1 **Article title:** Abiotic environmental factors driving the biomass and community structure of soil

2 bacteria in an arid region.

3

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21

22 **Abstract**

23 Microbial communities are important determinants of ecosystem functions in deserts. However,
24 bacterial communities and their relationship with edaphic conditions are poorly investigated in
25 these extreme ecosystems. Here we examined the community structure and biomass of bacteria,
26 including/focusing on nitrogen-fixing bacteria, across different soil habitats in Qatar, using high-
27 throughput sequencing and soil fatty acid profiling. To study bacterial community structure
28 correlations and its edaphic drivers, we determined soil physicochemical parameters. Soils in the
29 studied habitats were predominantly colonized by members of Proteobacteria, Actinobacteria,
30 and Chloroflexi, while nitrogen-fixing bacteria were sparse, and the proportion of unidentified
31 fungal taxa was relatively high. According to biomass estimates, there were more bacteria in soils
32 of shrub- and woodlands (known as rawda) in the Qatar Peninsula. This was mediated by the
33 high concentration of gram-positive bacterial fatty acid biomarkers, whereas gram-negative
34 bacterial biomarkers were more abundant in habitats with the highest salinity. Salinity also
35 appeared to alter the community composition of fungi as well as the diversity of bacteria. Overall,
36 soil phosphorus (P) concentration was positively correlated with the increase in diversity and
37 biomass of bacteria and exhibited a pronounced effect on the community composition. These
38 findings suggests P affects bacterial communities in various ways in these hot arid desert soils.

39

40 **Keywords:** Soil Bacterial diversity, Phospholipid fatty acid, High-throughput sequencing, Abiotic
41 stress, Arid regions, Soil physicochemical parameters.

42

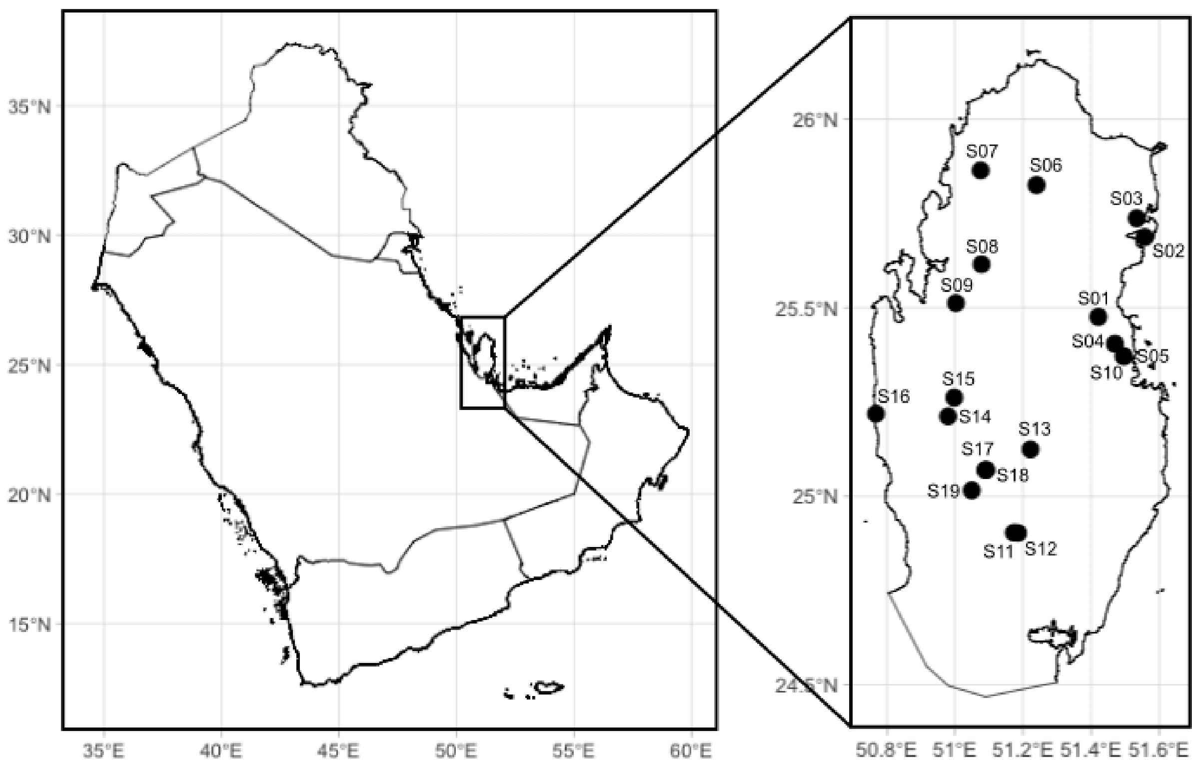
1. Introduction

Arid regions (or drylands), including desert, grassland, and savanna woodland biomes, encompass approximately 41% of the world's land surfaces and are expected to expand globally [1]. These biomes have several stresses, including soils typically low in organic matter and alkaline, low levels of available water that affect biological activities, drastic temperature fluctuations, and high solar radiation. Therefore, these biomes are biologically low-productive and have particularly sparse biota. However, the function and composition of microbial communities in desert soils are more diverse than thought previously and differ from those in other biomes [2–4], and the bacterial communities in drylands can differ significantly over short geographic distances [5]. Overall, soil microbes are critical for the functioning of ecosystems, including cycling of nutrients, decomposition of organic matter, productivity and diversity of plants, and regulating climate and pathogens [6,7]. In arid regions, soil microbes have even more influential role in contributing to (governing key bioprocesses, including additional functions) stabilizing soils, cycling of nutrients, and overall health of the environment [8–11].

