



Review

'Follow the Water': Microbial Water Acquisition in Desert Soils

Don A Cowan ^{1,*}, S. Craig Cary ², Jocelyne DiRuggiero ³ , Frank Eckardt ⁴, Belinda Ferrari ⁵ , David W. Hopkins ⁶, Pedro H. Lebre ¹, Gillian Maggs-Kölling ⁷, Stephen B. Pointing ⁸, Jean-Baptiste Ramond ^{1,9} , Dana Tribbia ⁵ and Kimberley Warren-Rhodes ¹⁰

- ¹ Centre for Microbial Ecology and Genomics, Department of Biochemistry, Genetics and Microbiology, University of Pretoria, Pretoria 0002, South Africa; pedro.lebre@up.ac.za (P.H.L.); jbramond@bio.puc.cl (J.-B.R.)
- ² School of Biological Sciences, University of Waikato, Hamilton 3216, New Zealand; craig.cary@waikato.ac.nz
- ³ Departments of Earth and Biology and Planetary Sciences, Johns Hopkins University, Baltimore, MD 21218, USA; jdiruggiero@jhu.edu
- ⁴ Department of Environmental and Geographical Science, University of Cape Town, Cape Town 7701, South Africa; frank.eckardt@uct.ac.za
- ⁵ School of Biotechnology and Biological Sciences, University of New South Wales, Sydney, NSW 2052, Australia; b.ferrari@unsw.edu.au (B.F.); d.tribbia@student.unsw.edu.au (D.T.)
- ⁶ Scotland's Rural College, West Mains Road, Edinburgh EH9 3JG, UK; david.hopkins@sruc.ac.uk
- ⁷ Gobabeb-Namib Research Institute, Walvis Bay 13013, Namibia; gillian@gobabeb.org
- ⁸ Department of Biological Sciences, National University of Singapore, Singapore 117558, Singapore; yncpsb@nus.edu.sg
- ⁹ Departamento Genética Molecular y Microbiología, Pontificia Universidad Católica de Chile, Santiago 7820436, Chile
- ¹⁰ NASA Ames Research Center, Moffett Field, CA 94035, USA; kim_lamma@yahoo.com
- * Correspondence: don.cowan@up.ac.za; Tel.: +27-82-879-9117

Abstract: Water availability is the dominant driver of microbial community structure and function in desert soils. However, these habitats typically only receive very infrequent large-scale water inputs (e.g., from precipitation and/or run-off). In light of recent studies, the paradigm that desert soil microorganisms are largely dormant under xeric conditions is questionable. Gene expression profiling of microbial communities in desert soils suggests that many microbial taxa retain some metabolic functionality, even under severely xeric conditions. It, therefore, follows that other, less obvious sources of water may sustain the microbial cellular and community functionality in desert soil niches. Such sources include a range of precipitation and condensation processes, including rainfall, snow, dew, fog, and nocturnal distillation, all of which may vary quantitatively depending on the location and geomorphological characteristics of the desert ecosystem. Other more obscure sources of bioavailable water may include groundwater-derived water vapour, hydrated minerals, and metabolic hydro-genesis. Here, we explore the possible sources of bioavailable water in the context of microbial survival and function in xeric desert soils. With global climate change projected to have profound effects on both hot and cold deserts, we also explore the potential impacts of climate-induced changes in water availability on soil microbiomes in these extreme environments.

Keywords: anhydrobiosis; desert soils; hyper-arid; microbiomes; desiccation; xerophily; moisture stress; water activity; water availability



Citation: Cowan, D.A.; Cary, S.C.; DiRuggiero, J.; Eckardt, F.; Ferrari, B.; Hopkins, D.W.; Lebre, P.H.; Maggs-Kölling, G.; Pointing, S.B.; Ramond, J.-B.; et al. 'Follow the Water': Microbial Water Acquisition in Desert Soils. *Microorganisms* **2023**, *11*, 1670. <https://doi.org/10.3390/microorganisms11071670>

Academic Editor: Lucia Cavalca

Received: 3 May 2023

Revised: 12 June 2023

Accepted: 16 June 2023

Published: 27 June 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

"Where there is water, there is life". This concept is believed to be almost universally true and has been a guiding principle in the search of past, and even extant, life on other planets [1–3]. Understanding how, and from where, microorganisms in xeric habitats can acquire water to support survival and metabolic activity is critical in understanding the functional ecology of Earth's drylands and how their soil microbiomes may respond to the effects of global climate change.

Water availability is widely accepted as the dominant driving force for the structure and function of microbial communities in both hot and cold desert soils [4–8]. Much microbial life on Earth cannot undergo cell division below a water activity of approx. 0.900, which is equivalent to a relative humidity of 90.0% [8,9]. Similarly, most microorganisms also cannot exhibit higher-order metabolic functions (such as respiration or photosynthesis) under conditions that are dryer than the lower water-activity value for cell division [10]. The exceptions are a small number of xerophilic or halophilic taxa that possess functional adaptations supporting cellular growth functions at lower water activity levels [8,10]. The apparent constraints of low water availability notwithstanding, even the most hyper-arid hot deserts, such as in the Atacama, the Namib, and the Sahara, harbour substantial populations of viable and functional microorganisms in soils and lithic niches [11–14].

However, many other parts of the biosphere, including Earth's subsurface and atmosphere, may exist, permanently or transiently, in a state of limited water activity. Much of the Earth's atmosphere, which represents a large-scale repository of microbial life [15,16], has a relative humidity of less than 80% [17].

The mandatory requirement for water is more exacting, however, and should probably be rephrased as 'where there is liquid water, there is life'. We acknowledge notable exceptions, such as the super-heated emission fluids of deep-sea hydrothermal vents [18] where temperatures are much too high ($>>120\text{ }^{\circ}\text{C}$) to sustain life. Those few terrestrial habitats where water is present but never (or very rarely) in a liquid form, such as the extreme polar deserts [19–21], harbour few (or possibly no) viable microorganisms. The apparent anomaly may be permafrost where, despite permanently frozen conditions, substantial populations of viable microorganisms exist [22], and there is solid evidence for in situ metabolic activity [23,24]. The possibility of micro-scale solute-rich liquid inclusions in permafrost horizons, containing metabolically active microorganisms, has been considered [25], but has not been definitively demonstrated.

There is also recent evidence that dry surfaces may acquire thin films or micrometre-sized droplets of water [26] that can support microbial survival during periods of desiccation. While this process has only been demonstrated on leaf surfaces and is driven by the deliquescence of aerosol-derived hygroscopic particles [27], it is not unreasonable to assume that similar processes may occur on rock surfaces, particularly where marine aerosols could provide a steady input of hygroscopic marine salts. This process might be of particular significance as a source of water input to exposed rock surfaces in coastal deserts, such as the Namib [28] and Atacama [29,30].

Given the current trends in global warming and the predictions of expanding deserts and drylands [31], we believe that developing understanding of complex interactions between soils, microbiomes, and the hydrological cycle is particularly important. Understanding both the qualitative and quantitative aspects of microbial water acquisition in desert soils may result in a re-evaluation of the functional roles, and ultimately, the ecosystem services, of desert soil microbiomes.

Here, we examine the potential sources of water for desert-soil microorganisms, the mechanisms by which microbial cells may access water, and the implications of global climate change for desert soil microbial communities.

2. Desert Soils and Their Water-Holding Capacity

Soils in deserts are typically classified within 5 of the 32 major soil groups in the FAO's World Reference Base for soils [32]; however, there is no single group that exclusively covers desert soils. The five most common soils in deserts are Arenosols, Leptosols, Cambisols, Calcisols, and Solonchaks. Arenosols are sandy soils that are usually easily eroded and have low water- and nutrient-holding capacities, typical of coastal and inland dunes and sand seas. Leptosols are thin soils over rock or gravel. Cambisols are relatively young soils in terms of pedogenic development (although more developed than Arenosols and Leptosols). Calcisols are soils with accumulations of calcium carbonate usually precipitated from the soil water due to evaporation at the surface. Solonchaks are soils in arid regions

with concentrations of salts due to evaporation (in contrast to highly salt-containing soils in coastal regions). Combinations of limited water and nutrient contents, shallowness, impenetrable hard layers, and high osmotic potential typically lead to limited water accessibility, restricting soil biological activity.

The distribution of water in a porous soil matrix is thermodynamically driven by a maximisation of the surface interactions with the internal surfaces of pores and voids. The surface interactions, including capillarity, lead to the narrowest pores becoming water-filled first when soil is gradually wetted, followed progressively larger pores. The water potential (effectively the force with which water is held in the soil pore space) is the combination of the matric effects (e.g., pore size distribution, pore connectivity, and neck size constrictions), pressure, humidity, gravity, and solute pressures, where these combined forces must be overcome for effective water extraction by plant roots or microorganisms. Under conditions of extreme dryness, liquid water is held only in the smallest soil pores and may therefore be inaccessible to soil microorganisms [33]. However, for many desert soils, where the sand-sized fraction predominates, pore distribution is dominated by larger pores because of the lower packing density of sand particles, and therefore, smaller forces acting to retain water; thus, physical accessibility is less of a restriction than the actual scarcity of water.

3. Sources of Bioavailable Water in Desert Ecosystems

3.1. Rainfall

Rainfall is the most obvious source of liquid water for Earth's terrestrial ecosystems. However, some hot deserts experience decadal periods between precipitation events [34], and some extremely cold deserts, such as the Antarctic McMurdo Dry Valleys, very rarely receive rainfall [35]. Precipitation events in the latter are in the form of occasional snowfall, where much of the settled snow does not melt but is lost back to the atmosphere via sublimation [36]. Surface snowmelt may only wet the upper 0.5–1.0 cm of soil (Figure 1 in [37]; Cowan, unpublished observations: see Figure 1a). Snow deposition on dry mineral surfaces is thought to provide water for shallow subsurface (2 to 5 mm depth) cryptoendolithic microbial communities [38].

