

1 ***The origin and role of biological rock crusts in rocky desert weathering***

2 ***Running title: Origin and role of BRC in arid rock weathering***

3 ***Authors:***

4 Nimrod Wieler¹, Hanan Ginat², Osnat Gillor^{1*#} and Roey Angel^{3*#}

5 * These authors contributed equally to this study

6 ***Affiliations***

7 ¹Zuckerberg Institute for Water Research, Blaustein Institutes for Desert Research, Ben Gurion
8 University of the Negev Sede Boqer Campus, Israel

9 ²The Dead Sea and Arava Science Center, Israel

10 ³Soil and Water Research Infrastructure and Institute of Soil Biology, Biology Centre CAS, Czechia

11

12 # Corresponding authors:

13 Roey Angel, Soil and Water Research Infrastructure and Institute of Soil Biology, Biology Centre CAS,
14 Czechia. Phone: +420-387-775847; e-mail: roey.angel@bc.cas.cz

15 Osnat Gillor, Zuckerberg Institute for Water Research, Blaustein Institutes for Desert Research, Ben
16 Gurion University of the Negev Sede Boqer Campus, Israel. Phone: +972-8-6596986; e-mail:

17 gilloro@bgu.ac.il

18

19 **Highlights/significance:**

- 20 • Tafoni (honeycomb) weathering patterns were observed at similar frequency and
21 magnitude in hard lime and dolomitic rocks originating from arid and hyperarid
22 environments, respectively, despite different lithologies and climate.
- 23 • In drylands, rock surfaces are colonised by an epilithic microbial community, dominated
24 by bacteria that form a biological rock crusts.
- 25 • The microbial communities on the hard lime and dolomitic rocks were dominated by
26 members of the phyla Proteobacteria and Actinobacteria that are typical to drylands.
- 27 • The two BRC communities were nevertheless distinct from each other, but also from the
28 surrounding soil and dust, showing the habitat filtering effect of the rock surfaces.
- 29 • Microbial and geological tools applied in this study suggest that in drylands biological
30 rock crusts mitigate rock weathering processes by forming an evaporation barrier.

31

32 **Keywords:** Arid; Cavernous weathering; Biological rock crust (BRC); Microbiome; Calcrete;

33 Dolocrete; Stable isotopes; FTIR; High-throughput sequencing

34

35

36 **Abstract**

37 In drylands, microbes that colonise rock surfaces were linked to erosion because water scarcity
38 excludes traditional weathering mechanisms. We studied the origin and role of rock biofilms in
39 geomorphic processes of hard lime and dolomitic rocks that feature comparable weathering
40 morphologies though originating from arid and hyperarid environments, respectively. We
41 hypothesised that weathering patterns are fashioned by salt erosion and mediated by the rock
42 biofilms that originate from the adjacent soil and dust. We used a combination of microbial and
43 geological techniques to characterise rocks morphologies and the origin and diversity of their
44 biofilm. Amplicon sequencing of the SSU rRNA gene suggested that bacterial diversity is low and
45 dominated by Proteobacteria and Actinobacteria. These phyla formed laminar biofilms only on rock
46 surfaces that were exposed to the atmosphere and burrowed up to 6 mm beneath the surface,
47 protected by sedimentary deposits. Unexpectedly, the microbial composition of the biofilms
48 differed between the two rock types and was also distinct from the communities identified in the
49 adjacent soil and settled dust, showing a habitat-specific filtering effect. Moreover, the rock
50 bacterial communities were shown to secrete extracellular polymeric substances that form an
51 evaporation barrier, reducing water loss rates by 65-75%. The reduced water transport rates
52 through the rock also limit salt transport and its crystallisation in surface pores, which is thought to
53 be the main force for weathering. Concomitantly, the biofilm layer stabilises the rock surface via
54 coating and protects the weathered front. Our hypothesis contradicts common models, which
55 typically consider biofilms as weathering-promoting agents. In contrast, we propose the microbial
56 colonisation of mineral surfaces acts to mitigate geomorphic processes in hot, arid environments.

57

58 **Introduction**

59 In arid and hyperarid stony deserts, bedrock surfaces are typically barren and free of vegetation
60 or continuous soil mantle. When these surfaces are exposed to atmospheric conditions, they
61 undergo weathering processes that shape the landscape (Smith, 2009). Weathering is an in-situ set
62 of processes that include physical, chemical and mechanical forces that result in the breakdown and
63 transport of the shattered fragments from the parent rock. Weathering can appear in a range of
64 sizes and morphologies (Smith, Warke, McGreevy, & Kane, 2005), including gravel shattering (Amit,
65 Harrison, Enzel, & Porat, 1996), surface crazing (Smith, 1988), ventifacts (Smith, 1988), microrills
66 (Smith, 1988; Sweeting & Lancaster, 1982) and cavernous patterns [also known as tafoni,
67 honeycomb or pitting (Mustoe, 1983; Viles, 2005)]. Weathering is an essential, though often
68 neglected, element in the overall denudation of hot deserts.

69 Cavernous weathering is one of the most frequently occurring weathering patterns that have
70 been observed in various regions across the globe, including humid and arid, cold and hot, coastal
71 and inland sites (Bruthans, Filippi, Slavík, & Svobodová, 2018). In the Negev Desert, Israel, cavernous
72 weathering patterns are common in carbonate rocks in arid and hyperarid regions. Upon exposure
73 to the atmosphere, these rocks develop a carbonate coating, termed calcrete or dolocrete
74 (respective to limestone or dolomite) by displacive and replacive cementation of calcium or
75 dolomite onto the rock surface (Wright & Wacey, 2004; Alonso-Zarza & Wright, 2010). Following the
76 cementation processes, typical honeycomb features are formed on the exposed parent rock,
77 typified by pits separated by thin walls that are coated by the calcrete or dolocrete. Recent studies
78 suggest that microbial activity also promotes the processes of calcrete and dolocrete formation
79 (Alonso-Zarza & Wright, 2010; Alonso-Zarza, Bustamante, Huerta, Rodríguez-Berriguete, & Huertas,
80 2016).

81 The accepted conceptual model for the formation of cavernous rock weathering in hot deserts
82 involves the presence of permeable rocks that are subjected to soluble salts and repeated episodes
83 of drying-rewetting cycles (Goudie, Wright, & Viles, 2002; Smith, 1988; Smith et al., 2005). The
84 proposed mechanisms assume that cavernous weathering results from physicochemical processes
85 including salt crystallization (Cooke, 1979; Scherer, 2004), incipient fractures (Amit et al., 1996),
86 exfoliation (Shtober-Zisu, Amasha, & Frumkin, 2017), or stress-erosion (Bruthans et al., 2014;
87 McArdle & Anderson, 2001). Recently, Bruthans and colleagues (2018) conclusively demonstrated
88 the superiority of the hydraulic hypothesis (moisture flux followed by salt crystallisation at the
89 boundary layer) over case hardening model, in a temperate climate.

90 In addition, biological mechanisms have been proposed to promote rock weathering through
91 mechanisms such as flaking via colony growth (Viles, 2012), acidification by bacterial extractions
92 (Garcia-Pichel, 2006; Warscheid & Braams, 2000) or alkalization during photosynthesis by
93 cyanobacteria (Büdel et al., 2004). In contrast, it was proposed that micro- and macro-organisms
94 colonisation can mitigate weathering in temperate, coastal regions (McIlroy de la Rosa, Warke, &
95 Smith, 2014; George E. Mustoe, 2010) through encrustation or protection from direct rain impact.
96 Yet, it is not clear which of these mechanisms dominates or what is the relative contribution of
97 chemical vs biological processes to weathering in arid environments.

98 Microorganisms colonising rocks form a hardy biofilm known as the biological rock crusts (BRC),
99 which is common in most arid and hyperarid regions worldwide (Gorbushina, 2007; Lebre, Maayer,
100 & Cowan, 2017; Pointing & Belnap, 2012). Epilithic communities colonising rock surfaces are
101 ubiquitous in arid environments, while hyperarid rocks, which experience increased radiation and
102 desiccation, are dominated by endolithic communities that colonise internal rock pores
103 (Makhalanyane et al., 2013; Pointing & Belnap, 2012; Viles, 1995). The BRC communities include
104 cyanobacteria and other phototrophic bacteria and heterotrophic bacteria, but very low

105 abundances of archaea, fungi or algae (Lang-Yona et al., 2018). However, the BRC inoculum was not
106 resolved and was proposed to originate from settled dust (Viles, 2008), or the surrounding soil
107 (Makhalanyane et al., 2015).