Bacteria from harsh conditions tend to have genes that improve tolerance to salinity, alkaline conditions, and changes in the osmotic conditions [12]. For example, the thick peptidoglycan cell of wall gram-positive bacteria make them more tolerant to drought [13], and there is growing evidence that microbial survival under water or carbon limitation is improved by adapting dormancy as a common strategy [3]. A comprehensive review article on microbial communities in oligotrophic environments suggests at least three strategies for how microorganisms conserve energy [3]. These are rhodopsin- bacteriochlorophyll-dependent light harvesting, degradation of organic energy reserves, and oxidation of some trace gases such as carbon monoxide and hydrogen from the atmosphere. Such characteristics seem to be present in members of Actinobacteria, Proteobacteria, and Chloroflexi, as they are dominants in deserts globally [3]. Still, other bacterial phyla can be predominant depending on local conditions or niches. In the Atacama desert, the soil surface was dominated by Actinobacteria species that are UV-

69 desiccation resistant. In contrast, halophilic bacteria from Proteobacteria or Firmicutes dominated
70 deeper layers with higher salt content [14]. However, studies of surface soils in the Gobi and
71 Taklamakan hot deserts and the Atacama desert reported a predominance of phylum Firmicutes
72 [8,15].
73 Global and continental scale studies have revealed that the structure of soil bacterial
74 communities are influenced by different drivers, including soil properties [16–18], climatic factors [1,19],
75 vegetation types [20] and nutrient concentration [16,21]. At the regional scale, typically, macronutrients
76 (carbon and nitrogen) and other soil factors (e.g., soil and pH characteristics) are often the drivers
77 of bacterial responses at the community level [22]. A global study of dryland soil bacteria revealed
78 that aridity level was the key factor for shaping bacterial composition [1]. A recent survey of bacterial
79 biodiversity of soils in high-altitude deserts suggests that organic matter and pH in soils primarily
80 influence the bacterial community composition [23]. Here we aim to study the diversity and
81 composition of nitrogen-fixing and total bacterial communities in soils across different Qatari
82 habitats in an arid region in relation to key soil parameters. We used DNA sequencing as well as
83 phospholipid fatty acid (PLFA) profiling to study the soil bacterial microbiome. Our goals were to
84 (1) study how composition and diversity differ in hot arid soils in the Qatar Peninsula and (2)
85 investigate the main factors affecting their diversity and abundance.
86
87 **2. Materials and methods**
88
89 **2.1 Study sites and sampling**
90 Qatar, a small limestone peninsula in the Persian Gulf, consists mainly of low-lying, arid, and
91 stony deserts. We collected soil samples from 19 sites across Qatar (Figure 1). The sites were
92 selected to represent various vegetation types (like saltmarsh, rawda, and sabkha) and
93 contrasting edaphic conditions with a minimal climatic variation. The study sites are distributed
94 over a geographically wide area; the closest locations are 0.16 km apart and the farthest 108 km.

Among the more intensively studied vegetation types were rawda and sabkha habitats, which are usually found in low-lying areas. Rawda (also known as roda or rawdah) soils are enriched with fine sand, silt, or loam that is washed down from the surrounding higher areas during rainy seasons and, therefore, are considered as good rangelands and can be used as farmlands as well as lands for the grazing of camels and cattle [24]. Sabkhas are characterized by high soil salinity and might be vegetated with halophytes and extremophiles or be barren [24]. The sampling was performed in the beginning of the relatively cool-rainy season in December 2018. The average annual rainfall is 50-90 mm, and the average daily temperature ranges from 18.5 ºC in January to 37 ºC in June. Samples were collected from each site (50 x 50 m), where 20 soil subsamples (5 cm in diameter and 5 cm deep) were collected and subsequently pooled. Pooled samples were air-dried for four days in the laboratory, thereafter homogenized, and stored in zip-lock plastic bags with silica gel to prevent absorption of moisture. More detailed information about selected sites and soil sampling is described in Adenan et al. (2021).



109 **Figure 1.** The geographic locations of sampling sites (S01-S19) in Qatar. Due to the close spacing
110 of some study sites, symbols may overlap.
111
112 **2.2 Chemical and phospholipid fatty acid analysis**
113 We measured total nitrogen (TN) and carbon (TC), nitrite (NO_2^-), nitrate (NO_3^-), total dissolved
114 salts (TDS), elemental contents (Ca, Cd, K, P, Mg, Pb), salinity, and pH [25]. In brief, we measured
115 soil parameters following validated methods (ISO/IEC 17025). We used Certified reference
116 material (PACS-3 marine sediment) to assess the accuracy and precision of the chemical
117 analyses.
118 For the lipid extraction and phospholipid fatty acid analysis, we followed standard
119 procedures [26–28]. Seven prokaryote-specific PLFAs: i15:0, i16:0, a15:0, a17:0, cy19:0, 10Me17:0,
120 and 10Me18:0 were used to assess the bacterial biomass by summing their concentration of [27].
121 We followed the fatty acid nomenclature of Frostegård et al. (1993).
122
123 **2.3 Molecular analysis**
124 We used DNeasy PowerSoil kit (Qiagen GmBH, Hilden, Germany) to extract DNA from soils
125 according to the manufacturer's instructions. We used bacterial primer pair 515F to amplify the
126 16S rRNA gene variable regions V3–V4 from the extracted DNA [29] and 926R [30], primer pair 19F
127 and 407R [31] specific to *nifH* gene, which encodes a subunit of the nitrogenase enzyme complex
128 related to nitrogen fixation efficiency. Unique 12-base Golay barcodes were used to tag Bacterial-
129 specific primers and the nifH gene-specific primers were equipped with Illumina Nextera XT
130 sequencing adapters (Illumina forward primer adaptor: 5′-
131 TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG-3′; Illumina reverse primer adaptor: 5′-
132 GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG-3′). The PCR mixture comprised 1 µl soil
133 DNA, 0.5 µl each of the primers (20 µM), 5 µl of 5x HOT FIREPol Blend Master Mix (Solis Biodyne,
134 Tartu, Estonia), and 18 µl nuclease-free water. We followed Otsing et al. (2021) for bacterial

135 amplicons, except that the PCR had 25 cycles of 95 °C for 30 s (instead of 30 cycles) [32]. For
136 nitrogen-fixing bacterial amplicons, we followed Sepp et al (2023) for the PCR [33]. 1% agarose gel
137 was used to check the success of the amplification, if the bands were low or not visible, the
138 samples were re-amplified by increasing cycles by two or three [34]. PCR and sequencing runs
139 included negative (nuclease-free water) and positive controls (bacteria from the nodules of
140 *Medicago sativa*). PCR products amplified with bacterial primer pairs were pooled at
141 approximately equimolar ratios as determined by gel band strength, except negative and positive
142 controls, from which 5 µl were added. We followed the manufacturer's instructions to purify
143 Bacterial amplicon libraries with FavorPrep™ Gel/PCR Purification Kit (Favorgen-Biotech Corp.,
144 Austria). Thereafter, the manufacturer's protocol were followed using the TruSeq DNA PCR-free
145 HT Library Prep kit (Illumina Inc., San Diego, CA, USA) when bacterial amplicon libraries were
146 subjected to ligation of Illumina adaptors, and using Illumina Nextera XT sample preparation kit
147 (Illumina Inc., San Diego, USA) when nitrogen-fixing bacterial amplicons were ligated. The
148 sequencing and ligation of Illumina adaptors were done at the Estonian Genome Center (Tartu,
149 Estonia) using Illumina MiSeq 2x300 bp paired-end mode.
150