The extent to which, and duration for which, soils retain water after precipitation is highly relevant to the capacity for soil microbiome functionality. Where present on desert soil surfaces, biological soil crusts (BSCs) are important in retaining precipitation that would otherwise be lost by evaporation or rapid infiltration to subsurface soil [39]. Both soil structure and composition are important in water retention [40] where, for example, clays such as sepiolite, palygorskite, and smectite, often associated with arid soil environments and evaporitic rock substrates, exhibit a very high water-holding capacity (250% of wt [16,41,42]). Organic substances in soils, such as plant biomass, humic acids, and particularly microbial extracellular polymeric substances (EPSs), are very hygroscopic. Water is less readily lost to evaporation or filtration in saline soils [43] and, while water in saline soils is generally considered to be less available for plant uptake, the hygroscopic matrices of microbial biofilms may compete effectively for salt- and clay-bound water [44].

Although long-term precipitation patterns in hyper-arid deserts, coupled with very high evaporation rates, may suggest that persistent microbial communities are not sustainable [45], there is clear evidence that specialized niches in below-ground soils and endoliths offer ephemeral microbial habitats after significant stochastic rainfall episodes [14,46–48].

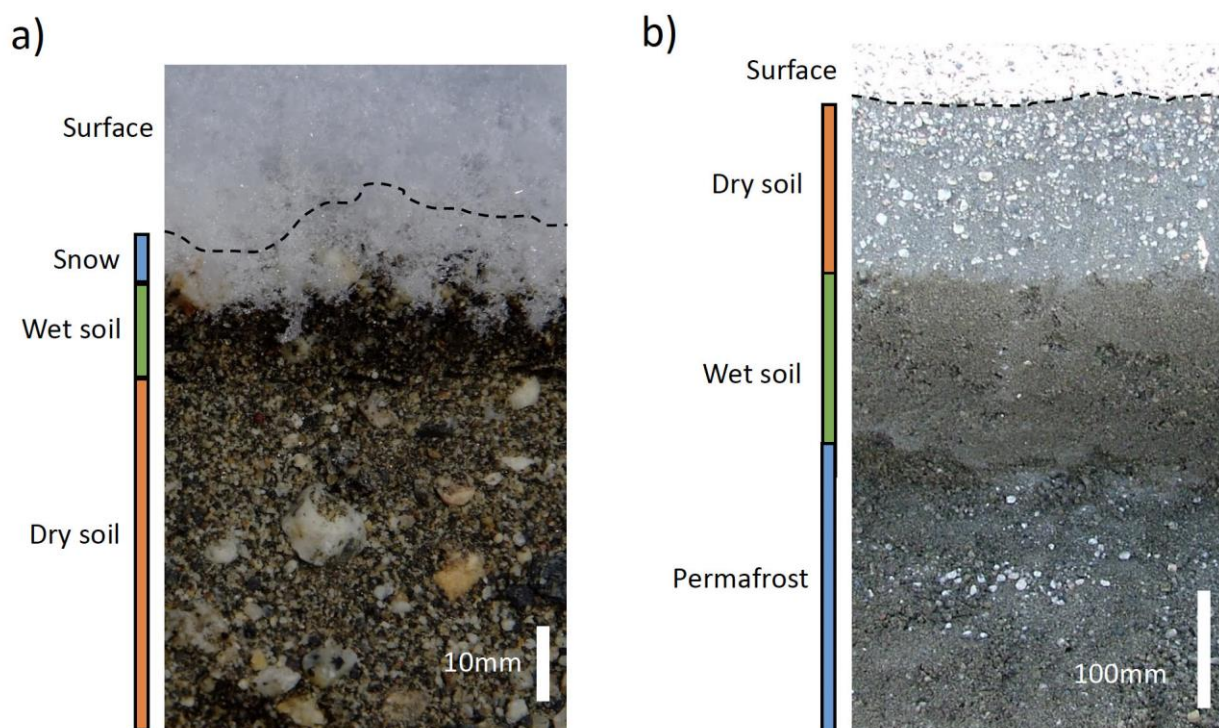


Figure 1. (a) Moist surface horizon (approx. 10 mm) from snowmelt (Miers Valley, East Antarctica, January 2012); (b) soil horizon profile, showing dry surface mineral soils, moistened active horizon, and frozen (permafrost) zone (Miers Valley, East Antarctica, January 2008).

3.2. Glacial Ice

Icecaps and other glacial masses might be considered as desert-like ecosystems, in that the consistently low temperatures typically characterizing all but the surface horizons of such environments can ensure that water is rarely, if ever, present in bioavailable liquid form. However, liquid water can exist on both the upper and lower surfaces of many glacial masses. For example, biologically active surface microbial communities are associated with the localized melting of many glacial masses, snow algae and cryoconite communities being two well-known examples. Both communities acquire liquid water from the frozen snow/ice substrate through the same mechanism: a reduction in albedo (reflected incident light) corresponding to an increase in the absorption of solar radiation (solar gain) [49]. In snow and ice algae (mostly *Chlamydomonadales* and *Zygnematales*, respectively), astaxanthin- and purpurogallan-rich pigmented cells absorb solar radiation with an associated heat-gain that melts frozen water (snow/ice) in the immediate vicinity of the cells [49]. Similarly, cryoconite holes are created by the deposition of dust particles and rock fragments/pebbles on snow and ice surfaces. The dark mineral particles are warmed by the absorption of solar radiation, and generate melt-wells in the ice surface, which rapidly become rich oases of metabolically active microbial life [50]. On the undersides of glacial masses, heat, generated by friction between the ice mass and the underlying rock surface, generates meltwater; sub-glacial liquid systems support substantial microbial populations [51].

3.3. Dew and Fog

In desert soil ecosystems, water may be available in the form of dew or fog inputs. Dew formation results from a balance between atmospheric relative humidity and temperature, where condensation occurs on surfaces when the balance exceeds the 'dew point' [52]. Dewfall is a relatively common occurrence in many hot semi-arid and arid (but not hyper-arid) deserts (up to 200 days per annum in some Negev Desert locations [53]) and is likely to make a significant contribution to the water input budgets of the surface (0–1 cm depth)

soils [54] and their microbiomes. Dew water input in the Badain Jaran Desert (northwest China) over a 5-month period amounted to a total of 3.4 mm, averaging 0.06 mm d^{-1} [55]. Dew is thought to be an important supplementary water source for desert vegetation. Soil surface lichens and surface microbiological communities (BSCs) have been shown to benefit from dew water inputs [56–58]. In the Atacama Desert, characteristic microkarstic features found on the surface layers of calcite rocks indicated that dew deposition might be an important source of liquid water for the endolithic communities inhabiting the calcite rock [30].

Fog water inputs are restricted to a limited number of coastal desert ecosystems, most notably the Namib (Namibia, south-western Africa) and Atacama (north-west Chile) deserts [34,59]. In the Namib Desert, fog generated off-shore by moist air over the Benguela Current is driven inland at night by onshore wind-flows, and can penetrate inland up to around 60 km [34]. At the coast, fog events are frequent (est. 40% events per annum [60]) and sustain extensive and well-characterized lichen fields [61]. This conclusion was recently supported by an extensive remote sensing drone survey of coastal Namib Desert lichen fields using advanced photogrammetry, which showed that *Xanthoparmelia* and *Stellanranga* spp. preferentially colonized ocean-facing rock surfaces, i.e., the direction from which fog originates [62].

Further inland, water capture from less frequent fog events sustains both specialist plants (e.g., Speargrass (*Stipagrostis sabulicola*) [63] and insect species (e.g., dune tenebrionid beetles [64]). However, salts and clay minerals may remain hydrated. In the Tarapacá Region of the Atacama Desert, gypsum crusts colonized by epilithic lichens and endolithic bacteria benefit from the coastal fog, called ‘camanchaca’, charged with humid air with a relative humidity close to 100% [65]. These frequent fog events [59] result in the continuous deliquescence of halite nodules in local salars, providing constant liquid water to the communities inhabiting the salt rocks [66,67]. This is also the only location in the desert where halite communities harbour the only eukaryote found in this system, a novel *Dolichomastix* alga [68].

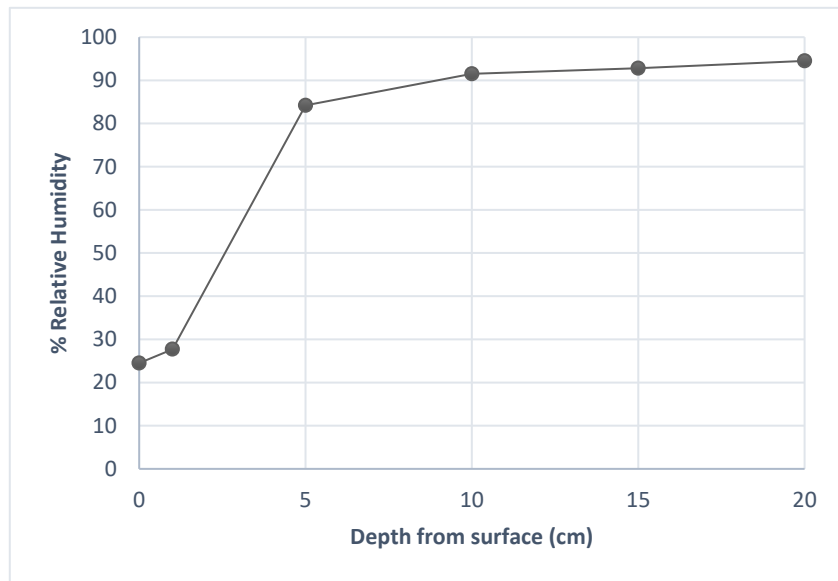
The role of fog water inputs in supporting soil microbiomes is much less clear. There is growing evidence that fog capture contributes bioavailable water for cryptic hypolithic communities [69], and supports microbial communities associated with desert plant rhizosheaths [70]. However, with the exception of some specialized plant species such as *S. sabulicola*, where captured fog water is channelled by specially adapted leaf structures down to the root zone [63], fog-derived water inputs are unlikely to penetrate, as liquid, to more than a few millimetres depth in desert pavements.