108 The goal of this study was to illuminate the origin and role of BRCs in cavernous weathering of
109 exposed limestone and dolomite rocks in arid and hyperarid regions. We predicted that the BRC
110 communities on exposed rock surfaces will resemble either the ever-present dust or the
111 surrounding soil, supporting a subset of adapted taxa from both sources. We further hypothesised
112 that the cavernous weathering morphologies of exposed rocks result from salt mobilisation by dew,
113 causing crystallisation pressure under atmospheric conditions. The developed rock biofilms clog the
114 surface rock pores through secretion of extracellular polymeric substances (EPS), lowering
115 evaporation and slowing the salt crystallisation, but also stabilising the exfoliated rocks preventing
116 further weathering. Thus, the presence of a BRC mitigates the geomorphic processes. To test our
117 hypotheses, we applied a holistic approach combining field observations, geological, geotechnical
118 and molecular microbiology characterisation elucidating BRCs' morphology, origin and role in arid
119 cavernous weathering.

120

121 ***Results and discussion***

122 ***Field and mineralogical observations***

123 Weathering features were observed in about 30% of exposed rocks sampled from both arid and
124 hyperarid sites. Neither the prevalence of weathering nor its morphology seemed to differ between
125 sites despite the different climates and underlying geology. In all cases, weathering type was
126 classified as tafoni or honeycomb weathering (Goudie, Viles, & Parker, 1997; Groom, Allen, Mol,
127 Paradise, & Hall, 2015; Fig. 1A), and it was coupled with the presence of sub-aerial biofilm,
128 burrowed underneath the surface and protected by sedimentary deposits (Fig. 1B). The weathering
129 and presence of the crusts were restricted to the atmospherically exposed parts of the rock. The
130 presence of identical weathering morphology and prevalence in different climates and lithologies
131 challenges the current model, which assumes that surface permeability, moisture and the presence
132 of salts as primary factors control weathering rates (Andrew S. Goudie et al., 2002; Smith, 1988;
133 Smith et al., 2005). However, the lack of correlation between tafoni weathering magnitude and
134 climate has already been reported (Brandmeier, Kuhlemann, Krumrei, Kappler, & Kubik, 2011).

135 To study the possible differences between these sites, we performed geological characterisation
136 of 10 limestone and dolomite rocks collected from the arid and hyperarid sites, respectively, testing
137 for mineral content, porosity, permeability and elasticity. As expected, our results showed different
138 lithological parameters between the limestone and dolomite rocks (Table 1), yet they displayed
139 similar weathering features. Moreover, petrographic thin section analysis showed that on both rock
140 types, crusts had developed to a similar thickness of 1-6 mm, irrespective of climatic conditions
141 including mean annual precipitation (Fig. 1C). However, microclimatic conditions, like dew or
142 surface temperature may impact local morphologies. Also, the thin sections showed that the crusts
143 are composed of masses of micritic to microsparitic minerals that form laminated structure (Fig.

144 1C). Such laminated structures indicate that the crusts are stage four terrestrial calcretes and
145 dolocretes, suggesting a mature crust phase (Alonso-Zarza & Wright, 2010). The calcretes and
146 dolocretes identified on the rocks' surface reject previously suggested impact of mineralised
147 networks or case hardening (McBride & Picard, 2004). In fact, the detection of mature calcretes
148 could serve as an indication of atmospheric exposure but was also suggested to result from biogenic
149 activity (Alonso-Zarza & Wright, 2010; Goudie, 1996).

150 ***Composition and chemical characteristics of the rock crusts***

151 To test our hypothesis that the crusts are biogenic and involved in rock weathering processes,
152 we characterised their origin and nature. An XRD analysis of the crust layers and bedrocks showed
153 that the crusts are composed of similar mineralogy as their respective host rocks, indicating that
154 local weathering, rather than dust deposition, is the source of crust generation (Table 1).

155 The biogenic nature of the crusts was confirmed using a cross-section analysis of the stable
156 carbon and oxygen isotopes ratios in the crust and host rock (Fig. 2A). For both limestone and
157 dolomite, values of $\delta^{13}\text{C}$ increased between the crust and the host rock layers and ranged from -
158 4.1‰ in the calcrete to -0.9‰ in the limestone bed, and from 0.2‰ in the dolocrete to 2.0‰ in the
159 dolomite bed. Such values are typical indicators to carbon isotope exchange of primary marine
160 CaCO_3 (abundant in the bedrock) with CO_2 released by microbial respiration (i.e. of carbon
161 originating from photosynthesis) with subsequent precipitation of pedogenic calcrete (Brlek &
162 Glumac, 2014; Mora, Driese, & Seager, 1991). Analysing $\delta^{13}\text{C}$, together with $\delta^{18}\text{O}$, compositions of
163 pedogenic carbonates is a useful way of reconstructing paleo-vegetation (e.g., C3/C4 plant ratio;
164 Ehleringer, Cerling, & Helliker, 1997; Mora et al., 1991). Our $\delta^{13}\text{C}$ results go along with $\delta^{13}\text{C}$ values
165 collected from speleothems (secondary mineral deposits formed in caves) collected in the central
166 and southern Negev Desert (Vaks, Bar-Matthews, Matthews, Ayalon, & Frumkin, 2010) that were

167 also dated to end of the Pliocene (the past 2.5 million years). The low ratio detected here (Fig 2A)
168 and by Vaks et al. (2010) suggest that the Negev region has been able to support only limited
169 vegetation for at least 2.5 Ga, if so then the role of the crust in shaping the morphology of the rock
170 surfaces was considerable. These results support the hypothesis that calcretes and dolocretes are
171 of biogenic origin, and therefore the crust can be referred to as BRC. Moreover, they indicate similar
172 developmental trajectory for both the calcretes and dolocretes that is independent of aridity or
173 lithological parameters.

174 In contrast, the trend in values of $\delta^{18}\text{O}$ differed between rock types. In the limestone rocks, the
175 ratio ranged from -3.0‰ to -6.8‰ between the BRC and the host rock, while in the dolomite it was
176 higher, ranging from -5.4‰ to -0.6‰. The decrease in $\delta^{18}\text{O}$ in the host limestone rock could be
177 explained by meteoric water substitution (Sandler, 2006). In contrast, the more negative $\delta^{18}\text{O}$
178 values in the dolomite compared to the host dolomite are attributed to isotopic differentiation of
179 meteoric water due to condensation (Rayleigh distillation) and could result from the large distance
180 from the Mediterranean Sea (that is the primary source of rainfall in the area) compared to closer
181 limestone rocks. In speleothems, similar patterns in $\delta^{18}\text{O}$ values were reported in the central and
182 southern Negev Desert (Vaks et al., 2010). The results suggest that the calcrete and dolomite
183 studied here have been experiencing arid to hyperarid climates since the Pleistocene, alluding to
184 the possible source of rain. A similar study conducted in the Thar Desert in India also inferred
185 sedimentary rocks stable isotope patterns to paleoclimate (Andrews et al., 1998).

186 To study the potential role of the BRC in the weathering process, its composition was
187 characterised using FTIR as was previously reported (Sheng, Yu, & Li, 2010). We focused on the
188 functional groups and element compositions in EPS or microbial aggregates and found a distinct
189 peak in the BRC layers ranging between 1020-1040 cm^{-1} in both limestone and dolomite rocks that
190 was absent from the host rocks (Fig. 2B). This peak is indicative of the presence of EPS from

191 bacterial origin (Shirshova, Ghabbour, & Davies, 2006), pointing to the significant components of
192 asymmetric and symmetric stretching of PO_2^- and $\text{P}(\text{OH})_2$ in phosphate as well as vibrations of C-OH
193 and C-C bonds found in polysaccharides and alcohols (Jiang et al., 2004). These results provide a
194 strong support for the biogenic nature of the crust, since EPS is a common feature of many if not
195 most biofilms (Drews, Lee, & Kraume, 2006). The detected EPS could serve several functions in BRC
196 such as dust-particle trap to collect the dust and its nutrients, a binding agent to individual
197 members of the biofilm (Davey & O'toole, 2000), or a protective agent by decreasing evaporation
198 and retaining moisture and shielding from radiation (Or, Smets, Wraith, Dechesne, & Friedman,
199 2007; Roberson & Firestone, 1992).

200 Based on these findings, we hypothesised that BRC could in fact act as a mitigator during the
201 weathering process by clogging the pores on the surface of the rock and thereby minimising
202 capillary rise. Consequently, crystallisation of dissolved salts, considered to be the primary
203 mechanism for rock weathering, is mitigated. To test this hypothesis, we performed a desiccation
204 experiment to estimate water loss from the rock surfaces covered with BRC. The results suggest
205 that both in limestone and dolomite rocks water moves through the rock and is lost to evaporation
206 two or three times faster in the absence of BRC than when it is present (Fig. 3). Considering that salt
207 transport due to hydraulic movement is a dominant weathering mechanism (Huinink, Pel, &
208 Kopinga, 2004), reduced evaporation due to BRC coverage will also inevitably lead to decrease
209 weathering rate. Moreover, the obtained results stand in contrast to similar measurements
210 performed on temperate sandy stones that showed no significant effect of BRC on water transport
211 rates (Slavík et al., 2017).

