Dryland microbiomes reveal community adaptations to desertification and climate change

Claudia Coleine[1,*], Manuel Delgado-Baquerizo[2], Jocelyne DiRuggiero[3,4], Emilio Guirado[5], Antoine L. Harfouche[6], Cesar Perez-Fernandez[7], Brajesh K. Singh[8,9], Laura Selbmann[1,10,*], and Eleonora Egidi[8,9]

[1]Department of Ecological and Biological Sciences, University of Tuscia, Viterbo, Italy.
[2]Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Sevilla, Spain.
[3]Department of Biology, Johns Hopkins University, Baltimore, MD, USA.
[4]Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MD, USA.
[5]Multidisciplinary Institute for Environment Studies "Ramón Margalef", Universidad de Alicante, Alicante, Spain.
[6]Department for Innovation in Biological, Agro-food and Forest systems, University of Tuscia, Viterbo, Italy.
[7]Universidad Privada Boliviana
[8]Global Centre for Land-Based Innovation, Western Sydney University, Penrith, Australia.
[9]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, Australia.
[10]Mycological Section, Italian Antarctic National Museum (MNA), Genoa, Italy.

Correspondence to: coleine@unitus.it, Largo dell'Università snc, Viterbo, 01100, Italy; selbmann@unitus.it, Largo dell'Università snc, Viterbo, 01100, Italy

Short title: Drylands microbiome under climate change

Abstract

Drylands account for 45% of the Earth's land area, supporting approximately 40% of the global population. These regions support some of the most extreme environments on Earth, characterized by extreme temperatures, low and variable rainfall, and low soil fertility. In these biomes, microorganisms provide vital ecosystem services and have evolved distinctive adaptation strategies to endure and flourish in the extreme. However, dryland microbiomes and the ecosystem services they provide are under threat due to intensifying desertification and climate change. In this review, we provide a synthesis of our current understanding of microbial life in drylands, emphasizing the remarkable diversity and adaptations of these communities. We then discuss anthropogenic threats, including the influence of climate change on dryland microbiomes and outline current knowledge gaps. Finally, we propose research priorities to address those gaps and safeguard the sustainability of these fragile biomes.

INTRODUCTION

Drylands are of paramount significance in their global distribution and the human population they support, regulating the global carbon (C), nitrogen (N), and water cycles [1]. Drylands constitute the largest terrestrial biome, covering about 45% of the global land surface and supporting almost half the world's cultivated systems and half of its livestock [2], encompassing a plethora of ecosystems such as rangelands, grasslands, woodlands, savannahs, deserts, scrublands, and dry forests. The global geographic classification of drylands is often based on the aridity index and encompasses all regions where this index is between 0.05 and 0.65 (Fig. 1a). In addition to water scarcity, drylands, particularly arid and hyper-arid systems, are characterized by polyextreme conditions [3, 4] such as high evaporation rates, extremely high solar ultraviolet (UV) radiation, and extremes of temperatures. Climate change and anthropogenic activities are making these challenging conditions even more extreme and unpredictable. Even small environmental changes could result in a severe alteration of the C balance, water availability, and the provision of multiple ecosystem services [5].

Drylands host a diverse array of microorganisms (hereafter dryland microbiomes) that can be free-living or symbiotic, associated with vascular plants, or within biological soil crusts (hereafter biocrusts). In drylands, microbiomes contribute to essential ecosystem functions, such as the formation of fertile islands, nutrient cycling, and climate regulation, while also providing the backbone for the ecological succession of vegetation in extreme regions [6]. Therefore, a potential loss of microbial diversity, and consequently loss of functionality, might dramatically compromise the productivity of dry regions.

Exploring dryland ecology, particularly belowground, and its response to climate change and other anthropogenic pressures is nowadays of primary importance. In this review, we provide a comprehensive synthesis of the most recent knowledge of the diversity and function of microbiomes inhabiting global drylands, although considering that there is a lack of data from several important deserts around the world. For example, major dry regions in North Africa, South America and Eurasia are still undersampled and understudied [e.g., 7,8]. Further, we discuss the major climate-driven and anthropogenic threats to these key members of the ecosystem, and adaptation strategies that might underpin microbial survival to the increasingly extreme conditions driven by climate change. We then outline a set of recommendations and directions that we hope will contribute to the design of more efficient conservation and restoration strategies to cope with increasing anthropogenic threats. The importance of vegetational attributes to dryland is not covered since it has been reviewed

3

87 elsewhere [e.g., 9] and our review primarily focuses on studies from natural systems within

88 drylands. However, we recognize that the overall dryland ecosystem, extending beyond wild

89 areas, encompasses land use types (e.g., farming) and niches (e.g., fertility islands), which

90 contribute to the definition of microbiomes in dryland ecosystems; however, these niches,

91 despite their significance, fall outside the scope of our current analysis.

92 **DRYLAND MICROBIOMES**

93 Top soils harbor the majority of dryland microbes, where they can exist as free-living

94 assemblages and in association with adapted vascular plants. However, in the most arid eco-

95 regions, they form interconnected assemblages known as biocrusts, which are typically

96 dominated by phototrophs cyanobacteria and chlorophycean algae [10]. The development of

97 biocrusts and soil heterotrophic communities results in enhanced soil stability (e.g., via the

98 release of exopolysaccharides), nutrient concentration, and water retention, which ultimately

99 favors the growth and development of vascular plants [9].

100 Drylands also support microbial communities specialized in the colonization of lithic

101 substrates. Particularly in hyper-arid regions, rocks provide a physical structure and porous

102 substrate, high water retention potential, and access to micronutrients (e.g., rock minerals),

103 forming epilithic, hypolithic, or endolithic assemblages [6]. Epiliths and hypolithic are

104 observed in drylands of almost all aridity classes; lichens, in particular, provide an attractive

105 niche for a multitude of microorganisms, constituting hotspots for microbial diversification

106 [11]. In hyper-arid regions, endoliths dominate and represent the utmost dryland specialists

107 [12].

108 **Bacteria and archaea**

109 Globally, members of *Actinobacteria*, *Alphaproteobacteria*, and *Chloroflexi* [15] dominate

110 drylands (Fig. 2 a,c). In soil, the dominant bacterial taxa belong to *Streptomyces mirabilis*,

111 *Geodermatophilus obscurus* as well as species from genera *Microcoleus, Phormidium,*

112 *Plectonema, Schizothrix, Nostoc, Modestobacter*, and *Sphingomonas* [8]. In contrast, N-

113 fixing bacteria are more abundant in biocrusts from hot drylands and include Proteobacteria,

114 *Azospirillum* spp.*,* Deinococcus-Thermus *Deinococcus* spp.*,* and cyanobacterial *Calothrix*

115 spp. [14] (Fig. 2b). Conversely, endolithic bacterial communities harbour more generalist

116 members of *Actinobacteria* (e.g., *Rubrobacter*, *Propionibacterium* and *Solirubrobacter),*

117 *Proteobacteria* (e.g., *Craurococcus*), and *Cyanobacteria* (e.g., *Chroococcidiopsis*) phyla.

4

118   Shotgun metagenomics has advanced our knowledge of the functional potential and

119   evolutionary pathways of microorganisms in these extreme environments, revealing how

120   drylands, and in particular hyper-arid soils, are a reservoir of new microbial entities harboring

121   potentially novel functional genes. Recent studies from the Atacama and Antarctic Deserts

122   revealed that the majority of dryland-associated microbial genomes lack representatives in

123   genomic public databases [15]. For example, the majority of new species of Antarctic

124   endoliths were found to belong to monophyletic bacterial clades that diverged from related

125   taxa 1.2 billion to 410 million years ago [16].

126   Among archaea, members of *Euryarchaeota* comprise the majority of sequences in highly

127   saline soils/rocks. In particular, haloarchaea are typically associated with high salt in soils

128   and halites [17]. A recent global survey of dryland soils showed that small-scale

129   heterogeneity induced by plants, rather than large-scale changes in environmental conditions

130   (e.g., soil pH), regulates the diversity, abundance, and co-occurrence network of nitrifying

131   archaeal communities, which also include taxa with adaptation to energy starvation and

132   extreme conditions [18].

133   **Fungi and algae**

134   High-throughput sequencing and cultivation approaches showed a high level of fungal

135   diversity in dry systems, inscribing these organisms among the most stress-tolerant

136   eukaryotic life forms on Earth [19-21]. Globally, the soil dryland mycobiome is dominated

137   by *Ascomycota*, followed by *Basidiomycota*, *Glomeromycota* and *Zygomycota*, with

138   *Alternaria*, *Fusarium*, *Chaetomium*, and *Cladosporium* as predominant genera. UV light,

139   seasonality, and sand content have been identified as the most environmental determining

140   critical shifts in community composition [21]. In contrast, our knowledge of biocrusts and

141   rock fungal diversity and function is still limited. Indeed, previous studies have mainly

142   focused on scattered localities [e.g., 22], while a systematic view of these mycobiomes at a

143   global scale is still lacking.

144   Especially in plant-free arid and hyper-arid regions, oxygenic photosynthetic organisms

145   are key primary producers. Such keystone organisms channel energy into the synthesis of

146   energy and carbon storage compounds or are known to accumulate energy reserves in

147   response to water stress or during the transition to dormancy. Among phototrophs,

148   *Cyanobacteria* are typically the dominant group (e.g., *Chroococcidiopsis* and *Nostoc*).

149   However, also green algae are widespread in drylands. The *Trebouxia genus* (family

150   *Trebouxiophyceae*) and, to a lower extent, the *Chlorophyceae* family dominate [22]. In

5

151 hypersaline systems, such as halite endoliths of the Atacama Desert, a unique alga of the

152 *Dolichomastix* genus was shown to significantly contribute to the photosynthesis and the

153 organic C budget of the community [23].

154 **Viruses**

155 Viruses are considered the most abundant biological entities on Earth, with high genomic

156 diversity and ecological and biogeochemical significance [24, 25]. Recent efforts led to

157 important advances in reporting uncharacterized lineages (e.g, cyanophages) in hyper-arid

158 deserts [26]. Recent studies reported on the extent of the rock-associated virome. For

159 example, a recent study reported transcriptionally active viruses of the order *Caudovirales*

160 and the families *Pleolipoviridae* and *Sphaerolipoviridae* in halite endoliths of the Atacama

161 Desert [23]. Analysis of putative extreme-tolerance genes and auxiliary metabolic genes,

162 provided evidence for a complex trade-off between viral predation and viral delivery of

163 extreme-tolerance genes to their hosts, thereby aiding in their survival [25, 27]. Yet, study

164 from Antarctic rocks [28], indicated high diversity but largely undescribed and spatially

165 structured communities.