3.4. Groundwater

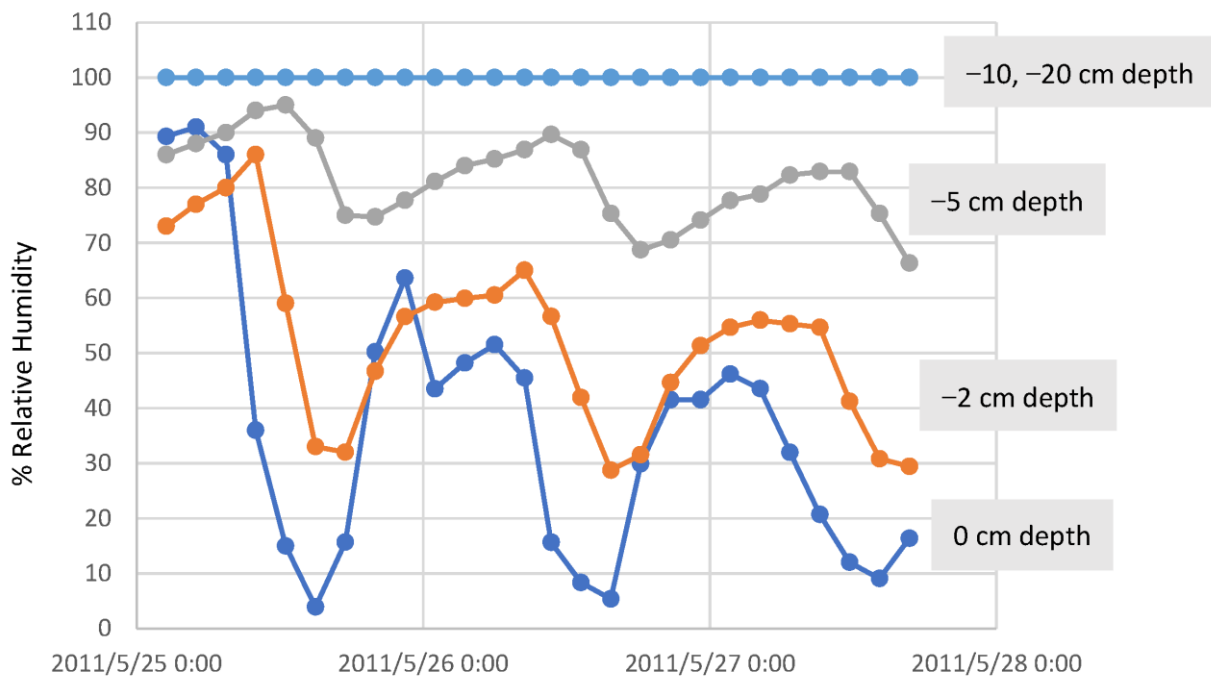
Even in the driest of deserts, water is present, but not always bioavailable. In cold deserts, permafrost layers, which may exist a few tens of centimetres or a few metres from the desiccated surface, are a potential source of bioavailable water for soil microbiomes [71]. The hydrologically active zone, the horizon above the permafrost that thaws and refreezes with seasonal cycles, provides a saturated soil profile at some distance below the desiccated surface horizon (Figure 1b). In some Antarctic and Arctic regions, such as the Windmill Islands (Ferrari, pers. comm.) and the Sør Rondane Mountains in East Antarctica, temperature fluctuations are so high during the summer months that surface soils may be subject to freeze–thaw cycles on a daily basis [72].

The presence of a saturated atmosphere at depth and a low surface relative humidity (Figure 2a) will generate a strong thermodynamic driver for the upward diffusion of high relative humidity (RH) water vapour [73,74], potentially available to shallow sub-surface microbial communities (see below). In hot deserts, groundwater may be able to fulfil a similar role, even though such subterranean liquid flows may be found tens or hundreds of metres below ground level. Measurements of soil atmospheric relative humidity values in shallow soil depth profiles in the central (hyper-arid zone) Namib Desert (Figure 2b) and the Atacama Desert (Figure 2c) are strongly suggestive of the upward transport of

subsurface water vapour [75], whether derived from deep subterranean groundwater or residual water from infrequent rainfall recharge.

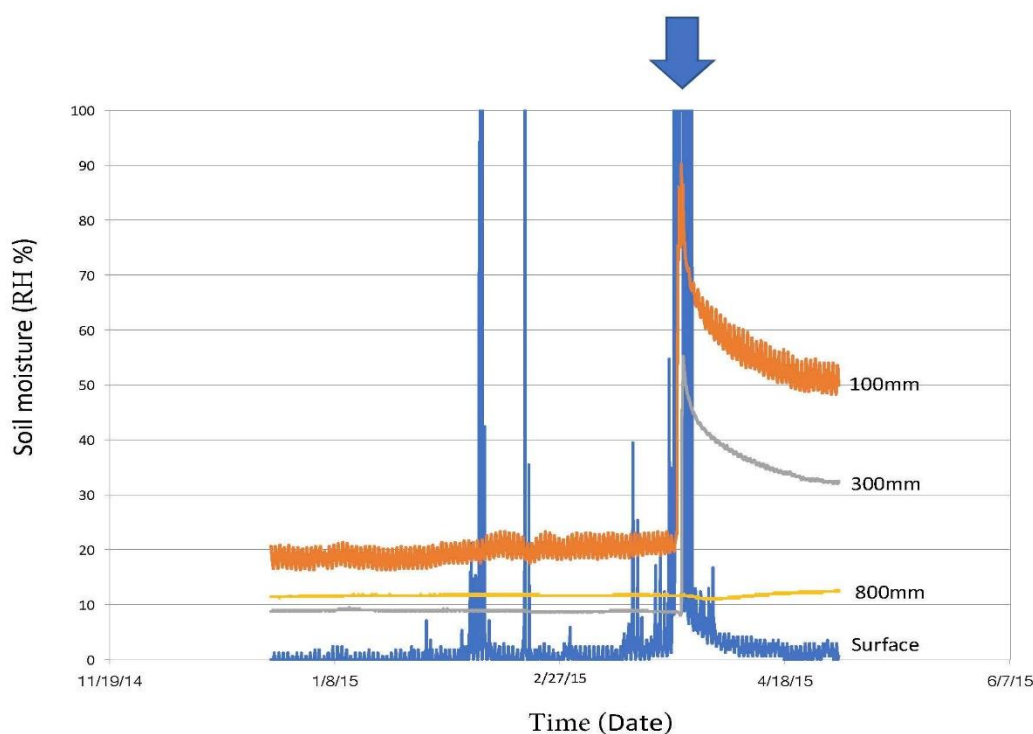


(a)



(b)

Figure 2. Cont.



(c)

Figure 2. (a) Soil %RH values (Thermochron DS1923 iButtons) across a 20 cm depth profile (Miers Valley, East Antarctica, January 2008; (b) 86 h iButton (Thermochron DS1923) record of % relative humidity values at specified depths in the soil profile (central Namib Desert, GPS S23.61 E15.17, May 2011); (c) temporal variation in soil moisture (%RH) in Atacama Desert soil horizons over a 6-month period, through a major rainfall event (blue arrow). Data from [45].

Irrespective of the origins of water vapour in desert soils, nocturnal distillation may also provide a mechanism for generating condensed (liquid) water in the upper soil horizons [40], under conditions where nocturnal soil surface temperatures are sufficiently low to yield measurable increases in shallow sub-surface soil water content [40].

3.5. Adsorption of Water from the Atmosphere

It has been well-established that fruticose lichens have the capacity to adsorb water from moist air [76], without the need for condensation processes. The capacity for microorganisms to acquire cellular water directly from the atmosphere (i.e., $H_2O(g)$) is not well established, although the permeability of the cell membrane to water molecules and the hypertonicity of the cellular cytoplasm suggest that this process is both physically and thermodynamically feasible. The close correlation between desert soil surface and shallow sub-surface relative humidity values (Figure 2b) suggests that the atmosphere of the near-surface (0 to 2 cm depth) soil horizon is in equilibrium with the above-surface atmosphere, and that water is potentially available to the shallow soil microbial communities that are able to adsorb it. One recent study suggested that, each night, an equivalent of $\sim 30 \mu m$ rainfall may enter the soils of the hyper-arid core of the Atacama Desert via atmospheric water vapour adsorption [77].

Whether microbial cells directly adsorb atmospheric moisture or not, there is good evidence that the biofilm structures in which most soil organisms reside do have this capacity. Most soil microbial communities are embedded in EPS matrices [78], composed of compositionally heterogeneous high-molecular-weight glycan polymers [79] that can constitute up to 90% of the biomass of a biofilm [80]. Such compounds are rich in free

hydroxyl (-OH) and amino (-NH₂) groups, both of which are strongly hydrophilic and contribute to the water-holding capacity of EPSs [81].

In addition, bacterial production and excretion of EPS constituents is strongly stimulated by exposure to stress, particularly sub-lethal heat [82] and osmotic stresses [7], and has been implicated in water retention in desert soil biocrust communities [83]. It has also been demonstrated that the hygroscopic properties of EPSs facilitate both the acquisition and retention of water from the atmosphere [84,85].

Microorganisms accumulate a wide array of low-molecular-weight organic solutes (including monosaccharide and oligosaccharide sugars, polyols, amino acids and their derivatives, ectoines and betaines [86]), at least some of which have been implicated in cellular responses to osmotic (including desiccation) stress [86]. The hygroscopic disaccharide trehalose, which is accumulated intracellularly in many organisms in response to desiccation [87], is capable of adsorbing and retaining water at atmospheric relative humidity values above 50% [88]. This mechanism of water acquisition by desiccated microbial cells is, at least theoretically, feasible in shallow subsurface microbial communities in both hot [89] and cold desert soils (see Figure 2a,b).

