Tracing elevational changes in microbial life and organic carbon sources in soils of the Atacama Desert

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Short title: Changes in Atacama Desert soil along an elevational transect

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Abstract

The Atacama Desert frequently serves as model system for tracing life under extremely dry conditions. We hypothesized that traces of life in the Atacama Desert follow distinct micro- and macro-scale gradients such as soil depth and elevation, respectively. Different depth intervals of surface soils (0-1, 1-5, and 5-10 cm) were sampled at five sites along an elevational transect near the Quebrada Aroma, spanning from the hyperarid core of the desert towards the arid Western Andean Precordillera (1,300 to 2,700 m a.s.l.), and from one additional site in the hyperarid core near Yungay. We determined the contents of major elements, pedogenic minerals and oxides, organic carbon (OC), and its $\delta^{13}C$ and $\delta^{15}N$ isotopic composition. The presence of living microorganisms was assessed by cultivation, and bacterial community composition was analyzed based on 16S rRNA gene sequencing. Additional information about past and present plant and microbial life was obtained from lipid biomarker analysis. We did not detect consistent micro-scale distributions for most of these proxies within the soils. However, concentrations of OC and of long-chain, plant wax-derived *n*-alkanes increased in soils along the aridity gradient towards the wetter sites, indicating the presence of past life at places presently not covered by vegetation. Likewise, bacterial abundance and diversity decreased as hyperaridity increased and the microbial community composition changed along the transect, becoming enriched in *Actinobacteria*. The distributional patterns of phospholipid fatty acids (PLFAs) confirmed the larger bacterial diversity at the higher, more humid sites compared to the drier ones. Archaeal isoprenoid glycerol dialkyl glycerol tetraethers (isoGDGTs) and bacterial branched (br)GDGTs, which can also indicate past life, did not follow a clear elevational trend and were absent at the driest site. Taken together, plant-derived and microbiological markers follow primarily the macro-scaled elevation and aridity gradient. Viable bacteria are present even at the driest sites, while detected biomolecules also indicate past life. The detection of past plant life in nowadays apparently lifeless regions suggests that conditions for life were less hostile in former times.

1. Introduction

The Atacama Desert (between 15°S and 27°S) is one of the driest places on Earth receiving on average less than 200 mm y^{-1} mean annual precipitation (Houston, 2006). Rainfall events in the hyperarid core of the desert (between 22°S and 26°S) may only be a few millimeters annually, often as a single event once in a decade (Warren-Rhodes et al., 2006). This hyperarid core of the desert is completely devoid of any higher plants. Sparse vegetation is primarily localized along the eastern and western side of the hyperarid core. In these regions, plants rely on fog moisture (coastal zones) (Cereceda et al., 2008; Schulz et al., 2011; Jaeschke et al., 2019) or irregular rainfalls (mainly north-eastern part) (Rundel, 1991), which are controlled by the El Niño Southern Oscillation and the Pacific Decadal Oscillation that vary with latitude and elevation (del Río et al., 2017; Houston 2006). The irregular availability of water results in a patchy distribution of life, which follows large-scale gradients including elevation or distance to the ocean, both affecting aridity (e.g. Ewing et al., 2008; Jones et al., 2018, Mörchen et al., 2019).

The presence of organic matter (OM) in soil can be indicative for past or present life, as remnants of dead organisms can be preserved in OM in form of biomolecules. OM has been detected in soils of the Atacama Desert, though at very low concentrations (2 - 125 µg g^{-1} organic carbon [OC]) (Fletcher et al., 2012; Valdivia-Silva et al., 2012) and particularly in labile forms such as carbohydrates or amino acids (Skelley et al., 2007). Clear assignments of biomolecules to vegetation sources have not yet been made in this particular environment. In addition, traces of microbial cells including the presence of phospholipid fatty acids (PLFA) (Connon et al., 2007; Ewing et al., 2007; Schulze-Makuch et al., 2018) or DNA (Crits-Christoph et al., 2013; Lester et al., 2007; Navarro-González et al., 2003; Schulze-Makuch et al., 2018) have been reported in OM. Evidence for viable microbial cells exists as well (Azua-Bustos et al., 2015; Bull and Asenjo, 2013). Earlier studies reported a variable abundance of organic carbon (OC) in different soil layers (Ewing et al., 2008; Lester et al., 2007; Valdivia-Silva et al., 2012), possibly reflecting changing OC input related to variable moisture availability in the past. Moreover, organic substances were found at specific places including for example halite crusts, within

or below biological structures, and even underneath rocks or within larger salt crystals (Azua-Bustos et al., 2011; Skelley et al., 2007). We thus can assume that besides large-scale precipitation gradients also small-scale gradients determine the occurrence of life and organic residues. Unravelling these vertical patterns in soil possibly provides additional keys to the understanding of past and present life in this desert.

Whenever plants or microbes have been active in soils, they likely left a fingerprint on other soil properties (Birkeland et al., 1978; Schwertmann, 1985). Vice versa, soil properties linked to aridity and related environmental conditions will be mirrored by differing accumulations of pedogenic minerals or salts (Schwertmann and Taylor, 1977), for example lime, gypsum, halite, as well as nitrates, phosphates, sulphates, and iodates (Bernhard et al., 2018; Clade et al., 2006; Ewing et al., 2006). Changes in soil properties thus likely coincide with changes in organic residues, which may undergo transformation processes over time.

Different analytical techniques are available to study organic residues and past or present life in more detail such as stable isotope, DNA-based or lipid biomarker analyses. The stable carbon isotopic composition ($\delta^{13}C$) of OC can be used as indicator for past changes in vegetation, its water-stress conditions, and OM turnover (Boutton, 1996; Peri et al., 2012; Staddon, 2004). Furthermore, stable nitrogen isotopic composition ($\delta^{15}N$) is a sensitive proxy to detect vegetation changes affected by mineralization processes and especially N-losses, which results in $\delta^{15}N$ enrichment (Schatz et al., 2011). Lipid biomarkers indicating life include, for example, plant-derived long-chain *n*-alkanes and fatty acids, microbial short-chain *n*-alkanes and fatty acids, bacterial phospholipid fatty acids (PLFAs) (Willers et al., 2015) and branched glycerol dialkyl glycerol tetraethers (brGDGTs) as well as archaeal isoprenoid tetraethers (isoGDGTs) (Schouten et al., 2013). While fatty acids, *n*-alkanes, and GDGTs are refractory compounds, PLFAs are biomarkers typically used to trace viable soil bacteria. However, under hyperarid conditions PLFA degradation may be extremely slow, thus PLFAs may potentially also reflect dormant or dead cells (Connon et al., 2007; Schulze-Makuch et al., 2018, Wilhelm et al., 2017),

104 although Ewing et al. (2007) argue that abiotic oxidation rates in surface soils are too high to support
105 PLFA preservation.

106 Microbial communities in the hyperarid core of the Atacama Desert are of low abundance and
107 low diversity (Azua-Bustos et al., 2015; Crits-Christoph et al., 2013; Drees et al., 2006; Navarro-
108 Gonzalez et al., 2003). The presence of viable cells can be assessed using e.g. microscopic staining
109 procedures or cultivation-dependent approaches, even though the abundance of microorganisms may
110 fall below the detection limit of these methods (Connon et al., 2007; Navarro-Gonzalez et al., 2003).
111 DNA-based, cultivation-independent approaches can reveal a more complete picture of microbial life.
112 However, it has to be considered that part of the DNA in soil can originate from dead cells or is
113 extracellular and thus does not represent viable organisms (Fletcher et al., 2011; Schulze-Makuch et
114 al., 2018).

115 In this study, we hypothesized that traces of life in the Atacama Desert follow distinct macro-
116 and micro-scale gradients that reflect the different availability of water. We collected surface soils that
117 were exposed to different levels of hyperaridity along an elevational gradient (1,340 to 2,720 m a.s.l.;
118 19°S). Samples at each site were taken from different depths (upper 10 cm; with three depth intervals),
119 thus representing a micro-scaled gradient in the surface soil. It was our aim to study soil properties,
120 microbial life and the origin and transformation of organic matter and find potential links between
121 these data by using a comprehensive set of analytical approaches, including stable C and N isotopes,
122 DNA-based and lipid biomarker analyses. Microbial life was characterized using cultivation-based
123 approaches to assess the presence of living cells, while DNA-based community profiling and lipid-
124 based analyses were performed to estimate abundance and study community composition. The
125 detection of long-chain *n*-alkanes in soil organic matter can potentially provide information about past
126 vegetation.