212 ***The microbial composition and origin of the BRCs***

213 To elucidate the identity of the bacterial communities on the limestone and dolomite BRCs, we
214 applied a multiplexed barcoded amplicon sequencing of the small subunit RNA gene (SSU rRNA). In
215 addition, we compared the BRC communities to those of samples of the surrounding soil and settled
216 dust in order to deduce the origin for the rock biofilm. As expected, we found poor and low-
217 diversity of the BRC communities. The communities of the BRC showed an average of 182 and 129
218 observed, 354 and 315 predicted phylotypes, and Shannon's H was 3.8 and 3.3 (Fig. 4A; Table S2),
219 for arid limestone and hyperarid dolomite, respectively, with no significant difference between the
220 rock types.

221 The surrounding soil was significantly richer and more diverse ($P < 0.05$) in the arid site (416 and 746
222 observed and predicted OTUs and Shannon's H = 5.6 on average), and equally rich but slightly more
223 diverse in the hyperarid site (221 and 466 observed and predicted OTUs and Shannon's H = 3.8, on
224 average. The diversity of the dust samples were as poor as the BRC's (169 and 107 observed
225 and predicted OTUs and Shannon's H = 3.0 and 1.5, on average) and did not differ between sites
226 (Fig. 4A; Table S2). The number of observed OTUs in the soil and their diversity scores were
227 somewhat lower in this study compared to reports from similar environments (Barberán, Henley,
228 Fierer, & Casamayor, 2014; Šťovíček, Kim, Or, & Gillor, 2017) however these could be due to
229 sequencing technologies and depth. The lower richness and diversity in hyperarid vs arid samples
230 and the BRC and dust vs. soil samples is expected and comparable with trends reported in other
231 works (Angel & Conrad, 2013; Barberán et al., 2014; Lang-Yona et al., 2018).

232 Beta-diversity analysis showed statistically significant differences between samples on the OTU-
233 level by climate, sample type, and to a small extent also their interaction, using variance
234 partitioning. These parameters were found to significantly contribute to the differences in bacterial
235 communities accounting for 22%, 40% and 3.8% of the variance (Fig. 4B, Table S3). Pairwise
236 comparisons further showed that the two BRCs significantly differed from one another ($P < 0.01$)

237 and also from their surrounding soil and dust samples ($P < 0.05$ in all cases; Table S3). The bacterial
238 community in the samples was typical for drylands, mostly dominated by members of the phyla
239 Proteobacteria, and Actinobacteria followed by Deinococcus–Thermus, Chloroflexi, Bacteroidetes,
240 Cyanobacteria, Acidobacteria, Firmicutes, and Gemmatimonadetes (Fig 4C, Table S4). Similar
241 communities have repeatedly been reported for arid and hyperarid soils and rocks (Angel & Conrad,
242 2013; Barberán et al., 2014; Lang-Yona et al., 2018). While cyanobacteria are typically the main
243 primary producers in the soil and rock communities (Weber, Büdel, & Belnap, 2016), recent studies
244 showed that other autotrophs may also contribute significantly to the energy balance of these
245 biofilms (Ji et al., 2017).

246 The BRCs of the two rock types differed in the relative abundance and composition of major
247 phyla. Most notably, Proteobacteria were significantly more dominant in the hyperarid compared to
248 the arid samples ($P = 0.02$) comprising on average 21% and 44% of the community in the limestone
249 and dolomite BRC, respectively. In contrast, the Actinobacteria showed an opposite trend ($P = 0.03$)
250 comprising on average 42% and 21% of the community in the limestone and dolomite BRC,
251 respectively. The two BRCs also differed in their composition of Firmicutes, Gemmatimonadetes and
252 Chloroflexi ($P < 0.03$; Fig 4C, Table S4).

253 The soil samples generally showed similar trends on the gross taxonomic level as their
254 respective BRC samples. While none of the phyla differed significantly between the hyperarid BRC
255 and the soil, the phyla Deinococcus–Thermus, Acidobacteria, Firmicutes, and Gemmatimonadetes
256 significantly differed between limestone BRC and the surrounding arid soil ($P < 0.04$; Table S4).
257 Lastly, the arid and hyperarid dust samples were dominated by members of the Proteobacteria,
258 with other phyla comprising only a minor fraction of the community (with a notable exception of
259 Bacteroidetes that dominated one of the dust samples). However, these differences were not
260 significant, probably due to the small sample size (Table S4).

261 Despite the general similarities in community composition between samples on the phylum
262 level, many of the OTUs found in each sample were unique to the BRC, soil or dust as evident by the
263 ternary diagrams (Fig. 4D). Direct analysis of the differences in the OTUs detected 130 (10%)
264 differentially abundant OTUs in the dolomite BRC and 74 (6%) differentially abundant OTUs in the
265 limestone BRC (Fig. S2). Similarly, several differentially abundant OTUs were also detected when
266 comparing the BRCs to their respective soil and dust samples. However, these differentially
267 abundant OTUs were fewer, probably due to the small dust sample size (Fig. S2).

268 The BRC bacterial communities were previously described (Kuhlman et al., 2006; Lang-Yona et
269 al., 2018; Wong, Lacap, et al., 2010; Wong, Lau, et al., 2010) but their origin and role in
270 geomorphological processes were not considered. Our results suggest that despite the similarity in
271 morphology and magnitude of rock weathering features in the arid limestone and hyperarid
272 dolomites, the two BRCs harboured distinct microbial communities, differing in over 16% of the
273 OTUs and their composition at the phylum level. Moreover, despite the spatial proximity and
274 continuous interaction between the limestone and dolomite surface to their respective surrounding
275 soils and dust particles, the bacterial communities of the BRCs were distinct. The abilities of bacteria
276 to disperse, settle and persist in a given location could be an important factor resulting in the
277 biogeographic patterns observed here. The difference between arid and hyperarid soil communities
278 could result from the local contribution of aeolian material that might affect the loess soil diversity
279 (Crouvi, Amit, Enzel, Porat, & Sandler, 2008). Alternatively, the hyperarid site experience slow
280 pedological processes while arid soil formation was enhanced (Amit et al., 2011) resulting in
281 disparate bacterial communities. The three matrices (BRC, soil and settled dust) studied here
282 sparsely shared their bacterial communities and specifically, the BRC community had little in
283 common with the soil or dust communities (Fig 4). This demonstrates the ecological filtering effect
284 of the rock surfaces, which imposes unique abiotic challenges on the microbes living on it (Horner-

285 Devine & Bohannan, 2006). This also suggests that the BRCs cannot be regarded as passive deposits of
286 microbial cells originating from the surrounding soil or dust, but rather it is a specific subset of
287 adapted microbes that can persist and form a biofilm under these unique conditions.

288 ***The role of BRC in arid rock weathering - synthesis***

289 Honeycomb weathering patterns are prevalent worldwide and are found in both humid and dry
290 ecosystems. According to contemporary models, this form of weathering is the result of the
291 transport of dissolved salts through the rock and their eventual crystallisation in surface pores,
292 leading to fractures and eventual flaking of rock material (Rodriguez-Navarro, Doehne, & Sebastian,
293 1999). In this study, we found that weathering patterns and magnitude are similar on rocks from
294 both arid and hyperarid sites, despite the differences in precipitation and lithologies. In arid and
295 hyperarid regions, BRCs were shown to form once the rock is exposed to the atmosphere (Pointing
296 & Belnap, 2012). A developed crust of biological origin was microscopically and isotopically
297 apparent on all weathered rocks and was shown to be supported by EPS (Fig. 2). Similar to
298 weathering magnitude, the BRCs showed no observable differences in form or depth despite the
299 different aridity and lithology. Both BRCs comprised bacterial taxa that are typical for xeric
300 environments (Pointing & Belnap, 2012) and included many heterotrophs but also dominant
301 phototrophs or otherwise autotrophic members (Fig. 4). The two BRCs did differ in their bacterial
302 communities at the OTU and higher taxonomical levels, demonstrating a discrepancy between
303 composition and function. The BRC communities also differed from their surrounding soil and dust,
304 indicative of the specialism of the colonising taxa to rock environment. In the absence of
305 mineralized networks or case hardening (i.e., addition of cementing agent to rock matrix material)
306 we conclude that calcrete and dolocrete were formed through the colonisation of microorganisms
307 and the secretion of EPS, serving as a thin biofilm (Brantley et al., 2011; Weber et al., 2016).

308 Our results further suggest that this biogenic layer mitigates evaporation and reduces water
309 transport, hence alleviating salt crystallisation pressure in the rock pores (Scherer, 2004).
310 Crystallization of calcium sulphate and sodium chloride solutions, which are abundant in these soils,
311 was shown to build pressure within pores and stress rocks (Scherer, 2004; Sperling & Cooke, 1985).
312 This process is enhanced under low relative humidity and rapid evaporation and compromises the
313 durability of the rocks (Rodriguez-Navarro & Doehne, 1999; Rodriguez-Navarro, Rodriguez-Gallego,
314 Chekroun, & Gonzalez-Muñoz, 2003). Our results suggest that the presence of BRC decreases
315 evaporation rates (Fig 3) and thus attenuate the crystallisation pressure and reduces damage to the
316 rocks. Moreover, the BRC may also stabilise the rock following exfoliation preserving the weathered
317 structure.