3.6. Hygroscopic Minerals and Surfaces

Mineral (and other) surfaces can acquire and retain thin films of water [90–92] that may exist from >1 mm depth down to molecular monolayers [93]. While the water in thicker surface films, typically acquired because of the presence of hygroscopic salts [94] or solutes [95], is thought to be bioavailable [96], it is uncertain whether thin surface water layers (<3 molecules thick) are in a liquid phase [96].

The presence of minute salt crystals on surfaces, derived from deposited sea spray in coastal deserts, can lead to deliquescence events (i.e., the formation of liquid brine as the salt absorbs water from the atmosphere). The phenomenon of salt deliquescence may be a primary driver for microbial life in much of the Atacama Desert, where cells and communities are typically active in thin layers of brine inside halite rocks [29,97] or in the NaCl-rich subsurface [97].

There is also recent evidence that endolithic microorganisms can access water from hydrated minerals [98]. Cyanobacteria growing as biofilms in gypsum (CaSO₄·2H₂O) minerals induce mineral dissolution accompanied by water extraction and the transformation of gypsum to anhydrite (CaSO₄). Given that many coastal desert soils, such as in the Namib and Atacama Deserts, are gypsum-rich, this phenomenon may be of considerable biological importance.

3.7. In Situ Hydro-Genesis

Apart from the various exogenous sources of biologically available water, all microbial cells have the capacity to generate water endogenously. The oxidative heterotrophic metabolism of carbohydrates is hydro-genic (water-generating: $C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O$), although it is unclear what proportion of intracellular water this (and related) metabolic processes may contribute. Oxygen stable-isotope analyses have suggested that, in actively growing cells, 70% of microbial intracellular water may be metabolically derived [99]. Notably, many intracellular metabolic processes are water-generating, including ligation, condensation, polymerization, and related reactions, in addition to oxidative metabolism.

Under desiccated conditions, when many cells may be in an anhydrobiotic state [99,100] with cellular activity limited to basal metabolic processes [100–104], hydro-genesis from carbohydrate metabolism may be limited. However, there is growing evidence that a recently discovered chemotrophic metabolism may even supplement cellular water in desiccated cells. Atmospheric trace gas assimilation, particularly hydrogen oxidation, has been observed in both hot and cold desert soil microbiomes [105–109]. This process, which uses newly described clades of assimilatory Ni–Fe hydrogenases [107] and is present in a wide range of aerobic soil bacterial phyla [108,109], not only provides the energy and reductant needed to support carbon fixation; the process is also hydro-genic ($2H_2 + O_2 = 2H_2O$).

While the quantitative contributions of this process to the cellular water budget have not yet been accurately determined, we have preliminary evidence that the kinetics of this process are remarkably fast, even in desiccated soils and at low temperatures (Belinda Ferrari, unpublished results). H_2 uptake rates in Antarctic soils (at $10\text{ }^\circ\text{C}$) were estimated at around $140\text{ pmol}\cdot\text{h}^{-1}\text{ g soil}_{\text{d.w.}}$ [108]. Using this value as an average over a 24 h period, this is equivalent to the addition of $3.4\text{ nmol } H_2O\cdot\text{g soil}$ ($0.06\text{ }\mu\text{g } H_2O\cdot\text{day}^{-1}\text{ g soil}$). Maximum H_2 uptake rates, measured for Antarctic Vestfold Hills and Windmill Island soils that have very high abundances of the atmospheric chemotrophic phyla *Actinobacteriota*, *Eremiobacterota* and *Ca. Dormibacterota*, were recorded as high as $421\text{ nmol}\cdot\text{h}^{-1}\text{ g soil}$ [100], equivalent to approx. $0.2\text{ mg } H_2O\cdot\text{day}^{-1}\text{ g soil}$). The scales of these values suggest that the hydro-genic contribution of H_2 oxidation in soils may not be altogether trivial over diel timescales.

The process of trace-gas-dependent hydro-genesis in microbial cells has the potential to realign current paradigms on the functional status and capacity of desert soil microbiomes. Recent transcriptomic data on microbial cellular function in hyper-arid soils suggest that a subset of microbial taxa retains some functionality under desiccated conditions [110,111]. Similarly, metaproteomic analyses of hyper-arid Antarctic Reeve Hill (Casey Station) soils show evidence of active expression of Ni-Fe hydrogenases and RuBisCO [105].

4. Implications of Climate Change

All climate models predict that the world's major hot desert regions will become hotter and drier [31]. This will directly affect water availability in soils, both from reduced inputs from rainfall, and from a reduction in the P/PET ratio (the aridity index: the ratio of precipitation to evapotranspiration; used in defining the severity of desert ecosystems [31]). The projected consequences of these changes include increased aridification (the expansion of the size of existing dryland and desert areas [112,113] and a transition of existing desert regions to a higher aridity status, e.g., from arid to hyper-arid). Any change in aridity status can have major impacts on both the macrobiology and the microbiology of affected areas, with the loss of the more desiccation- and heat-sensitive species (e.g., [114,115]), a reduction in primary production and soil organic carbon [116], and a reduction in the fixation of atmospheric nitrogen [117]. Both phototrophic and diazotrophic processes, which are crucial in soil nutrient cycling, are known to be very sensitive to cellular water activity [10,101].

Interestingly, under a warming climate regime, polar deserts are likely to become wetter as a result of increased glacial and permafrost melt and increased snowfall [118–120] with associated increases in fertility [121,122]. Such changes may lead to challenges for indigenous xerophilic microbiota which may be increasingly out-competed by the colonization and cosmopolitan r-strategists (rapidly growing microbes), resulting in homogenization and loss of biodiversity [123,124]. A recent investigation in the Windmill Islands region in East Antarctica showed that functional bacterial clades were vulnerable to change, with Gradient Forest modelling revealing 10–12% moisture thresholds as environmental tipping points that are likely to result in significant microbial community compositional shifts (Zhang, Wong, Czechowski et al., manuscript under review). Analysis of Antarctic soils sampled over a 14-year period confirmed this prediction, with wetter soils exhibiting higher relative abundances of microbial phototrophs (micro-algae and cyanobacteria) and fewer trace gas chemosynthetic bacteria (*Eremiobacterota*, *Ca. Dormibacterota*).

Increased water availability in continental Antarctic soils, via enhanced snowmelt and/or glacial melt, is therefore likely to dramatically impact soil microbial diversity and function. Moisture input from glacial meltwater to surface soils in the McMurdo Dry Valleys led to pronounced shifts in bacterial diversity [125] and activity [126]. Similarly, localized melting from persistent snow drifts has been shown to support metabolically active yeasts and filamentous fungi [127].

However, given the adaptability and resilience of microorganisms [128,129], the negative impacts of climate change on soil microbiomes may be less dramatic than on larger organisms such as plant and animal species [130]. In fact, several studies have shown that

drought-adapted bacterial and fungal species not only contributed to the overall resilience and stability of microbial communities [131,132], but also enhanced the resilience of the entire ecosystem [133–135].

The extent to which climate-induced changes in microbial community ecology will effect changes in function (at the micro-scale) and ecosystem servicing (at the macro-scale) is still a debated topic, in part due to the complexity of the interactions between the key players (fungi, bacteria, archaea, and viruses) within these communities and the ecosystem around them [136,137]. Such changes are, however, unlikely to be trivial [123]. Nonetheless, we believe that the concept of ‘where there is water, there is life’ remains an important paradigm. It is evident, however, that climate-induced changes in water availability are regionally highly heterogeneous, and the impacts on hot and cold deserts are likely to be very different, if not, in some instances, directly opposite.

Author Contributions: All authors contributed to the preparation of this manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: D.A.C. was supported by NRF SANAP grants 80256 and SNA14070974748. J.D.R. was supported by NASA grant # 80NSSC19K0470. J.-B.R. was funded through the 2019–2020 BiodivERSA joint call for research proposals (project GRADCATCH) under the BiodivClim ERA-Net COFUND programme via the Department of Science and Innovation (South Africa), and grant n°1210912 from ANID-Fondecyt (Chile).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: The authors gratefully acknowledge the staff of the Gobabeb-Namib Research Institute, where many of the discussions leading to the development of this article took place.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Daniel, R.M.; Finney, J.L.; Stoneham, M. The molecular basis of life: Is life possible without water? *Philosoph. Trans. R. Soc. Lond. B Biol. Sci.* **2004**, *359*, 1141–1328.
2. Williford, K.H.; Farley, K.A.; Stack, K.M.; Allwood, A.C.; Beaty, D.; Beegle, L.W.; Bhartia, R.; Brown, A.J.; de la Torre Juarez, M.; Hamran, S.E.; et al. The NASA Mars 2020 Rover Mission and the Search for Extraterrestrial Life. Chapter 11; In *From Habitability to Life on Mars*; Elsevier Publisher: Amsterdam, The Netherlands, 2018; pp. 275–308.
3. Rummel, J.D.; Beaty, D.W.; Jones, M.A.; Bakermans, C.; Barlow, N.G.; Boston, P.J.; Chevrier, V.F.; Clark, B.C.; De Vera, J.-P.P.; Gough, R.; et al. A new analysis of Mars “Special Regions”: Findings of the Second MEPAG Special Regions Science Analysis Group (SR-SAG2). *Astrobiology* **2014**, *14*, 887–968. [[CrossRef](#)] [[PubMed](#)]
4. Pointing, S.B.; Belnap, J. Microbial colonization and controls in dryland systems. *Nat. Rev. Microbiol.* **2012**, *10*, 551–562. [[CrossRef](#)]
5. Cary, S.C.; McDonald, I.R.; Barrett, J.E.; Cowan, D.A. On the rocks: The microbiology of Antarctic Dry Valley soils. *Nat. Rev. Microbiol.* **2010**, *8*, 129–138. [[CrossRef](#)]
6. Tiao, G.; Lee, C.K.; McDonald, I.R.; Cowan, D.A.; Cary, S.C. Rapid microbial response to the presence of an ancient relic in the Antarctic Dry Valleys. *Nat. Commun.* **2012**, *3*, 660. [[CrossRef](#)]
7. Lebre, P.; De Maayer, P.; Cowan, D.A. Xerotolerant prokaryotes: Surviving through a dry spell. *Nat. Rev. Microbiol.* **2017**, *15*, 285–296. [[CrossRef](#)]
8. Brown, A.D. Microbial water stress. *Bacteriol. Rev.* **1976**, *40*, 803–846. [[CrossRef](#)]
9. Stevenson, A.; Hamill, P.G.; O’Kane, C.J.; Kminek, G.; Rummel, J.D.; Voytek, M.A.; Dijksterhuis, J.; Hallsworth, J.E. *Aspergillus penicillioides* differentiation and cell division at 0.585 water activity. *Environ. Microbiol.* **2017**, *19*, 687–697. [[CrossRef](#)] [[PubMed](#)]
10. Stevenson, A.; Burkhardt, J.; Cockell, C.S.; Cray, J.A.; Dijksterhuis, J.; Fox-Powell, M.; Kee, T.P.; Kminek, G.; McGenity, T.J.; Timmis, K.N.; et al. Multiplication of microbes below 0.690 water activity: Implications for terrestrial and extra-terrestrial life. *Environ. Microbiol.* **2015**, *17*, 257–277. [[CrossRef](#)]
11. Gómez-Silva, B. Lithobiontic life: Atacama rocks are well and alive. *Anton. Leeuwenhoek* **2018**, *111*, 1333–1343. [[CrossRef](#)] [[PubMed](#)]
12. Cowan, D.A.; Hopkins, D.W.; Jones, B.E.; Maggs-Kölling, G.; Majewska, R.; Ramond, J.-B. Microbiomics of Namib Desert habitats. *Extremophiles* **2020**, *24*, 17–29. [[CrossRef](#)] [[PubMed](#)]

