2015), with the presence of UV protective bacterial pigments (Jacobs & Sundin, 2001; Kumar et al., 2015) and/or of effective DNA repair systems (Snider et al., 2009), the most significant mechanisms for increasing resistance. However, UV-B can also exert an indirect effect on soil bacteria due to shifts in plant development, photosynthate allocation, root biochemistry, root exudation (Caldwell et al., 2007; Rinnan et al., 2008), litter quality (Kotilainen et al., 2008) and litter photodegradation (Austin et al., 2016). Regarding UV-A radiation, fewer studies are available on its effects on soil bacteria (Jeffery et al., 2009; Kumar et al., 2015). It can also influence plant growth, including roots (Verdaguer et al., 2017), which might indirectly alter soil microbiota.

A reduction in soil moisture can directly alter the number and activity of soil microorganisms by dehydration or by reducing water availability (Naylor & Coleman-Derr, 2018; Preece et al., 2019). Drought will exert significant changes on the physical and chemical properties of the soil, affecting biological activity (Bérard et al., 2015; Karmakar et al., 2016). Some studies performed under drier conditions in Mediterranean ecosystems have reported that plant community composition, plant species richness and diversity (Shihan et al., 2017), along with changes in the root exudate profile, can influence the soil microbiome (Preece & Peñuelas, 2016). In general, researchers consider that bacteria will cope worse with a reduction in soil moisture than fungi, which could even improve their species richness and diversity (de Vries et al., 2018). Similar results have been found for soils in Mediterranean ecosystems (Flores-Rentería et al., 2015; Preece et al., 2019; Yuste et al., 2011). Indeed, according to Yuste et al. (2011), under a future scenario of drier conditions, a progressive replacement of soil bacteria by fungi could occur in Mediterranean regions.

Studies on the combined effects of climate change factors on soil microbiota are particularly relevant (Bérard et al., 2015; Yuste et al., 2011) since soil bacterial responses to one factor might be amplified, reduced or nullified by other factors. However, to our knowledge, there are no studies on the interactive effect between UV-B or UV-A radiation levels and drought on soil bacterial communities. In fact, most of the studies on the effect of UV radiation (or UV-B) and soil moisture on soil bacterial communities have focused on litter decomposition (Almagro et al., 2015; Bosco et al., 2016; Smith

et al., 2010). Soil bacteria changes can alter the biogeochemical cycles with so far unpredictable results at the ecological level (Bérard et al., 2015). Thus, there is a clear need for additional studies assessing the effect of UV-B and UV-A radiation on soil bacterial communities under reduced rainfall (RR) in Mediterranean ecosystems.

We aimed to address the impacts that UV-B and UV-A radiation along with decreased rainfall levels may exert on the structure of the soil bacterial community of a Mediterranean shrubland. Specifically, we expected soil bacteria to respond differently to UV radiation depending on the wavelength, with UV-B exerting a more negative impact than UV-A radiation. We also expected that UV radiation would exert a negative impact on soil bacteria when aggravated by rainfall reduction. Moreover, a shift in soil bacteria communities towards more resistant bacteria was anticipated. To validate these hypotheses, soil bacterial communities were taxonomically characterised using amplicon-based 16S rRNA gene sequencing, and their relationship with soil properties and enzymatic activities were investigated. Soil samples were collected in summer, the most stressful season in the Mediterranean Basin, as part of a field experiment conducted for almost 3 years in a shrub community subjected to different levels of UV radiation and rainfall.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

The study was conducted in the Gavarres Massif (41°91′N, 2°91′E, Girona, northeast of the Iberian Peninsula) in an area covered with a Mediterranean shrubland community dominated by *Arbutus unedo*, *Erica scoparia* and *Phillyrea angustifolia*. The experimental site was located about 250 m above sea level on a south-facing slope. Soils were mostly Inceptisols, classified as Typic Dystroxerept (Soil Survey Staff, 2014), with a sandy loam texture developed over a Palaeozoic granitic parent material. Climatological variables, such as precipitation and temperature, were constantly monitored at a meteorological station located 3 km away from the study site (Cassà de la Selva, Girona, northeast of the Iberian Peninsula).

Despite models predicting an increase in UV radiation, UV exclusion experiments are essential to determine the role of UV-A and UV-B radiation under field conditions, where it is often unfeasible to build an appropriate UV-enhancement experiment. Eighteen experimental plots (3 m × 3 m) were placed over a large shrubland area surrounded by forest. The experimental plots were covered with plastic shelters to control the UV radiation and rainfall. The shelters, which prevented rain from reaching the vegetation and soil, were set at an average height of 1.5 m and on a 10° south-facing slope. Three types of materials were used to construct the shelters to select the range of UV radiation reaching the vegetation and soil. Polycarbonate filters (2 mm thick, PC0100UV, PolimerTecnic, Girona, Spain) were used to exclude UV radiation almost completely (UV0 condition) while maintaining photosynthetic active radiation (Table S1). The UVA plots were covered using polyester filters (0.25 mm thick, Melinex, Ponscosta, Valencia, Spain) that excluded UV-B (<3% at the soil surface) but not UV-A (>52% transmittance) radiation. Last, 3 mm-thick methacrylate filters (MC0100XN, PolimerTecnic, Girona, Spain) were used in the UVAB plots, the purpose of which was to function as controls for the effect of the shelter on other environmental variables (e.g., temperature) without altering ambient UV-A and UV-B radiation (transmittance of these filters was 85% and 80.5% for UV-A and UV-B, respectively).