318 Arid weathering features, which lead to debris formation result from a dynamic balance
319 between the erosive salt forces and the mitigating effects of the BRC. The role of microbial biofilms
320 in the protection of surfaces from mineral weathering was extensively studied for biomineralisation
321 and sedimentation processes (Adams, Palmer, & Staley, 1992; Dupraz et al., 2009). Yet, the role of
322 BRC in weathering processes under atmospheric conditions in the desert has not been considered
323 before. We propose that microbial colonisation of mineral surfaces protects the rocks from
324 weathering by mitigating salt crystallisation and stabilising the weathered front. Rock weathering
325 processes are typically believed to be controlled at different scales ranging from the climatic scale,
326 down to local conditions at the site and eventually the microscale (Smith, 2009; Sperling & Cooke,
327 1985; Viles, 2001). The results presented here suggest that in arid environments, microscale
328 conditions determine the magnitude of weathering that shape the landscape.

329

330 **Materials and Methods**

331 **Study site**

332 We focused on two sites in the Negev Desert, Israel: Sede-Boqer – an arid site and Uvda Valley –
333 a hyperarid site (Fig. S1, Table 1). Both sites are rocky terrains underlined predominantly by
334 carbonate rock slopes consisting of limestone, dolomite, chalk, marl, clay and chert from the
335 Cretaceous to Eocene age. Our analyses compared samples from the limey Turonian age Shivta
336 Formation located in the arid region with samples from the dolomitic Turonian age Gerofit
337 Formation located in the hyperarid environment. The Negev Desert, Israel, maintains arid to
338 hyperarid conditions since the Holocene and has an aridity index (P/PET) of 0.05-0.005 (Amit et al.,
339 2010; Bruins, 2012) similar to other arid and hyperarid areas worldwide, e.g., the Namib and
340 Atacama Deserts (Azua-Bustos, Urrejola, & Vicuña, 2012; Viles & Goudie, 2007). The long-term
341 aridity of the Negev Desert makes it a reliable site for testing the cross-influence between BRCs and
342 geological substrates.

343 **Field sampling**

344 Twenty-four rock samples were collected along rocky slopes facing northward, comprising:
345 twelve limestone samples from the limey Turonian age Shivta Formation at the arid site
346 (30.88N34.78E, WGS 84 Grid; samples named: SB 1-12) and twelve dolomite samples from limey-
347 dolomitic Turonian age Gerofit Formation at the hyperarid site (29.94N34.97E, WGS 84 Grid;
348 samples named: UV 1-12) during November and December, 2014. Concomitantly, six soil samples
349 (ca. 500 g each) were collected, half from the arid (named: SBSoil 1-3) and a half from the hyperarid
350 (named: UVSoil 1-12) sites. Each rock or soil sample is a composite of four sub-samples that were
351 pooled and homogenised in the lab.

352 We also collected settled dust samples using glass beads traps (Goossens & Rajot, 2008). The
353 traps were placed on December 2013 and collected three months later in the arid (samples named:
354 SBDust 1-2) and hyperarid (samples named: UVDust 1-2) sites. Each dust sample was a composite of
355 two sub-samples that were pooled and homogenised in the lab.

356 ***Geological analyses***

357 The geological methods used in this study are based on direct field observations and detailed
358 characterisation of the subjected lithologies (i.e., Limestone and Dolomite) which included
359 morphology (thin sections), mineral components [X-ray powder diffraction (XRD)], porosity and
360 permeability (Automatic Gas Permeameter Porosimeter), and elastic properties (Schmidt hammer):
361 Petrographic thin sections, 30 μm thick, were prepared for each lithology to test the main
362 components in both the BRC and host rocks examined under a light microscope (Zeiss, Oberkochen,
363 Germany). XRD analysis of mineral components (Sandler et al., 2015) was conducted on the BRC and
364 host rocks using three replicates each. Powdered samples were scanned using X'Pert³ Powder
365 diffractometer equipped with a PIXcel detector (Panalytical Malvern, Almelo, Netherlands).
366 Scanning range was: 3 – 70° 2 θ , step size 0.013°, speed 70.1 s per step. Total effective porosity (ϕ)
367 and permeability (k) tests (Scherer, 1999) were performed using Automatic Gas Permeameter
368 Porosimeter (Core Laboratories, Houston, Texas, USA) on twelve rock core cylinder samples, with
369 18.5 mm radius and 26.5 mm height. Six samples were taken from each lithology, each set of six
370 samples were prepared in two orthogonal directions providing the normal to bedding and parallel
371 to bedding. Before testing porosity and permeability, samples were oven dried at a temperature of
372 110°C for 24 h. Schmidt hammer (Lassen, Aarhus, Denmark) tests were applied in the field (Goudie,
373 2016; Viles, Goudie, Grab, & Lalley, 2011). Twenty measurements were carried out for each
374 lithology.

375 ***FTIR and stable isotope analysis***

376 Fourier transform infrared spectroscopy (FTIR) analysis was conducted for testing the presence
377 of extracellular polymeric substances (EPS) on the rock surfaces while the host rock was used for
378 comparison. The spectra were recorded using a Vertex 70 FTIR spectrometer (Bruker, Billerica, MA,
379 USA) with a 4 cm^{-1} scan resolution. One to two mg of pulverised rock was taken from each sample
380 ($n = 2$), and the spectra were measured twice collected over a wavenumber range $4000\text{-}600\text{ cm}^{-1}$,
381 and a baseline correction was carried out. The spectral absorption bands, indicative for EPS, were
382 identified according to published information (Ferrando et al., 2018).

383 For $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analysis, 1-2 mg of rock surface powder (i.e., calcite or dolomite) was
384 obtained using a Microdrill (Dremel, Racine, WI, USA) along with a cross-section of the rock crust
385 and its host rock. Four profiles measurements of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were performed on samples UVSL
386 5-6 from the hyperarid site and NWSH 1-2 from the arid site. Measurements (in duplicate) of $\delta^{18}\text{O}\text{-H}_2\text{O}$
387 and $\delta^{13}\text{C}\text{-DIC}$ were performed on gas source isotope ratio mass spectrometer (GS-IRMS; Thermo Fisher
388 Scientific, Waltham, MA, USA) coupled to a Gas Bench II interface (Thermo) after CO_2 equilibration or CO_2
389 extraction by acidification for $\delta^{18}\text{O}\text{-H}_2\text{O}$ and $\delta^{13}\text{C}\text{-DIC}$, respectively. The samples were calibrated against
390 internal laboratory standards: Vienna Standard Mean Ocean Water (VSMOW) and carbonate
391 standard NBS19. $\delta^{13}\text{C}$ values were also referenced against VSMOW and valued for carbonate
392 relative to Vienna PeeDee Belemnite (VPDB) standard as previously described (Uemura et al., 2016)
393 with SD of 0.1‰. All values are reported in per-mil (‰).

394 ***Desiccation experiment***

395 To test the effect of biological rock crusts on water transport rates in the rock, clogging and
396 desiccation experiments were performed on sixteen rock core cylinders from both lithologies
397 (limestone and dolomite). Rock cylinders ($\varnothing 37\text{ mm}$, 6.5 cm) were drilled using a rock core drill. Each

398 set of eight rock cores from the two different lithologies included four rock cores that were kept
399 intact, and four rock cores that their BRC was mechanically removed using a diamond saw (Dremel,
400 Racine, WI, USA) to a depth of 5 cm. Each cylinder was immersed in distilled water for 72 h, covered
401 with epoxy (Devcon) and aluminium foil, leaving only the upper base of the crusted and bare
402 cylinders uncovered to allow evaporation. The cylinders were then weighed ($t=0$), incubated in an
403 oven dried at a temperature of 44 °C for 48 h and weighed every 2 h during the first 12 h and then
404 every 6 h to determine the residual water content. Second-degree polynomial functions were fitted
405 using function `stats::lm` to determine evaporation rates and compared using ANOVA in R.

406 ***DNA Extraction PCR amplification and sequencing***

407 For DNA extraction from all rocks, the surface (ca. 100 cm²) was scraped using a rasp (66-67 HRC
408 hardness; Dieter Schmid, Berlin, Germany) that was cleaned with 70% technical-grade ethanol
409 before each sampling. DNA was then extracted from 0.5 g of the homogenised sample using bead-
410 beating in the presence of a CTAB buffer and phenol, according to a previously published extraction
411 protocol (Angel, Claus, & Conrad, 2012). A 466-bp fragment of the *16S rRNA* gene was amplified
412 using the universal bacterial primers 341F (CCTAYGGGRBGCASCAG) and 806R
413 (GGACTACNNGGTATCTAAT) flanking the V3 and V4 region (Klindworth et al., 2012). Library
414 construction and sequencing were performed at a DNA Services Facility (University of Illinois at
415 Chicago, USA) using a MiSeq sequencer (Illumina, San Diego, CA, USA) in the 2 × 250 cycle
416 configuration (V2 reagent kit). The raw sequencing data were deposited into the EMBL-ENA SRA
417 database (<https://www.ebi.ac.uk/ena/>) and can be found under study accession [PRJNA381483](https://www.ebi.ac.uk/ena/record/PRJNA381483).