13. Mehda, S.; Muñoz-Martín, M.; Oustani, M.; Hamdi-Aïssa, B.; Perona, E.; Mateo, P. Lithic cyanobacterial communities in the polyextreme Sahara Desert: Implications for the search for the limits of life. *Environ. Microbiol.* **2022**, *24*, 451–474. [[CrossRef](#)] [[PubMed](#)]
14. Meslier, V.; Casero, M.C.; Dailey, M.; Wierzchos, J.; Ascaso, C.; Artieda, O.; McCullough, P.R.; DiRuggiero, J. Fundamental drivers for endolithic microbial community assemblies in the hyperarid Atacama Desert. *Environ. Microbiol.* **2018**, *20*, 1765–1781. [[CrossRef](#)]
15. Archer, S.D.J.; Lee, K.C.; Caruso, T.; Alcamí, A.; Araya, J.G.; Cary, S.C.; Cowan, D.A.; Etchebehere, C.; Gantsetseg, B.; Gomez-Silva, B.; et al. Contribution of soil bacteria to the atmosphere across biomes. *STOTEN* **2023**, *871*, 162137. [[CrossRef](#)]
16. Santl-Temkiv, T.; Amato, P.; Casamayor, E.O.; Lee, P.K.H.; Pointing, S.B. Microbial ecology of the atmosphere. *FEMS Microbiol. Rev.* **2022**, *46*, fuac009. [[CrossRef](#)] [[PubMed](#)]
17. Manabe, S.; Wetherald, R.T. Thermal equilibrium of the atmosphere with a given distribution of relative humidity. In *The Warming Papers: A Scientific Foundation for the Climate Change Forecast*; Archer, D., Pierrehumbert, R., Eds.; Wiley-Blackwell: Hoboken, NJ, USA, 2011; pp. 94–115.
18. Yang, Y.; Zhao, W.; Xiao, X. The upper temperature limit of life under high hydrostatic pressure in the deep biosphere. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* **2021**, *176*, 103604. [[CrossRef](#)]
19. McKay, C.P.; Davila, A.F.; Sun, H.J. Cold and Dry Limits of Life. In *Astrobiology: An Evolutionary Approach*; CRC Press: Boca Raton, FL, USA, 2014; pp. 271–281.
20. Goordial, J.; Davila, A.; Lacle, D.; Pollard, W.; Marinova, M.M.; Greer, C.W.; DiRuggiero, J.; McKay, C.P.; Whyte, L.G. Nearing the cold-arid limits of microbial life in permafrost of an upper Dry Valley, Antarctica. *ISME J.* **2016**, *10*, 1613–1624. [[CrossRef](#)]
21. Dragone, N.B.; Henley, J.B.; Holland-Moritz, H.; Diaz, M.; Hogg, I.D.; Lyons, W.B.; Wall, D.H.; Adams, B.J.; Fierer, N. Elevational constraints on the composition and genomic attributes of microbial communities in Antarctic soils. *mSystems* **2022**, *7*, e01330-21. [[CrossRef](#)]
22. Varsadiya, M.; Urich, T.; Hugelius, G.; Bárta, J. Microbiome structure and functional potential in permafrost soils of the Western Canadian Arctic. *FEMS Microb. Ecol.* **2021**, *97*, fiab008. [[CrossRef](#)]
23. Altshuler, I.; Hamel, J.; Turney, S. Species interactions and distinct microbial communities in high Arctic permafrost affected cryosols are associated with the CH₄ and CO₂ gas fluxes. *Environ. Microbiol.* **2019**, *21*, 3711–3727. [[CrossRef](#)]
24. Altshuler, I.; Raymond-Bouchard, I.; Magnuson, E.; Tremblay, J.; Greer, C.W.; Whyte, L.G. Unique high Arctic methane metabolizing community revealed through in situ ¹³CH₄-DNA-SIP enrichment in concert with genome binning. *Sci. Rep.* **2022**, *12*, e1160. [[CrossRef](#)]
25. Morozova, D.; Wagner, D. Highly resistant methanogenic archaea from Siberian permafrost as candidates for the possible life on Mars. *Int. J. Astrobiol.* **2007**, *6*, 59–87.
26. Grinberg, M.; Orevi, T.; Steinberg, S.; Kashtan, N. Bacterial survival in microscopic surface wetness. *eLife* **2019**, *8*, e48508. [[CrossRef](#)] [[PubMed](#)]
27. Burkhardt, J.; Hunsche, M. Breath figures on leaf surfaces-formation and effects of microscopic leaf wetness. *Front. Plant Sci.* **2013**, *4*, 422. [[CrossRef](#)]
28. Qu, E.; Omelon, C.; Oren, O.; Meslier, V.; Cowan, D.A.; Maggs-Kölling, G.; DiRuggiero, J. Trophic selective pressures organize the composition of endolithic microbial communities from global deserts. *Front. Microbiol.* **2020**, *10*, 2952. [[CrossRef](#)]
29. Davila, A.F.; Hawes, I.; Ascaso, C.; Wierzchos, J. Salt deliquescence drives photosynthesis in the hyperarid Atacama Desert. *Environ. Microbiol. Rep.* **2013**, *5*, 583–587. [[CrossRef](#)] [[PubMed](#)]
30. DiRuggiero, J.J.; Wierzchos, C.K.; Robinson, T.; Souterre, T.; Ravel, J.; Artieda, O.; Souza-Egipsy, V.; Ascaso, C. Microbial colonization of chasmoendolithic habitats in the hyper-arid zone of the Atacama Desert. *Biogeosciences* **2013**, *10*, 2439–2450. [[CrossRef](#)]
31. Greve, P.; Roderick, M.L.; Ukkola, A.M.; Wada, Y. The Aridity Index under global warming. *Environ. Res. Lett.* **2019**, *14*, 124006. [[CrossRef](#)]
32. IUSS Working Group WRB. World Reference Base for Soil Resources. In *International Soil Classification System for Naming Soils and Creating Legends for Soil Maps*, 4th ed.; International Union of Soil Sciences (IUSS): Vienna, Austria, 2022.
33. Wolf, A.B.; Vos, M.; de Boer, W.; Kowalchuk, G.A. Impact of matric potential and pore size distribution on growth dynamics of filamentous and non-filamentous soil bacteria. *PLoS ONE* **2013**, *8*, e83661. [[CrossRef](#)]
34. Eckardt, F.D.; Soderberg, K.; Coop, L.J. The nature of moisture at Gobabeb, in the central Namib Desert. *J. Arid Environ.* **2013**, *93*, 7–19. [[CrossRef](#)]
35. Obyrk, M.K.; Doran, P.T.; Fountain, A.G.; Myers, M.; McKay, C.P. Climate from the McMurdo Dry Valleys, Antarctica, 1986–2017: Surface air temperature trends and redefined summer season. *J. Geophys. Res. Atmos.* **2020**, *125*, e2019JD032180. [[CrossRef](#)]
36. Fountain, A.G.; Nylen, T.H.; Monaghan, A.; Basagic, H.J.; Bromwich, D. Snow in the McMurdo Dry Valleys, Antarctica. *Int. J. Climatol.* **2010**, *30*, 633–642. [[CrossRef](#)]
37. Hopkins, D.W.; Sparrow, A.D.; Novis, P.M.; Gregorich, E.; Elberling, B.; Greenfield, L. Controls on the distribution of productivity and organic resources in Antarctic Dry Valley soils. *Proc. R. Soc. B* **2006**, *273*, 2687–2695. [[CrossRef](#)] [[PubMed](#)]
38. Sun, H.J. Endolithic microbial life in extreme cold climate; Snow is required, but perhaps less is more. *Biology* **2013**, *2*, 693–701. [[CrossRef](#)]

