REVIEW ARTICLE

Microbial ecology of hot desert edaphic systems

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One sentence summary: This review surveys the latest research on the structure and function of microbial communities in hot desert terrestrial biotopes (which include soils, cryptic and refuge niches and plant-root-associated microbes) and the processes that govern their assembly.

ABSTRACT

A significant proportion of the Earth's surface is desert or in the process of desertification. The extreme environmental conditions that characterize these areas result in a surface that is essentially barren, with a limited range of higher plants and animals. Microbial communities are probably the dominant drivers of these systems, mediating key ecosystem processes. In this review, we examine the microbial communities of hot desert terrestrial biotopes (including soils, cryptic and refuge niches and plant-root-associated microbes) and the processes that govern their assembly. We also assess the possible effects of global climate change on hot desert microbial communities and the resulting feedback mechanisms. We conclude by discussing current gaps in our understanding of the microbiology of hot deserts and suggest fruitful avenues for future research.

Key words: deserts; soil; hypoliths; biological soil crusts; global change; community dynamics

INTRODUCTION

Just over a third of the planet's biomes may be considered as deserts (also known as dry/arid lands), constituting one-fifth of the Earth's total surface area (approximately 33.7×10^6 km^2; Fig. 1; Laity 2009). Indeed, a greater proportion of these land surfaces are under continual threat of desertification (transition of land towards greater aridity) as a result of anthropogenic activities and climate change (Schlesinger *et al.,* 1990; Le Houérou 1996; Wang, Chen and Dong 2006). These changes are likely to have devastating consequences both socioeconomically as well as environmentally (Grainger 2009), especially for human populations inhabiting these arid environments (currently estimated at 6% of the total population) (Ffolliott *et al.,* 2003). Desert environments are globally significant and currently store almost one-third of total terrestrial carbon (C) (Trumper, Ravilious and Dickson 2008). Improving our understanding of deserts offers

further potential for carbon sequestration through enhanced land management practices (Durant *et al.,* 2012).

While there is no unanimous consensus on what constitutes a 'desert', a number of factors are synonymous with these environments. For instance, a ubiquitous feature is the scant, erratic and low precipitation level, which is also a key basis for subclassification. Based on direct meteorological observations, a 'desert' can be defined as having a ratio of precipitation to potential evapotranspiration (P/PET) of less than 1 (UNEP 1992). Four key zones of aridity are further defined: subhumid (P/PET = 0.5–0.65), semiarid (0.2–0.5), arid (0.05–0.2) and hyperarid (<0.05) (Barrow 1992). Deserts are also characterized by extreme fluctuations in temperature, generally low nutrient status, high levels of incident ultraviolet (UV) radiation and strong winds (Lester, Satomi and Ponce 2007; Chamizo *et al.,* 2012; Stomeo *et al.,* 2013) (Table 1).
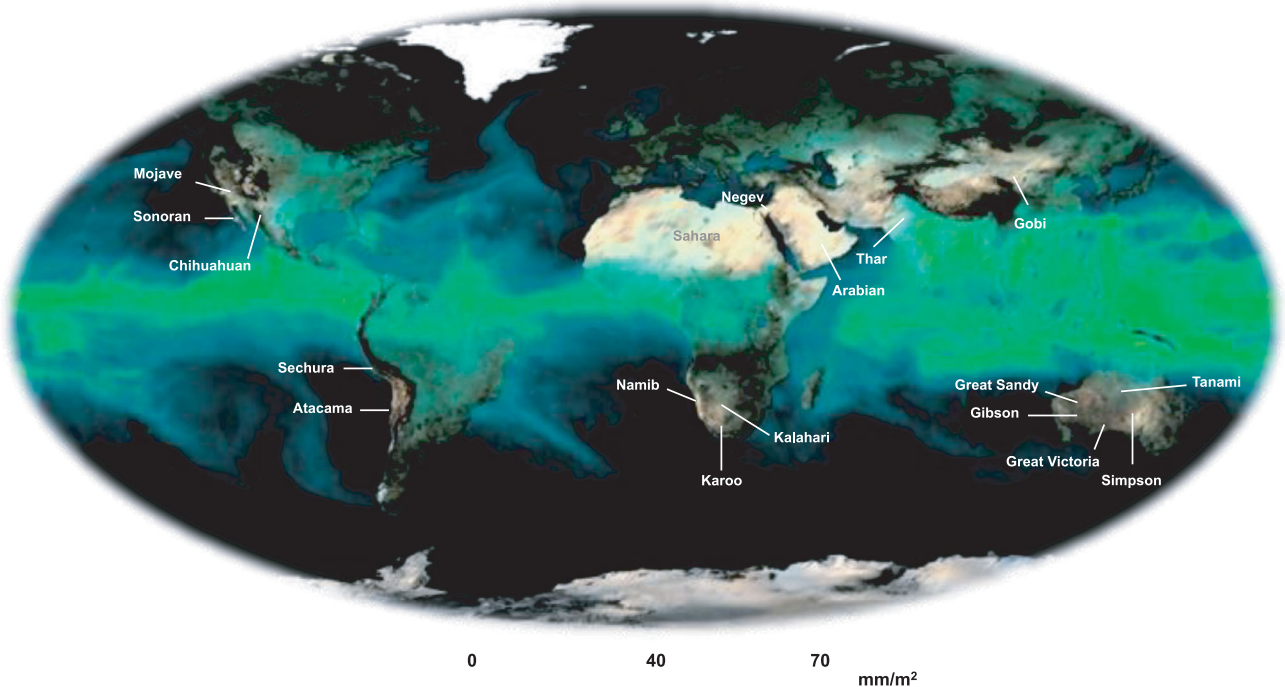
(A)
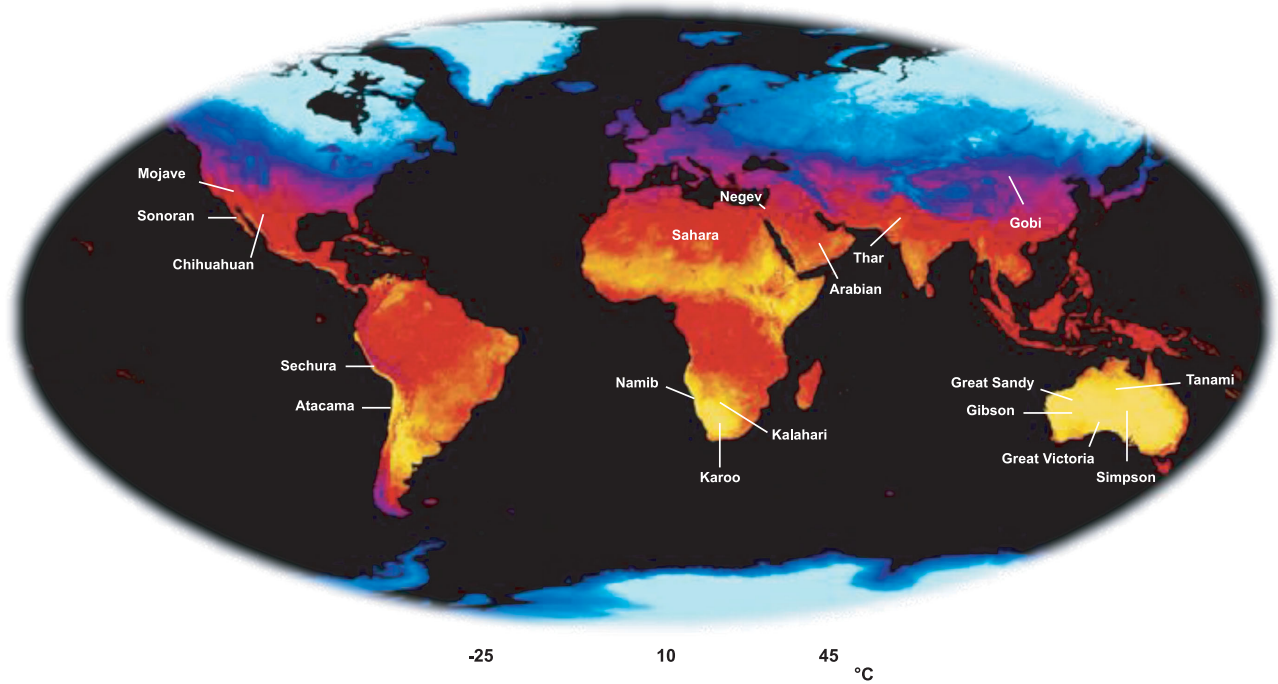
(B)

Figure 1. Global distribution of hot deserts with (**A**) land surface temperature (NEO, 2014) and (**B**) total precipitable water (NOAA, 2014) shown for January 2014.

In hot deserts, the combined effects of temperature fluctuations and aridity lead to unique adaptations in desert species. These adaptations are generally well understood for macroorganisms (plants and animals) (Berry and Bjorkman 1980; Evenari 1985). One consequence of the extremes of the desert environment is that the diversity of macrofauna is of-

ten limited in these systems and microorganisms may have a more influential role in governing key surface and subsurface bioprocesses.

Compared with higher organisms, relatively little is known of the specific mechanisms for microbial survival and adaption in hot desert ecosystems. To date, much of the research

Table 1. General characteristics (size, topography, physicochemical, pH and temperature) of globally distributed hot deserts.