127

128 **2. Materials and methods**

129 **2.1. Field sites and sampling**

Soil samples were collected from the surface soil (0-1, 1-5, and 5-10 cm depth) at two sites in the Atacama Desert centered around 69 – 70°W in February 2014 (Table 1). In the north (19°S), samples were taken at five locations along an elevational transect located north of the Quebrada Aroma and spanning from the hyperarid core of the desert towards the arid Precordillera of the Andes (Fig. 1). The study sites were defined as a compromise to obtain approx. equal increments in elevation and geographical distances between sites. However, the site at 2455 m a.s.l. does not perfectly fit into this pattern; it was chosen as first site along the transect with first occurrence of withered plants in an adjacently located depression. The transect is located along the central part of a planation surface formed 14.6 Ma ago on alluvial gravels (Evenstar et al., 2009). The surface gravels overlie Oligo-Miocene sediments and Paleocene and older igneous rocks (Fig. S1). It has a well-developed desert pavement (Evenstar et al., 2009). Water supply along the Aroma transect stems from northeasterly (monsoonal) airflows that bring convective precipitation from Amazonia during the austral summer (Garreaud et al., 2008; Houston and Hartley, 2003). Thus, there is a decrease in mean annual precipitation from 43.6 to 0 mm yr^{-1} and an increase in mean annual temperature from 13.5 to 17.7°C with decreasing elevation from 2,720 m a.s.l. to 1,340 m a.s.l. (Table 1).

For benchmarking, these samples were compared with samples from another well-known study site at Yungay, which is located in the hyperarid core of the Desert (24°S, 70°W, 1,020 m a.s.l.) (e.g. Azua-Bustos et al., 2015; Navarro-Gonzalez et al., 2003). Annual rainfall at this location is <2 mm yr^{-1} and mean annual temperatures are 14 – 16°C (McKay et al., 2003; Warren-Rhodes et al., 2006). Samples were taken from an alluvial fan with an age of around 2.1 Ma (Ewing et al., 2006), originating from granitic source rocks covered by sparse desert pavement and resting on a soil with atmospherically derived salts and dust. The collected sample material was extremely dry, hence it was collected in plastic bags and shipped to the laboratory under ambient conditions for further processing upon arrival.

2.2. Analyses of chemical and physical soil properties

Total nitrogen (TN) was analyzed with a Fisons NA 2000 elemental analyzer employing approx. 20 mg sample material according to DIN ISO 10694. Total OC was analyzed with a VarioMax elemental analyzer employing approx. 1 g of sample material (Elementar, Hanau, Germany) after removal of inorganic carbon (20% HCl, overnight, at room temperature). Both methods are based on dry combustion to CO_2 and quantification by a thermal conductivity detector. Inorganic carbon was analyzed via CO_2 pressure development after adding 15% HCl to the samples (DIN 19684). The pH value was assessed with a glass electrode (Thermo Fischer, Dreieich, Germany) in distilled water (1:2.5 w/w).

The oxalate-extractable Fe (Fe_o) was determined according to Schwertmann (1964) with NH_4 oxalate at pH 3.0 after shaking for 2 h in the dark. Total "free" Fe oxides (Fe_d) were determined by dithionite-citrate-bicarbonate (DCB) extraction after Mehra and Jackson (1958). The Fe concentration in the extracts was determined by inductively coupled plasma-optical emission spectroscopy (ICP-OES; Ultima 2, Horiba Scientific, Bensheim, Germany). The total extractable concentrations of Fe, P and S (Ex-Fe_{tot}, Ex-S_{tot}, Ex-Fe_{tot}) were quantified in an aqua regia digest (2 g soil, 7 mL concentrated HNO_3, 21 ml concentrated HCl). They were also analyzed using ICP-OES. Available phosphate was additionally determined following the Olsen-P extraction method (5 g soil, 100 ml 0.5M $NaHCO_3$, pH 8.5) according to Schoenau and O´Halloran (2008). Nitrate was measured photometrically in a $CaCl_2$ extract (5 g soil, 50 ml 0.01 M $CaCl_2$) according to Keeney and Nelson (1982).

Total contents of the elements S, Na, Mg, Si and P were estimated after removal of sand (>63 µm) with an energy dispersive X-ray fluorescence (ED-XRF) spectrometer (SPECTRO XEPOS, SPECTRO Analytical Instruments GmbH) on pellets produced from 8 g of sample material mixed with 2 g of wax binder (Fluxana Cereox). The amount of gypsum ($CaSO_4*H_2O$) was calculated from the ED-XRF data using the measured amount of S in the sample material.

Particle-size distribution was determined on two subsamples using a Laser Diffraction Particle Size Analyzer (LS13320, Beckman Coulter) by application of the Lorenz-Mie theory and calculating the percentaged size frequency within a size range of 0.04 – 2,000 µm (ISO 13320, 2009; Özer et al., 2010). Before the measurement, the samples were pretreated with 1.25 ml of 0.1 M $Na_4P_2O_7$ x $10H_2O$ for 12 h

in an overhead shaker to disperse the particles (Schulte and Lehmkuhl, 2018). Carbonates were not removed prior to measurement, as described in Schulte et al. (2016).

2.3. Stable isotope analyses

For stable isotope analyses of total OC, a sample aliquot was pre-treated with hydrochloric acid (5% HCl) in a water bath (50°C, 24 h) to completely remove inorganic carbon. Subsequently, samples were rinsed with distilled water three times and then freeze-dried. Samples were weighed before and after treatment to estimate the HCl-insoluble content as weight percent. For stable isotope analyses of TN, the untreated sample material was used. Samples were weighed into tin capsules to provide approx. 80 µg of C and 50 µg of N for analyses. Isotope ratios were measured using a continuous flow system that comprises an elemental analyzer (Euro EA 3000, Eurovector for C and Flash 2000, Thermo Scientific for N) attached to an isotope ratio mass spectrometer (IRMS; IsoPrime, Micromass for C, and Delta V Advantage, Thermo Scientific for N). Samples were combusted in a He atmosphere with an excess of oxygen in the elemental analyzer and the sample gas was transported into the IRMS in a continuous He flow through a series of traps and a GC column for purification and isolation of the target analytes (CO_2, N_2). The isotope ratios are expressed as δ values in per mil (‰) using the international standards Vienna PeeDee Belemnite (VPDB) for C and atmospheric nitrogen (AIR) for N. In addition to these calibration standards, laboratory standard materials were measured between samples to monitor the instrument performance yielding an analytical precision (1s) of ± 0.10‰ for C and of ± 0.15‰ for N isotope ratios. However, due to sample inhomogeneity some replicate analyses showed higher deviations.

2.4. Microbiological abundance and community analyses

For the cultivation-dependent estimation of bacterial cell numbers, 5 g of soil were suspended in 25 ml of phosphate buffer (120 mM, pH 8) and homogenized for 30 min at 60 rpm in an overhead shaker (REAX 2, Heidolph Instruments, Schwabach, Germany) followed by 5 min ultrasonication (USC-

T, VWR International, Darmstadt, Germany) to support dislodgement of bacterial cells from soil particles. 1 ml and 100 µl of the obtained suspensions were spread on agar plates, respectively. Moreover, a 5-fold serial dilution was prepared in microtiter plates and 5 µl droplets of each dilution step were pipetted onto squared agar plates. Two different media were used for the growth of bacterial cells, Nutrient Broth (NB), consisting of 3 g l^{-1} meat extract, 5 g l^{-1} peptone and 15 g l^{-1} agar, and Reasoner's 2A (R2A, VWR International). 50 mg l^{-1} of cycloheximide was added to each medium to suppress the growth of fungi. Plates were incubated at 30°C and evaluated for bacterial growth over a period of 4 weeks. The obtained cell counts served as proxy for the presence and abundance of viable cells, enabling a comparison between sites. The nutrient-rich NB medium was selected to allow the growth of a broad range of different bacteria, while R2A is less nutrient rich and may thus better reflect the conditions bacteria encounter in soil.

For the cultivation-independent analysis of the bacterial community composition, DNA was extracted from soil samples using a modified protocol after Nercessian et al. (2005). Each soil was extracted in two or four parallel assays. For each extraction assay, 0.5 g of soil were mixed with 500 µl of CTAB extraction buffer, 600 µl of phenol:chloroform:isoamylalcohol (PCI, 25:24:1), 60 µl of 10% sodium dodecyl sulfate, 60 µl of 10% lauroyl sarcosine, 100 µl of 0.1 M of sodium metaphosphate and 0.7 g of zirconium silicon beads (0.1 mm, BioSpec Products, Bartlesville, USA). Sodium metaphosphate was added to increase DNA recovery as it binds competitively to soil particles and thus increases DNA recovery (Pietramellara et al., 2001). Cell lysis was done using a bead beater at 30 kHz for 10 min (Tissue Lyser, Qiagen, Hilden, Germany). Upon centrifugation for 10 min at 16,000 g and 4°C, 1 volume of PCI was added to the supernatants, samples were inverted and then centrifuged for 10 min at 16,000 g and room temperature. Two volumes of 30% PEG 6000 in 1.6 M NaCl were added to the supernatant and incubated for 2 h. Afterwards the samples were centrifuged for 1 h at 17,000 g and 4°C. The pellets were washed with 70% ice-cold ethanol (-20°C) and resuspended in 25 µl PCR-grade water. The parallel DNA extracts were combined, further purified and concentrated using the CleanPCR kit (CleanNA; Alphen aan den Rijn, The Netherlands) and the magnetic stand MagStrip

(MagBio Europe Ltd.; London, United Kingdom) following the manufacturer's instructions, i.e., 17.5 µl of beads and 27.5 µl of buffer (20% PEG in NaCl) were given to 25 µl extracted DNA. The beads were washed with 70% ethanol and the purified DNA was eluted in 20 µl PCR-grade water. DNA was quantified using the Qubit Fluorometer (Thermo Fisher Scientific) and the QuantiFluor® dsDNA System (Promega, Mannheim, Germany).