166

167 Overall, new technologies have generated unprecedented amounts of sequencing data

168 giving us an ecosystem-wide view of the diversity, function, and biogeography of the global

169 dryland microbiomes (Fig. 1b). However, this wealth of data has uncovered several

170 knowledge gaps that require further investigation. For example, we have just begun to

171 comprehend the amplitude of microbial diversity in drylands with most of them remaining

172 undescribed. As such, extensive sampling studies are needed to describe the diversity,

173 distribution, and drivers of different microbial taxa. In particular, we have little understanding

174 of the interactions between the different life domains (e.g., bacteria and fungi; bacteria and

175 algae). In addition, studies should encompass more remote and less explored dryland areas

176 and neglected ecological niches (e.g., rocks) to capture the full spectrum of microbial

177 diversity. Moreover, the existing data predominantly focus on bacterial and fungal

178 communities, leaving a gap in our knowledge of other microorganisms and their roles in

179 these ecosystems. For example, viral contributions at the ecosystem level, including the role

180 of viruses in nutrient cycling and energy flow, spatial and temporal changes in biogeography,

181 and interactions with host populations remain poorly understood. Similarly, large-scale

182 surveys of microbes from higher taxa (e.g., protists) are still missing from drylands, although

6

183   micro-eukaryotes are abundant in arid ecosystems and show sensitivity to aridity on a global

184   scale [29].

185 **IMPACT OF CLIMATE AND ANTHROPOGENIC DRIVERS OF CHANGE ON**

186 **DRYLAND MICROBIOMES**

187   The main drivers of dryland microbial dynamics could be broadly categorized into factors

188   related to global climate (e.g., precipitation and temperature) and human activities (e.g.,

189   grazing, afforestation/deforestation, agriculture, fire management, urbanization, greenhouse

190   gas emission) [5] (Fig. 3). The consequences of these pressures on the drylands ecosystem

191   functioning include both direct effects (e.g., shifts in microbial community composition,

192   biodiversity loss) and indirect impacts via changes in physico-chemical soil properties (e.g.,

193   losses in C, nutrients, moisture, structure, decrease in pH, increase in salinity) [30]. Given the

194   fundamental role of microorganisms in supporting dryland functioning, microbial changes

195   associated with climate change and physical disturbance can result in important fertility and

196   multifunctionality loss that may lead to land degradation and desertification. It is estimated

197   that 25–35% of drylands are already degraded, with over 250 million people directly affected

198   and about one billion people in over one hundred countries at risk [31].

199 **Community responses to aridification**

200   Aridity is a major climatic driver of ecosystem structure and functioning in drylands [32].

201   Recent studies indicate that aridity has increased globally during recent decades and is

202   projected to increase significantly in the future due to changes in the amount and variability

203   of precipitation, combined with increasing temperature, and elevated atmospheric CO_2,

204   ultimately supporting the expansion of drylands [33]. These aridification processes can

205   dramatically affect the soil microbiome of dry ecosystems, due to reduction in vegetation

206   cover and decrease in N and C concentration [32] (Fig. 3). In fact, recent work suggests that

207   aridity thresholds regulate ecosystem function in drylands, and that increases in aridity can

208   negatively impact most microbial taxa and shift the compositional balance of key community

209   members [34]. In particular, even small intensifications in aridity levels can result in drastic

210   increases in the proportion of animal pathogens, and reductions in the proportion of

211   ectomycorrhizal fungi, soil C sequestration and plant cover [32, 35]. Recent evidence also

212   indicates that aridity thresholds can influence multiple physiological (e.g., soil microbial

213   metabolic activity and biomass carbon) and functional (nitrogen cycling and

214   multifunctionality) properties at the regional scale [35], while having drastic impacts on the

7

complex functional interactions between microbial species within soil ecological networks

and their multifunctionality [30,36]. This overall effect can be further exacerbated at the local

scale. For example, field experiments have found evidence that drought impacts the

community structure and activity of soil microorganisms in drylands from two continents,

with stronger responses detected in more mesic sites [37].

Global drying trends are also likely to impact complex biotic communities such as those

of biocrusts found in arid and hyper-arid systems. Experimental manipulation of climate has

evidenced rapid mortality of dominant biocrust species, resulting in a total collapse of the

surface biocrusts communities, and models concur that a warmer, drier future will generally

reduce the abundance and the rate of C fixation in biocrusts [38]. Such warming-induced

changes could reduce the physical stability of surface soils and their C storage potential.

However, despite their vulnerability, biocrusts are critical for regulating the responses of

multifunctionality to climate change and nutrient availability in arid ecosystems [39]. A

recent global soil survey provided evidence that soil microbial communities largely regulate

the impacts of increases in temperature, wetting-drying cycles and nutrient additions on

ecosystem multifunctionality [40].

Functional responses to aridification

Aridity can also impact the functional potential and adaptation strategies of dryland

communities. Dry conditions are challenging for microorganisms, which may suffer from

loss of water, damage to cellular membranes, accumulation of reactive oxygen species,

protein denaturation, and DNA damage. Survival in increasingly stressful environments

requires specialized mechanisms of adaptation (**Box 1**), and along aridity gradients, soil

communities are progressively enriched with genes related to these stress tolerance (e.g.,

DNA damage repair, cation transportation, sporulation and osmolyte biosynthesis), harbor

smaller and simplified genomes [41], and reduced community stability and interactions [24].

Consequently, increases in the incidence of stress tolerance/resource scavenging traits and

simplified co-occurrence patterns are likely outcomes of community-level adaptations to

increasing water-depletion driven by global change. For example, experimental drought in

Mediterranean-like grasslands of California has been found to trigger the upregulation of

transporter-related genes, as well as biosynthesis of cell membrane and wall compounds, and

compatible solutes [43]. However, under climate change, cold drylands, especially those from

arid (e.g., Eurasian steppe) or hyper-arid regions (e.g., Antarctic, Arctic) are most likely to

experience not only an intensified drought-induced aridity but also a large degree of warming

8

248 during the cold season. Such processes have been linked to microbial changes such as

249 increased microbial biomass, community complexity and metabolic potential for nitrogen

250 assimilation [44]. Consequently, shifts in the balance and occurrence of functional attributes

251 could be fundamentally different across hot and cold drylands, but investigations comparing

252 these contrasting biomes are currently lacking.

253

254 **An integrated multi-omics approach**

255 Overall, while the existence of adaptation traits, and traits trade-offs, has been postulated for

256 many microbial communities, studies focusing on trait-level consequences of climate change

257 are still scarce in drylands. This is mostly because attempts to match taxonomic,

258 physiological and functional profiles are mostly hampered by the limitation of gene target

259 amplicon sequencing, and the lack of a complete characterization of both taxonomic groups

260 and functional genes, especially from arid communities. Filling these gaps will require efforts

261 from multiple disciplines, including microbiology, ecology, bioinformatics, and Artificial

262 Intelligence to isolate, identify and characterize microbial species that inhabit global

263 drylands. A systematic investigation encompassing multi-omics approaches (metagenomics,

264 metabolomics, metaproteomics), culturing and *in situ* (e.g., using NanoSims) functional

265 activity assessments, will be essential to *i)* provide a more holistic understanding of eco-

266 evolutionary mechanisms of adaptation and metabolic potential of microbiomes in dry

267 environments and *ii)* unravel various co-existing energy acquisition pathways point to diverse

268 niches and the exploitation of available resources. Explicit consideration of environmental

269 conditions (e.g., arid vs hyper arid) and niche specialization (e.g., soil vs rock vs vegetation)

270 will provide valuable insights into the abilities of microorganisms to survive and function in

271 dry conditions and their significance in maintaining the ecological balance of these regions

272 worldwide. Additionally, most studies to date have focused on short-term responses to

273 drought and warming, but it is unclear how microbial communities will respond to prolonged

274 or permanent aridification processes. Long-term studies are needed to understand how

275 microbial communities will adapt to changing environmental conditions, and how these

276 adaptations will affect soil health and ecosystem functioning over time. In fact, shifts in

277 community functional balance mediated by climate change might potentially result in

278 functional changes, with feedback on biogeochemical cycles [45]. These associations might

279 be particularly important for the most arid regions of the world, where effects of soil

280 microbial diversity on ecosystem multifunctionality (e.g., via increasing organic matter

281 decomposition and nutrient transformation) are expected to prevail due to lack of vegetation

9

cover [36]. Overall, approaches that are strongly grounded in community-aggregated traits

(CATs) frameworks (e.g., the Y–A–S life history triangle) [43], show strong potential to help

linking future climate systems to the intrinsic ability of these communities to withstand and

recover from disturbance, and perform ecosystem functions.

Brown or green? Dryland greening as an understudied global driver

While the expansion of arid subtypes that become drier comprises the major outcome of

global change, there have been global trends in dryland greening (i.e., significant increases in

live green vegetation cover) at both the global and local scales [46]. The main drivers of this

phenomenon have been attributed to global increased atmospheric CO_2 levels (CO_2

fertilization), which improve vegetation water-use efficiency and, consequently, increase soil

moisture [47], as well as agricultural practices (e.g., irrigation) at the local scale [48]. Such

shifts in vegetation and water dynamics could significantly impact microbial communities in

these systems. For example, greater vegetation cover and establishment of fertility islands can

result in an increase in plant litter and root exudates, which serve as a source of organic

matter for microbes. This can lead to higher microbial biomass and diversity, which can

support more complex food webs and ecosystem processes, while also favoring microbial

communities that depend on labile carbon as a source of energy (i.e. copiotrophs) at the

expense of those adapted to low levels of nutrients (i.e. oligotrophs). Critically, increases in

microbial activity and respiration rates due to higher atmospheric CO_2 concentrations can

outpace the CO_2 fixation rate mediated by plants, further reinforcing CO_2 losses [49]. Yet,

increases in aridity may limit the positive influence of CO_2 and warming on plant

productivity [50]. Further experimental evidence is needed to understand the specific impacts

of vegetation cover and moisture increases on microbial community composition and

function, and the implications of these potential changes for microbial-mediated ecosystem

processes and services in drylands.