151 **2.4 Bioinformatic and statistical analysis**

152 Illumina 2x300 bp paired-end raw reads were processed using the LotuS pipeline, including
153 demultiplexing, quality-filtering, and chimera-checking [35]. Sequences were clustered into OTUs
154 at 97% similarity level using UPARSE. The taxonomic identity of each OTU was determined
155 based on the Silva database [36] and the International Nucleotide Sequence Database Consortium
156 (INSDc) by using BLAST search. USEARCH v10.0.240 was used for generating consensus OTU
157 sequences [37]. All taxonomically unidentifiable, archaeal, and eukaryotic OTUs were removed. All
158 global singletons or OTUs represented in positive or negative controls were removed. We used
159 functional predictive analysis to assign OTUs to functional groups (Functional Annotation of

160 Prokaryotic Taxa, FAPROTAX) [38]. Raw reads from targeted loci have been deposited in the NCBI
161 SRA (BioProject PRJNA944243).

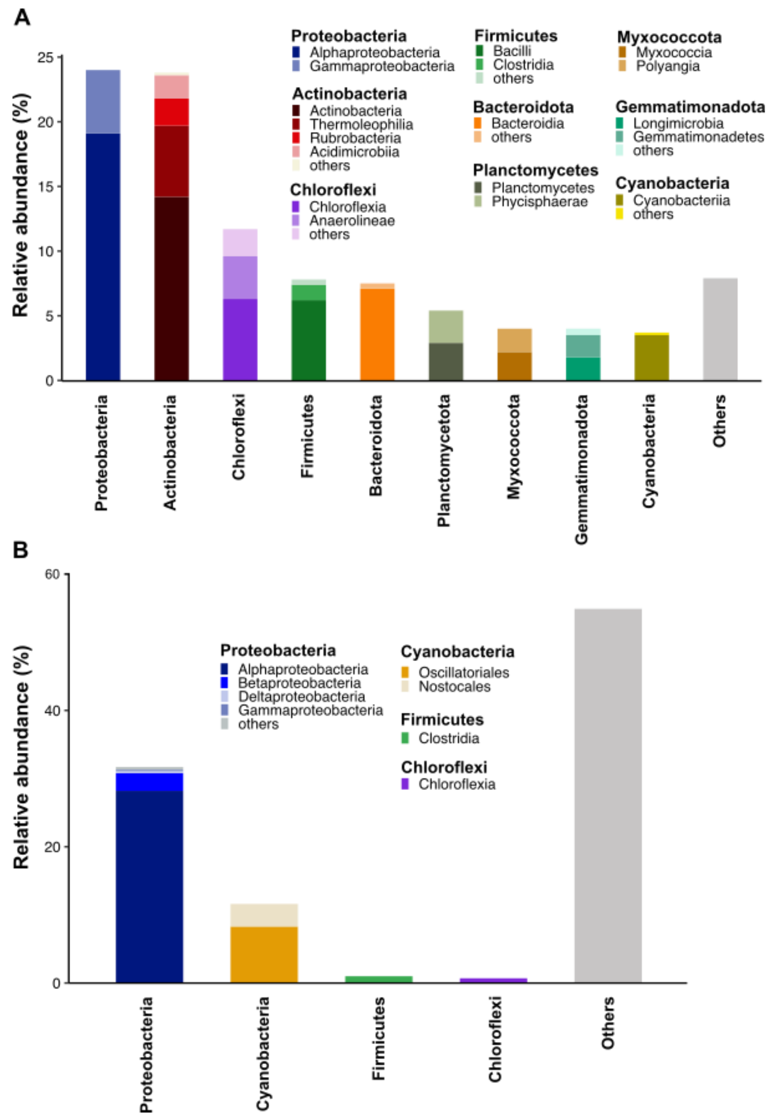
162 For analyzing the effect of soil abiotic variables on the species richness and diversity of
163 bacteria and nitrogen-fixing bacteria, individual variables were subjected to the best ordinary least
164 squares (OLS) multiple regression model selection. Species diversity of bacteria and nitrogen-
165 fixing bacteria were calculated based on OTU abundance, using the exponential of the Shannon
166 entropy of order q = 1 using R software [39] and implemented in the iNEXT package [40]. This
167 measure is more robust against biases arising from uneven sampling depth than the simple
168 number of OTUs [41]. Some of the soil nutrients (EC, NO_3^-, K, Ca, Mg) were log-transformed prior
169 to analyses to improve the distribution of residuals and reduce nonlinearity. We used the ANOVA
170 type II function in the *car* package in R [42] to detect soil parameters effect on the bacterial and N-
171 fixing bacterial diversity. The same analysis was also run to study soil parameters' impact on the
172 soil's bacterial fatty acid abundance.

173 To determine the effect of these factors on the bacterial and nitrogen-fixing bacterial
174 community composition, we used multivariate permutational analysis of variance as implemented
175 in the *adonis* function of the Vegan package of R [43]. The final multivariate models were
176 constructed based on forward selection criteria. For the data normalization, we transformed read
177 counts using the *varianceStabilizingTransformation* function in the DESeq2 package of R [44] as
178 suggested by McMurdie and Holmes [41]. Using the same parameters, nonmetric multidimensional
179 scaling (NMDS) ordinations were performed to visualize the differences in bacterial and nitrogen-
180 fixing bacterial community structure using the *metaMDS* function. The environmental factors were
181 fitted to the ordination plots using the *envfit* function of the Vegan package in R.
182