Name/location	Approx. size (km^2)	Topography	Approx. temperature range (°C)	Approx. precipitation (mm/yr)/ classification	Selection of soil characteristics	References
Sahara/Northern Africa	9 100 000	Gravel plains, sand, dunes, rock and desert pavement	−5–45	5–150 hyperarid–arid	pH: 7.6–7.9, OC[a] (%)[a] 0.1–1.2, N (%) 0.8–0.1	Osborne (2000), Badr El-Din SM et al. (2006), Benslama and Boulahrouf (2013)
Kalahari/Southwestern Africa	520 000	Sand sheets and longitudinal dunes	−10–45	100–250 arid–semiarid	pH: 7.7–8.7, OC (%) 0.1–0.5 N (%) 0.01–0.08	Dean et al. (1999), Lawson and Thomas (2002), Mosweu et al. (2013)
Namib/Southwestern Africa	81 000	Gravel plains, sand plains and dunes	5–45	5–100 hyperarid–arid	pH: 7.9–8.5, OC (%) 0.1–0.3 N (%) 0.03–0.05	Stomeo et al. (2013), Eckardt et al. (2013)
Karoo/South Africa	395 000	Gravel plains, bush lands and savannah	2–40	50–200 arid–semiarid	pH: 6.9–9, OC (%) 0.3–1.3 N (%) 0.02–0.06	Schmiedel and Jürgens (1999), Burke (2002)
Chihuahuan/North Central Mexico – Southwestern USA	455 000	Numerous mountain ranges with shrub covered flat basins	10–40	70–400 arid–semiarid	pH: 5.9–6.2, OC (%) 0.2–1.9 N (%) 0.07–0.1	Gallardo and Schlesinger (1992), Bell et al. (2008)
Mojave/Southwestern USA	152 000	Mountain chains, dry alkaline lake beds, calcium carbonate dunes	−10–50	30–300 arid–semiarid	pH: 7.1–9.4, OC (%) 0.04–0.1, N (%) 0.03–0.09	Schaeffer et al. (2003), Titus et al. (2002), Wood et al. (2005), Hereford et al. (2006)
Sonoran/Southwestern USA	312 000	Basins and plains bordered by mountain ridges	−10–50	70–400 arid–semiarid	pH: 5–8.6, OC (%) 0.4–2 N (%) 0.003–0.07	Parker (1991), Weiss and Overpeck (2005), Andrew et al. (2012)
Atacama-Sechura/Chile-Peru	105 000	Salt basins, sand plains and lava fields	−5–40	0–20 hyperarid	pH – 6.6–9.2, OC (%) 0.1–2.6, N (%) 0.01–0.15	Barros et al. (2008), Lester et al. (2007), Lacap et al. (2011), Crits-Christoph et al. (2013)
Arabian/Arabian Peninsula	2 300 000	Sand, gravel plains and rocky highlands	5–40	25–230 arid–semiarid	pH: 7–7.5, OC (%), N (%) /	Abdel Hafez (1982), Almazroui et al. (2012)
Thar/India and Pakistan	200 000	Rocky sand, dunes and saline soil	4–50	200–300 semiarid	pH: 7.9–8.1, OC (%) 0.3–0.4 N (%) 0.02–0.06	Pandey et al. (1995), Bhatnagar and Bhatnagar (2005), Tripathi et al. (2007), Rafique et al. (2008)
Gobi/Southern Mongolia	53 000	Grasslands, rocky outcrops and gravel plains	−20–30	30–100 arid	pH: 7.7–10.2, OC (%) 0.1–2.64, N (%) 0.05–0.25	Pankova (2008), Wesche et al. (2010), Kurapova et al. (2012)
Great Victoria/Southwestern Australia	350 000	Dunes, gravel plains and grassland	18–40	150–230 arid–semiarid	OC (%) 0.2	Pell et al. (1999), Grace et al. (2006)
Great Sandy/Northwestern Australia	285 000	Linear dunes, wide plains and saline lakes	10–40	250–370 semiarid	pH: 5.8–6, OC (%) 0.1–1.1 N (%) 0.05–0.09	Grigg et al. (2008), Grace et al. (2006)
Tanami/Northern Australia	185 000	Sandy plains, grassland and shrubs	10–40	300–500 semiarid	pH: 4.9–6.7, OC (%) 0.1–1.4, N (%) 0.01–0.08	Paltridge and Southgate (2001), Reith et al. (2012),
Simpson/Central Australia	180 000	Extensive dune-fields	5–40	50–400 semiarid	pH: 6.5–7, OC (%) 0.1–0.3 N (%) 0.05–0.07	Duncan and Dickman (2001), Islam et al. (2005), Free et al. (2013), Nano and Pavey (2013)
Gibson/Southern Australia	156 000	Sandy plains, rocky highlands and grassland	6–40	200–400 semiarid	OC (%) 0.06, N (%) /	Grace et al. (2006)
Negev/Israel	13 000	Dunes, sandy soil and rocky highlands	5–40	100–300 arid–semiarid	pH: 7.2–8, OC (%) 0.5–0.7 N (%) 0.006–0.04	Angel et al. (2010, 2013), Drahorad et al. (2013), Martirosyan and Steinberger (2014)

[a] organic carbon

on high temperature environments has focused on aquatic systems, with the dual objectives of curating the microbial taxa and exploiting genomes, genes and gene products for industrial processes (Stetter 1999; Haki and Rakshit 2003). We argue that from an ecological perspective, an improved understanding of the underlying community dynamics in arid soil biotopes is paramount for a number of reasons. For instance, it is critically important to understand the impacts of desertification on microbial ecosystem services (e.g. biogeochemical cycling of C and N).

It is now accepted that soil microbial communities are strongly influenced by environmental factors at different geographic scales (Lauber et al., 2009; Angel et al., 2010; Rousk et al., 2010; Stomeo et al., 2012). Desert environments, because of the range and severity of environmental factors, are an obvious target for fundamental research on the ecological and evolutionary processes which structure biological communities. Diversity of higher eukaryotic species has been directly related to system functionality, in particular the efficiency of resource utilization (Naeem et al., 1994; Tilman, Wedin and

Knops 1996; Naeem, Duffy and Zavaleta 2012). This relationship may also hold true for microbial guilds (Wittebolle *et al.,* 2009; Langenheder *et al.,* 2010), suggesting that losses in microbial diversity may directly impact desert biomes (Hooper *et al.,* 2012; Mace, Norris and Fitter 2012). Functional guilds with little or no redundancy [e.g. nitrogen (N) cyclers], which are particularly important in soil function and conservation (Philippot *et al.,* 2013), may be the most sensitive.

Here we review recent knowledge on the composition and structure of microbial communities found in hot deserts. We focus on soil, cryptic and plant-associated communities. Understanding microbial diversity, adaption and functionality in arid environments may improve efforts aimed at conservation, rehabilitation, sustainable land management practices and water resource planning in regions that are vulnerable to continued degradation (UNEP 2006).

MICROBIAL COMMUNITY STRUCTURE IN DESERT SOILS

Bacterial communities

Desert biomes have been shown to differ markedly from other biomes in terms of soil microbial community composition and function (Fierer *et al.,* 2012). A recent comparison of soil microbial communities across different biomes used metagenomic sequencing to demonstrate that both hot and cold deserts showed the lowest levels of phylogenetic and functional diversity (Fierer *et al.,* 2012). However, taxonomic diversity in desert soil biomes is, surprisingly, more diverse than initially assumed, traversing a number of key taxa.

Desert soils from across the world typically contain a number of ubiquitous phyla including Actinobacteria, Bacteroidetes and Proteobacteria (Chanal *et al.,* 2006; Connon *et al.,* 2007; Lester *et al.,* 2007; Fierer *et al.,* 2009). Actinobacteria, many of which show high homology to different families within the subclass Actinobacteridae (Neilson *et al.,* 2012), often prevail in desert soil phylogenetic surveys (Liu *et al.,* 2009; Goswami *et al.,* 2013; Makhalanyane *et al.,* 2013a). For example, Namib Desert soils (Fig. 2A and B) were dominated by actinobacterial phylotypes (44%) with high homology to *Rubrobacter, Arthrobacter, Thermopolyspora* and *Streptomyces* spp. (Drees *et al.,* 2006; Makhalanyane *et al.,* 2013a; Santhanam *et al.,* 2013). Members of these genera have also been found in cold deserts, with *Arthrobacter* sp. commonly isolated from Antarctic soil (Aislabie *et al.,* 2006). Although many of these groups are ubiquitous in all soil types, many Actinobacteria isolated from deserts soils appear to be novel species (Li *et al.,* 2005, 2006; Mayilraj *et al.,* 2006; Lester *et al.,* 2007; Luo *et al.,* 2012) of less common genera such as *Kocuria* (Li *et al.,* 2006; Gommeaux *et al.,* 2010) and *Frankia* (Connon *et al.,* 2007; Shash 2009; Makhalanyane *et al.,* 2013a). The presence of the pioneer genus *Frankia* may be vital in depauperate environments as significant contributors to soil fertility (Griffiths and McCormick 1984; Dommergues and Ganry 1986). Evidence that actinobacteria are a dominant phylum in arid environments is perhaps unsurprising, given their capacity for sporulation, wide metabolic (and degradative) capacity, competitive advantages via secondary metabolite synthesis and multiple UV repair mechanisms (Ensign 1978; McCarthy and Williams 1992; Chater and Chandra 2006; Gao and Garcia-Pichel 2011).

Bacteroidetes are also common in desert soils, which is surprising given the proposed copiotrophic phenotype of members

Figure 2. Hot desert landscapes: (**A**) Namib Desert gravel plains, (**B**) the dune-interdune landscape of the central Namib sand-sea, (**C**) the Negev Desert and (**D**) vegetated landscale of the Mojave Desert.

of this phylum (Fierer, Bradford and Jackson 2007a). Although, obviously, not all members of a given phylum necessary fall under the same ecological category. For example, Death Valley soils showed a number of phylotypes with high homology to members of the *Flavobacteriales* and to the genus *Adhaeribacter* of the class *Sphingobacteria* (Prestel *et al.*, 2013). Desert soil microbial isolation studies have shown an abundance of *Pontibacter* sp. from the family *Cytophagaceae* (Zhou *et al.*, 2007; Zhang *et al.*, 2009; Subhash, Sasikala and Ramana 2014). A *Pontibacter* isolate from the Taklamakan Desert (China) has been shown to have the capacity for nitrogen fixation (nitrogenase activity mediated by the *nif*H gene), the first of its kind for this genus (Xu *et al.*, 2014). Interestingly, isolates from Bacteroidetes often show optimum growth at high pH values, which is consistent with the generally alkaline character of desert soils (Lauber *et al.*, 2009).