The 16S rRNA gene fragment was amplified in triplicates per sample in a nested PCR approach. The first round consisted of a 10-µl PCR reaction mixture with 1x polymerase buffer, 0.2 µM of each primer, 0.8 µg μl^{-1} BSA, 0.25 µl AccuPrime DNA polymerase (Bioline GmbH, Luckenwalde, Germany), 1 µl of DNA template and PCR-grade water. The primer combination 9f/1492r (Heyer et al., 2002) was used and 30 cycles were applied (95°C, 20 s; 50°C, 20 s; 68°C, 90 s) upon initial denaturation at 94°C for 2 min. PCR was finalized by elongation at 72°C for 7 min. This first PCR was followed by a second PCR using the primers 515f/806r with sample-specific 8mer barcodes as published (Frindte et al., 2019). The second PCR was performed in 50 µl assays with 5 µl of template from the first round by applying a temperature profile consisting of initial denaturation, 30 cycles (94°C, 20 s; 50°C, 20 s; 68°C, 20 s) and final elongation as before. For the specific amplification of archaeal 16S rRNA genes the bacterial primer pair was replaced in the above described first-round PCR mixture by the archaeal primers 20f/958r (Ochsenreiter et al. 2003). The PCR was performed with 30 cycles (94°C, 20 s; 54°C, 20 s; 68°C, 60 s). The second PCR round was performed as described above, but with the barcoded primer 515f in combination with 958r and by applying 35 cycles with 30 s elongation time. The three technical replicates of each sample were pooled prior to DNA quantification using the QuantiFluor dsDNA system (Promega) in a plate reader (Tecan, Männedorf, Switzerland). PCR products of the different samples were pooled at equimolar ratios and the resulting pool was purified using the HighPrep magnetic beads system (Biozym) according to manufacturer's instructions. Illumina sequencing and library preparation was done by the Max Planck-Genome-centre Cologne. Sequencing was performed on an Illumina HiSeq system and generated paired-end (2x250 bp) reads.

The obtained sequence reads were oriented in the same direction using Cutadapt (Martin, 2011), followed by sample demultiplexing and trimming of primer sequences (error rate 0.15) in paired-end mode using Cutadapt in Qiime2. Quality filtering, read assembly, chimera checking and denoising was performed in DADA2 as implemented in Qiime2 (Bolyen et al., 2019) using default settings except truncation length of sequences, which was set to 200 bp for the forward read and 230 bp for the reverse read. As a result, an amplicon sequence variants (ASV) table was obtained (Callahan et al., 2017). The table was used to create a taxonomic table using the Greengenes naïve Bayes classifier (Version 13). Raw sequence reads have been deposited in the European Nucleotide Archive (PRJEB34989).

2.5. Lipid analyses

Soil samples taken from 0-10 cm depth at each site were homogenized and lipids were extracted from 100 g of dry soil in a Soxhlet apparatus with a mixture of dichloromethane and methanol (9:1, v:v; 48 h). The total lipid extract was saponified using methanolic KOH (0.5 M; 80°C, 2 h) and separated into neutral and acidic fractions by liquid-liquid extraction. After the addition of water, the neutral lipids were recovered using hexane, and fatty acids were extracted using dichloromethane following acidification with concentrated HCl (to pH 1). The neutral lipids were separated into polarity fractions using SiO_2 column chromatography (1% deactivated silica gel 60, 70-230 µm mesh size) and *n*-alkanes were recovered with hexane and GDGTs with methanol. Fatty acids were transesterified with methanolic HCl (95:5, v:v) to form fatty acid methyl esters (FAMEs). These were purified over a SiO_2-Na_2SO_4 column with dichloromethane and hexane (2:1). GDGTs were filtered through 0.45 µm PTFE filters using hexane:isopropanol (95:5, v:v). FAMEs and *n*-alkanes were identified using an Agilent 6890N gas chromatograph (GC) coupled to an Agilent 5975C mass spectrometer (MSD) and quantified using an Agilent 7890B GC with flame ionization detection (FID). The GC systems were equipped with a HP-5 column (30 m x 0.32 mm, 0.25 µm) and a DB-5MS column (50 m, 0.2 mm ID, 0.33 µm), respectively. The temperature program used was: 40°C (hold for 2 min) ramp to 140°C with 10°C min^{-1}

and to 320°C with 3°C min^{-1} (hold for 28 min). FAMEs and *n*-alkanes were quantified against authentic external standard mixtures. The GDGTs were analyzed using an Agilent 1290 Infinity ultra-high performance liquid chromatography (UHPLC) system coupled to an Agilent 6460 triple quadrupole mass spectrometry (QQQ-MS) system equipped with an atmospheric pressure chemical ionization (APCI) source following the method described by Peterse et al. (2012). Quantification was achieved using an internal C_{46} GDGT standard (Huguet et al., 2006).

The PLFAs were extracted following the method of Bossio and Scow (1998). Briefly, about 100 g of dry soil was extracted by shaking with phosphate buffer: chloroform:methanol (0.9:1:2, v:v:v). The total lipid fraction in the chloroform phase was separated on a SiO_2 column into glyco-, neutral-, and phospholipids using chloroform, acetone, and methanol, respectively. The phospholipid fraction was methylated with methanolic HCl and measured on the GC-MSD equipped with a HP-5 column (30 m x 0.32 mm, 0.25 µm) and using the temperature program: 50°C (2 min), ramped to 100°C with 15°C min^{-1}, followed by heating from 100 to 220°C with 2°C min^{-1}, and a final heating rate of 15°C min^{-1} to 240°C (held for 5 min). PLFAs were quantified against authentic external standard mixtures. Standard nomenclature is used to describe the PLFAs. They are designated by the total number of carbon atoms, number of double bonds, and the position of the double bond from the methyl (aliphatic) end (ω) of the molecule. The prefixes “a” and “i” refer to anteiso- and iso-branched fatty acids, respectively. The prefix “10Me” indicates methylation at C-10 from the carboxyl end of the molecule, and “cyc” indicates cyclopropane fatty acids.

2.6. Statistical analyses

The sequencing data were analyzed using multivariate approaches from the vegan package in Rstudio (Oksanen et al., 2018). To evaluate differences in community composition between samples, a Bray-Curtis distance matrix was calculated after Hellinger transformation from the ASV table and non-metric multidimensional scaling (NMDS)-plots were set up. The influence of environmental factors (i.e., numerically quantified soil properties) on bacterial community composition was visualized

in the NMDS plot using the Envfit algorithm. Differences in community composition between groups of samples were assessed via analysis of similarity (ANOSIM). To estimate the bacterial richness (Chao1) and Pilou's evenness, a rarefied ASV table with 2177 bacterial reads was used. Significant differences of soil properties in dependence on elevation or soil depth were proven using Kruskal-Wallis tests in OriginPro 8G. To assess differences in cultivable cell numbers along the Aroma transect one-way ANOVA was used on log-transformed data. Likewise, differences in alpha diversity were assessed by one-way ANOVA. Linear correlations between data were assessed based on Pearson correlation coefficients. In case of multiple comparisons, *P*-values were Bonferroni-Holm corrected to reduce type I errors.

3. Results

3.1. Soil properties

Variation of the soil properties determined along the Aroma elevational transect was primarily observed along the macro-scaled elevational gradient, while the micro-scaled gradient of soil depth only affected soil pH (Table 2, Table S1). The soils were generally moderately alkaline with pH values in the range of 7.4 to 8.8, consistently increasing from the surface to 10 cm soil depth. A change in pH with elevation and thus decreasing hyperaridity was not evident. Significant responses along the elevational gradient were observed for several other chemical soil properties (Table S1). Such a change was clearly evident for calcium carbonate, which was not detectable in the wetter sites of the Aroma transect in 2,720 and 2,455 m a.s.l., but became detectable with increasing dryness, reaching a maximum of 14.9 g kg^{-1} at the driest site 1,340 m a.s.l.. It was even higher in 10 cm depth at the Yungay site (18.4 g kg^{-1}). Even more pronounced was the accumulation of gypsum ($CaSO_4$) with decreasing elevation (Fig. 2), which was present at much higher concentrations (max. 33%) at the most hyperarid sites along the Aroma transect (1,680 and 1,340 m a.s.l.) than at the wetter sites. This is in agreement with increasing concentrations of total sulfur (Ex-S_{tot}) along the transect (Table 2). Similarly, the concentration of extractable nitrate (NO_3-N) increased at the lowest sites relative to the others

(around 1 mg kg^{-1} at 2,020, 2,455 and 2,720 m a.s.l. and between 3 and 175 mg kg^{-1} at the two lowest elevations), where it accumulated at higher concentrations in the deeper soil layers. Even higher values for nitrate were observed at Yungay (215 mg kg^{-1}), also in the deeper soil layers. Elemental analysis revealed an opposite trend for Si, which decreased with increasing dryness.