183 **3. Results**

184 **3.1 Identification of bacterial OTUs**

185 Altogether, 10,628 bacterial OTUs (1,306,756 reads) were identified in 19 sites. The number of
186 observed OTUs per site ranged from 439 to 5403 (average 3625). About 90% of all sequences
187 were classified at the phylum level. The five most abundant (dominant) bacterial phyla (among all
188 obtained sequences) were Proteobacteria (24.0%), Actinobacteria (23.8%), Chloroflexi (11.7%),
189 Firmicutes (7.8%) and Bacteroidota (7.5%). At the lower taxonomic levels, the five most dominant
190 classes were Alphaproteobacteria (19.1%), Actinobacteria (14.2%), Bacteroidia (7.1%),
191 Chloroflexia (6.3%) and Bacilli (6.2%) and five dominant orders Rhizobiales (8.0%), Bacillales
192 (5.5%), Sphingomonadales (5.2%), Solirubrobacterales (4.3%) and Micrococcales (4.0%; Figure
193 2A). At the genus level, *Microvirga* (phylum Proteobacteria), *Bacillus* (phylum Firmicutes), and
194 *Rubrobacter* (phylum Actinobacteria) were most abundant across all sites.
195 For nitrogen-fixing bacteria, 1035 OTUs (278,192 reads) were recovered from 14 sites;
196 the other five sites did not yield nitrogen-fixing bacterial sequence reads. The number of observed
197 OTUs for N fixing bacteria per site ranged from 43 to 537 (average 251). Almost half of the
198 nitrogen-fixing bacterial OTUs (492 OTUs) remained unidentified, but the most abundant phyla
199 detected were Proteobacteria (31.7%) and Cyanobacteria (11.6%). At the class level, the most
200 abundant ones were Alphaproteobacteria (28.2%), and order level Rhizobiales (25.2%), and
201 Nostocales (8.3%); other classes and orders were present with less than 4% (Figure 2B). Among
202 the identified functional groups of bacteria, most were aerobic chemoheterotrophs (63.7%),
203 followed by fermentative bacteria (6.9%), ureolytic bacteria (3.9%), manganese oxidizing bacteria
204 (3.8%), and nitrogen-fixing bacteria (3.6%) (Table S2, Supplementary Information). In all sites,
205 over 50% of the detected phenotypes belong to the aerobic chemoheterotrophs, except in site 7,
206 where it was 49.60%.
207



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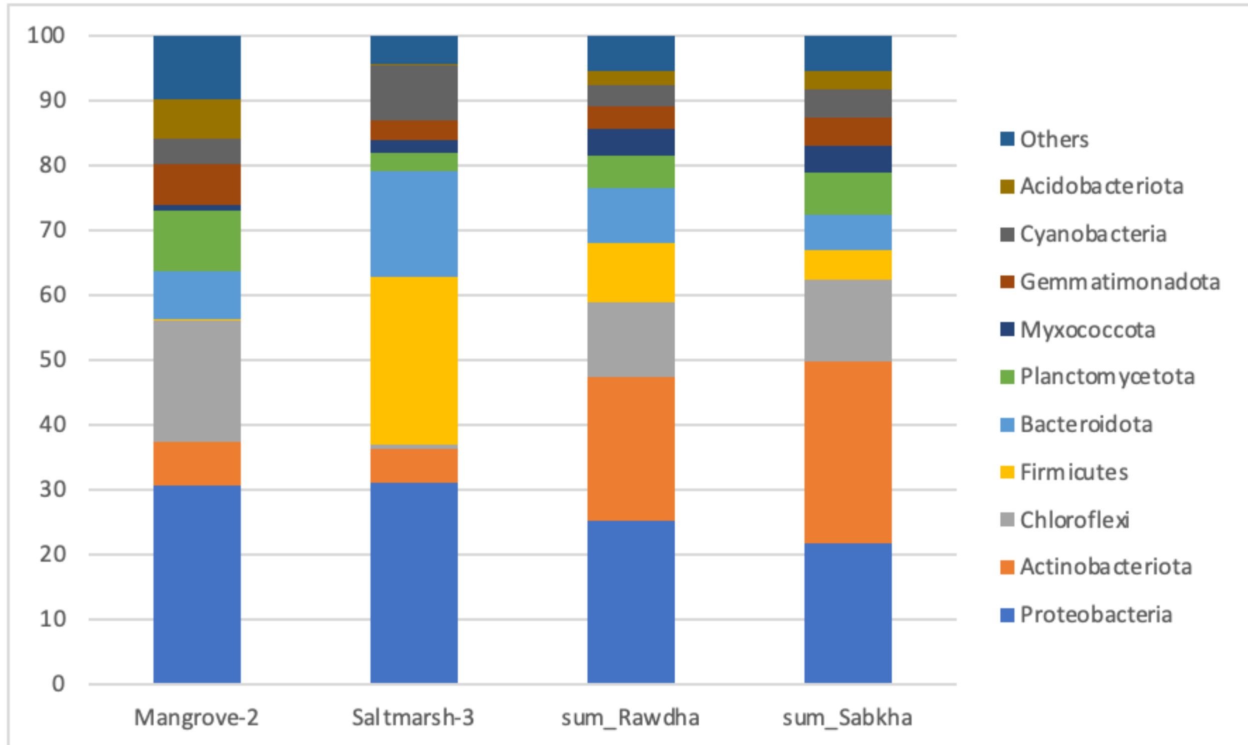
209

210 **Figure 2.** Relative abundance and composition of dominant soil bacteria in different habitats
211 across Qatar identified by A) 16S rRNA and B) *nifH* gene amplicon sequencing.

212

213 Based on the habitat types, Proteobacteria were equally abundant among all studied
214 habitats, whereas the other four most abundant phyla showed distinct occurrences among
215 habitats. Actinobacteria were often observed in the rawda and sabkha habitats and seldom in
216 saltmarsh and mangrove. Chloroflexi showed a high presence in the mangrove, rawda, and

217 sabkha and was scarce in the saltmarsh. The members of Firmicutes and Bacteroidota were more
218 often occurring in saltmarsh and less frequently in other habitats (Figure 3).
219



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221 **Figure 3.** Relative abundance and composition of dominant soil bacterial phylum by habitat types.
222

223 **3.2 Soil characteristics and their effects on bacterial diversity, biomass, and composition**

224 Soil chemical analyses revealed that all studied sites had slightly alkaline or alkaline soils (except
225 one sabkha site; mean±s.d.: pH value, 8.69±0.34), with very low N concentration, but with high
226 Ca content (mean±s.d.: 157090.21±75366.28 mg/kg). Among the other measured chemical
227 elements (Cd, K, Mg, P, Pb), the lowest concentrations were for heavy metals Cd and Pb. For
228 more details of soil chemical characteristics, see Adenan (2021). The highest bacterial diversity
229 (Shannon diversity index) was detected in one of the sabkha habitat sites (site 6), and the lowest
230 diversity was in saltmarsh (site 3). For N-fixing bacteria, the highest and lowest diversity was
231 found in sabkha sites, respectively, sites 7 and 10. However, it is worth noting that five locations

232 (including site 3) were unsuccessful in amplifying nitrogen-fixing bacteria. According to the
233 biomass, first there was no correlation with the bacterial diversity among the sites but there were
234 slightly more bacteria (=highest concentration of fatty acids) in rawda habitats. However, rawda
235 habitats showed one of the highest and lowest biomasses from all studied sites. In the case of
236 the highest level of bacterial biomass, this was due to the high concentration of biomarkers i15:0
237 and i16:0, characteristic of gram-positive bacteria. In contrast, the characteristic biomarker for
238 gram-negative bacteria was more abundantly detected from a sabkha site (site 10), mangrove,
239 and saltmarsh (Table S1).