Proteobacteria are globally distributed and were thought to be prominent members of desert soil bacterial communities (Chen *et al.*, 2003; Lester *et al.*, 2007; Spain, Krumholz and Elshahed 2009; Bachar, Soares and Gillor 2012; Lefèvre *et al.*, 2012). In a study comparing desert soil with agricultural soil bacterial communities, Proteobacteria phylotypes were 2-fold higher (retrieved by 16S rRNA gene amplicon pyrosequencing) in the desert soil communities, with the genus *Ochrobactrum* (Alphaproteobacteria) being most prevalent (Köberl *et al.*, 2011). Alpha-, Beta- and Gammaproteobacteria are often associated with soils receiving higher rates of organic carbon inputs (Fierer *et al.*, 2007a; Lopez *et al.*, 2013). However, Proteobacteria may be functionally important in nutrient-limited arid environments since members of this phylum are implicated in bacteriochlorophyll-dependent photosynthesis (Raymond 2008; Boldareva-Nuianzina *et al.*, 2013). It has also been demonstrated that proteobacterium isolates from the Gobi Desert are capable of conferring photosynthetic capacity to other phyla (e.g. Gemmatimonadetes) by horizontal gene transfer (Zeng *et al.*, 2014).

Other bacterial lineages identified in desert environments include Gemmatimonadetes, Firmicutes and Cyanobacteria (Bahl *et al.*, 2011; Lacap *et al.*, 2011; Makhalanyane *et al.*, 2013a; Richer *et al.*, 2014), and these phyla may be comparatively more abundant in desert soils than in other biomes (Fierer *et al.*, 2012). Interestingly, one study demonstrated that a higher abundance Gemmatimonadetes was significantly correlated with low soil moisture content [Pearsons coefficient (r) = 0.409 (DeBruyn *et al.*, 2011)]. Although Gemmatimonadetes are ubiquitously distributed in soils, virtually nothing is known of their physiology or ecology (DeBruyn *et al.*, 2011). To date, only six arid soil Gemmatimonadetes isolates have been described (Ludwig, Euzéby and Whitman 2008; DeBruyn *et al.*, 2011), which hampers determination of their physiologies and consequently assessment of their functional roles. In spite of this, it has been suggested that the abundance of these taxa in arid soils implies that they are important colonists (DeBruyn *et al.*, 2011).

Members of the phylum Firmicutes are also well represented in desert soils (Chanal *et al.*, 2006; Lester *et al.*, 2007; Prestel, Salamitou and DuBow 2008; Gommeaux *et al.*, 2010). Members of the Firmicutes, mainly the Clostridia class, have been shown to dominate the rhizospheric bacterial communities associated with Antarctic vascular plants (>30% of community in all samples; pyrosequencing data for 16S rRNA gene) (Teixeira *et al.*, 2010), emphasizing their importance in arid environments. Certain *Firmicutes* spp. (*Bacillus*, *Paenibacillus*, etc.) can form endospores, which facilitate survival under desiccating conditions. The rapid spore germination, non-

fastidious growth requirements and short doubling times of these aerobic taxa means that members of the Firmicutes are some of the most readily isolated microbial 'weeds' from arid soils.

Cyanobacteria are well represented in a range of hot and cold edaphic communities (Cary *et al.*, 2010; Whitton and Potts 2012). These photosynthetic taxa are particularly important in oligotrophic arid environments as they are implicated in the key biogeochemical cycling processes such as C or N utilization and stress response (Chan *et al.*, 2013). The capacity of Cyanobacteria to maintain photosynthetic metabolism in desert-like conditions (high radiation, desiccation, salt stress, etc.) has been demonstrated (Harel, Ohad and Kaplan 2004; Singh, Fernandes and Apte 2010; Chen *et al.*, 2013; Singh, Anurag and Apte 2013). For instance, the nitrogen-fixing *Anabaena* sp. exhibited radio tolerance at 6kGy doses, which is lethal for most bacteria (Singh *et al.*, 2013). This is comparable with other extremophilic organisms such as *Deinococcus radiodurans*, which have also been found in hot desert phylogenetic surveys (Lacap *et al.*, 2011). Cyanobacteria harbour a number of repair and tolerance mechanisms to counter the effects of UV irradiation (Fig. 3). In addition to synthesizing UV-absorbing/screening compounds such as scytonemin (Sorrels, Proteau and Gerwick 2009), it has been shown that many members have the capacity to efficiently repair the photosynthetic apparatus, primarily associated with photosystem II (PSII). Over 50% of PSII activity was detected in a *Microcoleus* sp. five minutes after rehydration (Harel *et al.*, 2004). It has been proposed that during high radiation, Cyanobacteria repair and assemble functional PSII through *de novo* synthesis of the D1 protein complex. This ability is variable between different groups, however, with *Nostoc* sp. shown to exhibit a higher tolerance for UV-B radiation when compared to both *Chlorella* and *Microcoleus* sp. (Chan *et al.*, 2013). This was attributed to the lower generation of reactive oxygen species (ROS) and a higher capacity to repair PSII and DNA damage. Seasonal variation in PSII activity has also been shown (Williams *et al.*, 2014). The molecular mechanisms used to tolerate high irradiation are tightly linked with those employed to counter desiccation mainly due to the comparative oxidative stresses associated (e.g. ROS production). This is exemplified by the array of ionizing-radiation-resistant organisms that have been isolated from desiccated environments (Rainey *et al.*, 2005). The high salt concentrations characteristic of many desert soils contribute to detrimental water loss in bacterial cells through ionic and osmotic stresses. Indeed, it has been shown that incubating cyanobacterial cells with 0.5M NaCl induces an irreversible loss of the oxygen-evolving activity of PSII and electron transport activity of PSI (Allakhverdiev *et al.*, 2000). Acclimation to salt stress is aided by an increase in unsaturated fatty acids in membrane lipids that facilitates the activation of the Na^+/H^+ antiporter(s) and/or H+ ATPase(s). Here, a decrease in Na^+ in the cystol can protect PSI and PSII against salt-induced inactivation (Allakhverdiev *et al.*, 2000). The accumulation of compatible solutes (e.g. trehalose, sucrose) is also crucial not only for osmoprotection (e.g. glucosylglycerol) but also for shielding enzymes during drying and depressing the phase transition temperature of dry lipids after desiccation, thus maintaining them in a liquid crystal state (Singh, Sinha and Hader 2002). These features, in coordination with a chemotactic ability that facilitates moisture-induced migration to the surface (Garcia-Pichel and Pringault 2001), confirm that cyanobacteria have a physiology adapted for survival and function arid environments. Cyanobacteria also contribute significantly to desert soil nutrient status through improving soil stability, moisture retention and fertility (Belnap and Gardner 1993). The ability of
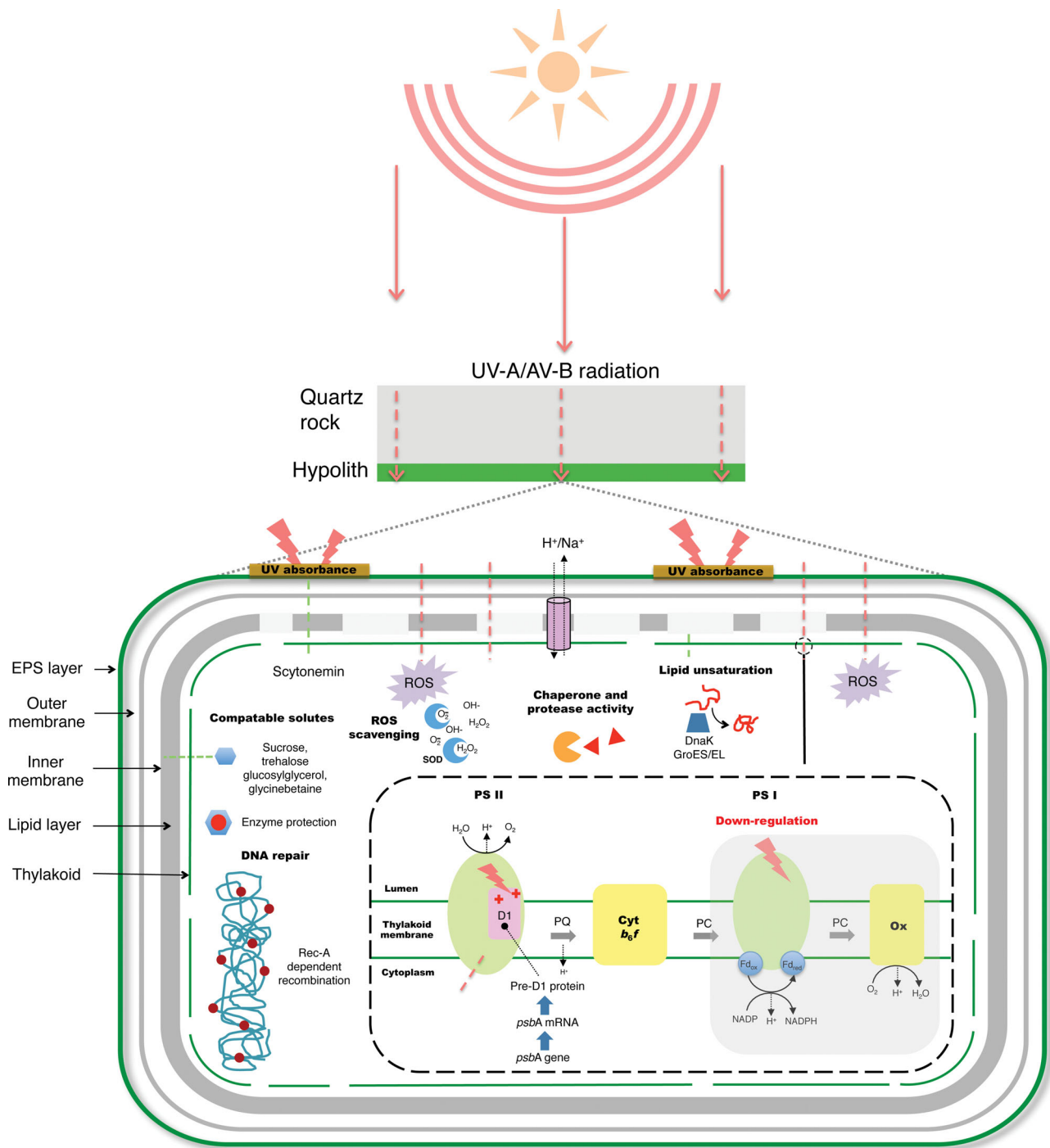
Figure 3. Resistance to photoinhibition and desiccation in Cyanobacteria. The synthesis of UV-screening pigments like scytonemin provides a barrier against UV-induced photodamage. The susceptibility of PSII to light-induced oxidative damage is countered by a highly efficient PSII repair system, whereby D1 protein is re-synthesized after degradation. This protein is encoded by the *psb*A gene, which is highly regulated at the transcriptional level with translational elongation also important. The downregulation of PSI in the thylakoid under high light conditions confers a physiological advantage as less ROS are produced. Chaperones such as groES/EL and DnaK are upregulated during desiccation and maintain proper protein function, with protease activity necessary for rapid turnover of unrequired proteins. A host of DNA repair mechanisms (e.g. RecA-mediated recombination) as well as mechanisms to reverse ROS damage [e.g. superoxide dismutases (SOD) activity] are also crucial in circumventing the effects of high irradiance and desiccation in Cyanobacteria. The unsaturation of fatty acids in membrane lipids also enhances tolerance to high light by protecting the photosynthetic machinery (e.g. facilitating Na+/H+ antiporter systems). PQ, plastoquinone; Cytb6f, cytochrome b6f complex; PC, plastocyanin; Fdox, ferredoxin; Fdred, ferredoxin–NADP reductase; O, terminal oxidase.