There was no systematic variation in the measured P parameters between samples, but a good correlation (Table S2) was observed between total P (Ex-P_{tot}) and P concentration determined by ED-XRF (R = 0.85, P <0.01). Likewise, no systematic variation was observed in pedogenic oxides across the macro- or micro-scaled gradients as evident from non-systematic changes in Fe_o/Fe_d ratios (Table 2) and in the ratios of Fe_d to Ex-Fe_{tot} (calculated from Table 2). Similarly, soil texture varied unsystematically with generally low clay contents (<22% at Yungay and <17% at Aroma) and inconsistent changes of the contents of silt and sand with soil depth or elevation (Table 2).

The OC concentrations in the Aroma soil samples decreased by a factor of 15.8 (from 1,648 to 104 mg kg^{-1} soil) with decreasing elevation (Table 2). Interestingly, the OC concentrations at Yungay (between 695 and 769 mg kg^{-1} soil) were not as low as in the driest Aroma site at 1,340 m a.s.l. In addition, OC contents varied at some Aroma sites strongly with soil depth, showing minimal values in the top centimeter at the least hyperarid sites (2,720 m a.s.l. and 2,020 m a.s.l.) and at Yungay (1,020 m a.s.l.). At other sites (Aroma 1,680 and 1,340 m a.s.l.) OC contents were higher in the top centimeter than at greater depth (Table 2). OC did not correlate significantly with any other chemical or physical soil property (except for $\delta^{13}C$, see below; Table S2). TN contents ranged between 125-392 mg kg^{-1} soil and increased at nearly all sites consistently from the first cm to 10 cm soil depth with no pronounced changes related to elevation (Table 2). The OC/TN ratio generally decreased with soil depth, except at Aroma 2,020 m a.s.l.. Furthermore, it decreased considerably by a factor of 12.2 (from about 6.1 to 0.5) as elevation decreased (numbers calculated from data in Table 2), potentially affected by the increasing nitrate contents, which accounted for more than half of the TN at Yungay (Table 2).

The isotopic data of $\delta^{13}C$ and $\delta^{15}N$ showed distinct changes with elevation (Tables 2 and S1). The most ^{13}C-enriched values of bulk soil OC were determined for the sites located at the highest elevation

(-22.7 to -23.9‰), while lower values (-24.3 to -28.0‰) were determined at all other sites including Yungay. The $\delta^{15}N$ values generally increased with increasing elevation along the Aroma transect, ranging from 5.0 to 13.2‰ (Table 2). However, the lowest $\delta^{15}N$ values were found at Yungay (between 2.9 and 3.5‰). Changes with soil depth were variable for both isotopic signals, but remarkably, both exhibited their maximum values at the depth containing the largest OC content. The two isotopic datasets were significantly positively correlated (Pearson correlation coefficient $R = 0.80$, $P < 0.05$, n = 18) (Table S2). A significant positive correlation was also observed between $\delta^{13}C$ and OC ($R = 0.84$, $P < 0.01$, n = 18).

3.2. Soil microbiology

The cultivation-dependent analysis revealed the presence of living microorganisms along the whole elevational transect, ranging from 10^2 to $>2x10^7$ colony forming units (CFUs) per gram soil (Fig. 3). Cell numbers decreased consistently with increasing hyperaridity (one-way ANOVA between sites, $P < 0.001$), while there was no consistent trend with soil depth. In some samples, cell numbers were close to or below the detection limit of 5 CFUs g^{-1} soil, especially at Aroma 1,680 m a.s.l. at 5 – 10 cm depth, where no colonies developed on either of the two media. Otherwise, the nutrient-poorer R2A medium supported the growth of bacteria at several of the driest sites along the Aroma transect and at Yungay better than the NB medium (Fig. 3, Table S3). The number of CFUs in soils from the hyperarid site Yungay corresponded best to those from soils taken at 2,020 and 2,455 m a.s.l. along the Aroma transect, as observed for OC.

The recovery of DNA (Table S4) can also serve as rough estimate for the abundance of microorganisms, even though it may underestimate the actual cell number in soil due to methodological limitations (Dineen et al., 2010; Lever et al., 2015). The data corresponded quite well to the results of the cultivation-dependent analysis with a Pearson correlation coefficient of $R = 0.70$ ($P = 0.001$, n = 18) for DNA content vs. log-transformed cell counts from NB medium as well as from R2A medium. Pearson correlation analyses were also performed between these microbial abundance

data and the soil properties (Table S5, Figure S3), revealing significant positive linear correlations of all three abundance parameters with OC (*R*-values between 0.73 and 0.78, *P* <0.02) and with $\delta^{13}C$ values (*R*-values between 0.72 and 0.77, *P* <0.02). DNA recovery correlated additionally to $\delta^{15}N$ (*R* = 0.77, *P* = 0.004). Correlations of the microbial abundance data to other soil properties were not evident, suggesting that OC is a major factor controlling bacterial abundance.

To analyze the bacterial community composition, amplicon sequencing of the 16S rRNA gene was performed. Negative controls were included to assess potential contaminations introduced during DNA extraction and PCR. These controls were weakly positive, but the microbial community composition in these samples differed markedly from those of the soil samples (Fig. S3), indicating that the results obtained for the soil samples were essentially unaffected by this contamination. PCR with samples from Yungay did not result in PCR products with the protocols applied here, possibly due to polymerase inhibition despite purification of the DNA extracts. The bacterial alpha diversity, assessed as estimated richness based on the Chao1 index, showed a strong and consistent decrease with increasing hyperaridity across the entire Aroma transect (641 ± 43 at 2,720 m a.s.l. and 75 ± 37 at 1,340 m a.s.l.) (Fig. S4). Similarly, bacterial evenness, quantified as Pielou's index, decreased consistently, but the decline started at sites below 2,455 m a.s.l. elevation (range from 0.88 ± 0.02 at 2,720 m a.s.l. to 0.66 ± 0.18 at 1,340 m a.s.l.) (Fig. S4). ANOVA confirmed the significance of the decline in dependence on elevation (*P* = 0.01 for Chao1, *P* = 0.04 for Pielou's evenness). At four of the five study sites, Chao1 diversity increased with increasing soil depth. However, this trend was not statistically significant due to strong deviations at one site (2,455 m a.s.l.). Community compositional differences between the soil samples were evaluated based on an NMDS plot, revealing a clear clustering according to aridity/elevation along the first axis (Fig. 4). ANOSIM confirmed the presence of these differences between samples from different sites along the transect (*R* = 0.72, *P* = 0.001). A further separation of the samples along the second NMDS axis was observed according to soil depth, but this separation of samples could not be statistically confirmed by ANOSIM (*R* = -0.02, *P* = 0.51), probably due to the strong effect of the factor elevation, which largely superimposed the depth-

related variation in the samples. Envfit was performed to assess whether the dissimilarities in bacterial community composition as visualized in the NMDS plot are correlated with environmental variables. The soil OC and Ex-Fe_{tot} contents showed a significant correlation, as well as $\delta^{13}C$ and $\delta^{15}N$ (Figure 4, Table S6). The fitting of these parameters was in a similar range (R^2 = 0.69 – 0.76, $P \leq 0.025$).

The bacterial community was dominated by different classes of *Actinobacteria* in all samples (26 – 95% relative abundance), followed by *Proteobacteria* (0.3 – 52%) and *Chloroflexi* (1.4 – 37%) (Fig. 5). Clear shifts in relative abundance in dependence on elevation were evident within the *Actinobacteria*, where members of the class *Thermoleophilia* dominated at the three highest elevations. The opposite was observed for the class *Rubrobacteria*, i.e., increasing relative abundance with increasing hyperaridity, especially at the two driest sites. *Verrucomicrobia* (class *Spartobacteria*), *Gemmatimonadetes* and *Bacteroidetes* (class *Saprospirae*) were of minor relative abundance at the least arid site and disappeared nearly completely with increasing hyperaridity. Changes in dependence on soil depth were also evident. *Rubrobacteria* (a class of the phylum *Actinobacteria*) accumulated at the soil surface, especially at the most hyperarid sites. Similarly, the class *Actinobacteria* showed decreasing relative abundance with increasing depth at nearly all sites (except at the driest site at 1,340 m a.s.l.). The class *Alphaproteobacteria* showed the same trend at the three least hyperarid sites, while the opposite trend, i.e., increasing abundance with soil depth) was observed at the two most hyperarid sites. In contrast, *Acidobacteria* subdivision 6, which was detected with low relative abundance if at all (<5.4%), increased consistently in abundance with increasing soil depth at all five sites.