Climate change and local drivers of change

Dryland microorganisms are highly vulnerable to physical disturbance both of natural and

anthropogenic nature. For example, they are known to be highly influenced by insects (e.g.,

ant nests) and mammal disturbance. Similarly, microorganisms are vulnerable to cropping

and grazing by livestock [51]. Crop cultivation and grazing accelerate erosion rates above

natural levels by reducing natural soil-stabilizing covers, such as native vegetation and

biocrusts, resulting in reduced bacterial biomass and shifts in the abundance of dominant

10

314 bacterial populations [52]. Changes in the dominance of microbial taxa associated with

315 grazing intensity can further influence the overall soil biodiversity and function of drylands.

316 This effect has been worsened by the adoption of management practices such as tillage,

317 which disrupts soil structure, accelerating surface runoff and topsoil C loss [53]. In some

318 regions of the world, such as Australia, introduction and encroachment of invasive species

319 (e.g., feral horses) has further contributed to soil erosion both directly, by removing surface

320 soil, and indirectly, by causing declines in plant cover, biomass and abundance [54].

321 Reduction in soil surface stability results in higher levels of soil movement, and thus

322 increases in soil erodibility and soil displacement by wind and water (Fig. 3).

323   Poor management practices are also responsible for increased soil acidification rates in

324 drylands, with deposition and leaching of N-based inorganic fertilizers being amongst the

325 major contributors to this process. During acidification, soils undergo various pH buffer

326 ranges associated with the weathering and liberation of different elements/constituents, such

327 as soluble aluminum, which can affect root growth by restricting access to water and

328 nutrients. Decreases in pH can also decrease soil microbial activity and diversity, affecting

329 agriculturally important associations, such as mycorrhizae and N fixing bacteria [55].

330   The combination of climatic, anthropogenic, and biotic processes ultimately results in soil

331 destabilization, nutrient depletion, and modified soil communities, consequently changing the

332 functional capabilities of soil in relation to C and N cycling, decomposition, and plant growth

333 [56]. As dryland microorganisms also contribute to global climate regulation through CO_2,

334 reactive N, and methane (CH_4) emissions, these processes will also likely alter the rate of

335 greenhouse gasses release relative to uptake, driving positive feedback and further

336 accelerating the rate of climate change. Empirical evidence is emerging in support of the

337 complex interactions between global and local factors and their potential impact on soil biota

338 and the processes they mediate. For example, a recent global study has evidenced that

339 increasing grazing pressure reduced ecosystem service delivery in warmer and species-poor

340 drylands, whereas positive effects of grazing were observed in colder and species-rich areas

341 [57]; similarly, herbivore exclusion in grasslands led to greater microbial metabolic quotient

342 (respiration rate/biomass unit) only at sites with lower soil organic C (< 1.7%) [58].

343   Despite these clear linkages, significant knowledge gaps exist in our understanding of

344 the interplay between local drivers of change and climatic factors on soil microbial

345 communities and the biogeochemical processes they mediate. This is mainly because

346 different drivers of change are often studied independently, especially when considering

347 microbial communities, although most terrestrial communities are exposed to different

11

348   physical, chemical, or biotic stressors that can move them out of their normal operating

349   range. In addition, there is a limitation in current studies that explore the relationship between

350   microbial composition and the environment at different scales. For example, global data

351   overlook the intricate variations in environmental filters such as soil composition,

352   topography, or disturbance patterns that occur within grid cells, posing an important question

353   on the point at which global or regional scale processes override fine scale processes on

354   individual sites. To improve our mechanistic understanding and predict the impact of

355   multiple disturbances on microbial communities and their taxonomic, functional and

356   metabolic attributes, it will be essential to design realistic experimental approaches

357   prioritizing those factors that are most likely to exert a strong influence on microbial

358   communities, using existing knowledge of global change (e.g., factorial experiments

359   considering drought, warming, and heatwaves). Conducting such experiments in a

360   coordinated fashion across different bioregions, where multiple indicators, including

361   taxonomic composition, functional genes and ecosystem processes, are measured using

362   standardized protocols, is also necessary to obtain a better understanding of the impact of

363   multiple disturbances on microbial communities at a global scale and define the role of local

364   conditions in modulating these interactions. This would involve comparing and contrasting

365   the responses of microbial communities to disturbances across different regions, climates,

366   and ecosystems. By doing so, we could assess the responsiveness of each metric at different

367   spatial extents and identify common patterns and mechanisms that operate across different

368   systems and understand how these are influenced by contextual variables such as land use,

369   management practices, and biotic interactions. Given the fundamental role of microorganisms

370   in supporting dryland functioning, it is essential to expand our knowledge on the impact of

371   both global and local drivers of change simultaneously to gain a better understanding of how

372   microbial communities respond to changing environmental conditions and assess how these

373   responses affect dryland functioning, and their vulnerability to degradation.

374   **CONCLUSIONS AND FUTURE DIRECTIONS**

375   Microorganisms are major players in drylands functioning with a key role in biogeochemical

376   cycling of elements essential for life [59]. While our understanding of biodiversity and the

377   ecological and physiological attributes of these fascinating organisms is rapidly progressing,

378   several outstanding questions and issues remain. At first glance, a major knowledge gap in

379   drylands microbial ecology is the extent of diversity and adaptation of microbial communities

380   in both soil and lithic substrates. Further, we have very limited understanding of

12

381 physiological, ecological, and evolutionary mechanisms that underpin adaptations of

382 microbes to their environments. We envisage that linking microbial traits with evolutionary

383 fitness and ecological dynamics through a trait-based approach will make it possible to better

384 understand mechanisms driving microbial adaptation and coexistence across niches [21].

385 Given the role of microorganisms in mediating feedback mechanisms to climate and

386 anthropogenic change, extending our knowledge on the functional attributes of these

387 communities will be of paramount importance in predicting the impact of future climate

388 change on these fragile and vulnerable communities.

389 Overall, the emerging body of literature focused on changes in aridity and climatic

390 patterns points to a shift in the distribution of microbial groups linked to soil stability,

391 vegetation, and biogeochemical cycling across the whole aridity spectrum. However,

392 significant knowledge gaps, highlighted above, still exist in our understanding on the

393 potential consequences of these processes and dryland functioning. In particular, empirical

394 data connecting soil microbial diversity and ecosystem functions across large environmental

395 gradients and how regional processes and climate change can affect this relationship, is

396 lacking. The interplay between taxonomic composition, functional attributes, and

397 environmental conditions holds the key to unraveling the mechanisms underlying microbial

398 responses to global change drivers. This knowledge will enable us to identify pivotal

399 transition points, assess the vulnerability of ecosystems, and develop effective strategies for

400 conservation and management. Expanding research efforts to bridge knowledge gaps and

401 promote interdisciplinary collaborations will pave the way for a comprehensive

402 understanding of dryland microbiomes and their role in sustaining ecosystem functioning in

403 the face of environmental challenges. Further, the consequences of CO_2 fertilization and

404 vegetation greening for dryland microorganisms should be also considered.

405 In-depth studies on dryland microorganisms are needed to assess the effectiveness of

406 biotechnological innovations in reverting climate- and human-driven issues, such as land

407 degradation and desertification. For example, recent research has demonstrated the potential

408 of utilizing biocrusts-associated cyanobacteria as biofertilizers for large-scale dryland

409 restoration efforts [60]. Their ability to fix C and N, improve soil aggregation, and provide a

410 favorable microhabitat for the colonization of heterotrophic microbial communities and later-

411 successional biocrusts species makes them particularly promising [61]. However, the

412 effectiveness of these techniques will likely depend on the type of disturbance, soil type,

413 climate conditions, and the ability to overcome technical limitations related to laboratory

414 cultivation, large-scale production and field-scale application. Similarly, harnessing the

13

unique genetic resources and stress adaptations provided by dryland microorganisms can also alleviate the negative effects of current agricultural practices. Emerging evidence shows that microbial communities from dry environments might mediate plant adaptation to drought [62]. Current and future assessments of the structure and function of dryland microbiomes, coupled with the development of significant approaches to increase their cultivability, will aid the development of effective and rationally designed microbial-based technologies for sustainable agriculture and forestry in these widespread ecosystems.

We also anticipate that remote sensing and artificial intelligence will play a central role in advancing dryland microbiomes research (Fig. 1b). Remote sensing could prove to be a valuable tool in studying the composition, structure, and functioning of these ecosystems, using, for instance, high-resolution satellites (e.g., Sentinel-2A/B multispectral imaging twin satellites with signals at 10m/pixel), miniature satellites (e.g., NASA biological CubeSat, BioSentinel), and drones equipped with sensors that reach a spatial resolution of less than 1m/pixel. Artificial Intelligence presents a powerful means to derive scientific insights from dryland microbiome data due to its ability to discover intricate patterns in large, highly complex datasets at an accelerated pace (see hypothetical example, Fig. 4). Moreover, with the growing availability of meta-omics data, the integration of these datasets becomes crucial for a comprehensive understanding of microbial community composition and functions. This integration not only holds potential in combining multi-omics data with environmental measures but also demonstrates promise in simultaneously exploring interactions across multiple dimensions of data [63-65].

These breakthroughs in the field will change policymakers' value of science in dryland ecosystems, including hyper-arid regions that are often neglected, underestimated, and overlooked. Core to the goal of these scientific explorations is the opportunity to guide future global decision-making policies on drylands biodiversity conservation and monitoring involving key stakeholders such as the UN Convention dealing with Land and Drought, and the Intergovernmental Panel on Climate Change. All these endeavors in drylands microbiome research are expected to lead us to a new age of holistic understanding of microbial life, develop innovative and desirable solutions for stemming biodiversity loss, shine the spotlight on the importance of this field, and ultimately understand and harness the power of the most abundant natural resources on our planet.

Data availability statement

14

448 Data sharing is not applicable to this article as no datasets were generated or analyzed during

449 the current study.