Table 2. Hot desert edaphic fungi and their potential ecological roles. N.D.: not determined.

Name	Desert	Functional role in desert soil systems	Technique	Reference
Aspergillus sp., *Penicillium* sp., *Acrophialophora* sp., *Aleternaria* sp.	Arid soils of Western Rajasthan (India)	Release of bioavailable phosphorous from organic phosphorous compounds	Culturing	Tarafdar *et al.* (1988)
Acaulospora sp., *Archaeospora* sp., *Entrophospora* sp., *Glomus* sp., *Paraglomus* sp.	Junggar Basin (Northwest China)	Arbuscular mycorrhizal fungi associated with desert ephemerals that probably play an important role in their development and maintenance	Culturing	Shi *et al.* (2007)
Phylotypes from the Ascomycota (mainly *Alternaria* sp. and *Acremonium* sp.) and Basidiomycota divisions	BSCs of the Colorado Plateau (USA)	The dark-pigmented *Alternaria* sp. may be involved in UV resistance of the BSC	DGGE	Bates and Garcia-Pachel (2009)
N.D.	Rock varnish from the Negev and Sinai deserts (Israel), the Mohave, Borrego and Sonoran desert regions (USA) and the Kalahari (South Africa)	Iron and Manganese precipitation. Protection against dessication and UV radiation.	Culturing/ microscopy	Krumbein and Jens (1981)
Arbuscular mycorrhizal fungi	Semiarid Mediterranean steppes (Spain)	Soil structuring and aggregation	Soil Hyphal length and glomalin content	Rillig *et al.* (2003)
Arbuscular mycorrhizal fungi	Sonoran Desert (USA)	As colonists of both roots and soils, they contribute to the creation of 'Resource-Island' soils by stabilizing windborne soil under plant canopies and enhancing plant colonization.	Spore count/ culturing/propagule density/mycelia formation	Carrillo-Garcia *et al.* (1999)
N.D.	Negev (Israel)	Biodegradation of recalcitrant organic matter (i.e. plant polymer)	Substrate utilization patterns	Oren and Steinberg (2008)

members of this phylum to withstand high levels of UV irradiation, desiccation and water stress (Cockell and Knowland 1999; Starkenburg *et al.*, 2011) is likely to provide a significant competitive advantage, demonstrated by a recent whole-genome transcriptional study which highlighted the capacity of a Cyanobacteria sp. to efficiently respond to soil moisture status (Rajeev *et al.*, 2013). Despite these advantages, cyanobacteria in the most extreme hyperarid deserts are generally restricted to protected sublithic niches, with only limited cell numbers in surface soils. For example, a recent study demonstrated that in Namib Desert hypolithic communities, over 10% of phylotypic sequences were affiliated to Cyanobacteria (Makhalanyane *et al.*, 2013). While the majority of clones demonstrated high homology to 'uncultured' cyanobacteria, many of the clones were affiliated to *Chroococcidiopsis*, a lineage with a global distribution in both hot and cold deserts (Bahl *et al.*, 2011). Interestingly, this study found no evidence of recent inter-regional gene transfer, suggesting that the global distribution of desert cyanobacteria is a product of an ancient evolutionary legacy and has not been significantly impacted by dispersal. This finding raises questions relating to large-scale biogeographic patterns in microbial communities, as to how these regional patterns relate to functional attributes, and what the resilience of this important desert soil taxon to the effects of climate change might be.

Fungal communities

Numerous fungal lineages have been reported from desert soil environments (Fierer *et al.*, 2012; Sterflinger, Tesei and Zakharova 2012; Chan *et al.*, 2013). The majority of studies on desert fungi have employed culture-based approaches with only a few studies using culture-independent methods. Early isolation studies, using soils from the Negev (Fig. 2C) and Sonoran deserts, showed a high level of fungal diversity (Ranzoni 1968; Taylor-George *et al.*, 1983), consistent with the general perception that fungi are one of the most stress-tolerant eukaryotic life forms on Earth (Waller *et al.*, 2005; Sterflinger *et al.*, 2012). Isolated phyla included members of both the *Basidiomycota* and *Ascomycota*, with high taxonomic diversity. For example, a culture-dependent survey of fungi from Makhtesh Ramon desert soil found 185 unique fungal species, dominated by ascomycetes (Grishkan and Nevo 2010), while a preliminary survey of Atacama desert soils recorded 12 genera, including *Cladophialophora, Cladosporium, Leptosphaerulina, Alternaria, Ulocladium, Eupenicillium, Aspergillus, Penicillium, Ascobolus, Monodictys, Periconia* and *Giberella* (Conley *et al.*, 2006). Both thermophilic and thermotolerant fungi have been isolated from hot desert soils (Moustafa, Sharkas and Kamel 1976; Titus, Nowak and Smith 2002).

Fungi are ecologically important in desert systems (Table 2) and have demonstrated different assimilation patterns from

those of the same species in other environments. For example, the utilization of plant polymers has been shown to be higher in desert fungi than in other taxa and may be crucial in shaping plant-associated microbial communities (discussed in greater detail below) (Oren and Steinberger 2008). A detailed overview of hot and cold desert fungi has been published by Sterflinger *et al.* (2012).

Archaeal communities

Archaeal taxa are relatively rare across many biomes but seem to be particularly abundant in desert soils (Fierer *et al.*, 2012), with *Thaumarchaeota* being the principal representative. All known organisms of this lineage are chemolithoautotrophic ammonia-oxidizers and may play important roles in biogeochemical cycling (Brochier-Armanet *et al.,* 2008), particularly in oligotrophic environments, which is exemplified by the preference of low ammonium concentrations by the thermophilic strain *Nitrososphaera gargensis* (optimal growth with 0.14 and 0.79 mM ammonium; Hatzenpichler *et al.,* 2008). A previous study on Tataouine Desert soils recovered archaeal phylotypes affiliated to thermophilic *Crenarchaeota* (Chanal *et al.,* 2006), although recent taxonomic revisions have moved some previous members of this phylum to the *Thaumarchaeota* (Brochier-Armanet *et al.,* 2008). Remarkably, metagenome sequencing of seven saline soils from the Kutch Desert in India found that halophilic euryarchaeota may constitute up to 40% of soil prokaryotic phylotypes (Pandit *et al.,* 2014).

A biogeographic survey across different ecosystems along a precipitation gradient, from the Israeli Negev Desert (Fig. 2D) in the south to the northern Mediterranean forests, demonstrated that differences in archaeal community composition between ecosystem types could be explained by the combined effects of precipitation gradient and vegetation cover (Angel *et al.,* 2010). In stark contrast, no differences in alpha diversity were found between the different ecosystems, suggesting that unlike macroorganisms, which are less diverse in desert areas, the diversity of archaea and bacteria seems to be less constrained by precipitation. However, fingerprinting techniques are not well suited for studies of comprehensive microbial diversity (Bent and Forney 2008) and these results should be interpreted with caution.

Viruses

Viruses, and more specifically phages (viruses infecting bacteria), are thought to be the most prevalent entities on earth (Rice *et al.,* 2001; Weinbauer 2004; Le Romancer *et al.,* 2007; Suttle 2007). In deserts, viruses and bacteriophages may have a more significant role in driving biogeochemical cycles than in other ecosystems since these environments are most likely microbially driven. Nevertheless, the ecological role of viruses in hot desert soils has rarely been examined (Prigent *et al.,* 2005; Fierer *et al.,* 2007a, 2012; Prestel *et al.,* 2008, 2013). One of the earlier studies used a strategy of exploring both extracellular phages and prophages inserted into bacterial genomes (Prigent *et al.,* 2005). Electron microscopy showed a higher than expected diversity of virus-like particles for this extreme environment, with morphotypes corresponding to three major families of tailed phages (*Myoviridae, Siphoviridae* and *Podoviridae*). Similarly, a study on Namib desert bacteriophages using a combination of electron microscopy and genomic approaches showed a surprisingly high number of phage-like morphotypes (over 20 distinct phage-like morphologies) (Prestel *et al.,* 2008), mostly belonging to the *Myoviridae* and *Siphoviridae* families of tailed bac-

teriophages. One surprising result from this study was the seemingly high diversity of *Myoviridae*-type bacteriophages, whose complex contractile tails with fragile caudal fibers were not expected to survive the harsh desert conditions. In contrast to the study from the Sahara desert, no phages belonging to the family *Podoviridae* were identified (Prigent *et al.,* 2005). More recently, a study on bacteriophages from Death Valley (USA), using random amplification and cloning of phage DNA in addition to electron microscopy and pulsed-field gel electrophoresis (Prestel *et al.,* 2013), revealed 11 distinct morphotypes all sharing structural traits with members of the order Caudovirales of tailed phages. An interesting observation from these studies was that many desert soil phages were present as active SOS-inducible prophages. Prestel *et al.* (2008) suggest that the environmental conditions in deserts may prevent the induction of these putative lysogens through UV exposure.

Fierer *et al.* (2007a) used metagenomic analysis and small-subunit RNA-based sequence analysis to compare the viral diversity of different biomes. The study, which compared soils from the Mojave Desert (e.g. Fig. 2C) to those of prairie and rainforest soils, was the first to profile viral communities using a metagenomic approach and showed that viral diversity was higher than initially expected. Results revealed that viral communities were taxonomically diverse and distinct from those in other environments (Fierer *et al.,* 2007a), and supported the general observation that viral communities in desert soil are principally members of the *Myoviridae, Podoviridae* and *Siphoviridae*. A smaller proportion of sequences in this study were similar to T4-like myophage and unclassified phages (Fierer *et al.,* 2007a).