An analysis of the archaeal community composition using specific primers revealed the predominant presence of the order *Nitrososphaerales* in all samples, being represented by different species of the genus *Nitrososphaera*. However, at the driest site (1,340 m a.s.l.) the number of reads representing this taxon were in a similar range as those of the negative controls. Thus, it cannot be excluded that these were false-positive signals in this particular sample. Nevertheless, we consider the detection of *Nitrososphaera* in all other samples as robust, because the PCR product and therewith

441 sequence read numbers were 1.5- to 21-fold higher compared to those in the negative controls,
442 indicating a more efficient amplification of the target genes, which can be attributed to a higher
443 number of the target genes in the DNA extract. Moreover, additional ASVs were detected in the
444 samples, being represented by high read numbers (at least 1,650 reads), which were not present in
445 the negative controls.
446
447 **3.3. Lipid biomarkers**
448 Lipid biomarker analysis revealed the presence of *n*-alkanes, fatty acids, and PLFAs in all samples
449 of the Aroma transect, even though at very low abundances at the two most hyperarid sites, while no
450 GDGTs were detectable at these most hyperarid sites (Fig. 6, Table S8). The concentrations of total
451 fatty acids (163 to 1812 ng g^{-1} dry weight [DW]) and PLFAs (99 to 974 ng g^{-1} DW) were one order of
452 magnitude higher than those of the *n*-alkanes (23 to 94 ng g^{-1} DW). GDGTs were present at very low
453 concentrations (205.9 pg g^{-1} DW to 11.0 ng g^{-1} DW) with lower abundances of isoGDGTs (205.9 pg g^{-1}
454 DW to 4.8 ng g^{-1} DW) and slightly higher brGDGT concentrations (2.8 to 6.7 ng g^{-1} DW), which is in good
455 agreement with previous data from the Atacama Desert (Wilhelm et al., 2017). In general, the
456 concentrations of all biomarkers except GDGTs decreased with decreasing elevation, i.e., with reduced
457 frequency of rare precipitation events. No reliable data were obtained for the Yungay reference site.
458 The *n*-alkanes were dominated by odd-numbered, long-chain homologues in the range of C_{21} to
459 C_{35} with relatively high carbon preference (CPI) indices, being indicative of little degraded, higher plant-
460 derived compounds (5.1 to 7.5; Table S8) except at the lowest, driest site at 1,340 m a.s.l. (1.8). The
461 total amount of the *n*-alkanes as well as their average chain length (ACL; 26.1 to 28.4) showed an
462 increase along the elevational transect, especially at the three highest sites.
463 The fatty acids were present in the range of C_{12} to C_{28} with even-numbered homologues being
464 the most abundant compounds (Table S8). The total abundance decreased strongly from the highest
465 to lowest Aroma site (1,827 to 152 ng g^{-1} DW) as well as the diversity of compounds. Several fatty acids
466 were present only at the highest, wettest site ($C_{17:0}$, $C_{18:2}$, $C_{21:0}$, $C_{25:0}$, $C_{28:0}$) and short-chain compounds

(C_{12}-C_{20}) became more abundant at the more hyperarid sites relative to long-chain homologues (C_{20}-C_{28}).

The absolute concentration and diversity of PLFAs also followed the elevational gradient (Fig. 6) and decreased strongly towards the lower, more hyperarid locations along the Aroma transect (Table 3). They particularly declined in abundance from the uppermost two locations (2,720 and 2,455 m a.s.l.) to the site at 2,020 m a.s.l., indicating that a higher biomass is promoted at higher elevation. Total abundances of bacterial cells per g soil DW, which were calculated using a conversion factor of 2.0 x 10^4 cells $pmol^{-1}$ PLFA (Connon et al., 2007; Schulze-Makuch et al., 2018; Willers et al., 2015), increased from 5.5 x 10^5 (at 1340 m a.s.l.) to 4.5 x 10^7 and 6.3 x 10^7 (at 2,720 and 2,455 m a.s.l.), respectively. Monounsaturated PLFAs were present at similar abundances at the two highest elevations, but not present at the two lowermost sites, while saturated PLFAs occurred in low but constant amounts at the three lower locations (Table 3). Likewise, the *Actinomycetes*-specific 10Me-PLFAs (Willers et al., 2015) were present at high and comparable concentrations (120 and 145 ng g^{-1} DW) at the two sites located at the uppermost elevations, while much lower amounts were determined at 2,020 and 1,680 m a.s.l. (11.7 and 1.0 µg g^{-1} DW) and they were not detectable at the lowest site.

GDGT concentrations did not follow a gradual trend along the elevational transect, but were present at higher abundances of 905 to 1691 pg g^{-1} DW at the three highest locations, at very low abundance at 1,680 m a.s.l. (31 pg g^{-1} DW), and not detected at the lowest site (Table S8). Isoprenoid and branched GDGTs occurred at very similar concentrations at the higher sites, but no brGDGTs were detected at the two lowest sites (Fig. 6). Crenarchaeol was the most abundant compound of the isoGDGTs, while brGDGTs were dominated by brGDGTs IIa and IIIa (combined 5- and 6-methyl isomers).

Significant correlations between the abundance of fatty acids, *n*-alkanes, PLFAs or GDGTs and soil properties were not evident when assessed by multiple Pearson correlation analyses with Bonferroni-Holm correction. Based on the fact that soil OC and stable isotopic signatures were linked

493 to microbial abundance parameters, we evaluated specifically whether this applies to lipids in a similar
494 way (Table S9, Fig. S5). A Pearson correlation analysis limited to the three parameters revealed a
495 significant positive correlation between abundance of fatty acids and OC content (R = 0.96, P <0.02),
496 as well as $\delta^{13}C$ (R = 0.94, P <0.02) and $\delta^{15}N$ (R = 0.98, P = 0.01). The same tendency was observed for
497 *n*-alkanes, though not statistically supported.

498

499 **4. Discussion**

500 **4.1. Physical and chemical soil properties and their correspondence to the macro-scaled**
501 **aridity gradient**

502 Water availability controls life in the Atacama Desert (Cáceres et al., 2007; Navarro-Gonzalez et
503 al., 2003), which in turn may alter or is related to soil properties. The surface soils along the Aroma
504 elevational transect clearly reflect the hyperaridity gradient in some of their physical, chemical, and
505 biological properties. They had increasing salt (nitrate), gypsum, and carbonate concentrations as
506 elevation decreased and hyperaridity increased (Fig. 2, Table 2), as reported for Atacama Desert soils
507 from other study sites (e.g. Ewing et al., 2006). The salt enrichment most likely reflects secondary
508 formation processes, e.g. when dissolved salts precipitate in the very surface soil, forming crusts upon
509 water evaporation, or the accumulation of salty dust on the surface, which can contribute to this
510 process at the drier sites. At the less dry sites at higher elevations, the salt, gypsum or carbonate
511 enrichment did not occur in the very surface soil but below 1 cm depth. This likely indicates that either
512 re-wetting by rare rain events contributed to the relocation of this material from the top centimeter
513 to greater depth, or the accumulation of dust having lower carbonate or gypsum contents occurred
514 on the surface.

515 Typical soil formation processes do not only comprise secondary salt enrichment, but also
516 chemical weathering, resulting in the formation of pedogenic oxides and secondary clay minerals
517 (Jenny, 1941; Schwertmann and Taylor, 1977; Schwertmann, 1985). However, we did not find any hint
518 to such processes, indicating that no intensive chemical weathering took place, likely due to the lack

519 of water. For example, the Fe_o/Fe_d ratio has been reported to increase with increasing humidity,
520 indicating an increasing activity of pedogenic processes (Bernhard et al., 2018), but such a shift was
521 not observed in our data with increasing water availability (Table 2). Bernhard et al. (2018) also pointed
522 out that clay formation increases in soils with increasing humidity. The non-systematically varying low
523 clay contents observed in our soils indicate that this pedogenic process was probably largely
524 suppressed by a lack of water at all sites.

525 Water does not only control soil formation but also the prevalence of different forms of life,
526 which all leave behind OC. The concentrations of OC followed the aridity trends along the transect
527 inversely, i.e., OC accumulation increased as hyperaridity declined. This clear trend along the macro-
528 scale gradient was not complemented by a consistent micro-scale gradient, i.e., changes of OC content
529 with depth were variable at the different sites. This suggests that there must be an interaction of OC
530 accrual, specific site properties at the micro-scale, and aridity.

531

532 **4.2. Aridity-related changes in soil organic material and isotopic signatures**

533 At the time of sampling, vegetation was absent at most of the sites. Only at the highest elevation
534 of the Aroma transect at 2,720 m a.s.l., sparsely occurring withered herbaceous plants such as *Atriplex*
535 sp. were present in immediate vicinity of the sample collection site (Fig. S1), likely contributing to the
536 highest OC concentrations observed at this site. The presence of long-chain aliphatic compounds
537 supports the hypothesis that a significant part of the soil OC originated from vegetation remains, e.g.
538 epicuticular waxes (Eglinton and Hamilton, 1967). Plant-derived OM was present even at the most
539 hyperarid sites, with very low CPI values (of *n*-alkanes) indicating its preservation over long time scales
540 under hyperarid conditions, which is in line with the recent findings by Wilhelm et al. (2017) on the
541 xeropreservation of lipid biomarkers in hyperarid Atacama soils.