The rainfall reaching each plot was collected in 310 L tanks located nearby. On half of the plots, after a precipitation event, the water was completely returned to the vegetation and soil, simulating natural rainfall (NR plots). On the other half, called reduced rainfall plots (RR), only 70% of the collected water was returned to the plots in spring, summer and autumn, and 90% in winter. These percentages were established considering the changes in precipitation expected for the Mediterranean Basin in the near future (Stocker et al., 2013). The experimental design was based on having three plots of each combination of UV (UV0, UVA and UVAB) and rainfall (NR and RR) levels. This experiment was conducted between August 2011 and June 2014. In February–March 2013, all the vegetation of the plots was burned by specialised firefighters and then allowed to recover naturally (Díaz-Guerra et al., 2018). Since the fire was conducted in winter, when the air temperature was low and plants were more hydrated, the severity of the fire was low. The soil samples for physicochemical analyses and microbiological characterisation were obtained between 15th to 25th June 2014, 34 months after the experiment was set up and 15 months after the controlled fire.

2.2 | Soil parameters

Five soil moisture and respiration measurements per plot were performed in situ at midday, on sunny days, in the center and at each corner of the plot. Soil moisture was determined as the percentage of volumetric water content by means of a time-domain reflectometer (FieldScout TDR 300 Soil Moisture Meter, Spectrum Technologies,

Inc. Aurora, IL 60504, USA) with two 20-cm probe rods. Soil respiration rates were measured with a portable InfraRed Gas Analyzer (IRGA; CIRAS-2 Portable Photosynthesis System, Amesbury, USA), connected to an SRC-1 Soil Respiration Chamber. Once the closed chamber (diameter 10 cm × height 15 cm) was placed on the soil surface, the flux of CO_2 was measured by the IRGA for 1 min. Carbon dioxide concentration was then calculated and expressed as g CO_2 m^{-2} h^{-1}. Data were calibrated according to soil temperature, which was taken just before the respiration measurement using a thermometer with a 10-cm probe rod (HANNA Instruments, Woonsocket, USA).

Five soil samples per plot from the surface of horizon A (0–5 cm depth) were collected after removing the leaf litter at the center and at each corner of the plot; then, samples were homogenised and pooled in a single composite sample per plot. Pooled samples were separated into aliquots for physicochemical and enzymatic determinations. Molecular work was performed using a single pooled sample per plot, thus reducing the number of replicates per treatment to three. This number of replicates would not be enough for an in-depth soil heterogeneity study but will provide relevant information on the effect of treatments. All collected samples were immediately chilled in a portable freezer and transported to the laboratory.

Once in the laboratory, samples were air-dried and sieved to 2 mm before the analyses. Soil pH was determined using 1:2.5 soil: water suspension. Soil electrical conductivity (EC) was measured in a 1:5 soil: water suspension. pH and EC were measured using a Crison 20 M pHmeter and a Crison micro CM 2200 conductimeter (Crison Instruments S.A., Barcelona, Spain), respectively. Soil organic carbon (SOC) was determined on 1 g of soil by the dichromate oxidation method in the presence of concentrated sulphuric acid (Hopmans & Bristow, 2001). Soil total nitrogen content (TN) was determined by using the Kjeldahl method (Hopmans & Bristow, 2001). One gram of soil was previously digested with sulphuric acid during 1 h at 175°C and 1.5 h at 370°C for organic N mineralization.

β-glucosidase activity was determined using ρNPG (0.05 M 4-nitrophenyl-β-D-glucopyranoside) as substrate in 0.5 g of dried soil. The concentration of ρNP released was determined spectrophotometrically at 398 nm and expressed as mg ρNP kg^{-1} h^{-1} (Masciandaro et al., 2008).

2.3 | DNA extraction

Nucleic acids were extracted from composite samples of each plot (conserved at −80°C) using the FAST DNA Spin kit for Soils (MP Biomedicals, California USA) with minor modifications. Briefly, 0.5 g of wet weight (WW) soil was used. Disruption of microbial cells was accomplished with a FastPrep®-24 Classic Instrument (MP Biomedicals, California USA) after two consecutive runs at 5.5 m/s for 45 s and cooling on ice 1 min before the two runs. DNA was finally eluted in 75 μl of low-ionic strength elution buffer. DNA extracts were distributed in aliquots and stored at −20°C.

The integrity of DNA extracts was assayed in a 2.0% agarose gel. The concentration of DNA was measured using the Qubit 2.0 fluorometer (Thermo Fisher) and the purity was evaluated using a Nanodrop 2000 spectrophotometer (Thermo Fisher Scientific, Wilmington, USA). No further purification steps to reduce protein contamination of DNA extracts were needed according to the A260/A280 ratios obtained (>1.8). The suitability of DNA extracts for downstream molecular applications was checked by PCR amplification using universal primers 27F and 1492R.

2.4 | Quantification of bacterial 16S rRNA genes

Bacterial 16S rRNA gene copies were quantified by quantitative PCR (qPCR). Reactions were performed with a 7500 Real-Time PCR system (Applied Biosystems, USA) using the SYBRGreen PCR Master mix. Standard curves were obtained using serial dilutions (10^2 to 10^7 gene copies) of linearized plasmids containing a positive insert for the 16S rRNA gene. All quantifications were run in duplicate. Amplification efficiency was 93%. Inhibition tests were performed prior to the analysis for each sample using an internal standard of 10^5 copies. No inhibition was considered when changes in the expected concentration of the internal standard were below a 10% difference.