MICROBIAL FUNCTIONALITY IN DESERT SOILS

We know surprisingly little about microbial functionality in desert soils. Metagenome data from a study focusing on a number of biomes showed that functional diversity, as represented by the abundances of genes implicated in nitrogen, potassium and sulphur metabolism, was lower in hot desert soils than in non-desert soils (Fierer *et al.,* 2012). However, functional alpha diversity (defined here as the average number of functional groups) has not been measured in desert soil microbial ecology, despite its importance when interpreting the diversity and distribution of genes across communities (Petchey and Gaston 2002; Green, Bohannan and Whitaker 2008; Raes *et al.,* 2011). Although desert soil microbial groups are abundant and span a number of taxa, nutrient cycling rates are lower in these depauperate biomes than in more mesic habitats, primarily due to moisture limitations and lower plant biomass (Fierer *et al.,* 2007a, 2012; Manzoni, Schimel and Porporato 2012). Arid soil-derived metagenomes show a higher abundance of genes associated with dormancy and stress response than non-arid biomes, a probable consequence of the evolutionary pressure of moisture- and thermal-stress events (Fierer *et al.,* 2012).

DESERT MICROBIAL COMMUNITY DYNAMICS

'Microbes are everywhere', but despite this ubiquity they are not in all places at all times. Indeed, many studies have shown that environmental factors such as water availability, N, salts, pH and temperature are important in explaining microbial community assembly in deserts (Angel *et al.,* 2010; Fierer *et al.,* 2012; Stomeo *et al.,* 2012; Garcia-Pichel *et al.,* 2013; Sher, Zaady and Nejidat 2013), findings which are consistent with the view that deterministic factors dominate bacterial community

assembly processes (Wang et al., 2013). However, it has also been demonstrated that stochasticity influences desert soil microbial communities at both global and local scales. Similar findings have been reported in above-ground environments, such as the phyllosphere of *Tamarix* trees across the Sonoran Desert (Finkel et al., 2012), where distance alone accounted for the variations in bacterial community composition.

Species interactions are also thought to be important in shaping desert microbial communities (Caruso et al., 2011; Stomeo et al., 2013). For instance, cyanobacteria drive the development of niche communities (as primary producers and N-fixers; Makhalanyane et al., 2013b) and may facilitate the persistence of other groups through the production of exopolysaccharides (EPS) which may aid in water uptake and retention (Hall-Stoodley, Costerton and Stoodley 2004). In contrast, antibiotic-resistance genes have been shown to be less abundant in desert soils than in non-desert soils (Fierer et al., 2012), suggesting that competitive interactions are not as important in shaping desert microbial communities as in mesic soil communities. In view of these contrasting findings, a greater focus on species interactions, the relative contributions of deterministic and stochastic processes and how these vary through time and with environmental gradients, is required.

LOCALIZED, CRYPTIC AND REFUGE NICHES

Microbial populations are inhomogeneously distributed in arid soil systems, particularly in the more 'extreme' hyperarid deserts. Where conditions allow, macroscopic surface communities (biological soil crusts, BSCs) develop. In more extreme desert habitats, where summer temperatures and desiccation processes exceed the limits of survival for surface BSCs, such communities are found only on the ventral surfaces of translucent pebbles and rocks (hypoliths). Neither BSC nor hypolithic communities show the same bacterial community structures as the surrounding surface soils (Connon et al., 2007; Makhalanyane et al., 2013a; Stomeo et al., 2013), but it is thought that desert soils may serve as a 'reservoir' from which the more specialized assemblages (BSCs and hypoliths) recruit keystone taxa (Makhalanyane et al., 2013a).

Biological soil crusts

BSCs are complex microbial communities colonizing interspace soil surfaces between patchily distributed plants and are widely distributed in both hot and cold deserts (Pointing and Belnap 2012). These communities consist of complex assemblages of different species, including algae, fungi, lichens and mosses together with photosynthetic and heterotrophic bacteria. Cyanobacteria are typically the dominant microorganisms in BSCs, in particular species of the genera *Microcoleus* (Belnap, Buedel and Lange 2003), *Phormidium, Tolypothrix* and *Scytonema* (Dojani et al., 2013).

Regional and local variations in the structures of BSCs have been identified in a number of deserts. For instance, BSCs in the Colorado Plateau of the southwest United States generally harbor abundant populations of Actinobacteria (Garcia-Pichel et al., 2003; Steven et al., 2012a,b), while this taxonomic group has been shown to be less abundant in BSCs from Oman or Australia (Abed et al., 2012). Even at small spatial scales, BSCs can show large differences in microbial community composition. These differences relate to microsite variations, such as local topography, shading or parental soil material (Steven et al., 2013). For example, BSCs associated with gypsum soils

harbor significantly larger populations of Actinobacteria and Proteobacteria and lower populations of Cyanobacteria compared to sandstone and shale soils (Steven et al., 2013). Variations in BSC community composition may also relate to differences in age, soil disturbance history, distance from plants and climatic regimes (Hawkes and Flechtner 2002; Gundlapally and Garcia-Pichel 2006; Housman et al., 2007; Strauss, Day and Garcia-Pichel 2012).

Biogeographic patterns in BSCs have also been investigated at a continental scale (Dvorak, Hasler and Poulickova 2012; Garcia-Pichel et al., 2013). For example, an analysis of the microbial community composition of BSCs across North America, resolved at the phylum level, recorded no statistically valid biogeographic patterns (Garcia-Pichel et al., 2013). In contrast, the use of phylogenies and molecular clocks calibrated from fossil DNA showed both a high diversity within *Microcoleus vaginatus* (an important primary producer within BSCs) and differences between continents (Dvorak et al., 2012); i.e. European strains could be separated from those in Asia and North America. These findings suggest that both geographic barriers and allopatric speciation are important in explaining cyanobacterial distribution in BSCs (Dvorak et al., 2012). Taken together, these studies indicate that microbial communities of BSCs display biogeographic patterns across different spatial scales that reflect their local environment as well as historical events.

BSCs make important contributions to the function of desert ecosystems and have been described as 'ecosystem engineers' (Jones, Lawton and Shachak 1994). For instance, these communities fix large amounts of atmospheric carbon dioxide (CO_2) (over 2.6 pg of C per year globally) (Elbert et al., 2012), regulate the temporal dynamics of soil CO_2 efflux and net CO_2 uptake (Castillo-Monroy et al., 2011), drive the activity of soil enzymes (Miralles et al., 2013), contribute to N turnover processes including N fixation (Elbert et al., 2012), nitrification (Castillo-Monroy et al., 2010) and denitrification (Abed et al., 2013) and mediate runoff-infiltration rates (Chamizo et al., 2012). The enrichment of nutrients in subcrust soils also stimulates increases in heterotrophic microbial and invertebrate populations, including bacteria, fungi and nematodes (Darby, Neher and Belnap 2007; Crenshaw et al., 2008). BSCs also contribute to soil stabilization, where filamentous fungi and cyanobacteria provide soil particle cohesion by penetrating through the uppermost soil layers (Pointing and Belnap 2012). Local hydrological cycles are influenced by BSCs, influencing factors such as the texture of soil aggregates and soil pore formation that determine water infiltration and retention (Belnap 2006). The influence of BSCs on these factors depends on the species composition and community morphology, which are in turn affected by historical events (e.g. disturbance) and by climate and soil properties. Collectively, BSCs are viewed as 'islands of fertility' in typical oligotrophic desert soil systems (Schlesinger et al., 1990).

Hypoliths

Most desert surfaces are covered, to a greater or lesser extent, with pebbles or rocks: the 'desert pavement' (Laity 2009). Translucent pebbles or rocks (mainly quartz or marble) are found in all major deserts (Azua-Bustos et al., 2011; Bahl et al., 2011; Caruso et al., 2011) and are a particularly important feature in hyperarid deserts due to the presence of 'hypolithic' microbial communities found on their ventral surfaces (Bahl et al., 2011). Such hypolithic communities may represent a sublithic extension of surface BSCs (Budel et al., 2009) or, in more extreme desert habitats, may represent discrete communities (Chan et al., 2012).

There appear to be multiple drivers for hypolithic community development, of which the principal (and necessary) driver is adequate light transmission (Warren-Rhodes *et al.,* 2013). Given the penetration of sufficient photosynthetically active radiation (PAR) to support cyanobacterial photosynthesis on the ventral or lateral surfaces, other factors which may dictate community development (and the frequency of colonization of suitable translucent substrates) are thought to include water availability (Lacap *et al.,* 2011), protection from incident UV radiation and excessive PAR (Schlesinger *et al.,* 2003; Cowan *et al.,* 2010; Wong *et al.,* 2010), desiccation (Warren-Rhodes *et al.,* 2006) and extremes of temperature (Warren-Rhodes *et al.,* 2006). The physical stability provided by the overlying rock (i.e. protection from physical disruption by wind) may also be a driver for hypolithic community development (Wong *et al.,* 2010).

In the hyperarid Atacama Desert, the rate of quartz rock hypolithic colonization is as low as approximately 3:4000 (Lacap *et al.,* 2011), whereas in the generally less arid Namib Desert colonization rates are above 95% (Warren-Rhodes *et al.,* 2013). An analysis of the photosynthetic responses of hypolithic communities in the tropical semiarid region of Australia (Tracy *et al.,* 2010) showed that photosynthetic activity was dependent on a soil moisture content of at least 15% (by mass). This finding provides a possible explanation for the very low hypolithic colonization rates in the hyperarid eastern Atacama Desert (compared to the more humid western coastal areas; Azua-Bustos *et al.,* 2011), and supports the observation that hypolithic communities in the western Namib Desert may be primarily supported by fog-derived moisture (Warren-Rhodes *et al.,* 2013). Hypolithic microbial community structure along an inverse fog-rainfall gradient across the central Namib Desert showed strong west–east discrimination (Stomeo *et al.,* 2013), indicating that water availability dictates higher resolution effects (such as microbial community composition) (Fig. 3).