39. Weber, B.; Belnap, J.; Budel, B.; Antoninka, A.J.; Barger, N.N.; Chaudhary, V.B.; Darrouzet-Nardi, A.; Eldridge, D.J.; Faist, A.M.; Ferrenberg, S.; et al. What is a biocrust? A refined, contemporary definition for a broadening research community. *Biol. Rev. Camb. Philos. Soc.* **2022**, *97*, 1768–1785. [[CrossRef](#)]
40. Francis, M.L.; Fey, M.V.; Prinsloo, H.P.; Ellis, F.; Mills, A.; Medinski, T. Soils of Namaqualand: Compensations for aridity. *J. Arid Environ.* **2007**, *70*, 588–603. [[CrossRef](#)]
41. Alvarez, A. Sepiolite: Properties and uses. In *Palygorskite–Sepiolite: Occurrences, Genesis and Uses. Developments in Sedimentology*; Singer, A., Galan, E., Eds.; Elsevier Science Publishers: Amsterdam, The Netherlands, 1984; Volume 37, pp. 253–287.
42. Francis, M.L. Effect of sepiolite and palygorskite on plant available water in Arenosols of Namaqualand, South Africa. *Geoderma Reg.* **2019**, *17*, e00022. [[CrossRef](#)]
43. Eckardt, F. Saline Soils. In *Encyclopaedia of Engineering Geology*; Encyclopaedia of Earth Sciences, Series; Bobrowsky, P.T., Marker, B., Eds.; Springer: Cham, Switzerland, 2018.
44. Cosby, B.J.; Hornberger, G.M.; Clapp, R.B.; Ginn, T. A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils. *Water Resour. Res.* **1984**, *20*, 682–690. [[CrossRef](#)]
45. Pfeiffer, M.; Morgan, A.; Heimsath, A.; Jordan, T.; Howard, A.; Amundson, R. Century scale rainfall in the absolute Atacama Desert: Landscape response and implications for past and future rainfall. *Quart. Sci. Rev.* **2021**, *254*, 106797. [[CrossRef](#)]
46. Schulze-Makuch, D.; Wagner, D.; Kounaves, S.P.; Mangelsdorf, K.; Devine, K.G.; de Vera, J.-P.; Schmitt-Kopplin, P.; Grossart, H.-P.; Parro, V.; Kaupenjohann, M.; et al. Transitory microbial habitat in the hyperarid Atacama Desert. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 2670–2675. [[CrossRef](#)]
47. Warren-Rhodes, K.A.; Lee, K.C.; Archer, S.D.J.; Cabrol, N.; Ng-Boyle, L.; Wettergreen, D.; Zacny, K.; Pointing, S.B.; NASA Life in the Atacama Project Team. Subsurface microbial habitats in an extreme desert Mars-analog environment. *Front. Microbiol.* **2019**, *10*, 69. [[CrossRef](#)] [[PubMed](#)]
48. Armstrong, A.; Valverde, A.; Ramond, J.B.; Makhalanyane, T.P.; Jansson, J.K.; Hopkins, D.W.; Aspray, T.J.; Seely, M.; Trindade, M.I.; Cowan, D.A. Temporal dynamics of hot desert microbial communities reveal structural and functional responses to water input. *Sci. Rep.* **2016**, *6*, 34434. [[CrossRef](#)] [[PubMed](#)]
49. Hotaling, S.; Lutz, S.; Dial, R.J.; Anesio, A.M.; Benning, L.G.; Fountain, A.G.; Kelley, J.L.; McCutcheon, J.; Skiles, S.M.; Takeuchi, N.; et al. Biological albedo reduction on ice sheets, glaciers, and snowfields. *Earth Sci. Rev.* **2021**, *220*, 103728. [[CrossRef](#)]
50. Anesio, A.M.; Lutz, S.; Christmas, N.A.M.; Benning, L.G. The microbiome of glaciers and ice sheets. *Biofilms Microbiomes* **2017**, *3*, 10. [[CrossRef](#)] [[PubMed](#)]
51. Skidmore, M.L.; Foght, J.M.; Sharp, M.J. Microbial life beneath a high Arctic glacier. *Appl. Environ. Microbiol.* **2000**, *66*, 3214–3220. [[CrossRef](#)]
52. Robinson, P.J. Temporal trends in United States dew point temperature. *Int. J. Climatol.* **2000**, *20*, 985–1002. [[CrossRef](#)]
53. Zangvil, A. Six years of dew observations in the Negev Desert, Israel. *J. Arid Environ.* **1996**, *32*, 361–371. [[CrossRef](#)]
54. Linacre, E.T. *Climate Data and Resources*; Routledge: London, UK, 1992; 366p.
55. Zhuang, Y.; Zhao, W.; Luo, L.; Wang, L. Dew formation characteristics in the gravel desert ecosystem and its ecological roles on *Reaumuria soongorica*. *J. Hydrol.* **2021**, *603*, 126932. [[CrossRef](#)]
56. Lange, O.L.; Geiger, I.L.; Schulze, E.D. Ecophysiological investigations on lichens of the Negev desert. *Oecologia* **1977**, *28*, 247–259. [[CrossRef](#)]
57. Pintado, A.; Sancho, L.G.; Green, T.G.A.; Blanquer, J.M.; Lázaro, R. Functional ecology of the biological soil crust in semiarid SE Spain: Sun and shade populations of *Diploschistes diacapsis* (Ach.). *Lumbsch. Lichenologist* **2005**, *37*, 425–432. [[CrossRef](#)]
58. Del Prado, R.; Sancho, L.G. Dew as a key factor for the distribution pattern of the lichen species *Teloschistes lacunosus* in the Tabernas Desert (Spain). *Flora* **2007**, *202*, 417–428. [[CrossRef](#)]
59. Cereceda, P.; Larrain, H.; Osses, P.; Fariás, M.; Egaña, I. The spatial and temporal variability of fog and its relation to fog oases in the Atacama Desert, Chile. *Atmos. Res.* **2008**, *87*, 312–323. [[CrossRef](#)]
60. Cermak, J. Low clouds and fog along the South-Western African coast—Satellite-based retrieval and spatial patterns. *Atmos. Res.* **2012**, *116*, 15–21. [[CrossRef](#)]
61. Schieferstein, B.; Loris, K. Ecological investigations on lichen fields of the Central Namib. *Vegetatio* **1992**, *98*, 113–128. [[CrossRef](#)]
62. Hinchliffe, G.; Bollard-Breen, B.; Cowan, D.A.; Doshi, A.; Gillman, L.N.; Maggs-Kolling, G.; Rios, A.D.L.; Pointing, S.B. Advanced photogrammetry to assess lichen colonization in the hyper-arid Namib Desert. *Front. Microbiol.* **2017**, *8*, 2083. [[CrossRef](#)] [[PubMed](#)]
63. Roth-Nebelsick, A.; Ebner, M.; Miranda, T.; Gottschalk, V.; Voigt, D.; Gorb, S.; Stegmaier, T.; Sarsour, J.; Linke, M.; Konrad, W. Leaf surface structures enable the endemic Namib desert grass *Stipagrostis sabulicola* to irrigate itself with fog water. *J. R. Soc. Interface* **2012**, *9*, 1965–1974. [[CrossRef](#)] [[PubMed](#)]
64. Hamilton, W.J.; Seely, M.K. Fog basking by the Namib Desert beetle, *Onymacris unguicularis*. *Nature* **1976**, *262*, 284–285. [[CrossRef](#)]
65. Wierzchos, J.; Cámara, B.; De Los Ríos, A.; Davila, A.F.; Almazo, I.M.S.; Artieda, O.; Wierzchos, K.; Gómez-Silva, B.; McKay, C.; Ascaso, C. Microbial colonization of Ca-sulfate crusts in the hyperarid core of the Atacama Desert: Implications for the search for life on Mars. *Geobiology* **2010**, *9*, 44–60. [[CrossRef](#)] [[PubMed](#)]
66. Azúa-Bustos, A.; González-Silva, C.; Mancilla, R.A.; Salas, L.; Gómez-Silva, B.; McKay, C.P.; Vicuña, R. Hypolithic cyanobacteria supported mainly by fog in the coastal range of the Atacama Desert. *Microb. Ecol.* **2011**, *61*, 568–581. [[CrossRef](#)]