2.5 | Barcoded amplicon sequencing of 16S rRNA genes and microbiome analyses

The hypervariable V4 region of the 16S rRNA gene was amplified using the primers 515F-806R and by applying the method previously described (Kozich et al., 2013), adapted to produce dual indexed Illumina compatible libraries in a single PCR step. The PCR products were normalised using Invitrogen SequalPrep DNA normalisation plates, and pooled samples were sequenced using an Illumina MiSeq PE250. Library preparation and sequencing were conducted at the RTSF Core facilities at the Michigan State University USA (https://rtsf.natsci.msu.edu/).

Raw sequences (942,993 reads for 16 out of 18 samples) were processed with DADA2 version 1.1.1 according to previously recommended methods (Callahan et al., 2016). First, the sequences were checked for quality

and, based on the obtained scores, truncated at positions 220 (forward reads) and 150 (reverse reads) to obtain mean quality scores over 30 for all positions. Reads exceeding a maximum number of expected errors (>2) or containing ambiguous bases were discarded. Forward and reverse reads were merged and chimeric sequences removed. Two replicates corresponding to reduced rainfall UVA-treated plots had very poor sequencing depth (<1500 reads), so were discarded from the analyses. A total of 4406 amplicon sequence variants (ASVs) contained a minimum of 2 sequences per sample (singletons discarded). ASV were classified according to the SILVA release 132 (www.arb-silva.de). The ASVs that could not be correctly assigned at the domain level (bootstrap below 75%), as well as those classified as mitochondria, chloroplasts, and eukaryotic related sequences (123 ASVs, 2.3% of total sequence reads), were removed from the data set. The final number of sequences per sample ranged from 19,988 to 47,488 (mean 35,379 sequences per sample).

Alpha diversity indexes (Shannon–Weiner and inverse of the Simpson) and richness (observed number of ASV) indicators were calculated using randomly collected subsets of ~19,500 sequences per sample. Ten iterations were performed and the mean values calculated. The microbial community structure was compared between samples by calculating the weighted UniFrac distances (Lozupone et al., 2011). Differences in the community structure were visualised using a Principal Coordinates Analysis (PCoA). Groups of samples using rainfall or UV radiation as treatments were statistically compared by means of analyses of similarity implemented in vegan: Community Ecology Package in R. Specific and shared ASVs among treatments were visualised as Venn diagrams using the ps_venn function in R. The sequences have been deposited in the Sequence Read Archive (SRA-NCBI) under Bioproject accession number PRJNA768312.

2.6 | Statistical analyses

All statistical tests were performed in R (R Core Team, 2014). Data were checked for normal distribution and homogeneity of variances using the Shapiro–Wilk and Bartlett's tests, respectively. Only β-glucosidase activity data were log-transformed to achieve normality. Correlations among physicochemical and biological variables were tested using Pearson's tests. ANOVAs and Tukey posthoc tests for multiple comparisons were used to test for the effects of rainfall (NR and RR) and UV radiation (UV0, UVA and UVAB) treatments, and possible interactions on measured soil physicochemical data and 16S rRNA gene abundances. For the microbial analysis, the combination of UV-A radiation and reduced rainfall (UVA_RR) was removed from the analysis, because two of the three samples yielded a very low sequencing depth (<1000 reads). Hence, one-way ANOVAs were performed to test differences between UV radiation conditions (UV0, UVA and UVAB) under NR, while two-way ANOVAs were applied to assess the effect of rainfall (NR and RR) and UV radiation (considering UV0 and UVAB conditions) treatments. Pairwise correlation tests of soil physicochemical data, activity rates, 16S rRNA gene densities, and estimated values of PCoA axis 1 and 2, were analysed using the stats package in R. All statistical tests were considered significant when $p \leq 0.05$, unless otherwise stated.

3 | RESULTS

3.1 | Soil properties and microbial activities

During the 15 months prior to soil collection, the soil moisture was approximately 23% lower in the RR plots than in the NR plots (Díaz-Guerra et al., 2018). At the moment of sampling for microbiological analyses (June 2014), soil moisture was also higher in the NR plots than RR plots, although the differences were only marginally significant (Table 1). Moreover, independently of the rainfall treatment, soil moisture tended to be higher in the UVA than in the UV0 plots, with the soil moisture for the UVAB plots not being different from the others (Table 1; ANOVA test, $p < 0.1$). Soil pH was slightly acidic, ranging from 5.73 to 6.90, and soil conductivity was low, ranging from 0.038 to 0.106 dS/m, especially for the plots receiving NR (Table 1).

Regardless of the rainfall conditions, SOC tended to be lower in the plots receiving ambient UV radiation (Table 1). Differences among UV radiation and rainfall conditions were not significant for soil C:N ratio or soil respiration. The interaction between the two factors was never significant (Table 1). Soil respiration and ß-glucosidase activity were the two proxies for soil microbial activity used in this study. However, whereas ß-glucosidase activity was positively correlated with TN and SOC (Pearson's correlation test, $p < 0.001$), soil respiration was not correlated with any of the analysed soil physicochemical variables (Figure S1), probably because of the narrow range of edaphic data variation of the studied soils in Les Gavarres (Table 1).