Hot desert hypolithic communities around the world are dominated by bacterial phylotypes, where the majority of taxa (approximately 80%) are affiliated to cyanobacteria, particularly members of the coccoid genus *Chroococcidiopsis* (Warren-Rhodes *et al.,* 2006; Tracy *et al.,* 2010; Azua-Bustos *et al.,* 2011; Bahl *et al.,* 2011; Lacap *et al.,* 2011; Makhalanyane *et al.,* 2013a). Filamentous cyanobacteria, closely related to *Scytonema* and *Nostoc* spp., have been recorded in Atacama hypoliths (Azua-Bustos *et al.,* 2011). Cyanobacterial groups with high homology to *Pleurocapsales, Oscillatoriales* and *Gloeocapsopsis* lineages also form a significant portion of hypolithic communities (Makhalanyane *et al.,* 2013a; Azua-Bustos *et al.,* 2014).

The dominance of cyanobacteria emphasizes the important role played by hypoliths in hot desert soils where, for example, unicellular N_2-fixing *Gloeothece* (*Gloeocapsa*) and heterocystous *Nostoc* may contribute substantially to soil N budgets (Boison *et al.,* 2004).

Heterotrophic bacteria belonging to the phyla Actinobacteria, Proteobacteria, Acidobacteria, Bacteroidetes and Chloroflexi also constitute significant proportions of all hypolithic communities (Lacap *et al.,* 2011; Makhalanyane *et al.,* 2013a). Actinobacterial phylotypes include a number of radiation tolerant taxa, such as *Rubrobacter* sp. (Lacap *et al.,* 2011; Makhalanyane *et al.,* 2013a). The N-fixing genus *Agrobacterium* (alpha-proteobacteria) is also abundant in hypolithons (Lacap *et al.,* 2011). It has been reported that *Agrobacterium tumefaciens* is responsive to specific phenolic compounds (acetosyringes), which are released from wounded plant tissue (Cho and Winans 2005). Interestingly, cyanobacteria are known to produce phenolic compounds which may protect them from

oxidative stressors (Pinero Estrada, Bermejo Bescos and Villar del Fresno 2001; Klejdus *et al.,* 2009). Acidobacteria form a minor fraction of the hypolithic microenvironment, with the majority of clones showing homology to uncultured *Acidobacterium* taxa (Makhalanyane *et al.,* 2013a). Bacteroidetes in Atacama hypoliths show homology to *Cytophaga* (Azua-Bustos *et al.,* 2011), and several hot desert hypolithic microbial communities have also shown phylotypic signals with high homology to the facultative methylotroph *Methylobacterium* sp. (Azua-Bustos *et al.,* 2011; Makhalanyane *et al.,* 2013a). *Methylobacterium* spp. which have been found, for instance, in Atacama (Azua-Bustos *et al.,* 2011) and Namib desert (Makhalanyane *et al.,* 2013a) hypoliths, are known to express proteins which allow for the use of methanol as both carbon and energy source (Green 2006). The presence of these taxa in hypolithons may indicate methylotrophic adaptation to single carbon metabolism within this niche, a further indicator of the importance of this group in driving functional processes.

The microbial diversity found in hypolithic communities largely mirrors that found in the surrounding soils, suggesting that hypolithic microbial communities selectively recruit from adjacent local populations (Makhalanyane *et al.,* 2013a). However, the kinetics of these processes are unknown, although it has been suggested that colonization is a slow (decadal-scale) process (Warren-Rhodes *et al.,* 2006).

Little is known about viruses and bacteriophages in desert hypolithic communities. The functional and taxonomic diversity of viruses have only recently been explored in desert hypolithic communities from the Namib. Phylogenetic analysis showed that bacteriophages belonging to the order *Caudovirales,* many of which infect *Bacillus* species, were prevalent. This is consistent with the previous work which showed that members of the *Bacilli* were dominant in Namib soils. However, the paucity of cyanophages (Adriaenssens *et al.,* 2014) was surprising since cyanobacteria are known to dominate hypolithic biomass (Chan *et al.,* 2012). The authors concurred with Prestel *et al.* (2013), who attributed this discrepancy to the fact that most sequences deposited in the databases used were derived from marine cyanophages, which differ from those in terrestrial environments.

Hypoliths are generally considered to be important physical elements of desert soil ecosystems. Hypolithic biomass and associated EPS layers are thought to contribute to soil stability around colonized rocks (Pointing *et al.,* 2007; Warren-Rhodes *et al.,* 2007). Hygroscopic EPS acts as a water reservoir after wetting events (including dew-fall; Gorbushina 2007) and as a possible mechanism for absorption of water vapour from the soil environment (de los Ríos, Cary and Cowan 2014). It has been recently proposed (Williams *et al.,* 2014) that EPS production during the wet season may serve as a protective mechanism against premature resurrection during the dry season.

DESERT MICROBIAL COMMUNITIES SHAPED BY PLANTS

In nutrient-limited environments, one of the most widely accepted theories of biological distribution is the 'resource island' hypothesis, which states that plants promote microbial heterogeneity in soils by enhancing soil fertility under their canopies (Herman *et al.,* 1995). Indeed, bacteria have been found to be more abundant under shrubs than in open soils (Bachar *et al.,* 2010). It has also been shown that bacterial and archaeal community compositions differ between shrub and intershrub sites in arid and semiarid soils, but not in mesic soils

(Angel *et al.,* 2010; Ben-David *et al.,* 2011; Bachar *et al.,* 2012). Gram-positive bacteria were found to be more abundant in soils under the shrub canopies, whereas cyanobacteria and anaerobic bacteria were prevalent in the inter-shrub soils. In direct contrast, active prokaryotic communities (Bacteria and Archaea) were found to be highly correlated with soil moisture but did not significantly differ between shrub and inter-shrub sites (Angel *et al.,* 2013). This result suggests that the spatial patterns obtained by the analysis of active communities cannot be extrapolated to predict the composition of total microbial communities (Angel *et al.,* 2013). Interestingly, the discrepancy between DNA- and RNA-based methodologies was less pronounced in Archaea than in Bacteria. The fact that members within the archaeal community have been found to be more resilient to energy starvation and extreme conditions (Maupin-Furlow, Humbard and Kirkland 2012), including high temperatures (Bowers and Wiegel 2011) and desiccation (Kendrick and Kral 2006) may explain these findings (Angel *et al.,* 2013). However, as the methodology used, i.e. terminal restriction fragment length polymorphism (T-RFLP) fingerprinting, is restricted to the most abundant microbial taxa, extrapolation to all members of the microbial community is not necessarily valid.

Studies focusing on the temporal variations of desert microbial communities are few. Nevertheless, it has been reported that seasonal rainfall was one of the primary triggers of major change in bacterial diversity in the vicinity of desert shrubs (Saul-Tcherkas, Unc and Steinberger 2013).

The issue of whether desert plant root systems select for unique rhizospheric and rhizoplanic microbial phylotypes (or communities) remains unresolved, not least because of difficulties in selecting appropriate 'controls' and the limited depth of many phylogenetic surveys. For example, members of the phylum *Acidobacterium* were associated with the rhizospheres of two native bunchgrasses (*Stipa hymenoides* and *Hilaria jamesii*) and the invading annual grass *Bromus tectorum,* but not found in inter-plant spaces colonized by biocrusts (Kuske *et al.,* 2002). Rhizospheric communities of King Clone (*Larrea tridentata*), an 11 700-year-old creosote bush ring in the Mojave Desert (Fig. 2D) (Jorquera *et al.,* 2012), analysed using both culturable and unculturable [PCR-denaturing gradient gel electrophoresis (DGGE)] methods, showed common taxa associated with agricultural plants, including species of *Proteobacteria*, *Bacteroidetes* and *Firmicutes* that commonly carry traits associated with the promotion of plant growth (Jorquera *et al.,* 2012). A phylogenetic comparison of desert plant rhizospheric communities (Andrew *et al.,* 2012) found few differences between the ecologically similar saguaro (*Carnegiea gigantea*) and cardon (*Pachycereus pringlei*) cacti. The authors concluded that desert rhizospheric bacterial communities were shaped primarily by soil characteristics and geographic location, with rhizospheric associations only being secondary factors. Similarly, bacterial community structures in the phyllosphere of *Tamarix* trees across Israel and the United States were found to be driven by climate (Finkel *et al.,* 2011), while community assembly within a region (i.e. the Sonora Desert) was found to be shaped by geographical distance (Finkel *et al.,* 2012), particularly for members of the *Betaproteobacteria*.

Mycorrhizal fungi play an important role in plant growth processes, including the transfer of nutrients, predominantly phosphorus (P) and N, and water (Parniske 2008), enhanced resistance to stress and, in some cases, protection against soil pathogens (Chagnon *et al.,* 2013). However, there is little information relating the abundance, distribution or interaction of mycorrhizal fungi with plants in deserts ecosystems. Fungal taxa belonging to the genera *Acaulospora, Archaeospora, Entrophospora, Glomus*

and *Paraglomus* have been isolated from soil around the roots of ephemeral plant communities (*Eremopyrum orientale, Gagea sacculifera, Plantago minuta, Tragopogon kasahstanicus* and *Trigonella arcuata*) in Junggar Basin, northwest China (Shi *et al.,* 2007). Members of *Sebacinaceae* were the dominant mycorrhizal fungi in all *Hexalectris* roots and were phylogenetically intermixed with ectomycorrhizal taxa (Taylor *et al.,* 2003). Six ITS RFLP types were identified, of which four were found in samples of *Hexalectris spicata* var. *spicata,* while the other two types were present in *H. spicata* var. *arizonica* and in *H. revoluta,* respectively. These results provide evidence for divergence in mycorrhizal specificity between closely related desert orchid taxa. However, most mycorrhizal fungi are not host-specific, and it is suggested that plants from the same or from different species may be interconnected by mycorrhizal fungal networks (van der Heijden and Horton 2009).