450

451 **BOX1: ENDURING THE EXTREMES: MAJOR ADAPTATIONS OF DRYLAND**

452 **MICROORGANISMS TO HYPER-ARID CONDITIONS**

453 Arid and hyper-arid regions are characterized by poly-extreme conditions (e.g., low water

454 availability combined with temperature fluctuations, salinity, and high UV radiation) that

455 require specialized mechanisms of adaptation. Microbial dryland specialists can produce

456 extracellular polymeric substances (EPSs) to retain water and nutrients, and synthesize

457 membranes rich in unsaturated fatty acids to maintain structural integrity [66]. They also

458 support important membrane proton and cation pumps that allow them to survive under high

459 pH environments [8]. Similarly, one of the major responses to harmful solar radiation is the

460 production of UV-absorbing/screening pigments such as carotenoids, scytonemin, and

461 mycosporine-like amino acids (MAAs), and melanin in fungi [67]. Microorganisms can also

462 accumulate compatible solutes in their cytoplasm to combat osmotic stress [7] (Fig. Box 1).

463 However, *de novo* production of compatible solutes is energetically expensive; thus,

464 microorganisms have evolved transport systems to uptake available solutes produced by other

465 community members, such as osmoprotectant uptake (Opu) proteins [68]. Yet, at the highest

466 salt concentration microorganisms, typically haloarchaea and a few bacteria, accumulate

467 potassium chloride (KCl) to balance the high osmotic pressure of their environment [69]. To

468 minimize cellular damage, some organisms such as the endolithic *Chroococcidiopsis*, have

469 evolved both the capacity to convert photosynthetically active solar radiation into chemical

470 energy using a complex molecular machinery and a number of acclimation and adaptive

471 mechanisms including orange carotenoid protein (OCP) and changes in the overall

472 composition of their photosynthetic apparatus [70]. To counteract a water-stressed

473 environment, fungi accumulate trehalose and intracellular glycerol as compatible solutes,

474 which protect cell membranes from desiccation and freezing damage [71]. Constitutively

475 melanized fungi have also evolved numerous morphological and osmotic adaptations to

476 survive extremely saline conditions such as meristematic growth, pigmentation (melanin in

477 cell walls), and changes in membrane composition and fluidity.

478 **Nutrient/energy sources**

15

479 Because of the scarcity of nutrients in hyper-arid drylands, microbial communities are almost

480 exclusively supported by the primary production of cyanobacteria and algae (i.e., autotrophs

481 vs. heterotrophic communities). A mean to obtain energy for heterotrophs is the light-driven

482 proton pump, bacteriorhodopsin, used by haloarchaea to augment their adenosine

483 triphosphate (ATP) budget; a similar light-harvesting system, xanthorhodopsin, is found in

484 the bacterium *Salinibacter* [72]. In drylands, atmospheric chemosynthesis supplements

485 photosynthetic primary production in cold desert soils in the high Arctic, Antarctica, Tibetan

486 Plateau and South Australian desert, with trace gas oxidation providing the energy and/or

487 carbon needed to sustain terrestrial ecosystems. Atmospheric hydrogen (H_2) oxidation via

488 [NiFe]-hydrogenases as a means to harvest electrons and (ribulose-1,5-biphosphate

489 carboxylase/oxygenase (RuBisCO) form IE have been reported for a broad range of bacteria,

490 including members of the *Actinobacteria*, *Acidobacteria*, and *Proteobacteria* Ca.

491 *Eremiobacterota* and Ca. *Dormibacterota* [73,74]. These processes are thought to play an

492 essential role in overcoming C and nutrient starvation in hyper-arid deserts with this *in situ*

493 metabolic hydrogenesis in specialized niche habitats may make a significant contribution to

494 water availability and, therefore, to water activity and metabolic capacity [75].

495 The acquisition of N is also essential for dryland communities. In biocrusts, heterocyst

496 cyanobacteria *Nostocales* and *Oscillatoriales* dominate, actively fixing N and emitting nitric

497 oxide and nitrous oxide [76]. Field experiments revealed that Antarctic communities had

498 significant nitrogenase activity, suggesting that they play an important role in nutrient cycling

499 in Antarctica soils [77]. It is thought that the high atmospheric deposition of nitrate over

500 millions of years, as a result of photochemical processes in the upper atmosphere, most likely

501 provides enough N to microbial communities of the desert. Indeed, pathways for uptake and

502 ammonia assimilation have been identified in metagenome-assembled genomes from gypsum

503 communities, indicating that deposited ammonia and nitrates might be major sources for N

504 [78]. At the functional level, the most abundant community members of Antarctic soil are

505 metabolically versatile aerobes, using ubiquitous atmospheric trace gasses, for persistence in

506 dormant state,   to meet their energy, and hydration needs via metabolic water production [15,

507 17]. The same strategy was found also crucial in endolithic microbiomes from Antarctica,

508 whose active metabolism is, as average, limited to 1,000 h per year [79].

509

510 **Ecological adaptations**

511 In addition to stress tolerance and resource-mining traits, it has been proposed that

512 cooperative interactions (e.g., metabolic interdependence, cross-feeding relationships [80])

16

might be enhanced to support microbial survival in response to restrictive conditions such as

those encountered in arid environments (e.g., oligotrophy) [80,81]. These interactions support

the survival of community members via mechanisms such as sharing of microbial byproducts

and contribute to the functioning and stability of their ecosystems [81]. Such complex

interactions are likely to establish during "windows of opportunity" (i.e. a short time window

in which environmental conditions drop long enough below the hostile average level)

allowing the organism enough time to develop tolerance and transition into more stable

existence [82]. Yet, while being considered a potential driving force for microbial

differentiation in important hyper-arid communities, such as those inhabiting rocks [83],

cooperative relationships have been directly observed in a relatively limited number of

communities (e.g., biocrusts) [84] and further manipulative studies and field surveys are

required to corroborate their role as an adaptation strategy in hyper-arid microbiomes.

REFERENCES

1. Lu N, Wang M, Ning B, Yu, D, Fu, B. Research advances in ecosystem services in drylands under global environmental changes. Curr. Opin. Environ. Sustain. 2018; 33:92–98.

2. Koutroulis, AG. Dryland changes under different levels of global warming. Sci. Total Environ. 2019;655:482–511.

3. Chevrier, V. F., Roy, R., Meslin, P. Y., Le Mouélic, S., Mathé, P. E., Rochette, P., & Bonello, G. Geochemical and spectral characterization of an altered Antarctic dolerite: implications for recent weathering on Mars. Planet. Space. Sci. 2020;194:105–106.

4. Davila, AF, Warren-Rhodes, K, DiRuggiero, J. The Atacama Desert: a window into late Mars surface habitability? in Mars Geological Enigmas (eds. Soare, S., Conway, S., Williams, J.-P. & Oehler, D.) 2021;333–355.

5. Martínez-Valderrama, J, Guirado, E, Maestre, FT. Desertifying deserts. Nat. Sustain. 2020;3: 572–575.

6. Wierzchos, J, de los Ríos A, Ascaso, C. Microorganisms in desert rocks: the edge of life on Earth. Int. Microbiol. 2012;15:173–183.

7. Leung, P. M., Bay, S. K., Meier, D. V., Chiri, E., Cowan, D. A., Gillor, O., et al. Energetic basis of microbial growth and persistence in desert ecosystems. mSystems 2020;5:e00495–19.

547   8.   Delgado-Baquerizo, M., Oliverio, A. M., Brewer, T. E., Benavent-González, A.,

548   Eldridge, D. J., Bardgett, R. D., et al. A global atlas of the dominant bacteria found in

549   soil. Science 2018;359:320–325.

550   9.   Maestre, F. T., Benito, B. M., Berdugo, M., Concostrina-Zubiri, L., Delgado-

551   Baquerizo, M., Eldridge, D. J., et al. Biogeography of global drylands. New Phytol.

552   2021;231:540–558.

553   10. Csotonyi, JT, Swiderski J, Stackebrandt, E, Yurkov V. A new environment for

554   aerobic anoxygenic phototrophic bacteria: biological soil crusts. Environ. Microbiol.

555   Rep. 2010;2: 651–656.

556   11. Hawksworth, DL, Grube, M. Lichens redefined as complex ecosystems. New Phytol.

557   2020;227:1281–1283.

558   12. Walker, JJ, Pace, NR. Endolithic microbial ecosystems. Annu. Rev. Microbiol.

559   2007;61:331–347.

560   13. Maestre, F. T., Delgado-Baquerizo, M., Jeffries, T. C., Eldridge, D. J., Ochoa, V.,

561   Gozalo, B., et al. Increasing aridity reduces soil microbial diversity and abundance in

562   global drylands. Proc. Natl. Acad. Sci. USA 2015;112:15684–15689.

563   14. Pombubpa, N, Pietrasiak, N, De Ley, P, Stajich, JE. Insights into dryland biocrust

564   microbiome: geography, soil depth and crust type affect biocrust microbial

565   communities and networks in Mojave Desert, USA. FEMS Microbiol. Ecol.

566   2020;96:fiaa125.

567   15. Ortiz, M., Leung, P. M., Shelley, G., Jirapanjawat, T., Nauer, P. A., Van Goethem,

568   M. W., et al. Multiple energy sources and metabolic strategies sustain microbial

569   diversity in Antarctic Desert soils. Proc. Natl. Acad. Sci. USA

570   2021;118:e2025322118.

571   16. Albanese, D., Coleine, C., Rota-Stabelli, O., Onofri, S., Tringe, S. G., Stajich, J. E.,

572   et al. Pre-cambrian roots of novel Antarctic cryptoendolithic bacterial lineages.

573   Microbiome 2021;9:63.

574   17. Cowan, D. A., Hopkins, D. W., Jones, B. E., Maggs-Kölling, G., Majewska, R., &

575   Ramond, J. B. Microbiomics of Namib Desert habitats. Extremophiles 2020;24:17–

576   29.

577   18. Trivedi, C., Reich, P. B., Maestre, F. T., Hu, H. W., Singh, B. K., & Delgado-

578   Baquerizo, M. Plant-driven niche differentiation of ammonia-oxidizing bacteria and

579   archaea in global drylands. ISME J. 2019;13:2727–2736.

580   19. Sterflinger, K, Tesei, D, Zakharova, K. Fungi in hot and cold deserts with particular

581   reference to microcolonial fungi. Fungal Ecol. 2012;5:453–462.