418 ***Sequence processing and analysis of bacterial communities***

419 Paired reads generated by the MiSeq platform were quality filtered and clustered into OTUs
420 using the UPARSE pipeline (Edgar, 2013), with modifications. Contig assembly was done using the

421 fastq_mergepairs command. Then, contigs were dereplicated with the derep_fulllength command,
422 and singleton sequences were removed. OTU centroids were then determined with the cluster_otus
423 command (set at 3% radius). Abundances of OTUs were determined by mapping the filtered contigs
424 (before dereplication, including singletons) to the OTU centroids using the usearch_global
425 command (set at 0.97% identity). Following these steps, a total of ca. 1.4 G reads remained. OTU
426 representatives were classified using mothur's implementation of a Naïve Bayesian sequence
427 classifier (Schloss et al., 2009; Wang, Garrity, Tiedje, & Cole, 2007) against the SILVA 119 SSU NR99
428 database (Quast *et al.*, 2013). All downstream analyses were performed in R V3.4.4 (R Core Team,
429 2016). Data handling and manipulation were done using package phyloseq (McMurdie & Holmes,
430 2013). For alpha-diversity analysis, all samples were subsampled (rarefied) to the minimum sample
431 size using bootstrap subsampling at 1000 iterations, to account for library size differences, while for
432 beta-diversity analysis library size normalisation was done using GMPR (Chen et al., 2018). The ACE
433 richness estimate (O'Hara, 2005) and Shannon's H diversity index were calculated using function
434 EstimateR in the vegan package (Oksanen et al., 2018) and tested using ANOVA and Tukey HSD in
435 the stats package. Variance partitioning and testing were done using PERMANOVA (McArdle &
436 Anderson, 2001) function vegan::adonis using Horn-Morisita distances. Differences in phyla
437 composition between the sample types were tested using the non-parametric Scheirer Ray Hare
438 Test (Mangiafico, 2018; function rcompanion::scheirerRayHare) followed by the *post hoc* Mann-
439 Whitney Test (function stats::wilcox.test) and FDR corrected using the Benjamini-Hochberg method
440 (Ferreira & Zwinderman, 2006; function stats::p.adjust). Detection of differentially abundant OTUs
441 was done using ALDEx2 (Fernandes et al., 2014). Plots were generated using packages ggplot2
442 (Wickham, 2016) and ggtern (Hamilton, 2017).

443

444 **References**

- 445 Adams, J. B., Palmer, F., & Staley, J. T. (1992). Rock weathering in deserts: Mobilization and concentration of
446 ferric iron by microorganisms. *Geomicrobiology Journal*, 10(2), 99–114.
447 <https://doi.org/10.1080/01490459209377910>
- 448 Alonso-Zarza, A. M., & Wright, V. P. (2010). Chapter 5 Calcretes. In *Developments in Sedimentology* (Vol. 61,
449 pp. 225–267). Elsevier. [https://doi.org/10.1016/S0070-4571\(09\)06105-6](https://doi.org/10.1016/S0070-4571(09)06105-6)
- 450 Alonso-Zarza, A. M., Bustamante, L., Huerta, P., Rodríguez-Berriguete, Á., & Huertas, M. J. (2016). Chabazite
451 and dolomite formation in a dolocrete profile: An example of a complex alkaline paragenesis in
452 Lanzarote, Canary Islands. *Sedimentary Geology*, 337, 1–11.
453 <https://doi.org/10.1016/j.sedgeo.2016.02.018>
- 454 Amit, R., Enzel, Y., Crouvi, O., Simhai, O., Matmon, A., Porat, N., ... Gillespie, A. R. (2011). The role of the Nile
455 in initiating a massive dust influx to the Negev late in the middle Pleistocene. *Geological Society of
456 America Bulletin*, 123(5–6), 873–889. <https://doi.org/10.1130/B30241.1>
- 457 Amit, R., Harrison, J. B. J., Enzel, Y., & Porat, N. (1996). Soils as a tool for estimating ages of Quaternary fault
458 scarps in a hyperarid environment — the southern Arava valley, the Dead Sea Rift, Israel. *CATENA*,
459 28(1–2), 21–45. [https://doi.org/10.1016/S0341-8162\(96\)00028-8](https://doi.org/10.1016/S0341-8162(96)00028-8)
- 460 Amit, R., Enzel, Y., Grodek, T., Crouvi, O., Porat, N., & Ayalon, A. (2010). The role of rare rainstorms in the
461 formation of calcic soil horizons on alluvial surfaces in extreme deserts. *Quaternary Research*, 74(02),
462 177–187. <https://doi.org/10.1016/j.yqres.2010.06.001>
- 463 Andrews, J. E., Singhvi, A. K., Kailath, A. J., Kuhn, R., Dennis, P. F., Tandon, S. K., & Dhir, R. P. (1998). Do stable
464 isotope data from calcrete record Late Pleistocene monsoonal climate variation in the Thar Desert of
465 India? *Quaternary Research*, 50(03), 240–251. <https://doi.org/10.1006/qres.1998.2002>
- 466 Angel, R., Claus, P., & Conrad, R. (2012). Methanogenic archaea are globally ubiquitous in aerated soils and
467 become active under wet anoxic conditions. *The ISME Journal*, 6(4), 847–862.
468 <https://doi.org/10.1038/ismej.2011.141>
- 469 Angel, R., & Conrad, R. (2013). Elucidating the microbial resuscitation cascade in biological soil crusts
470 following a simulated rain event. *Environmental Microbiology*, 15(10), 2799–2815.
471 <https://doi.org/10.1111/1462-2920.12140>
- 472 Azua-Bustos, A., Urrejola, C., & Vicuña, R. (2012). Life at the dry edge: Microorganisms of the Atacama
473 Desert. *FEBS Letters*, 586(18), 2939–2945. <https://doi.org/10.1016/j.febslet.2012.07.025>
- 474 Barberán, A., Henley, J., Fierer, N., & Casamayor, E. O. (2014). Structure, inter-annual recurrence, and global-
475 scale connectivity of airborne microbial communities. *Science of The Total Environment*, 487, 187–
476 195. <https://doi.org/10.1016/j.scitotenv.2014.04.030>

- 477 Brandmeier, M., Kuhlemann, J., Krumrei, I., Kappler, A., & Kubik, P. W. (2011). New challenges for tafoni
478 research. A new approach to understand processes and weathering rates. *Earth Surface Processes
479 and Landforms*, 36(6), 839–852. <https://doi.org/10.1002/esp.2112>
- 480 Brantley, S. L., Megonigal, J. P., Scatena, F. N., Balogh-Brunstad, Z., Barnes, R. T., Bruns, M. A., ... Yoo, K.
481 (2011). Twelve testable hypotheses on the geobiology of weathering. *Geobiology*, 9(2), 140–165.
482 <https://doi.org/10.1111/j.1472-4669.2010.00264.x>
- 483 Brlek, M., & Glumac, B. (2014). Stable isotopic ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) signatures of biogenic calcretes marking
484 discontinuity surfaces: a case study from Upper Cretaceous carbonates of central Dalmatia and
485 eastern Istria, Croatia. *Facies*, 60(3), 773–788. <https://doi.org/10.1007/s10347-014-0403-7>
- 486 Bruins, H. J. (2012). Ancient desert agriculture in the Negev and climate-zone boundary changes during
487 average, wet and drought years. *Journal of Arid Environments*, 86, 28–42.
488 <https://doi.org/10.1016/j.jaridenv.2012.01.015>
- 489 Bruthans, J., Filippi, M., Slavík, M., & Svobodová, E. (2018). Origin of honeycombs: Testing the hydraulic and
490 case hardening hypotheses. *Geomorphology*, 303, 68–83.
491 <https://doi.org/10.1016/j.geomorph.2017.11.013>
- 492 Bruthans, J., Soukup, J., Vaculikova, J., Filippi, M., Schweigstillova, J., Mayo, A. L., ... Rihosek, J. (2014).
493 Sandstone landforms shaped by negative feedback between stress and erosion. *Nature Geoscience*,
494 7(8), 597–601. <https://doi.org/10.1038/ngeo2209>
- 495 Büdel, B., Weber, B., Köhl, M., Pfanz, H., Sültemeyer, D., & Wessels, D. (2004). Reshaping of sandstone
496 surfaces by cryptoendolithic cyanobacteria: bioalkalization causes chemical weathering in arid
497 landscapes. *Geobiology*, 2(4), 261–268. <https://doi.org/10.1111/j.1472-4677.2004.00040.x>
- 498 Chen, L., Reeve, J., Zhang, L., Huang, S., Wang, X., & Chen, J. (2018). GMPR: A robust normalization method
499 for zero-inflated count data with application to microbiome sequencing data. *PeerJ*, 6, e4600.
500 <https://doi.org/10.7717/peerj.4600>
- 501 Cooke, R. U. (1979). Laboratory simulation of salt weathering processes in arid environments. *Earth Surface
502 Processes*, 4(4), 347–359. <https://doi.org/10.1002/esp.3290040405>
- 503 Crouvi, O., Amit, R., Enzel, Y., Porat, N., & Sandler, A. (2008). Sand dunes as a major proximal dust source for
504 late Pleistocene loess in the Negev Desert, Israel. *Quaternary Research*, 70(2), 275–282.
505 <https://doi.org/10.1016/j.yqres.2008.04.011>
- 506 Davey, M. E., & O'toole, G. A. (2000). Microbial biofilms: from ecology to molecular genetics. *Microbiology
507 and Molecular Biology Reviews*, 64(4), 847–867. <https://doi.org/10.1128/MMBR.64.4.847-867.2000>
- 508 Drews, A., Lee, C.-H., & Kraume, M. (2006). Membrane fouling - a review on the role of EPS. *Desalination*,
509 200(1–3), 186–188. <https://doi.org/10.1016/j.desal.2006.03.290>