3.2 | Soil bacterial 16S rRNA gene abundance and diversity

16S rRNA gene abundances ranged from 9.5 x 10^8 to 200 x 10^8 copies/g wet weight soil (Figure 1). Since the

TABLE 1 Soil properties measured (0–5 cm deep) at the time of sampling (June 2014)

Treatment	Moisture (%)	$pH_{1:2.5}$	$EC_{1:5}$ (dS/m)	SOC (%)	TN (%)	C:N ratio	Respiration ($g/m^2/h$)	ß-glucosidase (µg PNP/g DW/h)
RR								
UV0	5.95 (1.72)	6.2 (0.2)	0.081 (0.026)	1.35 (0.55)	0.102 (0.040)	13.18 (1.90)	0.30 (0.11)	104.1 (37.4)
UVA	7.47 (1.53)	6.4 (0.4)	0.078 (0.010)	1.47 (0.27)	0.112 (0.119)	13.48 (3.96)	0.38 (0.02)	108.6 (66.8)
UVAB	8.87 (0.17)	6.2 (0.3)	0.068 (0.024)	1.14 (0.13)	0.102 (0.027)	11.53 (2.26)	0.37 (0.09)	75.1 (16.4)
NR								
UV0	7.60 (3.59)	6.5 (0.3)	0.061 (0.020)	1.65 (0.32)	0.141 (0.048)	12.06 (1.76)	0.27 (0.03)	129.3 (65.2)
UVA	11.54 (0.98)	6.1 (0.3)	0.064 (0.012)	1.58 (0.16)	0.126 (0.016)	12.59 (1.42)	0.34 (0.15)	100.6 (16.31)
UVAB	9.13 (2.53)	6.0 (0.3)	0.050 (0.013)	1.13 (0.09)	0.081 (0.009)	13.93 (0.60)	0.30 (0.12)	65.2 (4.3)
Two-way ANOVA								
UV radiation	**0.090**	0.357	0.472	**0.073**	0.197	0.946	0.436	0.129
Rainfall	**0.064**	0.751	**0.069**	0.378	0.461	0.902	0.362	0.860
Interaction effect	0.306	0.332	0.964	0.684	0.265	0.343	0.911	0.761

Note: Values are means, with standard deviations in parentheses ($n = 3$).
Abbreviations: C:N, organic carbon content to nitrogen ratio; EC, electrical conductivity; SOC, organic carbon content; TN, total nitrogen content.
Note: p-values of two-way ANOVA tests with UV radiation and rainfall treatments as factors are shown (highlighted in bold when $p \leq 0.1$).

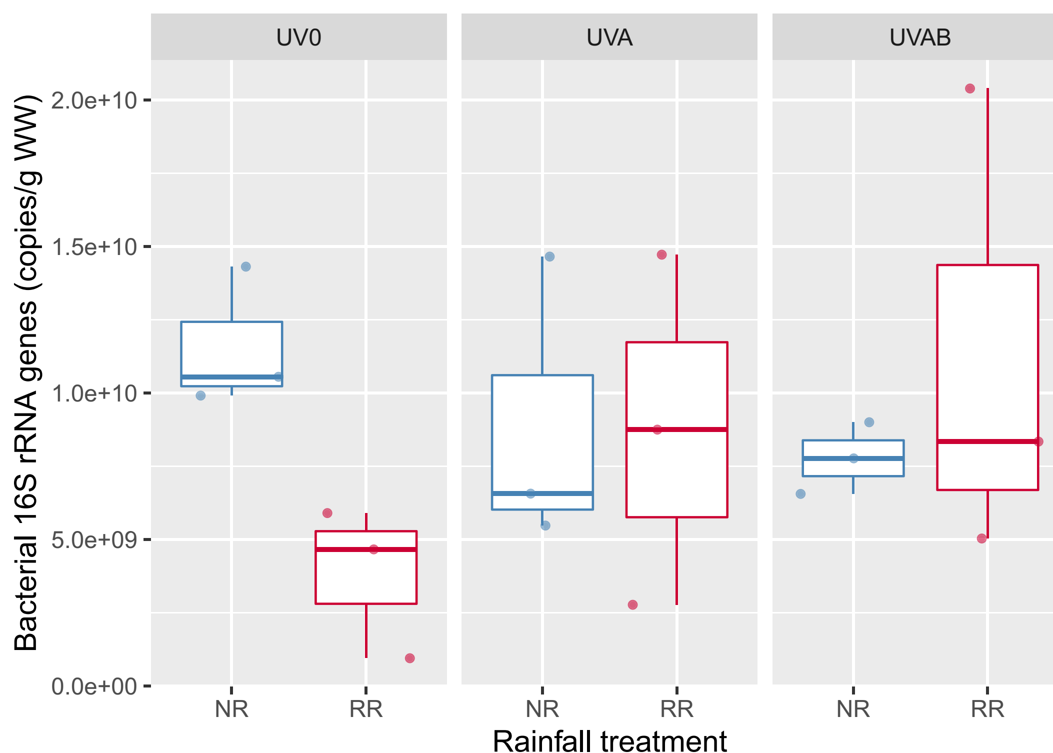

FIGURE 1 Box plot showing bacterial 16S rRNA gene abundance (copies/g WW) in the A horizon of soils according to UV radiation and rainfall treatments ($n = 3$). Colours refer to differences in the amount of rain received. NR, natural rain; RR, reduced rain; UV0, exclusion of ambient UV radiation; UVA, exclusion of ambient UV-B radiation; UVAB, near-ambient UV radiation; WW, wet weight

interaction between the UV radiation and rainfall treatments was almost significant ($p = 0.066$), the effect of one treatment within the levels of the other treatment was analysed. No significant differences were detected in 16S rRNA gene abundances among the different UV radiation conditions for either of the two rainfall levels applied (RR and NR). In contrast, there was an effect of the rainfall treatment in the plots that received no UV radiation (UV0), since the samples subjected to RR contained a significantly lower amount of 16S rRNA genes ($p = 0.018$) (Figure 1). A significant negative correlation between the abundance of the 16S rRNA gene and soil EC was found (Pearson's test, -0.52, $p < 0.05$), when the abundance data were log-transformed (Figure S1).