582 20. Makhalanyane, T. P., Valverde, A., Gunnigle, E., Frossard, A., Ramond, J. B., &

583   Cowan, D. A. Microbial ecology of hot desert edaphic systems. FEMS Microbiol.

584   Rev. 2015;39:203–221.

585 21. Egidi, E, Delgado-Baquerizo, M, Berdugo, M, Guirado, E, Albanese, D, Singh, BK,

586   Coleine, C. (2023). UV index and climate seasonality explain fungal community

587   turnover in global drylands. Global Ecol. Biogeogr. 2023;32(1):132-144.

588 22. Qu, E. B., Omelon, C. R., Oren, A., Meslier, V., Cowan, D. A., Maggs-Kölling, G.,

589   & DiRuggiero, J. Trophic selective pressures organize the composition of endolithic

590   microbial communities from global deserts. Front. Microbiol. 2019;10:2952.

591 23. Uritskiy, G., Tisza, M. J., Gelsinger, D. R., Munn, A., Taylor, J., & DiRuggiero, J.

592   Cellular life from the three domains and viruses are transcriptionally active in a

593   hypersaline desert community. Environ. Microbiol. 2021;23:3401–3417.

594 24. Kuzyakov, Y, Mason-Jones, K. Viruses in soil: nano-scale undead drivers of

595   microbial life, biogeochemical turnover and ecosystem functions. Soil Biol. Biochem.

596   2018;127:305–317.

597 25. Hwang, Y, Rahlff, J, Schulze-Makuch, D, Schloter, M, Probst, AJ. Diverse viruses

598   carrying genes for microbial extremotolerance in the Atacama Desert hyperarid soil.

599   mSystems 2021;6:e00385–21.

600 26. Adriaenssens, E. M., Kramer, R., Van Goethem, M. W., Makhalanyane, T. P., Hogg,

601   I., & Cowan, D. A. Environmental drivers of viral community composition in

602   Antarctic soils identified by viromics. Microbiome 2017;5:83.

603 27. Busse, L, Tisza, M, DiRuggiero, J. Viruses Ubiquity and Diversity in Atacama Desert

604   Endolithic Communities. Viruses, 2022;14(9):1983.

605 28. Ettinger, CL, Saunders, M, Selbmann, L, Delgado-Baquerizo, M, Donati, C,

606   Albanese, D, et al. Highly diverse and unknown viruses may enhance Antarctic

607   endoliths' adaptability. Microbiome 2023;11(1):1-8.

608 29. Oliverio, AM, Geisen, S, Delgado-Baquerizo, M, Maestre, FT, Turner, BL, Fierer, N.

609   The global-scale distributions of soil protists and their contributions to belowground

610   systems. Sci. Adv., 2020;6(4):eaax8787.

611 30. Delgado-Baquerizo, M., Doulcier, G., Eldridge, D. J., Stouffer, D. B., Maestre, F. T.,

612   Wang, J., et al. Increases in aridity lead to drastic shifts in the assembly of dryland

613   complex microbial networks. Land Degrad. Dev. 2020;31:346–355.

614 31. Burrell, AL, Evans, JP, De Kauwe, MG. Anthropogenic climate change has driven

19

615 over 5 million km of drylands towards desertification. Nat. Commun. 2020;11:3853
616 (2020).

617 32. Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao,
618 Y., Gaitán, J. J., et al. Global ecosystem thresholds driven by aridity. Science
619 2020;367:787–790.

620 33. Chai, R., Mao, J., Chen, H., Wang, Y., Shi, X., Jin, M., et al. Human-caused long-
621 term changes in global aridity. npj Clim. Atmos. Sci., 2021;4(1): 65.

622 34. Neilson, J.W., Califf, K., Cardona, C., Copeland, A., Van Treuren, W., Josephson,
623 K.L., et al. Significant impacts of increasing aridity on the arid soil microbiome.
624 MSystems 2017;2(3):10-1128.

625 35. Wang, C., Wang, X., Liu, D., Wu, H., Lü, X., Fang, Y., et al. Aridity threshold in
626 controlling ecosystem nitrogen cycling in arid and semi-arid grasslands. Nat.
627 Commun. 2014;5:4799.

628 36. Hu, W, Ran, J, Dong, L, Du, Q, Ji, M, Yao, S, et al. Aridity-driven shift in
629 biodiversity–soil multifunctionality relationships. Nat. Commun. 2021;12(1): 5350.

630 37. Ochoa-Hueso, R., Collins, S. L., Delgado-Baquerizo, M., Hamonts, K., Pockman, W.
631 T., Sinsabaugh, R. L., et al. Drought consistently alters the composition of soil fungal
632 and bacterial communities in grasslands from two continents. Glob. Chang. Biol.
633 2018;24:2818–2827.

634 38. Steven, B, Belnap, J, Kuske, CR. Chronic physical disturbance substantially alters the
635 response of biological soil crusts to a wetting pulse, as characterized by
636 metatranscriptomic sequencing. Front. Microbiol. 2018;9:2382.

637 39. Liu, Y. R., Delgado-Baquerizo, M., Trivedi, P., He, J. Z., Wang, J. T., & Singh, B. K.
638 Identity of biocrust species and microbial communities drive the response of soil
639 multifunctionality to simulated global change. Soil Biol. Biochem. 2017;107:208–
640 217.

641 40. Delgado-Baquerizo, M., Eldridge, D. J., Ochoa, V., Gozalo, B., Singh, B. K., &
642 Maestre, F. T. Soil microbial communities drive the resistance of ecosystem
643 multifunctionality to global change in drylands across the globe. Ecol. Lett.
644 2017;20:1295–1305.

645 41. Li, C, Liao, H, Xu, L, Wang, C, He, N, Wang, J, Li, X. The adjustment of life history
646 strategies drives the ecological adaptations of soil microbiota to aridity. Molecular
647 Ecol. 2022;31(10):2920–2934.

20

648 42. Zhang, C., Lei, S., Wu, H., Liao, L., Wang, X., Zhang, L., et al. Simplified microbial
649   network reduced microbial structure stability and soil functionality in alpine grassland
650   along a natural aridity gradient. Soil Biol. Biochem., 2024, 109366.

651 43. Malik, A.A., Swenson, T., Weihe, C., Morrison, E.W., Martiny, J.B., Brodie, E.L., et
652   al. Drought and plant litter chemistry alter microbial gene expression and metabolite
653   production. ISME J., 2020;14(9):2236–2247.

654 44. Zhang, X., Johnston, E. R., Li, L., Konstantinidis, K. T., Han, X. Experimental
655   warming reveals positive feedbacks to climate change in the Eurasian Steppe. ISME
656   J., 2017, *11*(4), 885-895.

657 45. Homyak, PM, Allison, SD, Huxman, TE, Goulden, ML, Treseder, KK. Effects of
658   drought manipulation on soil nitrogen cycling: A meta-analysis. Journal of
659   Geophysical Research: Biogeosciences 2017;122(12):3260–3272.

660 46. Zhang, W., Brandt, M., Penuelas, J., Guichard, F., Tong, X., Tian, F., & Fensholt, R.
661   Ecosystem structural changes controlled by altered rainfall climatology in tropical
662   savannas. Nat. Commun. 2019;10:671.

663 47. Gonsamo, A., Ciais, P., Miralles, D. G., Sitch, S., Dorigo, W., Lombardozzi, D., et al.
664   Greening drylands despite warming consistent with carbon dioxide fertilization effect.
665   Glob. Change Biol. 2021;27:3336–3349.

666 48. Zhu, Z., Piao, S., Myneni, R. B., Huang, M., Zeng, Z., Canadell, J. G., et al. Greening
667   of the Earth and its drivers. Nat. Clim. Change, 2016,*6*(8), 791-795.

668 49. Ogle, K. (2018). Hyperactive soil microbes might weaken the terrestrial carbon sink.

669 50. Piñeiro, J., Ochoa-Hueso, R., Delgado-Baquerizo, M., Dobrick, S., Reich, P. B.,
670   Pendall, E., Power, S. A. (2017). Effects of elevated CO2 on fine root biomass are
671   reduced by aridity but enhanced by soil nitrogen: A global assessment. Sci. Rep.,
672   2017;7(1):15355.

673 51. Wu, Y., Chen, D., Delgado-Baquerizo, M., Liu, S., Wang, B., Wu, J., .et al. Long-
674   term regional evidence of the effects of livestock grazing on soil microbial
675   community structure and functions in surface and deep soil layers. Soil Biol.
676   Biochem., 2022;168:108629.

677 52. Kuska, MT, Mahlein, AK. Aiming at decision making in plant disease protection and
678   phenotyping by the use of optical sensors. Eur. J. Plant Pathol., 2018;152:987-992.

679 53. Chowaniak, M., Głąb, T., Klima, K., Niemiec, M., Zaleski, T., & Zuzek, D. Effect of
680   tillage and crop management on runoff, soil erosion and organic carbon loss. Soil Use
681   Manag. 2020;36581–593.

21

682   54. Driscoll, D. A., Worboys, G. L., Allan, H., Banks, S. C., Beeton, N. J., Cherubin, R.
683   C., et al. Impacts of feral horses in the Australian Alps and evidence-based solutions.
684   Ecol. Manag. Restor. 2019;20:63–72.

685   55. Hackney, BF, Jenkins, J, Powells, J, Edwards, CE, De Meyer, S, Howieson, JG, et al.
686   Soil acidity and nutrient deficiency cause poor legume nodulation in the permanent
687   pasture and mixed farming zones of south-eastern Australia. Crop and Pasture Science
688   2019;70(12):1128-1140.

689   56. Orgiazzi, A, Panagos, P. Soil biodiversity and soil erosion: it is time to get married.
690   Glob. Ecol. Biogeogr. 2018;27:1155–1167.

691   57. Maestre, F. T., Le Bagousse-Pinguet, Y., Delgado-Baquerizo, M., Eldridge, D. J.,
692   Saiz, H., Berdugo, M., et al. Grazing and ecosystem service delivery in global
693   drylands. Science, 2022,*378*(6622), 915-920.

694   58. Risch, AC, Zimmermann, S, Schütz, M, Borer, ET, Broadbent, AAD, Caldeira, MC,
695   et al. Drivers of the microbial metabolic quotient across global grasslands. Glob. Ecol.
696   Biogeogr., 2023.