EFFECTS OF GLOBAL AND REGIONAL CHANGES ON DESERT MICROBIAL COMMUNITIES

Global surface temperatures are predicted to rise by 2 to 6°C over the next nine decades, potentially leading to dramatic shifts in the structure and functionality of terrestrial biological communities (Meehl *et al.,* 2007). Several recent studies have suggested that climatic change may specifically affect the composition of microbial communities in arid regions. For example, an increase in air temperature of 2–3°C over 4 yr was linked to a substantial reduction in BSC cover (ca. 44%) at two semiarid sites in Spain (Maestre *et al.,* 2013). In this study, atmospheric warming significantly increased soil CO_2 efflux and reduced soil net CO_2 uptake, lessening the capacity of drylands to sequester atmospheric CO_2. A latitudinal replacement in dominance between two key topsoil cyanobacteria (*M. vaginatus* and *M. steenstrupii*), driven by temperature, was observed in bacterial communities across arid North America (Garcia-Pichel *et al.,* 2013). Ecophysiological characterization demonstrated that one cyanobacterium (*M. vaginus*) was more psychrotolerant and less thermotolerant than the other (*M. steenstrupii*). This is in contrast to what is anticipated for plants and biocrust mosses, whose biogeography and mortality, respectively, have been shown to be primarily influenced by changes in precipitation events rather than a change in temperature (Reed *et al.,* 2012). The replacement of mosses by cyanobacteria led to substantial alterations in N cycling and soil fertility in south-west USA (Reed *et al.,* 2012). The results of this study suggest that changes in climate may lead to dramatic alterations in the composition of BSCs and hypoliths, both critical for nutrient input in depauperate environments. These changes are likely to result in reduced soil functionality in desert soils and other ecological consequences for soil fertility and erosion (Garcia-Pichel *et al.,* 2013).

Global and regional climate models predict altered precipitation patterns over multi-decadal timescales in most parts of the world (Solomon *et al.,* 2007). In arid regions, where low levels of soil moisture for extensive periods of time are common, a change in rainfall frequency and intensity may have serious implications for the soil microbial community structure. Indeed, soil microbial communities have been shown to respond to drought and precipitation variability in the Chihuahuan Desert (Clark *et al.,* 2009). Such effects are, however, not regionally homogeneous, as soil bacterial communities at a mid-elevation grassland site were most vulnerable to changes in precipitation frequency and timing, whereas fungal community structure

was most vulnerable in low desert scrub (Clark *et al.,* 2009). Simulated rainfall events have also been shown to impact desert microbial communities (Angel and Conrad 2013); Actinomycetales were the dominant bacterial order in dry biocrusts but showed a massive reduction in occurrence after artificial hydration events (Angel and Conrad 2013). A decline in a dominant population of Actinobacteria was also observed in Mediterranean soil cores following the first rainfall event after a dry summer (Placella, Brodie and Firestone 2012).

Elevated atmospheric CO_2 concentrations are expected to increase plant photosynthetic activity and the transfer of fixed carbon belowground (i.e. by root production and root exudation), which in turn could affect the composition of microbial communities. Such changes have been observed experimentally: the ratios of bacterial-to-total phospholipid fatty acids (PLFA)-C decreased and fungal-to-bacterial PLFA-C increased under elevated CO_2 compared with ambient conditions (Jin and Evans 2010). These changes in community composition, driven by the different growth rates of fungi and bacteria, may directly affect ecosystem processes (de Vries *et al.,* 2012).

Climate change effects are also expected to negatively impact the physiology of desert microbial communities. For instance, experimental warming decreased photosynthetic activity of soil lichens (Maphangwa *et al.,* 2012) and mosses (Grote *et al.,* 2010), ultimately reducing their growth and dominance within biocrusts (Escolar *et al.,* 2012; Reed *et al.,* 2012). However, little is known about the molecular mechanisms involved in the response of these communities to changes in environmental conditions, although a recent study has shed some light on molecular changes during desiccation-rewetting processes (Rajeev *et al.,* 2013). Using a metatranscriptomics approach, the authors showed that DNA repair and regulatory genes were rapidly but transiently induced during rehydration. Recovery of photosynthesis occurred within 1 h, accompanied by upregulation of anabolic pathways. The beginning of desiccation was characterized by the induction of genes for oxidative and photooxidative stress responses, osmotic stress response and the synthesis of C and N storage polymers (e.g. polyhydroxyalkanoates and cyanophycin), and by increased glycogen catabolism.

SENSITIVITY TO PHYSICAL DISTURBANCE

One of the projected impacts of increased desertification (and reduced grazing land) is increased pressure on marginal (arid and semiarid) lands. Microbial communities are sensitive to physical disturbance. For example, grazing destroyed the biocrusts at two sites in the Kalahari Desert, southern Botswana, with adverse effects on C sequestration and storage (Thomas 2012). Soil CO_2 efflux was significantly higher in sand-based soils where biocrusts were removed and in calcrete soils where the biocrust was buried under sand. Although no similar study has been reported from hot deserts, it has been documented that trampling impacts cold arid soil biocrust communities (Kuske *et al.,* 2012). Lichen, moss and bacterial (*M. vaginatus*) abundances were significantly reduced at three desert sites on the Colorado Plateau (USA), resulting in increased soil erosion and reduced C and N concentrations in surface soils. In parallel, members of the Actinobacteria, Chloroflexi and Bacteroidetes were more readily detected in the trampled areas compared to undisturbed biocrusts. Bacterial T-RFLP profiles exhibited much higher variability between field replicates at disturbed sites, indicating a transition towards an unstable community structure. Surprisingly, despite the negative impacts of trampling on the physical structure and composition of biocrust microbial communities, *M. vaginatus* could still be detected in surface soils after a decade of annual trampling, suggesting the potential for biocrust recovery over time. However, the formation of mature biocrusts has been shown to be an extremely slow (decadal-scale) process (Belnap and Gillette 1998).

IMPACT OF DESERT MICROBES ON ECOSYSTEMS

Soil microorganisms are important for the stability and productivity of deserts ecosystems, where plants are typically sparse (Belnap and Gardner 1993; Pointing *et al.,* 2007). For example, the physical structure of biocrust and hypoliths stabilizes the soil against wind and water erosion (Pointing and Belnap 2012). Biocrusts and hypolithic communities have been shown to increase soil fertility and soil moisture retention (Pointing and Belnap 2012), and thus influence the germination, survival and nutritional status of the widely spaced vascular plants. Additionally, dark cyanobacterial and lichen pigments in biocrusts decrease surface albedo, influencing local and regional temperatures (Kuske *et al.,* 2012). Therefore, the disturbance of desert microbial communities and desert pavements may be regarded as a major contributor to the desertification process (Pointing and Belnap 2012, 2014). On a global scale, the loss of forests and drylands to desertification and use for crop production will reduce the abundance of ecto- and ericoid mycorrhizas and increase the abundance of arbuscular mycorrhizas (Johnson *et al.,* 2013). As arbuscular mycorrhizal fungi have been found to increase organic carbon decomposition under elevated CO_2 concentrations (Cheng *et al.,* 2012), these changes may have major implications for belowground C sequestration. This, together with the fact that desertification reduces plant cover, could have extensive consequences for the biogeochemical cycles of C, N and P (Delgado-Baquerizo *et al.,* 2013). For example, dryland ecosystems will be able to store less carbon both above- and belowground, compromising their ability to mitigate increased levels of atmospheric CO_2.

RESEARCH GAPS AND FUTURE DIRECTIONS

Our understanding of desert microbial communities has greatly improved with the advent of modern molecular technologies. Recent advances in high-throughput sequencing platforms (Soon, Hariharan and Snyder 2013; Subramanian *et al.,* 2013), mass spectrometry (Monge *et al.,* 2013; Segata *et al.,* 2013) and bioinformatics tools (McKenna *et al.,* 2010; Kouskoumvekaki, Shublaq and Brunak 2013) have all facilitated in-depth comparative studies of microbial ecology and function. These studies have led to an exponential increase in the volumes of publicly available sequence data, which has greatly facilitated cross-investigator and cross-system meta-analysis (e.g. Auguet, Barberan and Casamayor 2010; Delmont *et al.,* 2011). However, although many examples of meta-'omics' studies of various soil environments have been reported (e.g. metagenomics, Allen *et al.,* 2009; metatranscriptomics, Bailly *et al.,* 2007; metaproteomics, Benndorf *et al.,* 2007; metabolomics, Gelsomino and Azzellino 2011), there are few examples where these tools have been applied to studies related to desert soil microbial communities.

While we are now beginning to appreciate the 'true bacterial diversity' of desert environments, we still lack a comprehensive understanding of the fungal and viral component. Most

studies of desert soil niches show that bacterial phyla dominate, and detailed knowledge of the diversity (and function) of fungal and archaeal lineages remains incomplete. The role of virus and phage populations remains completely unresolved. In order to fully understand the patterns underlying community assembly in these environments, the use of polyphasic approaches focusing on all lineages is essential. It is expected that smaller organisms (mostly bacteria) are likely to follow different community assembly mechanisms rather than larger organisms (fungi), owing in part to dispersal limitation (Schmidt *et al.,* 2014).

The relationship between desert plants and microbial communities also remains largely unresolved. For example, it is not clear whether desert plants are linked to microbial communities (such as biocrusts) via mycorrhizal networks. While mycorrhizal fungi have not been detected in biocrusts, glomalin, which often indicates the presence of mycorrhizal associations, seems to be abundant in biocrusts (Pointing and Belnap 2012).

The interactions of microbial communities, specifically aspects relating to microbial food webs, may be fruitful pursuits in desert research. Understanding the interaction networks underpinning nutrient cycling in depauperate environments may contribute to an understanding of how biodiversity influences function in these systems.

The majority of studies focused on the diversity and roles of microorganisms in desert ecosystems are derived from a limited number of desert sites (situated mainly in America and Australia) and from single time points. Many other deserts, in particular those in Asia and Africa remain largely unexplored by microbial ecologists. Incorporating more geographically diverse samples into future research, particularly with the inclusion of a temporal dimension, will improve our understanding of desert microbial communities over a wider range of both spatial- and timescales. An improved appreciation of the intrinsic and extrinsic mechanisms that influence desert microbial communities will strengthen our ability to predict the impacts of climate or land-use change, and to develop management strategies for protection prior to, or restoration following, disturbance events. For example, initiatives such as 'The Earth Microbiome Project' (http://www.earthmicrobiome.org) have the potential to contribute hugely to addressing this information deficit.

Linking community structure to function also remains a central challenge in microbial ecology. Although there is a growing perception that the functional capacity of microbial communities can be predicted from phylotypic profiles (Langille *et al.,* 2013) or more targeted functional gene screening such as via GeoChip® analysis (He *et al.,* 2007), there remains a very wide gulf between potential metabolic capacity and *in vivo* functionality. Scope for *in situ* functional analyses of microbial communities in soils, in the wider context of the soil microenvironment, remains enormous. Future studies should also focus on biotic interactions between functional guilds, how environmental variables moderate such interactions and how both affect biogeochemical processes.