Observed bacterial richness (S_{obs}) that is the number of ASVs per unit sample, varied from 2.81 to 3.02 (Figure 2). Rarefaction curves of richness and Shannon–Weiner's diversity indexes at different sampling depths reflected an almost complete saturation (Figure S2). No significant differences in species richness in response to UV radiation (UV0 and UVAB plots) and/or rainfall treatments were detected, including when the effect of the UV radiation was analysed within NR.

Shannon–Weiner's diversity indexes were fairly homogeneous in all samples, ranging from 6.56 to 7.06. Higher diversity values were found in the plots where reduced rainfall was applied (RR) than in the NR plots ($F = 5.035$, $p = 0.049$), and they were more pronounced in UV0 treatments, although the interaction between UV radiation and rainfall was not significant ($F = 0.821$, $p = 0.386$). Calculation of the inverse of the Simpson diversity index (InvSimpson), a more realistic measurement of diversity for fairly homogenous communities, reinforced the differences between the RR and the NR plots receiving no UV radiation, with the interaction between the two factors almost significant in this case ($F = 4.217$, $p = 0.067$, Figure 2). When the Shannon–Weiner and InvSimpson indexes were analysed within the NR treatment, there were no significant differences among the three UV conditions (Figure 2).

Principal Coordinates Analysis was used to detect sample distribution according to treatments (Figure S3). Differences between RR and NR treatments could not be confirmed with an Adonis test using weighted Unifrac distances ($F = 1.007$, $p = 0.384$, 999 permutations), thus revealing a high heterogeneity of microbial communities within the natural and the reduced rainfall plots. The rainfall treatment seemed to have a similar effect on the microbial communities as the UV radiation treatment according to the magnitude of the F statistic in the Adonis

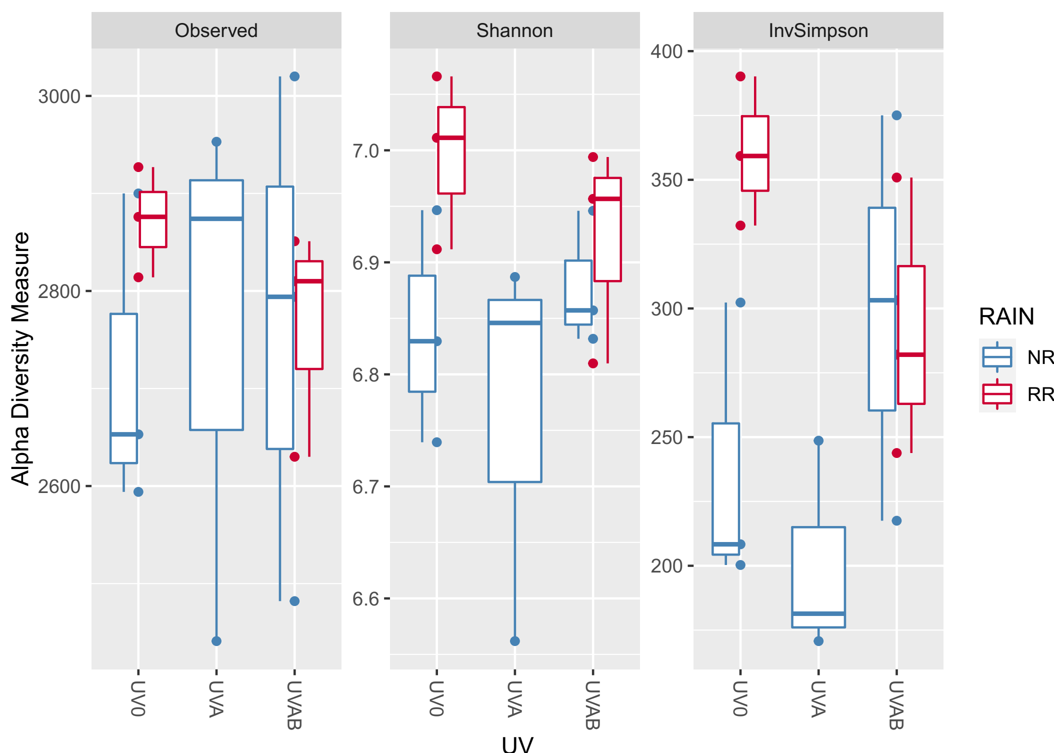

FIGURE 2 Alpha diversity indicators for soil samples collected in June 2014. Box plots are organised according to UV radiation and rainfall conditions. Observed, number of observed ASVs; Shannon, Shannon-Weiner diversity index; InvSimpson, the inverse of the classical Simpson's diversity estimator; NR, natural rain; RR, reduced rain; UV0, exclusion of ambient UV radiation; UVA, exclusion of ambient UV-B radiation; UVAB, near-ambient UV radiation

test (F = 0.988, $p = 0.434$). Axis.1 of the PCoA correlated negatively with pH (Pearson coefficient − 0.59, $p < 0.05$), whereas EC and soil moisture correlated significantly with Axis.2 (Pearson coefficients 0.63, $p < 0.05$, and −0.67, $p < 0.01$, respectively).