697   59. Jansson, JK, Hofmockel, KS. Soil microbiomes and climate change. Nat. Rev.
698   Microbiol. 2020;18:35–46.

699   60. Chamizo, S. Soil inoculation with cyanobacteria: reviewing its potential for
700   agriculture sustainability in drylands. Agric. Res. Technol. 2018;18

701   61. Maier, S., Tamm, A., Wu, D., Caesar, J., Grube, M., Weber, B. Photoautotrophic
702   organisms control microbial abundance, diversity, and physiology in different types of
703   biological soil crusts. ISME J. 2018;12:1032–1046.

704   62. Lau, JA, Lennon, J. T. Rapid responses of soil microorganisms improve plant fitness
705   in novel environments. Proc. Natl. Acad. Sci. USA 2012;109:14058–14062.

706   63. Harfouche, A. L., Jacobson, D. A., Kainer, D., Romero, J. C., Harfouche, A. H.,
707   Mugnozza, G. S., et al. Accelerating climate resilient plant breeding by applying next-
708   generation artificial intelligence. Trends Biotechnol. 2019;37:1217–1235.

709   64. Streich, J., Romero, J., Gazolla, J. G. F. M., Kainer, D., Cliff, A., Prates, E. T., et al.
710   Can exascale computing and explainable artificial intelligence applied to plant
711   biology deliver on the United Nations sustainable development goals?. Curr Opin.
712   Biotechnol., 2020;61:217-225.

713   65. Harfouche, AL, Nakhle, F, Harfouche, AH, Sardella, OG, Dart, E, Jacobson, DA.
714   primer on artificial intelligence in plant digital phenomics: embarking on the data to
715   insights journey. Trends Plant Sci., 2023;28(2):154-184.

22

716 66. Pereira, S., Zille, A., Micheletti, E., Moradas-Ferreira, P., De Philippis, R., &

717   Tamagnini, P. Complexity of cyanobacterial exopolysaccharides: composition,

718   structures, inducing factors and putative genes involved in their biosynthesis and

719   assembly. FEMS Microbiol. Rev. 2009;33:917–941.

720 67. Casero, MC, Ascaso, C, Quesada, A, Mazur-Marzec, H, Wierzchos, J. Response of

721   endolithic *Chroococcidiopsis* strains from the polyextreme Atacama Desert to light

722   radiation. Front. Microbiol. 11:614875 (2021).

723 68. Teichmann, L, Kümmel, H, Warmbold, B, Bremer, E. OpuF, a new *Bacillus*

724   compatible solute ABC transporter with a substrate-binding protein fused to the

725   transmembrane domain. Appl. Environ. Microbiol., 2018;84(20):e01728-18.

726 69. Uritskiy, G., Getsin, S., Munn, A., Gomez-Silva, B., Davila, A., Glass, B., et al.

727   Halophilic microbial community compositional shift after a rare rainfall in the

728   Atacama Desert. ISME J. 2019;13:2737–2749.

729 70. Chen, L., Deng, S., De Philippis, R., Tian, W., Wu, H., & Wang, J. UV-B resistance

730   as a criterion for the selection of desert microalgae to be utilized for inoculating desert

731   soils. Am. J. Appl. Psychol. 2013;25:1009–1015.

732 71. Coleine, C, Stajich, JE, Selbmann, L. Fungi are key players in extreme ecosystems.

733   Trends Ecol. Evol. (2022) doi:10.1016/j.tree.2022.02.002.

734 72. Oren, A. Thermodynamic limits to microbial life at high salt concentrations. Environ.

735   Microbiol. 2011;13:1908–1923.

736 73. Jordaan, K., Lappan, R., Dong, X., Aitkenhead, I. J., Bay, S. K., Chiri, E., et al.

737   Hydrogen-oxidizing bacteria are abundant in desert soils and strongly stimulated by

738   hydration. mSystems 2020;5:e01131–20.

739 74. Ray, A. E., Zaugg, J., Benaud, N., Chelliah, D. S., Bay, S., Wong, H. L., et al.

740   Atmospheric chemosynthesis is phylogenetically and geographically widespread and

741   contributes significantly to carbon fixation throughout cold deserts. ISME J.,

742   2020;16(11):2547-2560.

743 75. Cowan, D. A., Ferrari, B. C., McKay, C. P. (2022). Out of thin air? Astrobiology and

744   atmospheric chemotrophy. Astrobiology, *22*(2), 225-232.

745 76. Rodriguez-Caballero, E., Belnap, J., Büdel, B., Crutzen, P. J., Andreae, M. O.,

746   Pöschl, U., Weber, B. Dryland photoautotrophic soil surface communities endangered

747   by global change. Nat. Geosci. 2018;11:185–189.

748 77. Cowan, D. A., Sohm, J. A., Makhalanyane, T. P., Capone, D. G., Green, T. G. A.,

749   Cary, S. C., Tuffin, I. M. Hypolithic communities: important nitrogen sources in

750   Antarctic Desert soils. Environ. Microbiol. Rep. 2011;3:581–586.

751   78. Ertekin, E, Meslier, V, Browning, A, Treadgold, J, DiRuggiero, J. Rock structure

752   drives the taxonomic and functional diversity of endolithic microbial communities in

753   extreme environments. Environ. Microbiol. 2021;23:3937–3956.

754   79. Coleine, C., Albanese, D., Ray, A. E., Delgado-Baquerizo, M., Stajich, J. E.,

755   Williams, T. J., et al. Metagenomics untangles potential adaptations of Antarctic

756   endolithic bacteria at the fringe of habitability. Sci. Total Environ., 2024, *917*,

757   170290.

758   80. Cavaliere, M., Feng, S., Soyer, O. S., Jiménez, J. I. Cooperation in microbial

759   communities and their biotechnological applications. Environm. Microbiol., 2017,

760   *19*(8), 2949-2963.

761   81. Ciccarese, D., Micali, G., Borer, B., Ruan, C., Or, D., Johnson, D. R. Rare and

762   localized events stabilize microbial community composition and patterns of spatial

763   self-organization in a fluctuating environment. ISME J., 2022, *16*(5), 1453-1463.

764   82. van Belzen, J., Fivash, G. S., Hu, Z., Bouma, T. J., Herman, P. M. A probabilistic

765   framework for windows of opportunity: the role of temporal variability in critical

766   transitions. J. R. Soc. Interface., 2022, *19*(190), 20220041.

767   83. Coleine, C., Delgado-Baquerizo, M., Albanese, D., Singh, B. K., Stajich, J. E.,

768   Selbmann, L., Egidi, E. Rocks support a distinctive and consistent mycobiome across

769   contrasting dry regions of Earth. FEMS Microbiol. Ecol. 2022;98:fiac030.

770   84. Rossi, F., Mugnai, G., De Philippis, R. Complex role of the polymeric matrix in

771   biological soil crusts. Plant and Soil, 2018, *429*, 19-34.

772   85. Egidi, E., Delgado-Baquerizo, M., Plett, J. M., Wang, J., Eldridge, D. J., Bardgett, R.

773   D., et al. A few Ascomycota taxa dominate soil fungal communities worldwide. Nat.

774   Commun. 2019;10:2369.

775   86. Meslier, V., Casero, M. C., Dailey, M., Wierzchos, J., Ascaso, C., Artieda, O., et al.

776   Fundamental drivers for endolithic microbial community assemblies in the hyperarid

777   Atacama desert. Environ. Microbiol., *20*, 1765–1781 (2018).

778   87. Lebre, P. H., De Maayer, P. Cowan, D. A. Xerotolerant bacteria: surviving through a

779   dry spell. Nat. Rev. Microbiol., 2017*, 15*, 285–296.

780   88. Finstad, K. M., Probst, A. J., Thomas, B. C., Andersen, G. L., Demergasso, C.,

781   Echeverría, A., et al. Microbial community structure and the persistence of

782   cyanobacterial populations in salt crusts of the hyperarid Atacama Desert from

783   genome resolved metagenomics. Front. Microbiol., 2017, 8, 1435.

24

784   89. Lacap-Bugler, D. C., Lee, K. K., Archer, S., Gillman, L. N., Lau, M. C., Lee, C. K.,

785   et al. Global diversity of desert hypolithic cyanobacteria. Front. Microbiol. 2017, 8,

786   248744.

787

788   **AUTHORS CONTRIBUTIONS**

789   C.C., E.E., M.D-B., J.D.R., B.K.S., and A.H. formulated the review and identified the themes

790   to be covered, with contributions from all co-authors. C.C., E.E., J.D.R., and A.L.H.

791   developed and designed the figures. All authors contributed to the first draft of the

792   manuscript and edited the article before submission.