542 Indications on the origin or processes acting on soil OC and TN may also be derived from their
543 isotopic composition. We observed highest $\delta^{13}C$ values for OC at the least hyperarid site (Aroma at
544 2,720 m a.s.l.), where very sparse vegetation was evident and microbial abundance, diversity and OC

were highest, which is in agreement with findings of earlier studies (Ewing et al., 2008; Quade et al., 2007). Ewing et al. (2008) proposed the existence of a specific C cycle for hyperarid soils, consisting of C input primarily from atmospheric deposition, reflecting external biological activity, and OC degradation by biotic as well as abiotic processes, i.e., photodegradation, which results in the retention of isotopically depleted photodegradation products, leading to lower $\delta^{13}C$ values in hyperarid soil. The higher $\delta^{13}C$ values at the least hyperarid site may additionally be the result of OC input from C_4 plants such as *Atriplex* and CAM plants such as *Browningia candelabris*, which were growing at that site and have higher $\delta^{13}C$ values compared to C_3 plants (Díaz et al., 2016; Quade et al., 2007; Ramond et al., 2018). However, even C_3 desert plants show higher $\delta^{13}C$ values compared to the global average of C_3 plants, linked to a higher water-use efficiency and more frequent stomatal closure (Díaz et al., 2016; Quade et al., 2007). Moreover, microbial decomposition will result in OC enriched in ^{13}C, while isotopically depleted CO_2 is respired, as discussed by Bernhard et al. (2018). The higher microbial cell numbers observed with decreasing hyperaridity will likely contribute to higher microbial decomposition rates. The good correlation between bacterial community composition and $\delta^{13}C$ values substantiates this assumption (Fig. 4). Taken together, there are non-mutually exclusive explanations for the observed shift in $\delta^{13}C$ values, being highest at the least hyperarid site.

We observed a positive correlation between $\delta^{13}C$ and $\delta^{15}N$ values along the elevational transect (Table S2), similar as reported by Díaz et al. (2016). The $\delta^{15}N$ values increased with decreasing hyperaridity (Table 2), which is in contrast to the concept of decreasing $\delta^{15}N$ in soils from hotter and/or dryer ecosystems (Craine et al., 2015), but it supports the finding of Wang et al. (2014), who observed a bell-shaped response curve, with again decreasing $\delta^{15}N$ towards hyperaridity. The maximum $\delta^{15}N$ values, which were determined at Aroma 2,720 m a.s.l., were even higher than those in the study of Wang et al. (2014), but in a similar range as those of Atacama Prepuna soils (Díaz et al., 2016) and those reported for some Namib Desert soils (Ramond et al., 2018). The decreasing $\delta^{15}N$ values under hyperarid conditions are probably linked to a transition from a primarily biologically mediated soil N cycle to a dominantly abiotic one with increasing hyperaridity, characterized by a slow accumulation

of atmospheric N (Ewing et al., 2007). We observed a high accumulation of nitrate in soils with increasing hyperaridity, even though this was not reflected in TN in our data (Table 2). Major processes taking place in the most hyperarid soils are probably N-deposition and gaseous losses, primarily of NH_3 volatilization and to some extent also by photolytic transformation of N at the soil surface (Ewing et al., 2007). Wang et al. (2014) state that nitrogen input processes result in soil $\delta^{15}N$ values close to zero, while positive values, as observed at our study sites, result from isotope discrimination during output processes, causing ^{15}N enrichment. NH_3 volatilization has a high fractionation factor (Robinson, 2001), and is thus likely contributing to the positive $\delta^{15}N$ values observed at the most hyperarid sites. Re-deposition of ^{15}N-enriched nitrate or ammonium may reinforce the enrichment. The even higher $\delta^{15}N$ values observed at the least hyperarid Aroma site may result from additional biological processes, of which nitrification and denitrification have the strongest fractionation factors (Robinson, 2001), but also microbial and plant ammonium assimilation, which have lower fractionation factors, may contribute to this process, especially when biological activity increases following a rainfall event. This is in line with the finding that OC, microbial abundance, diversity and lipid concentrations increased with decreasing hyperaridity along the Aroma transect (Table 2, Fig. 3, Fig. S4, Fig. 6). It is further supported by the good correlation between bacterial community compositional data and $\delta^{15}N$ values (Fig. 4) and in line with the detection of nitrifying archaea of the genus *Nitrososphaera*, which were identified based on amplicon sequencing (Table S7) as well as the detection of crenarchaeol as marker for these archaea (Schouten et al., 2013) (Fig. 7, Table S8). Thus, the higher $\delta^{15}N$ values observed at wetter Aroma sites likely reflect the integrated outcome of a more open N cycling system with more N preservation (e.g. increased accumulation of cell debris).

4.3. Decreasing microbial abundance and diversity with increasing aridity

Despite the absence of plants and very low OC concentrations at most sites, we found evidence for microbial life even at the driest locations of our study, i.e., bacterial cells could be cultivated from samples taken at nearly all sites. The presence of living microbial cells was further substantiated by

597 the PLFA analyses (Table 3) and the detection of microbial residues, including monounsaturated $C_{16:1}$
598 and $C_{18:1}$ fatty acids and crenarchaeol. We determined a consistent decrease in cell numbers as well as
599 in DNA concentrations towards the hyperarid core of the desert (Fig. 3, Table S4), which coincided
600 with decreasing abundances of short-chain fatty acids and PLFAs towards the core (Fig. 7, Table 3).
601 The range of cell numbers determined by cultivation as well as based on PLFAs in this study is in good
602 agreement with earlier reports, where cell numbers ranged from close to or below the detection limit
603 up to approx. 10^5 cells g^{-1} soil for hyperarid sites (Connon et al., 2007; Crits-Christoph et al., 2013;
604 Fletcher et al., 2011; Lester et al., 2007; Maier et al., 2004; Navarro-Gonzales et al., 2003; Drees et al.,
605 2006; Valdivia-Silva et al., 2016). Higher cell numbers, often in the range of 10^5 to 10^7 cells g^{-1} soil,
606 were reported for arid sites and more than 10^7 for semi-arid desert soils (Bernhard et al., 2018; Crits-
607 Christoph et al., 2013; Drees et al., 2006; Valdivia-Silva et al., 2016). However, this is still several orders
608 of magnitude below the abundance of microorganisms in soils of other biomes (5×10^7 to 2×10^{10} cells
609 g^{-1} soil; Torsvik et al., 2002; Whitman et al., 1998). The PLFA-based estimates resulted in slightly higher
610 cell numbers compared to the numbers of cultivated cells determined on NB and R2A plates. This may
611 either be due to the fact that a substantial number of cells in these soils cannot be cultivated, well-
612 known from other studies (Amann et al., 1995; Lloyd et al., 2018), or PLFAs are better preserved in
613 these hyperarid soils, representing to some extent past life (Connon et al., 2007; Schulze-Makuch et
614 al., 2018, Wilhelm et al., 2017).

615 The decrease in bacterial cell numbers with decreasing elevation and increasing hyperaridity
616 was accompanied by a decrease in microbial diversity towards the hyperarid core of the desert, as
617 evident from amplicon sequencing and PLFA data (Table 3, Fig. S4). Decreasing microbial diversity has
618 been reported in previous studies along large transects spanning from arid to hyperarid conditions
619 (Crits-Christoph et al., 2013; Navarro-Gonzalez et al., 2003). In the study of Neilson et al. (2012), a
620 narrower gradient within the transition zone from aridity to hyperaridity was analyzed, but only slight
621 changes in diversity were observed. No decrease in diversity was observed in a transect study ranging
622 from arid to Mediterranean conditions (Angel et al., 2010). These findings suggest that bacterial

communities withstand arid conditions still quite well, while a clear reduction in abundance and diversity appears to occur under hyperarid conditions.

4.4. Changes in microbial community composition in soils along the aridity gradient

Bacterial community composition in all samples was dominated by the presence of the phyla *Actinobacteria*, *Proteobacteria* and *Chloroflexi*. Among these, especially *Actinobacteria* are known to represent a dominant group in bacterial communities in hyperarid desert soils, but also the presence of *Chloroflexi* is well documented (Connon et al., 2007; Crits-Christoph et al., 2013; Drees et al., 2006; Lester et al., 2007; Lynch et al., 2012; Lynch et al., 2014, Neilson et al., 2012; Schulze-Makuch et al., 2018; Vikram et al., 2015). Members of these phyla appear to be particularly well adapted to life under hyperarid conditions. Indeed, some *Actinobacteria* are characterized by a high tolerance to desiccation and solute stress, capable of forming resting stages, and having multiple UV repair mechanisms and a wide metabolic spectrum (Makhalanyane et al., 2015; Mohammadipanah and Wing, 2016).