3.3 | Soil bacterial community structure and composition

Taxonomical assignations of the ASVs at different levels showed that Proteobacteria (27%, of sequences), Actinobacteria (20%), Planctomycetes (16%), Verrucomicrobia (17%), and Acidobacteria (8%) were the most abundant phyla in all the samples. Altogether these phyla accounted for more than 85% of the sequences (Figure 3). At lower taxonomic ranks, *Alphaproteobacteria*, particularly members of the DA111 group (*Rhodospirilalles*) (4.5%) and *Bradyrhizobiaceae* (3.1%), were the most representative. Furthermore, within the Acidobacteria, common soil bacteria such as *Solibacteraceae* and *Acidobacteraceae* were among the most abundant families, accounting for more than 2% of the sequences.

Relative abundances of the sequences at the phylum level were fairly similar, independently of the use of UV radiation or rainfall levels as the grouping variables. However, some effects of treatments were found at a lower taxonomic level. The *Solirubrobacterales* group YNFPP1 belonging to Actinobacteria appeared to be slightly enriched in the UVAB plots compared to the other radiation conditions, its relative abundances accounting for more than 2.1% of sequences compared with 1.3% of sequences. On the other hand, *Mycobacteraceae* and *Gaiellales*, also from the Actinobacteria phylum, were less abundant in the NR samples than in the RR samples. In contrast, *Planctomycetaceae* and soil group DA 101 were slightly more abundant in the NR samples than in the RR samples. Venn diagrams showed the presence of some specific ASVs, which could be found selectively in some treatments (Figure 3), although, in all cases, specific taxa were represented at very low abundance. For instance, the 561 ASVs shared between the UV0 and the UVAB samples accounted for less than 2.8% of the total sequence reads, but this figure was below 0.5% in all other cases. Most ASVs that were specific to a condition could not be observed in all the replicates within the group.

DESeq tests were also conducted (alpha value 0.1) to assess for relevant differences at the ASV level in response to UV radiation or rainfall treatments. The tests were conducted pairwise using UV radiation conditions as the

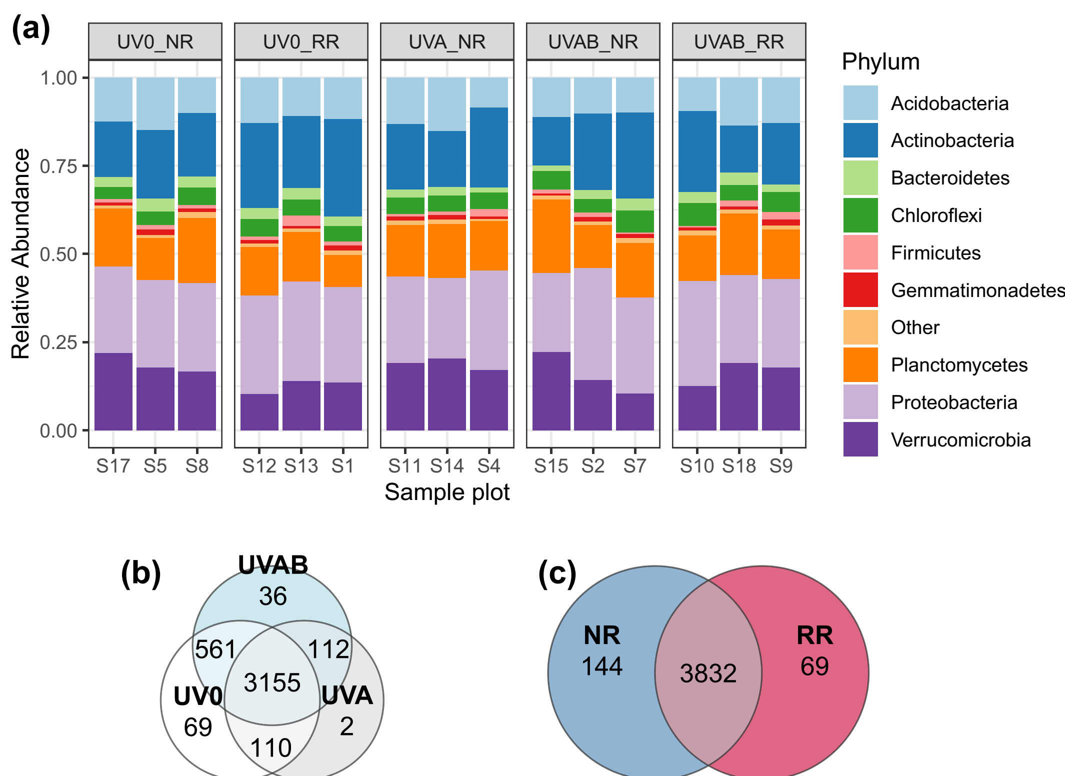

FIGURE 3 (a) Relative abundance of sequences according to main phyla. Only phyla accounting for more than 0.5% of sequences in any of the samples are shown. (b) Venn diagram of shared and specific ASVs in UV-treatments. (c) Venn diagram of shared and specific ASVs in rain-treatments. NR, natural rain; RR, reduced rain; UV0, exclusion of ambient UV radiation; UVA, exclusion of ambient UV-B radiation; UVAB, near-ambient UV radiation

TABLE 2 Taxa (ASVs) showing significant differential abundances according to pair-wise DESeq analyses

	Mean relative abundances in group (% sequence reads)						
	UV0 ($n = 3$)	UVA ($n = 3$)	UVAB ($n = 3$)	p	NR ($n = 9$)	RR ($n = 6$)	p
Acidobacteria Pyrinomonadaceae RB4	<0.01	<0.01	0.24 (0.24)	***	0.08 (0.08)	0.03 (0.03)	NS
Chloroflexi Unident. *Ktedonobacteraceae*	<0.01	0.02 (0.01)	0.17 (0.10)	*	0.06 (0.04)	0.04 (0.02)	NS
Gemmatimonadetes Unident. *Longimicrobiaceae*	0.19 (0.19)	<0.01	<0.01	***	0.06 (0.06)	<0.01	NS
Verrucomicrobia '*Candidatus* Xiphinematobacter'	0.10 (0.05)	0.21 (0.02)	0.14 (0.04)	NS	0.15 (0.03)	0.02 (0.01)	**

Note: Mean relative abundances (%) and standard errors of the mean (in parentheses) are indicated for differential taxa. Comparisons according to UV treatments were performed only for the NR subset.