809   **Ethics declarations**

810   **Ethics approval and consent to participate**

811   Not applicable.

812

813   **Consent for publication**

814   All authors consent to publication of this article.

815 **COMPETING INTERESTS**

816 The authors declare that they have no competing interests.
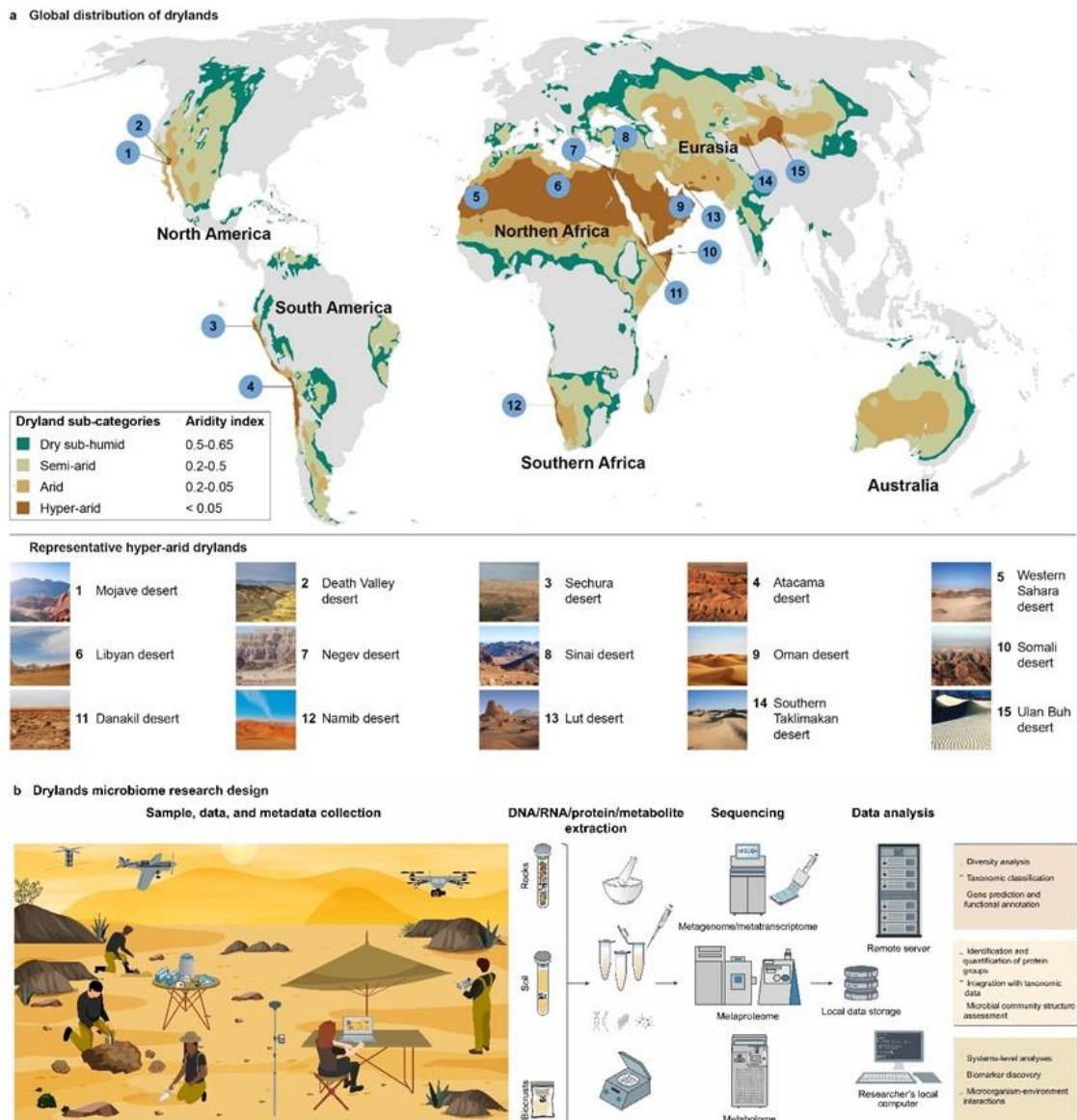
818
819 **Fig. 1. Global distribution and microbiome research design of drylands.** (a).Distribution of
820 drylands worldwide according to the United Nations (UN) Convention to Combat Desertification and
821 the Convention on Biological Diversity definitions using the aridity zone map created by the UN
822 Environment Programme Drylands are categorized into four sub-groups (each marked with a specific
823 color) based on their aridity index. Sites of fifteen representative global hyper-arid drylands are
824 marked on the map (b). Schematic illustration of drylands microbiome research, from designing the
825 experiment to collecting time-series samples and high-resolution data, analyzing meta-omics datasets
826 and to providing insights into microbial ecosystems response to desertification and climate change
827 Remote sensing platforms based on large and small satellite (CubeSat) constellations that work in
828 unison as well as unmanned aerial vehicles (coordinated teams of drones) carrying imaging sensors
829 (red-green-blue (RGB), multispectral, hyperspectral, thermal infrared, and light detection and ranging
830 (LiDAR)) offer new ways to study dryland microbiome ecosystems and dynamics by providing
831 spectroscopic and ranging data and capturing finer detail of biodiversity, including the microbial soil,
832 biocrusts, and rocks inhabitants. Microbiome data (metagenomics, metatranscriptomics,

833 metaproteomics, and metabolomics) of soil, rocks, and biocrusts, generated by state-of-the-art high-
834 throughput sequencing platforms, allow for rapid time course studies and large sample analyses.
835 Biological samples are labeled with quick response codes and information about each sample (when it
836 was collected, where it was collected from, what kind of sample it is, and what were the
837 environmental conditions at the time of sampling) and methods used in the experiments should be
838 recorded in the experimental metadata Data and metadata are stored locally on a data storage device
839 (e.g., a network attached storage), accessed by the researcher's local computer, and transmitted to a
840 remote server, with significant computing power, to analyze meta-omics data and their associated
841 metadata.
842

28

a   Microbial diversity of drylands soil

Dry sub-humid   Semi-arid   Arid

Bacteria

Acidimicrobiia	Bacteroidia
Acidobacteriia	Blastocatellia
Actinobacteria	Chloroflexia
Alphaproteobacteria	Deltaproteobacteria

Gammaproteobacteria	Phycisphaerae
Gemmatimonadetes	Planctomycetacia
KD4-96	Rubrobacteria
MB-A2-108	Thermoleophilia

Verrucomicrobiae

Dry sub-humid   Semi-arid   Arid

Fungi

Agaricomycetes	Dothideomycetes
Agaricostilbomycetes	Eurotiomycetes
Archaeorhizomycetes	GS35

Lecanoromycetes	Olpidiomycetes
Leotiomycetes	Paraglomeromycetes
Lichinomycetes	Pezizomycetes

Pezizomycotina	
Taphrinomycetes	
Tritirachiomycetes	

b   Microbial diversity of dryland biocrusts and lithic habitats

Biocrusts   Rocks   Halite

Acidobacteria	Chloroflexi
Actinobacteria	Crenarchaeota
Armatimonadetes	Cyanobacteria
Bacteroidetes	Deinococcus/Thermi

Euryarchaeota	Proteobacteria
Firmicutes	Nitrososphaerota
Gemmatimonadetes	Verrucomicrobia
Planctomycetes	Others

c   Overview of the most representative genera in drylands

| Microbial taxonomy	Phylum	Family	Genus	Soil	Biocrusts	Rocks
Bacteria	Actinobacteria	Geodermatophilaceae	Geodermatophilus	✓		
		Streptomycetaceae	Streptomyces	✓		
	Bacteroidetes	Salinibacteraceae	Salinibacter	✓	✓	
	Cyanobacteria	Cyanophyceae	Chroococcidiopsis	✓	✓	✓
			Nostoc	✓	✓	✓
			Scynotema		✓	
	Firmicutes	Bacillaceae	Bacillus	✓		
	Proteobacteria	Sphingomonadaceae	Sphingomonas	✓		
		Azotobacteraceae	Azotobacter	✓		✓
Archaea	Euryarchaeota	Halococcaceae	Halococcus		✓	✓
	Nanohalarchaeota	Nanosalinaceae	Candidatus Nanopetramus			✓
	Nitrososphaerota	Nitrososphaeraceae	Nitrososphaera	✓		
		-	Candidatus Nitrosodeserticola	✓		
Fungi	Ascomycota	Cladosporiaceae	Cladosporium	✓		
		Incertae sedis	Cryomyces			✓
		Hypocreaceae	Acremomium		✓	
		Lecanoraceae	Carbonea		✓	✓
			Lecidella		✓	✓
		Lentitheciaceae	Darksidea	✓		
		Pleosporaceae	Alternaria	✓	✓	
		Teratosphaeriaceae	Friedmanniomyces			✓
			Neocatenulostroma			✓
Algae	Chlorophyta	Dunaliellaceae	Dunaliella	✓		✓
		Mamiellaceae	Dolichomastix			✓
		Trebouxiophyceae	Trebouxia	✓	✓	✓
Virus	Uroviricota	Siphoviridae	-	✓	✓	✓
		Myoviridae	-	✓	✓	✓
		Podoviridae	-	✓	✓	✓

843

Fig. 2. Overview of drylands microbiome diversity. (a). Relative abundances of different bacterial and fungal groups at the global scale. Relative abundances were calculated based on the number of reads retrieved by amplicon sequencing (16S ribosomal RNA (rRNA) gene and internal transcribed spacer (ITS) regions for bacteria and fungi, respectively). 16S rRNA and ITS datasets were obtained from soil global datasets [8, 85], which include samples collected in drylands ranging from sub-humid

849 to arid regions (Spain (Europe)), China, Australia, North Africa, North America, and South America).
850 (b). Most abundant microbial taxa found in biocrusts, rocks, and halites based on data from [14, 22,
851 61, 69, 78, 86-89]. Data are presented from samples collected in dry regions worldwide, including
852 Colorado Plateau (Colorado) Mojave Desert and Joshua Tree National Park (California), Canadian
853 Arctic (Canada), Victoria Land (Continental Antarctica), Atacama Desert (Chile), Negev Desert
854 (Israel), Northern Cape Province (South Africa), Libyan Desert, Australia, and Taklimakan Desert
855 and Tibetan Plateau (China). (c). Microbial taxonomy, phylum, family- and genus-level assignments,
856 and ecological niches of the most notable examples of dryland microorganisms. Hyphens (-) mean
857 that the taxonomy classification of sequences is not available at a given level. KD4-96, uncultured
858 *Chloroflexi*; MB-A2-108, uncultured *Actinobacteria*; GS35, uncultured *Ascomycota*.