A clear grouping of the samples according to their origin from different elevations along the Aroma transect was observed (Fig. 4). Similar findings were reported in other studies (Crits-Christoph et al., 2013; Drees et al., 2006). Most evident was a substantial increase in the relative abundance of *Rubrobacteria*, a class of *Actinobacteria* (Fig. 5). This group of bacteria has been detected as a widespread and dominant colonizer of desert soils in other studies (Crits-Christoph et al., 2013; Neilson et al., 2012; Lacap et al 2011; Connon et al., 2007; Holmes et al., 2000). Besides the macro-scale variation, micro-scale variation was observed in bacterial community composition (Fig. 4, Fig. 5). Most responsive to this factor were the classes *Actinobacteria*, which showed decreasing abundance with depth, and the low-abundant class *Acidobacteria* subdivision 6, which showed increasing abundance with depth. Soil-depth related differences in microbial community composition have recently been reported in a few other Atacama Desert soil studies, though over a larger depth range (Schulze-Makuch et al., 2018; Warren-Rhodes et al., 2019). As even the deeper subsoil may show peaking concentrations in organic matter (Mörchen et al., 2019), future studies should likely include

649 even deeper subsoils across the desert to understand past and present niches of life. The patterns we
650 observed in bacterial community composition were best explained by soil organic carbon content and
651 extractable total iron, besides a correlation to $\delta^{13}C$ and $\delta^{15}N$ ratios (Fig. 4, Table S6), while other soil
652 properties such as carbonate, nitrate or gypsum content, which also varied clearly with elevation
653 (Table S1), were less relevant. In addition to the deterministic processes, i.e., control by soil properties
654 and water availability, which cause environmental filtering, stoichiometric processes such as dispersal
655 limitation or ecological drift may also play a role in community shaping (Caruso et al., 2011; Evans et
656 al., 2017; Zhou and Ning, 2017).

657 The detected PLFAs derived mainly from gram-negative bacteria (monounsaturated and
658 cyclopropyl PLFAs), from *Actinobacteria* (10-Me PLFAs), and (at much lower abundance) gram-positive
659 bacteria (branched) as observed in previous studies (Connon et al., 2007; Neilson et al., 2012; Schulze-
660 Makuch et al., 2018). At the two least hyperarid sites, several branched PLFAs including 10Me-$C_{17:0}$
661 were detected, indicative for *Actinomycetes* (Zelles, 1999), which are members of the class
662 *Actinobacteria*. Some fungal PLFAs such as $C_{18:1\omega9}$ and $C_{16:1\omega5}$ and $C_{20:1\omega9}$ were also detected,
663 predominantly at the highest elevations (Ruess and Chamberlain, 2010). Although these PLFAs occur
664 also in bacteria or plants, both fungi and mycorrhizal plants are common in the arid regions of the
665 Chilean deserts (Dhillion et al., 1995; Gonçalves et al. 2015), making them a likely source of $C_{16:1\omega5}$ and
666 $C_{20:1\omega9}$. None of these bacterial groups was present at the driest site at 1,340 m a.s.l., where only
667 saturated PLFAs ($C_{16:0}$ and $C_{18:0}$) were detectable, which are non-specific. Sequencing revealed the
668 predominance of *Actinobacteria*, as well as some *Chloroflexi* at these sites, but specific markers of
669 these taxa remained below the detection limit at these sites (Fig. 5).

670 Similar to OC, PLFAs, DNA or cell numbers, both isoGDGTs and brGDGTs concentrations followed
671 the general elevational trend (Fig. 6), with the exception of a slight increase at site 2,020 m a.s.l. Similar
672 proportions of isoGDGTs and brGDGTs abundances were observed at the higher elevations (Fig. 6).
673 The detection of *Acidobacteria* subdivision 6 at these sites is intriguing in this context, because this
674 group possesses substantial quantities of 6-methyl *iso*-diabolic acid, the likely precursor for the orphan

675 bacterial 6-methyl brGDGTs in soils (Sinninghe Damsté et al., 2018). The relative abundances among
676 isoGDGTs were very similar in the Aroma samples with crenarchaeol and its isomer being the dominant
677 isoGDGTs contributing 49 – 63%. These are biomarkers for ammonia-oxidizing *Thaumarchaeota*
678 groups I.1a (*Nitrosopumilus* lineage) and I.1b (*Nitrososphaera* lineage) (Jung et al. 2014; Sinninghe
679 Damsté et al., 2012). The presence of *Nitrosophaera* was confirmed by amplicon sequencing. The
680 presence of this ammonium-oxidizing archaeon has recently been reported for arid and even some
681 hyperarid sites in the Atacama Desert (Schulze-Makuch et al., 2018). However, archaea in general and
682 potentially nitrifying *Thaumarchaeota* have not consistently been detected in hyperarid desert soils
683 even when specific primers were applied for their detection (Azua-Bustos et al., 2018, Azua-Bustos et
684 al., 2015, Crits-Christoph et al., 2013), indicating spatial patchiness concerning their distribution. The
685 chemolithoautotrophic lifestyle of these organisms probably supports their survival in the desert soils,
686 where organic carbon is scarce.
687
688 **5. Conclusions**
689 In this study, a comprehensive set of chemical, physical, microbial, and lipid biomarker analyses
690 was applied to elucidate the possibility that life in the Atacama Desert follows distinct micro- and
691 macro-scale gradients. Intriguingly, differences at micro-scale resolution, here tested by different soil
692 depths in the very surface soil (0 - 10 cm depth), were mostly not consistent over the whole transect,
693 in part because aridity and soil depth interacted with, e.g. lime, gypsum, and OC accumulation. The
694 strongest evidence for micro-scaled variation was seen in the microbial data, but the identification of
695 underlying controls on this micro-scaled heterogeneity demands further in-depth studies. Clear
696 gradients of plant-derived OC and microbial life were observed in response to the macro-scale
697 gradient, which is primarily driven by water-availability. These gradients were in part non-linear, and
698 were evident for chemical soil properties as well as for biodiversity. The lack of linear correlations
699 between microbial data and further chemical soil properties may be due to non-linear dependencies,
700 possibly modulated by differences in nutrient use efficiencies. Our analyses showed that it is feasible

to obtain signals of life even in the most hyperarid sites of the desert, but further in-depth analyses are now needed to better differentiate between past and present life. This includes the differentiation of microbial markers, which can represent fragments of former life, of dead, dormant or viable cells. The detected organic marker molecules from plants (*n*-alkanes) may be taken as indicator for the presence of past life in the hyperarid core of the desert. Their detection suggests that life might have been better supported in that region in former times, the disentangling of the involved time-scales now warranting further attention.

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Figure legends:

Fig. 1: Location of sampling sites along the Aroma transect.

Fig. 2: Gypsum content in soils along the Aroma transect.

Fig. 3: Bacterial colony forming units (CFU) in Atacama Desert soil samples taken along the Aroma transect. Cell numbers were determined on nutrient-rich NB and less nutrient-rich R2A medium. Mean values and standard deviation of two experimental replicates are shown.

Fig. 4: NMDS plot showing the dissimilarities in bacterial community composition between samples taken along the Aroma transect. Samples from different elevations along the transect are encoded by color, while the symbol shape indicates soil depth. Arrows are projected on the plot to visualize the impact of those soil properties that explain a significant amount of variation in community composition according to Envfit analysis. Detailed Envfit results are provided in Table S6.

Fig. 5: Bacterial community composition in soil samples from the Aroma transect. Colors indicate different phyla, while classes within phyla are labelled by line patterns. The labelling of soil samples from different depths is as follows: A = 0 – 1 cm, B = 1 – 5 cm, C = 5 – 10 cm. The group “others” includes all taxa with a relative abundance below 2% in all samples.

Fig. 6: Lipid concentrations in samples from the Aroma transect (composite sample from 0-10 cm).

Fig. 7: Relative abundance of GDGTs in samples from the Aroma transect (composite sample from 0-10 cm).

Table 1. Description of sampling sites. Samples were taken from 0 - 1 cm, 1 - 5 cm and 5 - 10 cm soil depth intervals.

Region	Sampling site[1]	Geographic location	Elevation	Distance to coast [km]	MAT[2] [°C]	MAP[3] [mm yr^{-1}]	Vegetation	Sampling date
Aroma	Ar_2720	S 19°31'42.7''; W 69°22'43.2''	2720 m	86.80	13.5[4]	43.6[4]	*Browningia candelabris, Atriplex* sp.[6]	23.02.2014
	Ar_2455	S 19°33'02.0''; W 69°25'38.5''	2455 m	80.93	15.7[4]	11.1[4]	absent[7]	23.02.2014
	Ar_2020	S 19°35'44.8''; W 69°30'26.8''	2020 m	73.37	15.7[4]	11.1[4]	absent	23.02.2014
	Ar_1680	S 19°39'18.6''; W 69°35'31.5''	1680 m	59.49	17.7[4]	0[4]	absent	23.02.2014
	Ar_1340	S 19°46'53.1''; W 69°40'02.4''	1340 m	50.82	17.7[4]	0[4]	absent	23.02.2014
Yungay	Yu_1020	S 24°06'06.1''; W 70°01'05.8''	1020 m	49.18	14-16[5]	<2[5]	absent	18.02.2014

[1] Nomenclature of sampling sites as follows: name of location_elevation.