240 Several soil parameters showed a significant effect on bacterial diversity and biomass. In
241 both cases, soil P concentration showed a consistent significant effect (Table 1). In addition, there
242 was an effect of total dissolved salts and total C on bacterial diversity and pH value, Ca and Mg
243 concentrations on bacterial biomass. The diversity of N-fixing bacteria was affected by soil Mg
244 concentration (F-value=5.849, p=0.034). Both bacterial diversity and biomass correlated
245 positively with soil P concentration (Figure 4). Otherwise, bacterial diversity correlated also with
246 the concentration of K (p-value = 0.009) and bacterial biomass with the concentration of Mg (p-
247 value < 0.001). The concentration of Mg also correlated positively with the diversity of N-fixing
248 bacteria (p-value = 0.006) among the studied variables. Neither Cd or Pb had any significant
249 effects on bacterial diversity or biomass.

250

251 **Table 1.** Analysis of variance for the effect of selected soil parameters on
252 bacterial diversity (A) and biomass (B). Bold typeface indicates statistical
253 significance (*P* < 0.05).

A. Factors	**df**	**F**	**P**
Total dissolved salts	1	**28.729**	**<0.001**

Total C	1	**6.2704**	**0.028**
Ca	1	3.6795	0.079
Cd	1	4.5873	0.053
Mg	1	3.4961	0.086
P	1	**12.773**	**0.004**
Residuals	12		

254

B.

Factors	**df**	**F**	**P**
pH	1	**7.444**	**0.026**
Salinity	1	2.157	0.180
Total dissolved salts	1	2.271	0.170
Total C	1	2.895	0.127
NO_3^-	1	4.199	0.075
Ca	1	**6.589**	**0.033**
K	1	4.661	0.063
Mg	1	**5.395**	**0.049**
P	1	**9.282**	**0.016**
Pb	1	4.919	0.057
Residuals	8		

255

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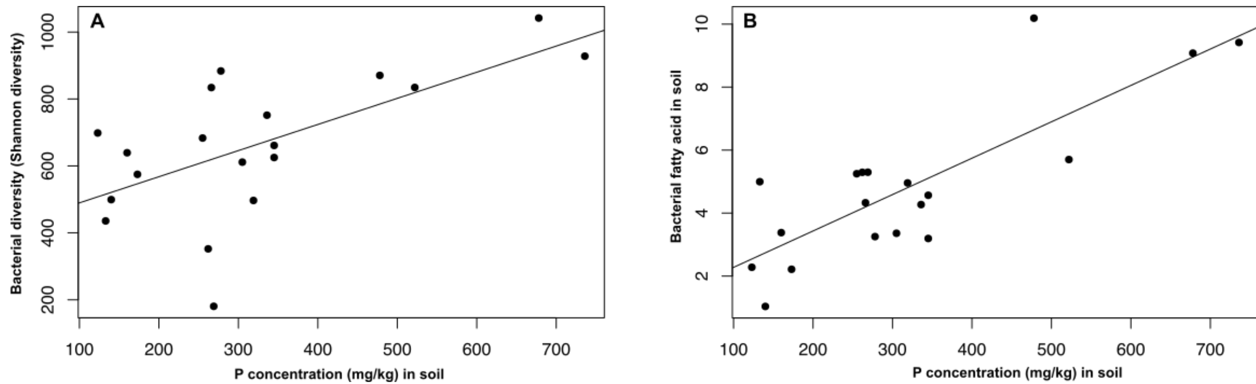

258

259 **Figure 4.** Bacterial diversity **(**A) and biomass (B) in relation to P concentration in soil.

260

261 The community composition of all bacteria was significantly affected by P concentration ($F_{1,15}$ =
262 3.201, P>0.001), salinity ($F_{1,15}$ = 2.907, P=0.001) and Cd concentration ($F_{1,15}$ = 1.748, P=0.036)
263 explaining 14.0%, 12.7% and 7.6% of variation, respectively (Fig S2). The community composition
264 of nitrogen-fixing bacteria was significantly affected by Mg ($F_{1,11}$ = 1.620, P = 0.010) and Cd ($F_{1,11}$
265 = 1.418, P = 0.038), explaining 11.5 and 10.1% of variation, respectively.

266

267 **4. Discussion**

268 We detected that bacterial diversity and biomass were both significantly affected by soil P
269 concentrations. However, we found no correlation between bacterial diversity and biomass among
270 the sites. Previous studies have shown that PLFA profiling and 16S rRNA gene metabarcoding
271 results are broadly comparable [45]. In addition, soil P was an important factor for bacterial
272 community structure. Phosphate was observed to be an important factor for soilborne microbial
273 community across many Dutch soils [46,47]. Also, several other studies have found that microbial
274 distributions are affected by P availability in soils [48–50]. While we did not include vegetation
275 structure in our study, microbial communities in deserts have been suggested to be more affected

276 by vegetation than soil properties [51,52]. Similarly, bacterial communities can enhance the growth
277 of plants in arid soils [53]. The highest bacterial biomass roughly follows the results of arbuscular
278 mycorrhizal (AM) fungal richness from the same sites [25]. There seemed to be slightly more
279 bacteria, especially gram-positive bacteria, in rawda habitats. This suggests that bacteria likely
280 play an essential role in why these habitats are favored by most wild plants and frequently used
281 as farmlands and for the grazing of camels and cattle.