859
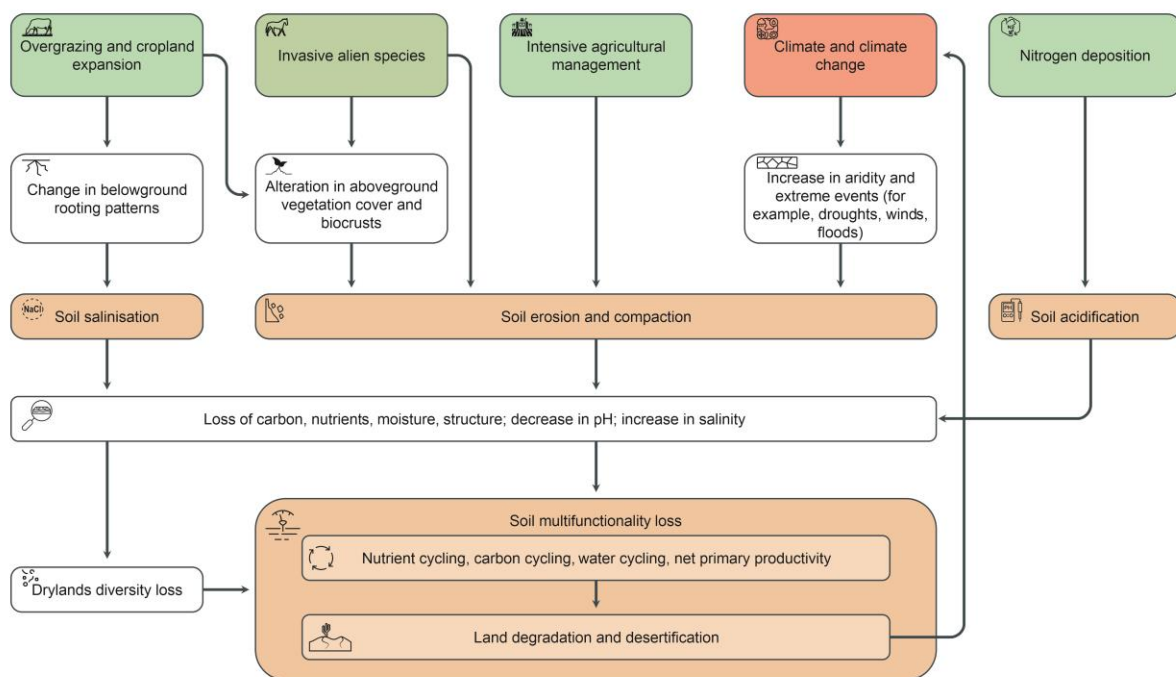
860

861 **Fig. 3. Drivers of land degradation and desertification in drylands.** Dryland soils are vulnerable to
862 a range of physical (e.g., increase in aridity, droughts, winds, and floods), human-induced (e.g.,
863 nitrogen deposition via fertilization, overgrazing and intensive cropping), and biotic (e.g., invasive
864 alien species) disturbances. These disturbances increase the rate of soil salinization, erosion and
865 compaction, whose consequences include both direct effects (e.g., shifts in microbial community
866 composition and biodiversity loss) and indirect impacts via changes in physico-chemical soil
867 properties (e.g., loss of carbon, nutrients, moisture, structure, decrease in pH, and increase in salinity).
868 If not properly managed, these pressures can result in land degradation and, in arid areas,
869 desertification, which will further accelerate the rate of climate change. Through cascading effects, the
870 drylands microbiome can ultimately impact ecosystem health and functioning.
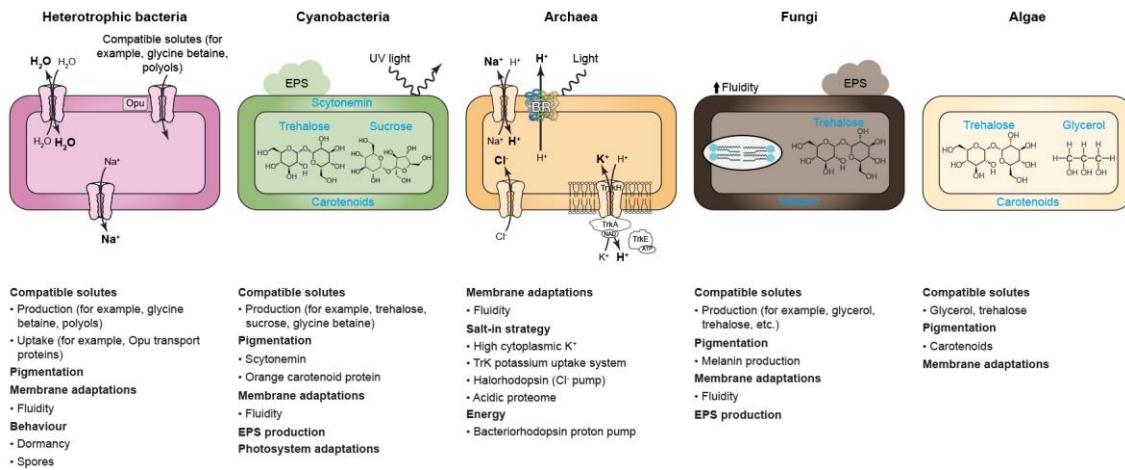
871

872
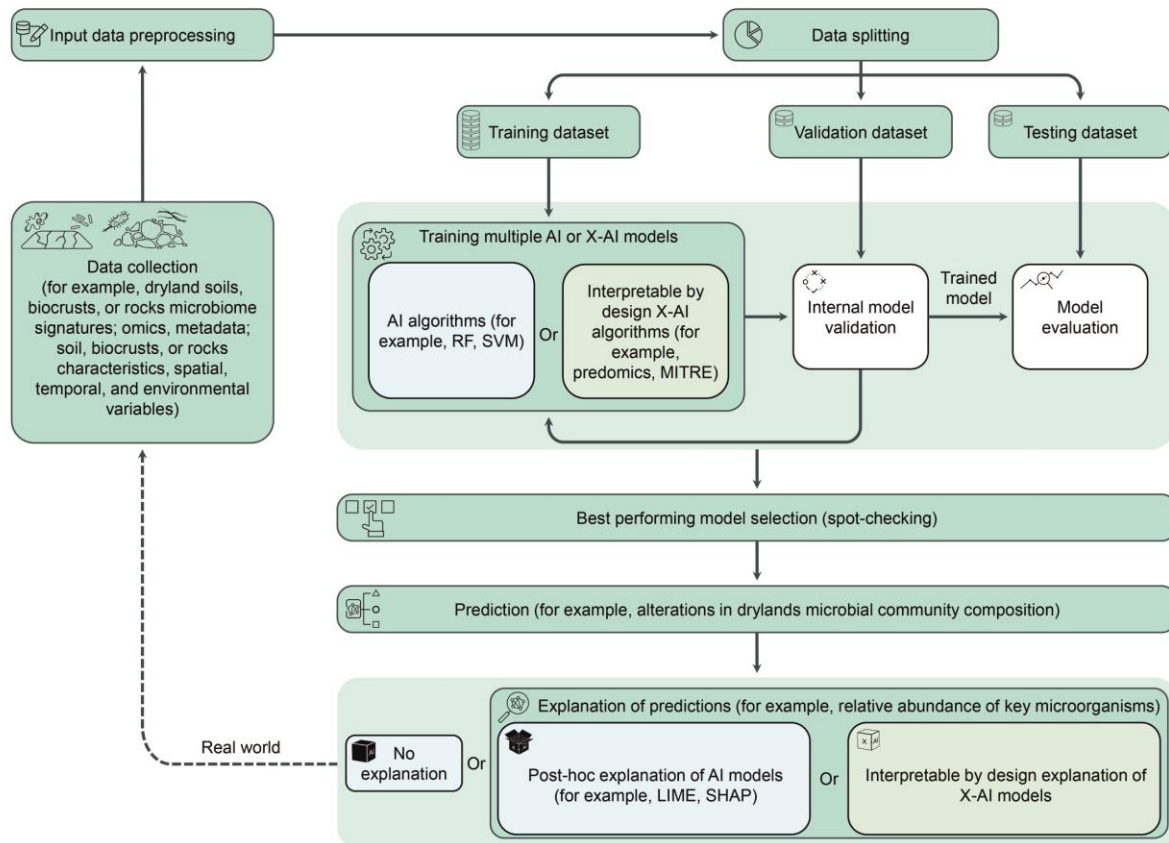
Fig. 4. A hypothetical example of applying artificial intelligence (AI) to microbiome research.
For instance, for searching for microbial signatures to predict alterations in microbial communities in
dryland soils, biocrusts, or rock samples. Real-world data are converted to a clean dataset to be used
as input for the algorithm through data preprocessing. Data is then split into three subsets: training
dataset used to fit the model, validation dataset for internal validation of the model where its accuracy
is estimated and hyper parameters are tuned, and testing dataset to provide an unbiased evaluation of
the final model. Multiple AI algorithms such as random forest (RF) and support vector machine
(SVM) or interpretable by design X-AI algorithms such as predomics and MITRE can be trained at
the same time using the same dataset. A model from the best-performing algorithm is selected through
spot-checking to make predictions. Producing explanations revolve around two approaches: using
post-hoc algorithms like Shapley additive explanations (SHAP) or local interpretable model-agnostic
explanations (LIME) to open the black box by identifying important patterns and features underlying
their predictions, or using interpretable by design models to explain their own predictions.

886

Heterotrophic bacteria

Compatible solutes
- Production (for example, glycine betaine, polyols)
- Uptake (for example, Opu transport proteins)

Pigmentation

Membrane adaptations
- Fluidity

Behaviour
- Dormancy
- Spores

Cyanobacteria

Compatible solutes
- Production (for example, trehalose, sucrose, glycine betaine)

Pigmentation
- Scytonemin
- Orange carotenoid protein

Membrane adaptations
- Fluidity

EPS production

Photosystem adaptations

Archaea

Membrane adaptations
- Fluidity

Salt-in strategy
- High cytoplasmic K^+
- TrK potassium uptake system
- Halorhodopsin (Cl- pump)
- Acidic proteome

Energy
- Bacteriorhodopsin proton pump

Fungi

Compatible solutes
- Production (for example, glycerol, trehalose, etc.)

Pigmentation
- Melanin production

Membrane adaptations
- Fluidity

EPS production

Algae

Compatible solutes
- Glycerol, trehalose

Pigmentation
- Carotenoids

Membrane adaptations

887

888 **Box 1 Figure Legend**

889 **Major molecular and cellular adaptations of dryland microorganisms.** The figure depicts
890 examples of the main adaptation strategies (compatible solutes, pigmentation, membrane adaptations,
891 extracellular polymeric substance (EPS) production, salt-in strategy, photosystem adaptations, energy,
892 and behavior) of dryland microorganisms according to their taxonomic classification (heterotrophic
893 bacteria, cyanobacteria, archaea, fungi, and algae). ATP, adenosine triphosphate; BR,
894 bacteriorhodopsin; Cl-, chloride anion; H^+, hydrogen ion; H_2O, water; Na^+, sodium ion; NAD,
895 nicotinamide adenine dinucleotide; Opu, osmoprotectant uptake; K^+, potassium ion; Trk, potassium
896 uptake system, including TrkA, TrkE and TrkH proteins; UV, ultraviolet.

897