- 510 Dupraz, C., Reid, R. P., Braissant, O., Decho, A. W., Norman, R. S., & Visscher, P. T. (2009). Processes of
511 carbonate precipitation in modern microbial mats. *Earth-Science Reviews*, 96(3), 141–162.
512 <https://doi.org/10.1016/j.earscirev.2008.10.005>
- 513 Edgar, R. C. (2013). UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nature Methods*,
514 10(10), 996–998. <https://doi.org/10.1038/nmeth.2604>
- 515 Ehleringer, J. R., Cerling, T. E., & Helliker, B. R. (1997). C₄ photosynthesis, atmospheric CO₂, and climate.
516 *Oecologia*, 112(3), 285–299. <https://doi.org/10.1007/s004420050311>
- 517 Fernandes, A. D., Reid, J. N., Macklaim, J. M., McMurrough, T. A., Edgell, D. R., & Gloor, G. B. (2014). Unifying
518 the analysis of high-throughput sequencing datasets: characterizing RNA-seq, 16S rRNA gene
519 sequencing and selective growth experiments by compositional data analysis. *Microbiome*, 2, 15.
520 <https://doi.org/10.1186/2049-2618-2-15>
- 521 Ferrando, D., Toubiana, D., Kandiyote, N. S., Nguyen, T. H., Nejdat, A., & Herzberg, M. (2018). Ambivalent
522 role of calcium in the viscoelastic properties of extracellular polymeric substances and the
523 consequent fouling of reverse osmosis membranes. *Desalination*, 429, 12–19.
524 <https://doi.org/10.1016/j.desal.2017.12.006>
- 525 Ferreira, J. A., & Zwinderman, A. H. (2006). On the Benjamini–Hochberg method. *The Annals of Statistics*,
526 34(4), 1827–1849. <https://doi.org/10.1214/009053606000000425>
- 527 Garcia-Pichel, F. (2006). Plausible mechanisms for the boring on carbonates by microbial phototrophs.
528 *Sedimentary Geology*, 185(3–4), 205–213. <https://doi.org/10.1016/j.sedgeo.2005.12.013>
- 529 Goossens, D., & Rajot, J. L. (2008). Techniques to measure the dry aeolian deposition of dust in arid and semi-
530 arid landscapes: a comparative study in West Niger. *Earth Surface Processes and Landforms*, 33(2),
531 178–195. <https://doi.org/10.1002/esp.1533>
- 532 Gorbushina, A. A. (2007). Life on the rocks. *Environmental Microbiology*, 9(7), 1613–1631.
533 <https://doi.org/10.1111/j.1462-2920.2007.01301.x>
- 534 Goudie, A. S., Viles, H. A., & Parker, A. G. (1997). Monitoring of rapid salt weathering in the central Namib
535 Desert using limestone blocks. *Journal of Arid Environments*, 37(4), 581–598.
536 <https://doi.org/10.1006/jare.1997.0297>
- 537 Goudie, A. S. (2016). Quantification of rock control in geomorphology. *Earth-Science Reviews*, 159, 374–387.
538 <https://doi.org/10.1016/j.earscirev.2016.06.012>
- 539 Goudie, A. S., Wright, E., & Viles, H. A. (2002). The roles of salt (sodium nitrate) and fog in weathering: a
540 laboratory simulation of conditions in the northern Atacama Desert, Chile. *CATENA*, 48(4), 255–266.
541 [https://doi.org/10.1016/S0341-8162\(02\)00028-0](https://doi.org/10.1016/S0341-8162(02)00028-0)
- 542 Goudie, A.S. (1996). Organic agency in calcrete development. *Journal of Arid Environments*, 32(2), 103–110.
543 <https://doi.org/10.1006/jare.1996.0010>

- 544 Groom, K. M., Allen, C. D., Mol, L., Paradise, T. R., & Hall, K. (2015). Defining tafoni: Re-examining
545 terminological ambiguity for cavernous rock decay phenomena. *Progress in Physical Geography*,
546 39(6), 775–793. <https://doi.org/10.1177/0309133315605037>
- 547 Hamilton, N. (2017). *ggtern: An Extension to “ggplot2”, for the Creation of Ternary Diagrams*. Retrieved from
548 <https://CRAN.R-project.org/package=ggtern>
- 549 Horner-Devine, M. C., & Bohannon, B. J. M. (2006). Phylogenetic clustering and overdispersion in bacterial
550 communities. *Ecology*, 87(sp7), S100–S108. [https://doi.org/10.1890/0012-9658\(2006\)87\[100:PCAOIB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[100:PCAOIB]2.0.CO;2)
- 551
- 552 Huinink, H. P., Pel, L., & Kopinga, K. (2004). Simulating the growth of tafoni. *Earth Surface Processes and*
553 *Landforms*, 29(10), 1225–1233. <https://doi.org/10.1002/esp.1087>
- 554 Ji, M., Greening, C., Vanwonterghem, I., Carere, C. R., Bay, S. K., Steen, J. A., ... Ferrari, B. C. (2017).
555 Atmospheric trace gases support primary production in Antarctic desert surface soil. *Nature*.
556 <https://doi.org/10.1038/nature25014>
- 557 Jiang, W., Saxena, A., Song, B., Ward, B. B., Beveridge, T. J., & Myneni, S. C. B. (2004). Elucidation of
558 functional groups on gram-positive and gram-negative bacterial surfaces using infrared spectroscopy,
559 10.
- 560 Klindworth, A., Pruesse, E., Schweer, T., Peplies, J., Quast, C., Horn, M., & Glockner, F. O. (2012). Evaluation of
561 general 16S ribosomal RNA gene PCR primers for classical and next-generation sequencing-based
562 diversity studies. *Nucleic Acids Research*, 41(1), e1–e1. <https://doi.org/10.1093/nar/gks808>
- 563 Kuhlman, K. R., Fusco, W. G., La Duc, M. T., Allenbach, L. B., Ball, C. L., Kuhlman, G. M., ... Crawford, R. L.
564 (2006). Diversity of microorganisms within rock varnish in the Whipple Mountains, California. *Applied*
565 *and Environmental Microbiology*, 72(2), 1708–1715. [https://doi.org/10.1128/AEM.72.2.1708-](https://doi.org/10.1128/AEM.72.2.1708-1715.2006)
566 1715.2006
- 567 Lang-Yona, N., Maier, S., Macholdt, D. S., Müller-Germann, I., Yordanova, P., Rodriguez-Caballero, E., ...
568 Weber, B. (2018). Insights into microbial involvement in desert varnish formation retrieved from
569 metagenomic analysis. *Environmental Microbiology Reports*, 10(3), 264–271.
570 <https://doi.org/10.1111/1758-2229.12634>
- 571 Lebre, P. H., Maayer, P. D., & Cowan, D. A. (2017). Xerotolerant bacteria: surviving through a dry spell. *Nature*
572 *Reviews Microbiology*, 15(5), 285–296. <https://doi.org/10.1038/nrmicro.2017.16>
- 573 Makhalanyane, T. P., Valverde, A., Birkeland, N.-K., Cary, S. C., Marla Tuffin, I., & Cowan, D. A. (2013).
574 Evidence for successional development in Antarctic hypolithic bacterial communities. *The ISME*
575 *Journal*, 7(11), 2080–2090. <https://doi.org/10.1038/ismej.2013.94>