282 Similar to other global desert ecosystem studies [3,54–58], Proteobacteria, Actinobacteria,
283 and Chloroflexi predominated different habitats across Qatar. However, slight differences can still
284 be expected, as previous studies of microbes in barchan sand dunes in Qatar and soils in Saudi
285 Arabia identified Actinobacteria, Firmicutes, and Proteobacteria as the dominant phyla [59,60].
286 Similar results have also been found in soils in Kuwait that harbored mainly Actinobacteria, and
287 Proteobacteria [61]. Yet, our results showed that some phyla displayed distinct occurrences among
288 habitats. For example, members of Firmicutes were more often occurring in saltmarsh and less
289 in other habitats. A similar trend of Firmicutes favoring saline environments has been reported
290 from deeper layers of desert soils with a higher salt content, dominated by halophilic bacteria from
291 Firmicutes [14].

292 In the case of nitrogen-fixing bacteria, which play an essential role in supporting plants in
293 desert soils [62–64], almost half of the OTUs were left unidentified, highlighting that we lack genomic
294 information for these bacteria and therefore we were able to recognize only the dominance by
295 Proteobacteria (Alphaproteobacteria and Betaproteobacteria) and Cyanobacteria. These phyla
296 are traditionally considered as the major groups of nitrogen fixation population, however the
297 enrichment of refence sequence databases and the advance of technology has recently revealed
298 the predominance of previously-undervalued *Deltaproteobacteria* within Proteobacteria at the
299 global level (Masuda et al., 2022).

300 Salinity is one of the major drivers of microbial communities globally (Lozupone & Knight,
301 2007). It often also affects the microbial communities in drylands and desert ecosystems [58,65,66].

302 Salinity is frequently shown to negatively impact bacterial biomass and diversity [67,68]. However,
303 there exists salt-tolerant phylotypes and phenotypes that have a positive relationship with the
304 salinity [66]. Our results show the effect of salinity on the total bacterial communities and the effect
305 of total dissolved salts on bacterial diversity. Sites with the highest salinity concentration seem to
306 have the highest gram-negative bacterial biomass. This is similar to findings around a hypersaline
307 lake in Iran [69]. They speculated that this was due to the higher synthesis of glutamate and
308 lipopolysaccharides in the membrane in G- bacteria compared to G+ bacteria, both of which are
309 believed to support a greater stress tolerance [69,70]. However, others have argued that G+ bacteria
310 could be favored over G- bacteria in saline conditions. As G+ bacteria have both inducible and
311 constitutive osmolyte production, while in G- bacteria only synthesis of osmolytes is induced by
312 salt and water stress [71,72]. Zhang et al. (2019) also had a deeper look at the impact of salinity on
313 bacterial phenotypes, but determined only a significant positive relationship with the relative
314 abundance of the anaerobic phenotype. Our phenotype detection revealed mostly aerobic
315 chemoheterotrophs.

316

317 **5. Conclusions**

318 Our study determined that Proteobacteria and Actinobacteria were predominant phyla along
319 different hot arid desert soils in the Qatar Peninsula and the diversity of bacteria was consistent
320 among different habitats, only bacterial biomass was highest in rawda habitats. This was due to
321 the high concentration of fatty acids of gram-positive bacteria, whereas gram-negative bacteria
322 were more abundant in the sites with the highest concentration of salinity. Nevertheless, soil P
323 concentration was the major driver of bacterial diversity and biomass and composition at the
324 community level. We propose that further experimental studies may shed additional light on the
325 effect of P concentration on bacterial communities in harsh environmental conditions.

326

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331 **Author contributions**

332 Conceptualization; JMA, LT. Funding acquisition; JMA. Investigation; JO, SA, TV, JMA, TA.
333 Methodology; JO, JMA, TA, LT, AMS. Supervision; JMA, TAA, LT, AMS. Visualization; JO.
334 Roles/Writing - original draft; JO, JMA. Writing - review & editing; JO, MB, TV, SKS, SA, AMS,
335 MA, LT, MZ, TA, JMA.
336

337 **Compliance with Ethical Requirements**

338 This article does not contain any studies on human or animal subjects
339

340 **Declaration of competing interests**

341 The authors declare no competing financial interests.
342

343 **Data availability statement**

344 Raw reads from targeted loci have been deposited in the NCBI SRA (BioProject PRJNA944243)
345

346 **References**

347 1. Maestre, F. T. *et al.* Increasing aridity reduces soil microbial diversity and abundance in
348 global drylands. *Proceedings of the National Academy of Sciences* **112**, 15684–15689
349 (2015).
350 2. Fierer, N. *et al.* Cross-biome metagenomic analyses of soil microbial communities and their
351 functional attributes. *Proceedings of the National Academy of Sciences* **109**, 21390–21395
352 (2012).

353 3. Leung, P. M. *et al.* Energetic Basis of Microbial Growth and Persistence in Desert
354 Ecosystems. *mSystems* **5**, e00495-19 (2020).
355 4. Vasar, M. *et al.* Global soil microbiomes: A new frontline of biome-ecology research. *Global*
356 *Ecology and Biogeography* **31**, 1120–1132 (2022).
357 5. Ronca, S., Ramond, J.-B., Jones, B., Seely, M. & Cowan, D. Namib Desert dune/interdune
358 transects exhibit habitat-specific edaphic bacterial communities. *Frontiers in Microbiology* **6**,
359 (2015).
360 6. Delgado-Baquerizo, M. *et al.* Multiple elements of soil biodiversity drive ecosystem functions
361 across biomes. *Nat Ecol Evol* **4**, 210–220 (2020).
362 7. van der Heijden, M. G. A., Martin, F. M., Selosse, M.-A. & Sanders, I. R. Mycorrhizal
363 ecology and evolution: the past, the present, and the future. *New Phytologist* **205**, 1406–
364 1423 (2015).
365 8. An, S., Couteau, C., Luo, F., Neveu, J. & DuBow, M. S. Bacterial diversity of surface sand
366 samples from the Gobi and Taklamaken deserts. *Microbial ecology* **66**, 850–860 (2013).
367 9. Feng, W. *et al.* Dominant soil bacteria and their ecological attributes across the deserts in
368 northern China. *European Journal of Soil Science* **71**, 524–535 (2020).
369 10. Makhalanyane, T. P. *et al.* Microbial ecology of hot desert edaphic systems. *FEMS*
370 *microbiology reviews* **39**, 203–221 (2015).
371 11. Neilson, J. W. *et al.* Significant impacts of increasing aridity on the arid soil microbiome.
372 *MSystems* **2**, e00195-16 (2017).
373 12. Delgado-Baquerizo, M. *et al.* A global atlas of the dominant bacteria found in soil. *Science*
374 **359**, 320–325 (2018).
375 13. Battistuzzi, F. U. & Hedges, S. B. A major clade of prokaryotes with ancient adaptations to
376 life on land. *Molecular biology and evolution* **26**, 335–343 (2009).
377 14. Schulze-Makuch, D. *et al.* Transitory microbial habitat in the hyperarid Atacama Desert.
378 *Proceedings of the National Academy of Sciences* **115**, 2670–2675 (2018).