Abbreviations: RR, reduced rain; NR, natural rain; NS, not significant; UV0, exclusion of ambient UV radiation; UVA, exclusion of ambient UV-B radiation; UVAB, near-ambient UV radiation.

Note: Adjusted p-values for UV or rain comparisons are indicated, *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

confronting variable, but only in the NR plots. Significant differences at the $p < 0.1$ level were observed for relatively low abundant ASVs, suggesting a limited effect of the UV treatment on the microbiome composition (Table 2). In general, unidentified *Longimicrobiaceae* (Gemmatimonadetes) were higher in the UV0 plots compared to the UVA or the UVAB plots, especially in the NR condition. In contrast, *Pyrinomonadaceae* (Acidobacteria) and *Ktedonobacteraceae* (Chloroflexi) were dominant in the UVAB plots when compared to the UV0 plots. No significant differences were found between the UVA and UVAB plots. Regarding rain conditions, only '*Candidatus* Xiphinematobacter' (Verrucomicrobia) had on average a higher relative concentration in soils from the NR plots than from the RR plots.

4 | DISCUSSION

4.1 | Soil bacterial community

Slightly acid to neutral soil pHs have been associated with high bacterial richness and diversity (Delgado-Baquerizo & Eldridge, 2019; Fierer & Jackson, 2006; Rousk et al., 2010), which is consistent with the high values found in our study (Figure 1). Indeed, in a Mediterranean forest (Curiel Yuste et al., 2014), soils with slightly acidic pH have shown alpha diversity indexes (Shannon–Weiner–Weaver or Simpson diversity indexes) similar to those reported here, and higher than those described in more alkaline soils (Flores-Rentería et al., 2015; Moroenyane et al., 2018). The most abundant bacterial phyla found in the studied soils are mostly in line with those reported in previous studies of Mediterranean Basin soils (Janssen, 2006; Preece et al., 2019; Siles et al., 2014), with a clear dominance of Proteobacteria (27% in the studied plots) and specifically of *Alphaproteobacteria* (Janssen, 2006; Preece et al., 2019; Siles et al., 2014; Spain et al., 2009). However, what stands out most in Les Gavarres soil is the high abundance of *Planctomycetes* (~16%), since, in most studies, including those carried out in Mediterranean forests, *Planctomycetes* ranged from 0% to 10% (Bastida et al., 2013; Buckley et al., 2006; Janssen, 2006; Preece et al., 2019). In a depth profile, Ivanova et al. (2016) reported a significant variation of *Planctomycetes* abundance, which was highest at the topsoil, and this was related to the enrichment of C and N availability at this depth. Specifically, in the studied soils of Les Gavarres, SOC ranged from 1.13% to 1.65% and TN from 0.08% to 0.14% in the upper 5 cm depth. Positive correlations between SOC and TN with *Planctomycetes* were found in a study with different organic amendment-treated soils (0.15%–1.7% of SOC and 0.07%–0.25% of TN), suggesting that organic carbon exerts a deep control over members of the phylum (Bastida et al., 2013). Nevertheless, the small variations observed in the present study would not affect soil functioning, including respiration and ß-glucosidase activity, at the 0–5 cm depth range (Table 1), probably pointing to a low involvement of *Planctomyces* in these activities.

4.2 | UV radiation and rainfall treatment effects on soil bacterial abundance and diversity

UV radiation and rainfall effects on soil bacterial communities were studied 15 months after a low severity burning of the vegetation of the experimental plots. The effects of wildfires on soil microbial communities are greatly dependent on the severity of the fire (Rodríguez

et al., 2018; Sáenz de Miera et al., 2020). For instance, bacterial biomass did not change in a semiarid environment after analysing a 14-year wildfire chronosequence (Muñoz-Rojas et al., 2016). In another study, 6 months after a low severity fire, the physicochemical and microbial properties of soils did not differ significantly from the pre-burning situation (Pourreza et al., 2014). In the present study, key soil parameters that could affect soil bacteria, such as pH, moisture and organic matter, did not vary either after the controlled fire (Díaz-Guerra et al., 2018). Although vegetation burning might have had an effect on the original soil microbial communities, the goal of the present study was to analyse the effects of UV radiation and rain after burning.