67. Warren-Rhodes, K.A.; McKay, C.P.; Boyle, L.N.; Wing, M.R.; Kiekebusch, E.M.; Cowan, D.A.; Stomeo, F.; Pointing, S.B.; Kaseke, K.F.; Eckardt, F.; et al. Physical ecology of hypolithic communities in the central Namib desert: The role of fog, rain, rock habitat and light. *J. Geophys. Res.* **2013**, *118*, 1451–1460. [[CrossRef](#)]
68. Uritskiy, G.; Tisza, M.J.; Gelsinger, D.R.; Munn, A.; Taylor, J.; DiRuggiero, J. Cellular life from the three domains and viruses are transcriptionally active in a hypersaline desert community. *Environ. Microbiol.* **2021**, *23*, 3401–3417. [[CrossRef](#)]
69. Marasco, R.; Mosqueira, M.J.; Fusi, M.; Ramond, J.-B.; Merlino, G.; Booth, J.M.; Maggs-Kölling, G.; Cowan, D.; Daffonchio, D. Rhizosheath microbial community assembly of sympatric desert speargrasses is independent of the plant host. *Microbiome* **2018**, *6*, 215. [[CrossRef](#)] [[PubMed](#)]
70. Robinson, C.K.; Wierzchos, J.; Black, C.; Crits-Christoph, A.; Ma, B.; Ravel, J.; Ascaso, C.; Artieda, O.; Valea, S.; Roldán, M.; et al. Microbial diversity and the presence of algae in halite endolithic communities are correlated to atmospheric moisture in the hyper-arid zone of the Atacama Desert. *Environ. Microbiol.* **2015**, *17*, 299. [[CrossRef](#)]
71. Uritskiy, G.; Munn, A.; Dailey, M.; Gelsinger, D.R.; Getsin, S.; Davila, A.; McCullough, P.R.; Taylor, J.; DiRuggiero, J. Environmental factors driving spatial heterogeneity in desert halophile microbial communities. *Front. Microbiol.* **2020**, *11*, 578660. [[CrossRef](#)]
72. Mikucki, J.; Auken, E.; Tulaczyk, S.; Virginia, R.A.; Schamper, C.; Sørensen, K.I.; Doran, P.T.; Dugan, H.; Foley, N. Deep groundwater and potential subsurface habitats beneath an Antarctic Dry Valley. *Nat. Commun.* **2015**, *6*, 6831. [[CrossRef](#)]
73. Batista, R.F.; Reichert, J.; Holthusen, D.; Batistão, A.C.; Daher, M.; Schünemann, A.L.; Filho, E.I.F.; Schaefer, C.E.G.R.; Francelino, M.R. Freeze–thaw cycles affecting rheological properties of Antarctic soils. *Geoderma* **2022**, *428*, 116220. [[CrossRef](#)]
74. Evans, D.D.; Thames, J.L. *Water in Desert Ecosystems*; US/IBP Synthesis Series; Academic Press: Cambridge, MA, USA, 1981; Volume 11, 280p.
75. Du, C.; Yu, J.; Wang, P.; Zhang, Y. Analysing the mechanisms of soil water and vapour transport in the desert vadose zone of the extremely arid region of northern China. *J. Hydrol.* **2018**, *558*, 592–606. [[CrossRef](#)]
76. Lange, O.L.; Green, T.C.A.; Melzer, B.; Meyer, A.; Zellner, H. Water relations and CO₂ exchange of the terrestrial lichen *Teloschistes capensis* in the Namib fog desert: Measurements during two seasons in the field and under controlled conditions. *Flora* **2006**, *201*, 268–280. [[CrossRef](#)]
77. Glaser, D.M.; Hartnett, H.E.; Finn, D.R.; Perez-Montañó, S.; Cadillo-Quiroz, H.; Desch, S. Water vapor adsorption provides daily, sustainable water to soils of the hyperarid Atacama Desert. *Astrobiology* **2022**, *22*, 1222. [[CrossRef](#)]
78. Kaur, N.; Dey, P. Bacterial exopolysaccharides as emerging bioactive macromolecules: From fundamentals to applications. *Res. Microbiol.* **2023**, *174*, 104024. [[CrossRef](#)]
79. Fleming, H.-C.; Wingender, J. Relevance of microbial extracellular polymeric substances (EPSs)—Part I: Structural and ecological aspects. *Water Sci. Technol.* **2001**, *43*, 1–8. [[CrossRef](#)]
80. Wu, B.; Wang, H.; Li, W.; Dai, X.; Chai, X. Influential mechanism of water occurrence states of waste-activated sludge: Potential linkage between water-holding capacity and molecular compositions of EPS. *Water Res.* **2022**, *213*, 118169. [[CrossRef](#)] [[PubMed](#)]
81. Wang, L.-L.; Wang, L.-F.; Ren, X.-M.; Ye, X.-D.; Li, W.-W.; Yuan, S.-J.; Sun, M.; Sheng, G.P.; Yu, H.-Q.; Wang, X.K. pH dependence of structure and surface properties of microbial EPS. *Environ. Sci. Technol.* **2012**, *46*, 737–744. [[CrossRef](#)] [[PubMed](#)]
82. Nguyen, H.T.; Razafindralambo, H.; Blecker, C.; N’yapo, C.; Thonart, P.; Delvigne, F. Stochastic exposure to sub-lethal high temperature enhances exopolysaccharides (EPS) excretion and improves *Bifidobacterium bifidum* cell survival to freeze–drying. *Biochem. Eng. J.* **2014**, *188*, 85–94. [[CrossRef](#)]
83. Baubin, C.; Ran, N.; Siebner, H.; Gillor, O. Divergence of biocrust active bacterial communities in the Negev Desert during a hydration-desiccation cycle. *Microb. Ecol.* **2023**, *86*, 474–484. [[CrossRef](#)] [[PubMed](#)]
84. Costa, O.Y.A.; Raaijmakers, J.M.; Kuramae, E.E. Microbial extracellular polymeric substances: Ecological function and impact on soil aggregation. *Front. Microbiol.* **2018**, *9*, 1636. [[CrossRef](#)]
85. Flemming, H.C.; Wingender, J.; Szewzyk, U.; Steinberg, P.; Rice, S.A.; Kjelleberg, S. Biofilms: An emergent form of bacterial life. *Nat. Rev. Microbiol.* **2016**, *14*, 563–575. [[CrossRef](#)]
86. Da Costa, M.S.; Santos, H.; Galinski, E.A. An overview of the role and diversity of compatible solutes in Bacteria and Archaea. *Adv. Biochem. Eng. Biotechnol.* **1998**, *61*, 118–153.
87. Wyatt, T.T.; Golovina, E.A.; van Leeuwen, M.R.; Hallsworth, J.E.; Wösten, H.A.; Dijksterhuis, J. Decreases in bulk water and mannitol and accumulation of trehalose and trehalose-based oligosaccharides define a two-stage maturation process towards extreme stress resistance in ascospores of *Neosartorya fischerii* (*Aspergillus fischerii*). *Environ. Microbiol.* **2014**, *17*, 383–394. [[CrossRef](#)]
88. Fakes, M.G.; Dali, M.V.; Haby, T.A.; Morris, K.R.; Varia, S.A.; Serajuddin, A.T. Moisture sorption behaviour of selected bulking agents used in lyophilized products. *PDA J. Pharm. Sci. Technol.* **2000**, *54*, 144–149.
89. Bosch, J.; Marais, E.; Maggs-Kölling, G.; Ramond, J.B.; Lebre, P.H.; Eckardt, F.; Cowan, D.A. Water inputs across the Namib Desert: Implications for dryland edaphic microbiology. *Front. Biogeogr.* **2022**, *14*, e55302. [[CrossRef](#)]
90. Ewing, G.E. Thin film water. *J. Phys. Chem. B* **2004**, *108*, 15953–15961. [[CrossRef](#)]
91. Wang, J.; Kalinichev, A.G.; Kirkpatrick, R.J. Effects of substrate structure and composition on the structure, dynamics, and energetics of water at mineral surfaces: A molecular dynamics modeling study. *Geochim. Cosmochim. Acta* **2006**, *70*, 562–582. [[CrossRef](#)]
92. Mohlmann, D. Widen the belt of habitability. *Orig. Life Evol. Biosph.* **2012**, *42*, 93–100. [[CrossRef](#)]
93. Mohlmann, D. Are nanometric films of liquid undercooled interfacial water bio-relevant? *Cryobiology* **2009**, *58*, 256–261. [[CrossRef](#)] [[PubMed](#)]