- 576 Makhalanyane, T. P., Valverde, A., Gunnigle, E., Frossard, A., Ramond, J.-B., & Cowan, D. A. (2015). Microbial
577 ecology of hot desert edaphic systems. *FEMS Microbiology Reviews*, *39*(2), 203–221.
578 <https://doi.org/10.1093/femsre/fuu011>
- 579 Mangiafico, S. (2018). *rcompanion: functions to support extension education program evaluation*. Retrieved
580 from <https://CRAN.R-project.org/package=rcompanion>
- 581 McArdle, B. H., & Anderson, M. J. (2001). Fitting multivariate models to community data: a comment on
582 distance-based redundancy analysis. *Ecology*, *82*(1), 290–297. [https://doi.org/10.1890/0012-9658\(2001\)082\[0290:FMMTCD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2)
- 584 McBride, E. F., & Picard, M. D. (2004). Origin of honeycombs and related weathering forms in Oligocene
585 Macigno Sandstone, Tuscan coast near Livorno, Italy. *Earth Surface Processes and Landforms*, *29*(6),
586 713–735. <https://doi.org/10.1002/esp.1065>
- 587 McIlroy de la Rosa, J. P., Warke, P. A., & Smith, B. J. (2014). The effects of lichen cover upon the rate of
588 solutional weathering of limestone. *Geomorphology*, *220*, 81–92.
589 <https://doi.org/10.1016/j.geomorph.2014.05.030>
- 590 McMurdie, P. J., & Holmes, S. (2013). phyloseq: an R package for reproducible interactive analysis and
591 graphics of microbiome census data. *PLOS ONE*, *8*(4), e61217.
592 <https://doi.org/10.1371/journal.pone.0061217>
- 593 Mora, C. I., Driese, S. G., & Seager, P. G. (1991). Carbon dioxide in the Paleozoic atmosphere: Evidence from
594 carbon-isotope compositions of pedogenic carbonate. *Geology*, *19*(10), 1017.
595 [https://doi.org/10.1130/0091-7613\(1991\)019<1017:CDITPA>2.3.CO;2](https://doi.org/10.1130/0091-7613(1991)019<1017:CDITPA>2.3.CO;2)
- 596 Mustoe, G. E. (1983). Cavernous weathering in the Capitol Reef Desert, Utah. *Earth Surface Processes and*
597 *Landforms*, *8*(6), 517–526. <https://doi.org/10.1002/esp.3290080603>
- 598 Mustoe, G. E. (2010). Biogenic origin of coastal honeycomb weathering. *Earth Surface Processes and*
599 *Landforms*, *35*(4), 424–434. <https://doi.org/10.1002/esp.1931>
- 600 O'Hara, R. B. (2005). Species richness estimators: how many species can dance on the head of a pin? *Journal*
601 *of Animal Ecology*, *74*(2), 375–386. <https://doi.org/10.1111/j.1365-2656.2005.00940.x>
- 602 Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., ... Wagner, H. (2018). *vegan:*
603 *community ecology package*. Retrieved from <https://CRAN.R-project.org/package=vegan>
- 604 Or, D., Smets, B. F., Wraith, J. M., Dechesne, A., & Friedman, S. P. (2007). Physical constraints affecting
605 bacterial habitats and activity in unsaturated porous media – a review. *Advances in Water Resources*,
606 *30*(6–7), 1505–1527. <https://doi.org/10.1016/j.advwatres.2006.05.025>
- 607 Pointing, S. B., & Belnap, J. (2012). Microbial colonization and controls in dryland systems. *Nature Reviews*
608 *Microbiology*, *10*(8), 551–562. <https://doi.org/10.1038/nrmicro2831>

- 609 Roberson, E. B., & Firestone, M. K. (1992). Relationship between desiccation and exopolysaccharide
610 production in a soil *Pseudomonas* sp. *Applied and Environmental Microbiology*, 58(4), 1284–1291.
- 611 Rodriguez-Navarro, C., & Doehne, E. (1999). Salt weathering: influence of evaporation rate, supersaturation
612 and crystallization pattern. *Earth Surface Processes and Landforms*, 24(3), 191–209.
613 [https://doi.org/10.1002/\(SICI\)1096-9837\(199903\)24:3<191::AID-ESP942>3.0.CO;2-G](https://doi.org/10.1002/(SICI)1096-9837(199903)24:3<191::AID-ESP942>3.0.CO;2-G)
- 614 Rodriguez-Navarro, C., Doehne, E., & Sebastian, E. (1999). Origins of honeycomb weathering: The role of salts
615 and wind. *Geological Society of America Bulletin*, 111(8), 1250–1255. [https://doi.org/10.1130/0016-7606\(1999\)111<1250:OOHWTR>2.3.CO;2](https://doi.org/10.1130/0016-7606(1999)111<1250:OOHWTR>2.3.CO;2)
- 617 Rodriguez-Navarro, C., Rodriguez-Gallego, M., Chekroun, K. B., & Gonzalez-Muñoz, M. T. (2003).
618 Conservation of Ornamental Stone by *Myxococcus xanthus*-Induced Carbonate Biomineralization.
619 *Applied and Environmental Microbiology*, 69(4), 2182–2193.
620 <https://doi.org/10.1128/AEM.69.4.2182-2193.2003>
- 621 Scherer, G. W. (2004). Stress from crystallization of salt. *Cement and Concrete Research*, 34(9), 1613–1624.
622 <https://doi.org/10.1016/j.cemconres.2003.12.034>
- 623 Schloss, P. D., Westcott, S. L., Ryabin, T., Hall, J. R., Hartmann, M., Hollister, E. B., ... Weber, C. F. (2009).
624 Introducing mothur: open-source, platform-independent, community-supported software for
625 describing and comparing microbial communities. *Applied and Environmental Microbiology*, 75(23),
626 7537–7541. <https://doi.org/10.1128/AEM.01541-09>
- 627 Sheng, G. P., Yu, H. Q., & Li, X. Y. (2010). Extracellular polymeric substances (EPS) of microbial aggregates in
628 biological wastewater treatment systems: A review. *Biotechnology Advances*, 28(6), 882–894.
629 <https://doi.org/10.1016/j.biotechadv.2010.08.001>
- 630 Shirshova, L. T., Ghabbour, E. A., & Davies, G. (2006). Spectroscopic characterization of humic acid fractions
631 isolated from soil using different extraction procedures. *Geoderma*, 133(3–4), 204–216.
632 <https://doi.org/10.1016/j.geoderma.2005.07.007>
- 633 Shtober-Zisu, N., Amasha, H., & Frumkin, A. (2017). Inland notches: lithological characteristics and climatic
634 implications of subaerial cavernous landforms in Israel: Inland Notches: Lithological characteristics
635 and climatic implications. *Earth Surface Processes and Landforms*, 42(12), 1820–1832.
636 <https://doi.org/10.1002/esp.4135>
- 637 Slavík, M., Bruthans, J., Filippi, M., Schweigstillová, J., Falteisek, L., & Řihošek, J. (2017). Biologically-initiated
638 rock crust on sandstone: Mechanical and hydraulic properties and resistance to erosion.
639 *Geomorphology*, 278, 298–313. <https://doi.org/10.1016/j.geomorph.2016.09.040>
- 640 Smith, B. J. (1988). Weathering of superficial limestone debris in a hot desert environment. *Geomorphology*,
641 1(4), 355–367. [https://doi.org/10.1016/0169-555X\(88\)90007-4](https://doi.org/10.1016/0169-555X(88)90007-4)

- 642 Smith, B. J. (2009). Weathering Processes and Forms. In A. J. Parsons & A. D. Abrahams (Eds.),
643 *Geomorphology of Desert Environments* (pp. 69–100). Dordrecht: Springer Netherlands.
644 https://doi.org/10.1007/978-1-4020-5719-9_4
- 645 Smith, B. J., Warke, P. A., McGreevy, J. P., & Kane, H. L. (2005). Salt-weathering simulations under hot desert
646 conditions: agents of enlightenment or perpetuators of preconceptions? *Geomorphology*, *67*(1–2),
647 211–227. <https://doi.org/10.1016/j.geomorph.2004.03.015>
- 648 Sperling, C. H. B., & Cooke, R. U. (1985). Laboratory simulation of rock weathering by salt crystallization and
649 hydration processes in hot, arid environments. *Earth Surface Processes and Landforms*, *10*(6), 541–
650 555. <https://doi.org/10.1002/esp.3290100603>
- 651 Šťovíček, A., Kim, M., Or, D., & Gillor, O. (2017). Microbial community response to hydration-desiccation
652 cycles in desert soil. *Scientific Reports*, *7*, 45735. <https://doi.org/10.1038/srep45735>
- 653 Sweeting, M. M., & Lancaster, N. (1982). Solutions and wind erosion forms on limestone in the Central Namib
654 Desert. *Z. Geomorphology N. F.*, *26*(2), 197–207.
- 655 Uemura, R., Nakamoto, M., Asami, R., Mishima, S., Gibo, M., Masaka, K., ... Shen, C.-C. (2016). Precise oxygen
656 and hydrogen isotope determination in nanoliter quantities of speleothem inclusion water by cavity
657 ring-down spectroscopic techniques. *Geochimica et Cosmochimica Acta*, *172*, 159–176.
658 <https://doi.org/10.1016/j.gca.2015.09.017>
- 659 Vaks, A., Bar-Matthews, M., Matthews, A., Ayalon, A., & Frumkin, A. (2010). Middle-Late Quaternary
660 paleoclimate of northern margins of the Saharan-Arabian Desert: reconstruction from speleothems
661 of Negev Desert, Israel. *Quaternary Science Reviews*, *29*(19–20), 2647–2662.
662 <https://doi.org/10.1016/j.quascirev.2010.06.014>
- 663 Viles, H. (1995). Ecological perspectives on rock surface weathering: Towards a conceptual model.
664 *Geomorphology*, *13*(1–4), 21–35. [https://doi.org/10.1016/0169-555X\(95\)00024-Y](https://doi.org/10.1016/0169-555X(95)00024-Y)
- 665 Viles, H. (2005). Self-organized or disorganized? Towards a general explanation of cavernous weathering.
666 *Earth Surface Processes and Landforms*, *30*(11), 1471–1473. <https://doi.org/10.1002/esp.1287>
- 667 Viles, H., Goudie, A., Grab, S., & Lalley, J. (2011). The use of the Schmidt Hammer and Equotip for rock
668 hardness assessment in geomorphology and heritage science: a comparative analysis. *Earth Surface
669 Processes and Landforms*, *36*(3), 320–333. <https://doi.org/10.1002/esp.2040>
- 670 Viles, H.A., & Goudie, A. S. (2007). Rapid salt weathering in the coastal Namib Desert: Implications for
671 landscape development. *Geomorphology*, *85*(1–2), 49–62.
672 <https://doi.org/10.1016/j.geomorph.2006.03.025>
- 673 Viles, H. A. (2001). Scale issues in weathering studies. *Geomorphology*, *41*(1), 63–72.
674 [https://doi.org/10.1016/S0169-555X\(01\)00104-0](https://doi.org/10.1016/S0169-555X(01)00104-0)