The results obtained in the UV0 plots support a negative effect of rainwater reduction on the abundance of bacteria, which is consistent with previous studies (de Vries et al., 2018; Maestre et al., 2015). However, our results also indicate that the effect of precipitation on soil bacterial abundance under UV radiation is lower (Figure 1). Under more xeric conditions, greater exposure to UV radiation increases litter decomposition rates, mostly attributable to the stimulation of photodegradation, although a synergistic effect on soil bacteria has not been disregarded (Baker & Allison, 2015; Smith et al., 2010). Under sunlight, greater nutrient availability through increasing photo-mineralization could favour bacterial development (Pieristè et al., 2020). Bacterial alpha diversity can be either unaffected (Naylor & Coleman-Derr, 2018), or decreased by sudden drought periods (de Vries et al., 2018; Flores-Rentería et al., 2015; Preece et al., 2019). However, in this study, the bacterial diversity indexes were higher under RR (Figure 2), similar to the findings of other studies involving long-term drought periods (Bastida et al., 2019; Preece et al., 2019). A high bacterial diversity in soils with a long history of drought responds to an adaptation of the bacterial community to these conditions (Preece et al., 2019), favouring drought-tolerant phenotypes (Curiel Yuste et al., 2014). Nevertheless, differences in alpha diversity indexes in response to rainfall conditions were mainly observed in the UV0 plots. This would suggest that solar UV radiation could exert a negative effect on soil bacterial diversity under drier conditions, counteracting a possible effect of long-term drought.

4.3 | UV radiation and rainfall treatment effects on soil bacterial composition

Enrichment of bacterial species with enhanced resistances to drought conditions and UV radiation was analysed at lower taxonomic ranks. Shifts in specific bacteria in response to solar UV radiation and rainfall reduction, but not in response to the combination of both factors, were detected. Specifically, the *Solirubrobacter* group YNFPP1 (*Actinobacteria*), tended to be more present in soils receiving near-ambient solar UV radiation (UVAB plots), although the differences were not significant. The ecological significance of this genus remains poorly understood (Li et al., 2015; Poncelet et al., 2014), but it was one of the key genera found in a sand desert exposed to extreme environmental conditions, including intense solar UV radiation (Sun et al., 2018), which could indicate a higher UV-B tolerance. Within the *Acidobacteria* phylum, one ASV from the *Pyrinomonadaceae* family was also more abundant in the UVA and the UVAB plots than in the UV0 plots. Many *Acidobacteria* exhibit carotenoid-related pigments which could favour their tolerance to solar UV radiation (Pinto et al., 2021). In contrast, an unidentified *Longimicrobiaceae* (*Gemmatimonadetes* phylum) was less abundant in the UVA and UVAB plots under NR. Last, an unidentified *Ktedonobacteraceae* (*Chloroflexi* phylum) was also more abundant in the UVAB soils than in the UV0 ones. In addition, it was recently observed that *Ktedonobacter* bacteria were more prevalent in surface snow where they were exposed to higher UV radiation (Maccario et al., 2019).

Some differences in the bacterial community composition have also been related to rainfall. In the present study, the relative abundance of *Planctomycetes* decreased under RR, which is consistent with the most widespread response previously reported (Naylor & Coleman-Derr, 2018). In moisture-limited soils, it is also common to observe a decrease in *Verrucomicrobia* (Naylor & Coleman-Derr, 2018). Accordingly, we detected that an ASV identified as '*Candidatus* Xiphinematobacter' (*Chtoniobacteraceae*, *Verrucomicrobia*) was significantly higher in the NR plots than in the RR plots. In contrast, a higher relative abundance of *Gaiellaceae* (Actinobacteria phylum) was found under RR. Hermans and coworkers reported that soil abundance of *Gaiellaceae* was negatively correlated with the soil C:N ratio (Hermans et al., 2017). Given that in the present study no effect of the rainfall treatment was observed on soil C:N (Table 1), other non-measured soil physicochemical properties should be considered. In a previous study, differences in *Gaiellaceae* abundance were related to cation exchange capacity and soil nutrient content (Barbosa et al., 2015).

5 | CONCLUSIONS

The microbiome of the studied soils of Les Gavarres massif, especially in terms of microbial richness and diversity, is consistent with data reported for slightly acidic pH

soils. Our study showed that long-term RR and UV filtering did not severely affect soil bacterial communities, despite there being small changes in the composition and relative abundance of some taxa. The relative abundance of *Planctomycetes* was unexpectedly high and tended to increase in drier conditions which could be related to the long-term application of rain reduction treatment. At lower taxonomic ranks (family and genus level), UV radiation caused a relative enrichment of bacteria adapted to harsh conditions, although differential taxa always occurred at low abundances (<0.2%). Contrary to what was expected, exposure to UV-A or UV-B radiation was not determinant to explain differences in microbial communities. Nevertheless, our results support a synergistic effect of UV radiation and water availability on soil bacterial communities. RR caused a decrease in bacterial abundance and increased diversity only in the UV0 plots (not receiving UV radiation) but not in other treatments. The limited effects observed in the soil microbial community structure of the studied Mediterranean shrublands could be the result of a high resilience of microbial communities after a low severity vegetation burning event, although more studies would be needed to confirm this.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Conceiving the work: Dolors Verdaguer, Laura Llorens, Lluís Bañeras, Sébastien Massart, Laura Díaz-Guerra. *Designing the work*: Dolors Verdaguer, Laura Llorens, Lluís Bañeras and Sébastien Massart. *Experiment design and maintenance*: Laura Díaz-Guerra, Dolors Verdaguer, Laura Llorens. *Generation and analysis of data*: Laura Díaz-Guerra, Elena Hernández-del Amo, Maria Gispert, Sébastien Massart. *Drafting the manuscript*: Lluís Bañeras, Dolors Verdaguer. *Revising the manuscript*: All authors. *Approving final article*: Lluís Bañeras, Dolors Verdaguer.

DATA AVAILABILITY STATEMENT

Sequences have been deposited in the Sequence Read Archive (SRA-NCBI) under Bioproject accession number PRJNA768312. Will be publicly available after publication.

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SUPPORTING INFORMATION

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