[2]MAT = mean annual temperature

[3]MAP = mean annual precipitation

[4]Análisis de los Recursos Hídricos de la Quebrada de Aroma Región de Tarapacá ; Gobierno de Chile Ministerio de obras públicas direccion general de aguas división de estudios y planificación [2013]

[5] Warren-Rhodes et al. (2006)

[6] futher unidentified herbaceous plant species were present at this site

[7] very first withered plants appeared in a depression adjacent to the sampling site

Table 2. Selected soil properties determined in soils taken at different depth along the Aroma transect (Ar) and at Yungay (Yu).[1]

Site	Depth	pH[2]	$CaCO_3$	OC	TN	NO_3-N	$\delta^{13}C$	$\delta^{15}N$	Olsen-P	Ex-P_{tot}[3]	Ex-S_{tot}[3]	Ex-Fe_{tot}	Fe_o	Fe_d	Fe_o/Fe_d	Na	Mg	Si	P	Clay <2 µm	Silt 2-63 µm
	cm		g kg^{-1}	mg kg^{-1}	mg kg^{-1}	mg kg^{-1}	‰	‰	mg kg^{-1}	g kg^{-1}	g kg^{-1}	g kg^{-1}	g kg^{-1}	g kg^{-1}		g kg^{-1}	g kg^{-1}	g kg^{-1}	g kg^{-1}	%	%
Ar_2720	0-1	7.5	0.0	822	165	0.4	-23.9	9.1	7.2	0.88	0.12	32.7	0.36	8.38	0.042	14.4	11.6	253.6	1.11	3.9	33.1
	1-5	8.1	0.0	1648	270	1.1	-22.7	13.2	6.1	1.20	0.13	32.4	0.34	8.11	0.042	9.7	14.6	254.6	1.53	7.7	41.7
	5-10	8.8	0.0	1457	320	0.7	-23.6	12.5	5.5	1.71	0.18	34.5	0.54	5.79	0.093	6.9	15.6	251.4	1.50	12.1	48.8
Ar_2455	0-1	7.6	0.0	524	145	0.5	-25.4	7.2	5.6	0.96	0.15	33.8	0.27	8.00	0.034	14.2	13.7	257.8	1.19	5.2	35.6
	1-5	7.9	0.0	539	150	1.1	-25.8	7.4	5.6	0.94	0.17	33.9	0.28	8.16	0.034	12.1	15.7	256.1	1.23	7.8	37.5
	5-10	8.3	0.0	498	150	0.0	-27.0	6.8	4.0	0.49	0.09	31.0	0.22	7.10	0.031	14.1	12.6	243.6	0.69	4.8	20.8
Ar_2020	0-1	7.7	0.0	363	125	0.6	-26.4	6.6	5.3	0.80	0.12	28.9	0.19	6.65	0.028	17.8	12.2	267.3	1.17	2.8	20.7
	1-5	8.5	0.0	424	150	1.0	-26.2	7.1	1.7	1.05	0.21	33.6	0.19	6.13	0.032	8.8	18.2	256.0	1.19	8.7	34.7
	5-10	8.4	6.0	696	235	1.0	-24.3	7.3	2.1	1.32	0.46	30.9	0.15	3.31	0.045	6.0	25.3	249.8	1.23	5.7	18.4
Ar_1680	0-1	7.8	2.1	254	140	6.1	-25.9	7.7	3.7	0.96	0.52	31.1	0.39	7.53	0.052	11.2	18.7	240.3	1.24	14.8	40.8
	1-5	8.0	9.5	130	140	8.5	-27.0	7.6	2.1	0.97	2.93	28.3	0.35	5.60	0.063	10.1	23.8	231.9	1.19	16.2	33.9
	5-10	8.3	9.1	131	255	175	-26.8	6.0	4.4	0.88	12.70	23.0	0.22	4.00	0.054	22.2	22.1	192.0	0.89	8.3	20.4
Ar_1340	0-1	7.9	14.3	185	135	3.3	-26.6	6.2	3.1	0.77	1.64	29.2	0.26	6.87	0.037	17.3	14.5	249.2	1.05	5.4	14.2
	1-5	8.1	14.9	104	130	11	-27.8	5.5	5.9	0.64	31.18	23.9	0.27	5.33	0.051	34.5	13.4	173.7	0.60	1.5	13.7
	5-10	8.4	6.4	109	155	52	-28.0	5.0	7.6	0.68	24.55	22.9	0.16	5.18	0.031	33.5	12.2	156.9	0.52	1.2	10.1
Yu_1020	0-1	7.4	8.2	694	170	69	-26.9	3.4	13.2	0.61	6.15	15.3	0.16	3.45	0.048	10.9	13.2	184.4	0.82	6.6	14.0
	1-5	8.0	15.8	769	218	215	-26.2	3.5	2.9	0.74	8.90	20.1	0.20	5.13	0.038	12.9	19.3	189.2	0.80	21.3	27.8
	5-10	8.0	18.4	711	392	184	-26.8	2.9	3.6	0.49	33.20	16.2	0.19	3.92	0.049	23.0	18.0	166.2	0.62	15.7	17.0

[1] Sand content can be calculated as 100% minus clay content (%) minus silt content (%)

[2] Measured in H_20

[3] EX-P_{tot}, Ex-S_{tot} and Ex-Fe_{tot} = aqua-regia extractable P and S, respectively

Table 3: Phospholipid fatty acid (PLFA) concentrations in soils from the Aroma transect taken at 0 – 10 cm depth. Concentrations are given in ng g^{-1} dry weight (DW).[1]

PLFA	Ar_2720	Ar_2455	Ar_2020	Ar_1680	Ar_1340
14:0	0.9	5.5	n.d.	n.d.	n.d.
i-15:0	12.4	12.1	n.d.	n.d.	n.d.
a-15:0	8.2	9.3	n.d.	n.d.	n.d.
15:0	5.5	4.9	n.d.	n.d.	n.d.
i-16:1ω7	3.8	8.9	0.3	n.d.	n.d.
i-16:0	33.3	36.1	2.4	0.4	n.d.
16:1ω9	2.3	3.5	0.2	n.d.	n.d.
16:1ω7	19.7	85.9	2.0	n.d.	n.d.
16:1ω5	7.6	5.8	n.d.	n.d.	n.d.
16:0	63.1	175.3	3.3	2.1	5.3
10Me16:0	49.6	91.04	4.5	n.d.	n.d.
i-17:1ω7	13.0	14.8	0.5	n.d.	n.d.
br17:0	28.8	22.9	5.89	n.d.	n.d.
i-17:0	14.6	10.1	n.d.	n.d.	n.d.
a-17:0	19.2	13.5	n.d.	n.d.	n.d.
17:1ω7	7.8	13.7	1.0	n.d.	n.d.
cyc17:0	32.5	100.6	1.3	n.d.	n.d.
C17:0	37.4	18.0	1.4	0.8	n.d.
10Me17:0	8.2	8.2	0.7	n.d.	n.d.
brC18:0	5.3	2.45	n.d.	n.d.	n.d.
i-18:1ω9	3.9	9.4	1.2	n.d.	n.d.
18:1ω9	66.7	73.4	3.1	n.d.	n.d.
18:1ω7	25.0	17.6	0.8	n.d.	n.d.
18:1ω5	8.4	n.d.	n.d.	n.d.	n.d.
18:0	29.9	29.0	2.7	1.8	1.9
10Me18:0	62.1	45.3	6.5	1.0	n.d.
br19:0	5.2	5.89	0.8	n.d.	n.d.
cyc19:0	14.3	7.2	0.2	n.d.	n.d.
19:0	3.4	1.89	n.d.	n.d.	n.d.
20:1ω9	9.9	10.9	0.3	n.d.	n.d.
20:0	8.1	5.1	0.78	n.d.	n.d.
22:0	2.9	12.01	n.d.	n.d.	n.d.
24:0	1.7	0.4	n.d.	n.d.	n.d.
Sum	614.5	860.6	39.7	6.0	7.2
MONO[2]	168.1	243.9	9.3	0.0	0.0
SAT[3]	152.9	252.2	8.1	4.6	7.2
Actinomycetes[4]	119.8	144.6	11.7	1.0	0.0
Cells g^{-1} DW[5]	4.5×10^7	6.3×10^7	2.9×10^6	0.4×10^6	5.5×10^5

[1] n.d.: not detected / below detection limit

[2] MONO: *i*-16:1, 16:1ω9, 16:1ω7, 17:1ω9, *a*-17:1, 17:1ω7, *i*-18:1ω9, 18:1ω9, 18:1ω7, 18:1ω5, 20:1ω9

[3] SAT: 14:0, 15:0, 16:0, 17:0, 18:0, 19:0, 20:0. 22:0, 24:0

[4] *Actinomycetes*: 10Me-PLFAs

[5] conversion factor: 2.0×10^4 cells $pmol^{-1}$ PLFA