- 675 Viles, H. A. (2008). Understanding dryland landscape dynamics: do biological crusts hold the key? *Geography*
676 *Compass*, 2(3), 899–919. <https://doi.org/10.1111/j.1749-8198.2008.00099.x>
- 677 Viles, H. A. (2012). Microbial geomorphology: A neglected link between life and landscape. *Geomorphology*,
678 157–158, 6–16. <https://doi.org/10.1016/j.geomorph.2011.03.021>
- 679 Wang, Q., Garrity, G. M., Tiedje, J. M., & Cole, J. R. (2007). Naïve Bayesian classifier for rapid assignment of
680 rRNA sequences into the new bacterial taxonomy. *Applied and Environmental Microbiology*, 73(16),
681 5261–5267. <https://doi.org/10.1128/AEM.00062-07>
- 682 Warscheid, T., & Braams, J. (2000). Biodeterioration of stone: a review. *International Biodeterioration &*
683 *Biodegradation*, 46(4), 343–368. [https://doi.org/10.1016/S0964-8305\(00\)00109-8](https://doi.org/10.1016/S0964-8305(00)00109-8)
- 684 Weber, B., Büdel, B., & Belnap, J. (Eds.). (2016). *Biological Soil Crusts: An Organizing Principle in Drylands* (1st
685 ed. 2016 edition). New York, NY: Springer.
- 686 Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York, USA: Springer-Verlag. Retrieved
687 from <http://ggplot2.org>
- 688 Wong, F. K. Y., Lacap, D. C., Lau, M. C. Y., Aitchison, J. C., Cowan, D. A., & Pointing, S. B. (2010). Hypolithic
689 microbial community of quartz pavement in the high-altitude tundra of Central Tibet. *Microbial*
690 *Ecology*, 60(4), 730–739. <https://doi.org/10.1007/s00248-010-9653-2>
- 691 Wong, F. K. Y., Lau, M. C. Y., Lacap, D. C., Aitchison, J. C., Cowan, D. A., & Pointing, S. B. (2010). Endolithic
692 microbial colonization of limestone in a high-altitude arid environment. *Microbial Ecology*, 59(4),
693 689–699. <https://doi.org/10.1007/s00248-009-9607-8>
- 694 Wright, D. T., & Wacey, D. (2004). Sedimentary dolomite: a reality check. *Geological Society, London, Special*
695 *Publications*, 235(1), 65–74. <https://doi.org/10.1144/GSL.SP.2004.235.01.03>
- 696

697 **Figure legends**

698 **Figure 1. A.** Comparable weathering features in the exposed limestone and dolomite rocks on
699 both sites as noted in field outcrops (hammer for scale, 30 cm long). **B.** Visual presence of a rock
700 crust with similar thickness (3-6 mm) in both rock types. The crust's mineralogical composition
701 matched that of the host rock. **C.** Thin-section analysis of the rocks showing lamination structure in
702 the BRCs. Dashed lines indicate the interface between BRC host rocks. BRC's mineralogy includes
703 micritic to microsparitic dolomitic or calcitic crystals.

704
705 **Figure 2. A.** Fourier Transform Infrared (FTIR) analysis of limestone (top) and dolomite (bottom)
706 BRCs indicating the presence of extracellular polymeric substances (EPS) molecules through the
707 distinctive peak ranging between $1020-1040\text{ cm}^{-1}$, which was absent from the host rocks. **B.** Carbon
708 and oxygen isotope-ratio depth profiles of the limestone (top) and dolomite (bottom) BRC's in
709 comparison to their host rocks.

710
711 **Figure 3.** Desiccation of rock cores in the presence and absence of BRC as a function of time,
712 following full hydration. The curves indicate a second-degree polynomial line fitting (all fitted curves
713 were statistically significant from each other in ANOVA tests with P values < 0.01 and $R^2 > 0.95$).

714
715 **Figure 4.** Microbial community features of the BRCs, the surrounding soils and settled dust in
716 the two studied sites. **A.** Comparison of the richness in the form of observed no. of OTUs (S obs.)
717 and the predicted number of OTUs (ACE index), and a comparison of α -diversity (Shannon's H Index)
718 between the different sample types. Identical lower-case letters indicate no statistical difference
719 between groups in a Tukey's HSD test. **B.** Clustering of sample types using a PCoA ordination based
720 on Horn-Morisita distance matrix. Identical lower-case letters indicate no statistical difference

721 between groups in a pairwise PERMANOVA test. Ellipses denote 95% confidence intervals around
722 the arid and hyperarid samples assuming multivariate normal distribution. **C.** Composition of
723 bacterial phyla in the different sample types (see Table S4 for results of statistical tests in the
724 relative abundance of different phyla between sample types). **D.** Relative contribution of each
725 bacterial OTU to the community composition of each sample type. Top – arid site, bottom –
726 hyperarid site (see Figure S2 for statistical detection of preferentially abundant OTUs between each
727 sample-type pair.

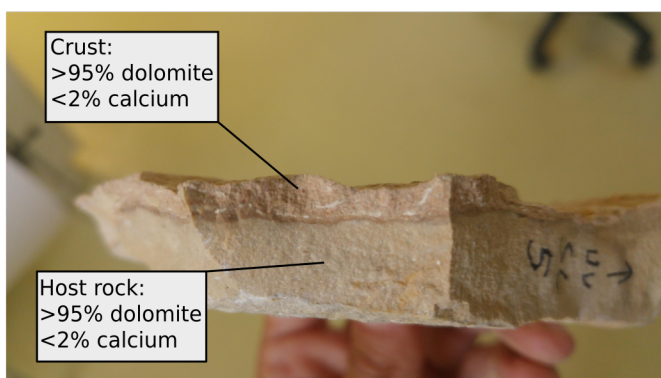
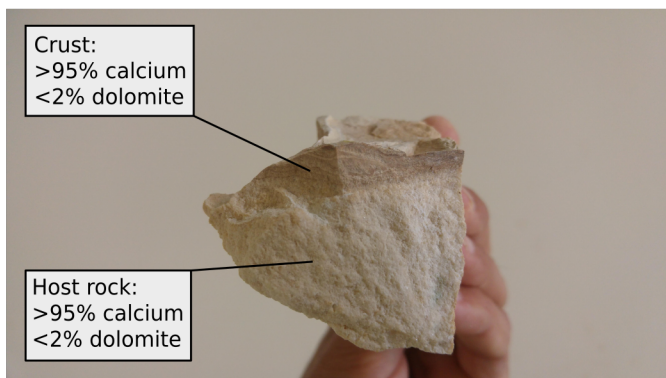
728 **Tables**

729 Table 1. Geological parameters of the subjected lithologies

Rock properties	Limestone (arid; Shivta Formation)			Dolomite (hyperarid; Gerofit Formation)		
	Dolomite	Calcium	Quartz	Dolomite	Calcium	Quartz
BRC mineralogy (%)	0	95	3	90	2	1
Host rock mineralogy (%)	0	95	0	95	0	1
Porosity (%)	13.5 ± 2.2			8.25 ± 1.3		
Permeability (miliDarcy)	0.1 – 3.8			0.05 – 0.41		
Surface penetration resistance (kg cm ⁻¹)	100 – 365			130 – 230		

730

731

A**Limestone (arid)****Dolomite (hyperarid)****B****C**