379 15. Maza, F. *et al.* Soil bacterial communities from the Chilean Andean highlands: taxonomic
380 composition and culturability. *Frontiers in bioengineering and biotechnology* **7**, 10 (2019).
381 16. Bahram, M. *et al.* Structure and function of the global topsoil microbiome. *Nature* **560**, 233–
382 237 (2018).
383 17. Fierer, N. & Jackson, R. B. The diversity and biogeography of soil bacterial communities.
384 *Proceedings of the National Academy of Sciences* **103**, 626–631 (2006).
385 18. Lauber, C. L., Hamady, M., Knight, R. & Fierer, N. Pyrosequencing-based assessment of
386 soil pH as a predictor of soil bacterial community structure at the continental scale. *Applied*
387 *and environmental microbiology* **75**, 5111–5120 (2009).
388 19. Zhou, J. *et al.* Temperature mediates continental-scale diversity of microbes in forest soils.
389 *Nature communications* **7**, 1–10 (2016).
390 20. Prober, S. M. *et al.* Plant diversity predicts beta but not alpha diversity of soil microbes
391 across grasslands worldwide. *Ecol Lett* **18**, 85–95 (2015).
392 21. Leff, J. W. *et al.* Consistent responses of soil microbial communities to elevated nutrient
393 inputs in grasslands across the globe. *Proceedings of the National Academy of Sciences*
394 **112**, 10967–10972 (2015).
395 22. Karimi, B. *et al.* Biogeography of soil bacteria and archaea across France. *Science*
396 *advances* **4**, eaat1808 (2018).
397 23. Osman, J. R. *et al.* The bacterial communities of surface soils from desert sites in the
398 eastern Utah (USA) portion of the Colorado Plateau. *Microbiological Research* **244**, 126664
399 (2021).
400 24. Al-Thani, R. F. & Yasseen, B. T. Biological Soil Crusts and Extremophiles Adjacent to
401 Native Plants at Sabkhas and Rawdahs, Qatar: The Possible Roles. *FEM* **4**, 55 (2018).
402 25. Adenan, S. *et al.* Diversity of arbuscular mycorrhizal fungi and its chemical drivers across
403 dryland habitats. *Mycorrhiza* **31**, 685–697 (2021).

404 26. Frostegård, Å., Tunlid, A. & Bååth, E. Phospholipid fatty acid composition, biomass, and
405 activity of microbial communities from two soil types experimentally exposed to different
406 heavy metals. *Applied and Environmental Microbiology* **59**, 3605–3617 (1993).
407 27. Frostegård, A. & Bååth, E. The use of phospholipid fatty acid analysis to estimate bacterial
408 and fungal biomass in soil. *Biology and Fertility of soils* **22**, 59–65 (1996).
409 28. van Aarle, I. M. & Olsson, P. A. Fungal lipid accumulation and development of mycelial
410 structures by two arbuscular mycorrhizal fungi. *Applied and Environmental Microbiology* **69**,
411 6762–6767 (2003).
412 29. Caporaso, J. G. *et al.* Global patterns of 16S rRNA diversity at a depth of millions of
413 sequences per sample. *Proceedings of the national academy of sciences* **108**, 4516–4522
414 (2011).
415 30. Parada, A. E., Needham, D. M. & Fuhrman, J. A. Every base matters: assessing small
416 subunit rRNA primers for marine microbiomes with mock communities, time series and
417 global field samples. *Environmental microbiology* **18**, 1403–1414 (2016).
418 31. Ueda, T., Suga, Y., Yahiro, N. & Matsuguchi, T. Remarkable N2-fixing bacterial diversity
419 detected in rice roots by molecular evolutionary analysis of nifH gene sequences. *Journal of*
420 *bacteriology* **177**, 1414–1417 (1995).
421 32. Otsing, E., Anslan, S., Ambrosio, E., Koricheva, J. & Tedersoo, L. Tree Species Richness
422 and Neighborhood Effects on Ectomycorrhizal Fungal Richness and Community Structure in
423 Boreal Forest. *Frontiers in Microbiology* **12**, (2021).
424 33. Sepp, S.-K. *et al.* Global diversity and distribution of nitrogen-fixing bacteria in the soil.
425 *Frontiers in Plant Science* **14**, (2023).
426 34. Davison, J. *et al.* Temperature and pH define the realised niche space of arbuscular
427 mycorrhizal fungi. *New Phytologist* (2021) doi:https://doi.org/10.1111/nph.17240.
428 35. Hildebrand, F., Tadeo, R., Voigt, A. Y., Bork, P. & Raes, J. LotuS: an efficient and user-
429 friendly OTU processing pipeline. *Microbiome* **2**, 1–7 (2014).

430 36. Quast, C. *et al.* The SILVA ribosomal RNA gene database project: improved data
431 processing and web-based tools. *Nucleic acids research* **41**, D590–D596 (2012).
432 37. Edgar, R. C. Search and clustering orders of magnitude faster than BLAST. *Bioinformatics*
433 **26**, 2460–2461 (2010).
434 38. Louca, S., Parfrey, L. W. & Doebeli, M. Decoupling function and taxonomy in the global
435 ocean microbiome. *Science* **353**, 1272–1277 (2016).
436 39. R Core Team. *R: A language and environment for statistical computing*. (R Foundation for
437 Statistical Computing, 2019).
438 40. Chao, A. *et al.* Rarefaction and extrapolation with Hill numbers: a framework for sampling
439 and estimation in species diversity studies. *Ecological monographs* **84**, 45–67 (2014).
440 41. McMurdie, P. J. & Holmes, S. Waste Not, Want Not: Why Rarefying Microbiome Data Is
441 Inadmissible. *PLOS Computational Biology* **10**, e1003531 (2014).
442 42. Fox, J. *et al.* Package ‘car’. *Vienna: R Foundation for Statistical Computing* **16**, (2012).
443 43. Oksanen, J. *et al.* Vegan: community ecology package. (2017).
444 44. Love, M. I., Huber, W. & Anders, S. Moderated estimation of fold change and dispersion for
445 RNA-seq data with DESeq2. *Genome Biology* **15**, 550 (2014).
446 45. Orwin, K. H., Dickie, I. A., Holdaway, R. & Wood, J. R. A comparison of the ability of PLFA
447 and 16S rRNA gene metabarcoding to resolve soil community change and predict
448 ecosystem functions. *Soil Biology and Biochemistry* **117**, 27–35 (2018).
449 46. Kuramae, E., Gamper, H., van Veen, J. & Kowalchuk, G. Soil and plant factors driving the
450 community of soil-borne microorganisms across chronosequences of secondary succession
451 of chalk grasslands with a neutral pH. *FEMS Microbiology Ecology* **77**, 285–294 (2011).
452 47. Kuramae, E. E. *et al.* Soil characteristics more strongly influence soil bacterial communities
453 than land-use type. *FEMS Microbiology Ecology* **79**, 12–24 (2012).