94. Qvit-Raz, N.; Jurkevitch, E.; Belkin, S. Drop-size soda lakes: Transient microbial habitats on a salt-secreting desert tree. *Genetics* **2008**, *178*, 1615–1622. [[CrossRef](#)]
95. Burch, A.Y.; Zeisler, V.; Yokota, K.; Schreiber, L.; Lindow, S.E. The hygroscopic biosurfactant syringafactin produced by *Pseudomonas syringae* enhances fitness on leaf surfaces during fluctuating humidity. *Environ. Microbiol.* **2014**, *16*, 2086–2098. [[CrossRef](#)] [[PubMed](#)]
96. Stevenson, A.; Hallsworth, J.E. Water and temperature relations of soil Actinobacteria. *Environ. Microbiol. Rep.* **2014**, *6*, 744–755. [[CrossRef](#)]
97. Azua-Bustos, A.; Fairén, A.G.; Silva, C.G.; Carrizo, D.; Fernández-Martínez, M.; Arenas-Fajardo, C.; Fernández-Sampedro, M.; Gil-Lozano, C.; Sánchez-García, L.; Ascaso, C.; et al. Inhabited subsurface wet smectites in the hyperarid core of the Atacama Desert as an analog for the search for life on Mars. *Sci. Rep.* **2020**, *10*, 19183. [[CrossRef](#)]
98. Huang, W.; Erteki, E.; Wang, T.; Cruz, L.; Dailey, M.; DiRuggiero, J.; Kisailus, D. Mechanism of water extraction from gypsum rock by desert colonizing microorganisms. *Proc. Natl. Acad. Sci. USA* **2020**, *117*, 10681–10687. [[CrossRef](#)]
99. Kreuzer-Martin, H.W.; Ehrlinger, J.R.; Hegg, E.L. Oxygen isotopes indicate most intracellular water in log-phase *Escherichia coli* is derived from metabolism. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 17337–17341. [[CrossRef](#)]
100. Leung, P.M.; Bay, S.; Meier, D.; Chiri, E.; Cowan, D.A.; Gillor, O.; Woebken, D.; Greening, C. Energetic and trophic basis of microbial persistence in desert ecosystems. *mSystems* **2020**, *5*, e00495-19. [[CrossRef](#)]
101. Bosch, J.; Varliero, G.; Hallsworth, J.; Dallas, T.D.; Hopkins, D.; Frey, B.; Kong, W.; Lebre, P.; Makhalanyane, T.P.; Cowan, D.A. Microbial anhydrobiosis. *Environ. Microbiol.* **2021**, *23*, 6377–6390. [[CrossRef](#)] [[PubMed](#)]
102. Katoh, H.; Asthana, R.K.; Ohmori, M. Gene expression in the cyanobacterium *Anabaena* sp. PCC7120 under desiccation. *Microb. Ecol.* **2004**, *47*, 164–174. [[CrossRef](#)] [[PubMed](#)]
103. LeBlanc, J.C.; Gonçalves, E.R.; Mohn, W.W. Global response to desiccation stress in the soil actinomycete *Rhodococcus jostii* RHA1. *Appl. Environ. Microbiol.* **2008**, *74*, 2627–2636. [[CrossRef](#)] [[PubMed](#)]
104. Rapoport, A.; Golovina, E.A.; Gervais, P.; Dupont, S.; Beney, L. Anhydrobiosis: Inside yeast cells. *Biotechnol. Adv.* **2019**, *37*, 51–67. [[CrossRef](#)] [[PubMed](#)]
105. Ji, M.; Greening, C.; Van Wouterghem, I.; Carere, C.R.; Bay, S.K.; Steen, J.A.; Montgomery, K.; Lines, T.; Beardall, J.; van Dorst, J.; et al. Atmospheric trace gases support primary production in Antarctic desert surface soil. *Nature* **2017**, *552*, 400–403. [[CrossRef](#)]
106. Jordaan, K.; Lappan, R.; Dong, X.; Aitkenhead, I.J.; Bay, S.K.; Chiri, E.; Wieler, N.; Meredith, L.K.; Cowan, D.A.; Chown, S.L.; et al. Hydrogen-oxidising bacteria are abundant in hot desert soils and strongly stimulated by hydration. *mSystems* **2020**, *5*, e01131. [[CrossRef](#)]
107. Ortiz, M.; Leung, P.M.; Shelley, G.; Jirapanjawan, T.; Nauer, P.A.; Van Goethem, M.W.; Bay, S.K.; Islam, Z.F.; Jordaan, K.; Vikram, S.; et al. Multiple energy sources and metabolic strategies sustain microbial diversity in Antarctic desert soils. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2025322118. [[CrossRef](#)]
108. Ray, A.E.; Zaugg, J.; Benaud, N.; Chelliah, D.S.; Bay, S.; Wong, H.L.; Leung, P.M.; Ji, M.; Terauds, A.; Montgomery, K.; et al. Atmospheric chemosynthesis is phylogenetically and geographically widespread and contributes significantly to carbon fixation throughout cold deserts. *ISME J.* **2022**, *16*, 2547–2560. [[CrossRef](#)]
109. Greening, C.; Grinter, R. Microbial oxidation of atmospheric trace gases. *Nat. Rev. Microbiol.* **2022**, *20*, 513–528. [[CrossRef](#)] [[PubMed](#)]
110. León-Sobrino, C.; Ramond, J.-B.; Maggs-Kölling, G.; Cowan, D.A. Nutrient acquisition, rather than stress response over diel cycles, drives microbial transcription in a hyper-arid Namib Desert soil. *Front. Microbiol.* **2019**, *10*, 1045. [[CrossRef](#)]
111. Gunnigle, E.; Frossard, A.; Ramond, J.B.; Guerrero, L.; Seely, M.; Cowan, D.A. Diel-scale temporal dynamics recorded for bacterial groups in Namib Desert soil. *Sci. Rep.* **2017**, *7*, 40189. [[CrossRef](#)]
112. Midgley, G.F.; Bond, W.J. Future of African terrestrial biodiversity and ecosystems under anthropogenic climate change. *Nat. Clim. Change* **2015**, *5*, 823–829. [[CrossRef](#)]
113. Beck, H.E.; Zimmermann, N.E.; McVicar, T.R.; Vergopolan, N.; Berg, A.; Wood, E.F. Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Sci. Data* **2018**, *5*, 180214. [[CrossRef](#)] [[PubMed](#)]
114. Corrado, R.; Cherubini, A.M.; Pennetta, C. Early warning signals of desertification transitions in semiarid ecosystems. *Phys. Rev. E* **2014**, *90*, 062705. [[CrossRef](#)] [[PubMed](#)]
115. Román-Palacios, C.; Wiens, J.J. Recent responses to climate change reveal the drivers of species extinction and survival. *Proc. Natl. Acad. Sci. USA* **2019**, *117*, 4211–4217. [[CrossRef](#)]
116. Change, C. *The IPCC Scientific Assessment*; Houghton, J.T., Jenkins, G., Ephraums, J.J., Eds.; Cambridge University Press: Cambridge, UK, 1990.
117. Olivares, J.; Bedmar, E.J.; Sanjuán, J. Biological nitrogen fixation in the context of global change. *Molec. Plant-Microb. Interact.* **2013**, *26*, 486–494. [[CrossRef](#)]
118. Hassol, S.J. *Impacts of a Warming Arctic-Arctic Climate Impact Assessment*; Cambridge University Press: Cambridge, UK, 2004; 139p.
119. Barrett, J.E.; Virginia, R.A.; Wall, D.H.; Doran, P.T.; Fountain, A.G.; Welch, K.A.; Lyons, W.B. Persistent effects of a discrete warming event on a polar desert ecosystem. *Glob. Change Biol.* **2008**, *14*, 2249–2261. [[CrossRef](#)]
120. Cowan, D.A.; Ah Tow, L. Endangered Antarctic environments. *Ann. Rev. Microbiol.* **2004**, *58*, 649–690. [[CrossRef](#)] [[PubMed](#)]
121. Gutt, J.; Isla, E.; Xavier, J.C.; Adams, B.J.; Ahn, I.; Cheng, C.C.; Colesie, C.; Cummings, V.J.; di Prisco, G.; Griffiths, H.; et al. Antarctic ecosystems in transition—Life between stresses and opportunities. *Biol. Rev.* **2021**, *96*, 798–821. [[CrossRef](#)]

122. Lee, J.R.; Raymond, B.; Bracegirdle, T.J.; Chadès, I.; Fuller, R.A.; Shaw, J.D.; Terauds, A. Climate change drives expansion of Antarctic ice-free habitat. *Nature* **2017**, *547*, 49–54. [[CrossRef](#)]
123. Cavicchioli, R.; Ripple, W.J.; Timmis, K.N.; Azam, F.; Bakken, L.R.; Baylis, M.; Behrenfeld, M.J.; Boetius, A.; Boyd, P.W.; Classen, A.T.; et al. Scientists' warning to humanity: Microorganisms and climate change. *Nat. Rev. Microbiol.* **2019**, *17*, 569–586. [[CrossRef](#)] [[PubMed](#)]
124. Colby, G.A.; Ruuskanen, M.O.; St. Pierre, K.A.; St. Louis, V.L.; Poulain, A.J.; Aris-Brosou, S. Warming climate is reducing the diversity of dominant microbes in the largest high Arctic lake. *Front. Microbiol.* **2020**, *11*, 561194. [[CrossRef](#)] [[PubMed](#)]
125. Lee, K.C.; Caruso, T.; Archer, S.D.J.; Gillman, L.N.; Lau, M.C.; Cary, S.C.; Lee, C.K.; Pointing, S.B. Stochastic and deterministic effects of a moisture gradient on soil microbial communities in the McMurdo Dry Valleys of Antarctica. *Front. Microbiol.* **2018**, *9*, 2619. [[CrossRef](#)]
126. Niederberger, T.D.; Sohm, J.A.; Tirindelli, J.; Gunderson, T.; Capone, D.G.; Carpenter, E.J.; Cary, S.C. Diverse and highly active diazotrophic assemblages inhabit ephemerally wetted soils of the Antarctic Dry Valleys. *FEMS. Microbiol. Ecol.* **2012**, *82*, 376–390. [[CrossRef](#)] [[PubMed](#)]
127. Rao, S.; Chan, Y.; Lacap, D.C.; Hyde, K.D.; Pointing, S.B.; Farrell, R.L. Low-diversity fungal assemblage in an Antarctic Dry Valleys soil. *Polar Biol.* **2011**, *35*, 567–574. [[CrossRef](#)]
128. Philippot, L.; Griffiths, B.S.; Langenheder, S. Microbial community resilience across ecosystems and multiple disturbances. *Microbiol. Mol. Biol. Rev.* **2021**, *85*, e00026–20. [[CrossRef](#)]
129. Uritskiy, G.; Getsin, S.; Munn, A.; Gomez-Silva, B.; Davila, A.; Glass, B.; Taylor, J.; DiRuggiero, J. Halophilic microbial community compositional shift after a rare rainfall in the Atacama Desert. *ISME J.* **2019**, *13*, 2737–2749. [[CrossRef](#)]
130. Cruz-Martínez, K.; Suttle, K.; Brodie, E.; Power, M.E.; Andersen, G.L.; Banfield, J.F. Despite strong seasonal responses, soil microbial consortia are more resilient to long-term changes in rainfall than overlying grassland. *ISME J.* **2009**, *3*, 738–744. [[CrossRef](#)]
131. Hawkes, C.V.; Keitt, T.H. Resilience vs. historical contingency in microbial responses to environmental change. *Ecol. Lett.* **2015**, *18*, 612–625. [[CrossRef](#)]
132. Evans, S.E.; Wallenstein, M.D. Climate change alters ecological strategies of soil bacteria. *Ecol. Lett.* **2014**, *17*, 155–164. [[CrossRef](#)] [[PubMed](#)]
133. Mariotte, P.; Canarini, A.; Dijkstra, F.A. Stoichiometric N:P flexibility and mycorrhizal symbiosis favour plant resistance against drought. *J. Ecol.* **2017**, *105*, 958–967. [[CrossRef](#)]
134. Fiodor, A.; Singh, S.; Pranaw, K. The contrivance of plant growth promoting microbes to mitigate climate change impact in agriculture. *Microorganisms* **2021**, *9*, 1841. [[CrossRef](#)] [[PubMed](#)]
135. Dimkpa, C.; Weinand, T.; Asch, F. Plant-rhizobacteria interactions alleviate abiotic stress conditions. *Plant Cell Environ.* **2009**, *32*, 1682–1694. [[CrossRef](#)] [[PubMed](#)]
136. De Vries, F.; Liiri, M.; Bjoernlund, L.; Bowker, M.A.; Christensen, S.; Setälä, H.M.; Bardgett, R.D. Land use alters the resistance and resilience of soil food webs to drought. *Nat. Clim. Change* **2012**, *2*, 276–280. [[CrossRef](#)]
137. Orwin, K.; Wardle, D.A. Plant species composition effects on belowground properties and the resistance and resilience of the soil microflora to a drying disturbance. *Plant Soil* **2005**, *278*, 205–221. [[CrossRef](#)]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.