454 48. Liu, L., Gundersen, P., Zhang, T. & Mo, J. Effects of phosphorus addition on soil microbial
455 biomass and community composition in three forest types in tropical China. *Soil Biology and*
456 *Biochemistry* **44**, 31–38 (2012).
457 49. Oliverio, A. M. *et al.* The Role of Phosphorus Limitation in Shaping Soil Bacterial
458 Communities and Their Metabolic Capabilities. *mBio* **11**, e01718-20 (2020).
459 50. Tan, H. *et al.* Long-term phosphorus fertilisation increased the diversity of the total bacterial
460 community and the phoD phosphorus mineraliser group in pasture soils. *Biol Fertil Soils* **49**,
461 661–672 (2013).
462 51. Li, S. *et al.* Fertile islands lead to more conspicuous spatial heterogeneity of bacteria than
463 soil physicochemical properties in a desert ecosystem. *CATENA* **206**, 105526 (2021).
464 52. Zuo, Y. *et al.* Plant cover of Ammopiptanthus mongolicus and soil factors shape soil
465 microbial community and catabolic functional diversity in the arid desert in Northwest China.
466 *Applied Soil Ecology* **147**, 103389 (2020).
467 53. Ayangbenro, A. S. & Babalola, O. O. Reclamation of arid and semi-arid soils: The role of
468 plant growth-promoting archaea and bacteria. *Current Plant Biology* **25**, 100173 (2021).
469 54. Bay, S. K. *et al.* Chemosynthetic and photosynthetic bacteria contribute differentially to
470 primary production across a steep desert aridity gradient. *ISME J* **15**, 3339–3356 (2021).
471 55. Belov, A. A., Cheptsov, V. S. & Vorobyova, E. A. Soil bacterial communities of Sahara and
472 Gibson deserts: Physiological and taxonomical characteristics. *AIMS Microbiol* **4**, 685–710
473 (2018).
474 56. Liu, L. *et al.* Development of bacterial communities in biological soil crusts along a
475 revegetation chronosequence in the Tengger Desert, northwest China. *Biogeosciences* **14**,
476 3801–3814 (2017).
477 57. Liu, Y. *et al.* Differences in bacterial community structure between three types of biological
478 soil crusts and soil below crusts from the Gurbantunggut Desert, China. *European Journal*
479 *of Soil Science* **70**, 630–643 (2019).

480 58. Ren, M. *et al.* Diversity and Contributions to Nitrogen Cycling and Carbon Fixation of Soil
481 Salinity Shaped Microbial Communities in Tarim Basin. *Frontiers in Microbiology* **9**, 431
482 (2018).
483 59. Khan, M. A. & Khan, S. T. Microbial communities and their predictive functional profiles in
484 the arid soil of Saudi Arabia. *SOIL* **6**, 513–521 (2020).
485 60. Majid, S. A. *et al.* Microbial Characterization of Qatari Barchan Sand Dunes. *PLOS ONE* **11**,
486 e0161836 (2016).
487 61. Quoreshi, A. M. *et al.* Untangling the bacterial community composition and structure in
488 selected Kuwait desert soils. *Applied Soil Ecology* **138**, 1–9 (2019).
489 62. Bessadok, K. *et al.* Diversity of rhizobia isolated from Tunisian arid soils capable of forming
490 nitrogen-fixing symbiosis with Anthyllis henoniana. *Journal of Arid Environments* **188**,
491 104467 (2021).
492 63. Rolli, E. *et al.* Improved plant resistance to drought is promoted by the root-associated
493 microbiome as a water stress-dependent trait. *Environmental Microbiology* **17**, 316–331
494 (2015).
495 64. Tian, Y. *et al.* Exploring the structural changes in nitrogen-fixing microorganisms of
496 rhizosheath during the growth of Stipagrostis pennata in the desert. *Bioscience Reports* **41**,
497 BSR20201679 (2021).
498 65. Thompson, L. R. *et al.* A communal catalogue reveals Earth's multiscale microbial diversity.
499 *Nature* **551**, 457 (2017).
500 66. Zhang, K. *et al.* Salinity Is a Key Determinant for Soil Microbial Communities in a Desert
501 Ecosystem. *MSystems* **4**, e00225-18 (2019).
502 67. Egamberdieva, D., Renella, G., Wirth, S. & Islam, R. Secondary salinity effects on soil
503 microbial biomass. *Biol Fertil Soils* **46**, 445–449 (2010).

504 68. Yan, N. & Marschner, P. Response of microbial activity and biomass to increasing salinity
505 depends on the final salinity, not the original salinity. *Soil Biology and Biochemistry* **53**, 50–
506 55 (2012).
507 69. Barin, M., Aliasgharzad, N., Olsson, P. A. & Rasouli-Sadaghiani, M. Salinity-induced
508 differences in soil microbial communities around the hypersaline Lake Urmia. *Soil Research*
509 **53**, 494–504 (2015).
510 70. Kaur, A., Chaudhary, A., Kaur, A., Choudhary, R. & Kaushik, R. Phospholipid fatty acid – A
511 bioindicator of environment monitoring and assessment in soil ecosystem. *Current Science*
512 **89**, 1103–1112 (2005).
513 71. Baumann, K. & Marschner, P. Effects of salinity on microbial tolerance to drying and
514 rewetting. *Biogeochemistry* **112**, 71–80 (2013).
515 72. Harris, R. F. Effect of water potential on microbial growth and activity. *Water potential*
516 *relations in soil microbiology* **9**, 23–95 (1981).
517
518