The integration of mathematical models and *in vivo* data may also shed light on functionality in desert ecosystems. Recently, predictions of the responses of microbial guilds to climate change were investigated through the development of temporal ecological response models (Lester *et al.,* 2014). These models, derived from biophysical data across spatial gradients in well-studied environments, could be used to make predictions of ecological changes in understudied arid environments.

REFERENCES

Abdel-Hafez S. Survey of the mycoflora of desert soils in Saudi Arabia. *Mycopathologia* 1982;**80**:3–8.

Abed RMM, Lam P, De Beer D, *et al.* High rates of denitrification and nitrous oxide emission in arid biological soil crusts from the Sultanate of Oman. *ISME J* 2013;**7**:1862–75.

Abed RMM, Ramette A, Huebner V, *et al.* Microbial diversity of eolian dust sources from saline lake sediments and biological soil crusts in arid Southern Australia. *FEMS Microbiol Ecol* 2012;**80**:294–304.

Adriaenssens EM, Van Zyl L, De Maayer P, *et al.* Metagenomic analysis of the viral community in Namib Desert hypoliths. *Environ Microbiol* 2014, DOI: 10.1111/1462-2920.12528.

Aislabie JM, Chhour K-L, Saul DJ, *et al.* Dominant bacteria in soils of Marble Point and Wright Valley, Victoria Land, Antarctica. *Soil Biol Biochem* 2006;**38**:3041–56.

Allakhverdiev SI, Sakamoto A, Nishiyama Y, *et al.* Ionic and osmotic effects of NaCl-induced inactivation of photosystems I and II in Synechococcus sp. *Plant Physiol* 2000;**123**:1047–56.

Allen HK, Moe LA, Rodbumrer J, *et al.* Functional metagenomics reveals diverse *β*-lactamases in a remote Alaskan soil. *ISME J* 2009;**3**:243–51.

Almazroui M, Nazrul Islam M, Athar H, *et al.* Recent climate change in the Arabian Peninsula: annual rainfall and temperature analysis of Saudi Arabia for 1978–2009. *Int J Climatol* 2012;**32**:953–66.

Andrew DR, Fitak RR, Munguia-Vega A, *et al.* Abiotic factors shape microbial diversity in Sonoran Desert Soils. *Appl Environ Microbiol* 2012;**78**:7527–37.

Angel R, Conrad R. Elucidating the microbial resuscitation cascade in biological soil crusts following a simulated rain event. *Environ Microbiol* 2013;**15**:2799–815.

Angel R, Pasternak Z, Soares MIM, *et al.* Active and total prokaryotic communities in dryland soils. *FEMS Microbiol Ecol* 2013;**86**:130–8.

Angel R, Soares MI, Ungar ED, *et al.* Biogeography of soil archaea and bacteria along a steep precipitation gradient. *ISME J* 2010;**4**:553–63.

Auguet JC, Barberan A, Casamayor EO. Global ecological patterns in uncultured Archaea. *ISME J* 2010;**4**:182–90.

Azua-Bustos A, Gonzalez-Silva C, Mancilla RA, *et al*. Hypolithic cyanobacteria supported mainly by fog in the coastal range of the Atacama Desert. *Microb Ecol* 2011;**61**:568–81.

Azua-Bustos A, Zuniga J, Arenas-Fajardo C, *et al*. *Gloeocapsopsis AAB1*, an extremely desiccation-tolerant cyanobacterium isolated from the Atacama Desert. *Extremophiles* 2014;**18**:61–74.

Bachar A, Al-Ashhab A, Soares MIM, *et al*. Soil microbial abundance and diversity along a low precipitation gradient. *Microb Ecol* 2010;**60**:453–61.

Bachar A, Soares MIM, Gillor O. The effect of resource islands on abundance and diversity of bacteria in arid soils. *Microb Ecol* 2012;**63**:694–700.

Badr El-Din SM RS, Zahra MK, Zidan WMH. Microbial diversity in two Egyptian soils. *Catrina* 2006;**1**:111–8.

Bahl J, Lau MC, Smith GJ, *et al*. Ancient origins determine global biogeography of hot and cold desert cyanobacteria. *Nat Commun* 2011;**2**:163.

Bailly J, Fraissinet-Tachet L, Verner M-C, *et al*. Soil eukaryotic functional diversity, a metatranscriptomic approach. *ISME J* 2007;**1**:632–42.

Barros N, Feijóo S, Salgado J, *et al*. The dry limit of microbial life in the Atacama Desert revealed by calorimetric approaches. *Eng Life Sci* 2008;**8**:477–86.

Barrow C. *World Atlas of Desertification*, **Vol. 3**. Middleton N, Thomas D (eds). London: Edward Arnold, 1992, 249.

Bates ST, Garcia-Pichel F. A culture-independent study of free-living fungi in biological soil crusts of the Colorado Plateau: their diversity and relative contribution to microbial biomass. *Environ Microbiol* 2009;**11**:56–67.

Bell C, McIntyre N, Cox S, *et al*. Soil microbial responses to temporal variations of moisture and temperature in a chihuahuan desert grassland. *Microb Ecol* 2008;**56**:153–67.

Belnap J. The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrol Process* 2006;**20**:3159–78.

Belnap J, Buedel B, Lange OL. Biological soil crusts: characteristics and distribution. In: Belnap J, Lange OL (eds). *Biological Soil Crusts*. Berlin, Germany: Springer-Verlag, 2003, 3–30.

Belnap J, Gardner JS. Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium Microcoleus vaginatus. *West N Am Naturalist* 1993;**53**:40–7.

Belnap J, Gillette DA. Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. *J Arid Environ* 1998;**39**:133–42.

Ben-David EA, Zaady E, Sher Y, *et al*. Assessment of the spatial distribution of soil microbial communities in patchy arid and semi-arid landscapes of the Negev Desert using combined PLFA and DGGE analyses. *FEMS Microbiol Ecol* 2011;**76**:492–503.

Benndorf D, Balcke GU, Harms H, *et al*. Functional metaproteome analysis of protein extracts from contaminated soil and groundwater. *ISME J* 2007;**1**:224–34.

Benslama O, Boulahrouf A. Impact of glyphosate application on the microbial activity of two Algerian soils. *Int J Curr Microbiol App Sci* 2013;**2**:628–35.

Bent SJ, Forney LJ. The tragedy of the uncommon: understanding limitations in the analysis of microbial diversity. *ISME J* 2008;**2**:689–95.

Berry J, Bjorkman O. Photosynthetic response and adaptation to temperature in higher plants. *Ann Rev Plant Physio* 1980;**31**:491–543.

Bhatnagar A, Bhatnagar M. Microbial diversity in desert ecosystems. *Curr Sci India* 2005;**89**:91–100.

Boison G, Mergel A, Jolkver H, *et al*. Bacterial life and dinitrogen fixation at a gypsum rock. *Appl Environ Microb* 2004;**70**:7070–7.

Boldareva-Nuianzina EN, Bláhová Z, Sobotka R, *et al*. Distribution and origin of oxygen-dependent and oxygen-independent forms of Mg-protoporphyrin monomethylester cyclase among phototrophic proteobacteria. *Appl Environ Microb* 2013;**79**:2596–604.

Bowers KJ, Wiegel J. Temperature and pH optima of extremely halophilic archaea: a mini-review. *Extremophiles* 2011;**15**:119–28.

Brochier-Armanet C, Boussau B, Gribaldo S, *et al*. Mesophilic Crenarchaeota: proposal for a third archaeal phylum, the Thaumarchaeota. *Nat Rev Microbiol* 2008;**6**:245–52.

Budel B, Darienko T, Deutschewitz K, *et al*. Southern African biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency. *Microb Ecol* 2009;**57**:229–47.

Burke A. Properties of soil pockets on arid Nama Karoo inselbergs–the effect of geology and derived landforms. *J Arid Environ* 2002;**50**:219–34.

Carrillo-Garcia Á, La Luz D, León JL, *et al*. Nurse plants, mycorrhizae, and plant establishment in a disturbed area of the Sonoran Desert. *Restor Ecol* 1999;**7**:321–35.

Caruso T, Chan Y, Lacap DC, *et al*. Stochastic and deterministic processes interact in the assembly of desert microbial communities on a global scale. *ISME J* 2011;**5**:1406–13.

Cary SC, McDonald IR, Barrett JE, *et al*. On the rocks: the microbiology of Antarctic Dry Valley soils. *Nat Rev Microbiol* 2010;**8**:129–38.

Castillo-Monroy AP, Bowker MA, Maestre FT, *et al*. Relationships between biological soil crusts, bacterial diversity and abundance, and ecosystem functioning: Insights from a semi-arid Mediterranean environment. *J Veg Sci* 2011;**22**:165–74.

Castillo-Monroy AP, Maestre FT, Delgado-Baquerizo M, *et al*. Biological soil crusts modulate nitrogen availability in semi-arid ecosystems: insights from a Mediterranean grassland. *Plant Soil* 2010;**333**:21–34.

Chagnon PL, Bradley RL, Maherali H, *et al*. A trait-based framework to understand life history of mycorrhizal fungi. *Trends Plant Sci* 2013;**18**:484–91.

Chamizo S, Cantón Y, Lázaro R, *et al*. Crust composition and disturbance drive infiltration through biological soil crusts in semiarid ecosystems. *Ecosystems* 2012;**15**:148–61.

Chamizo S, Cantón Y, Miralles I, *et al*. Biological soil crust development affects physicochemical characteristics of soil surface in semiarid ecosystems. *Soil Biol Biochem* 2012;**49**:96–105.

Chan Y, Lacap DC, Lau MC, *et al*. Hypolithic microbial communities: between a rock and a hard place. *Environ Microbiol* 2012;**14**:2272–82.

Chan Y, Van Nostrand JD, Zhou J, *et al*. Functional ecology of an Antarctic Dry Valley. *P Natl Acad Sci USA* 2013;**110(22)**:8990–95.

Chanal A, Chapon V, Benzerara K, *et al*. The desert of Tataouine: an extreme environment that hosts a wide diversity of microorganisms and radiotolerant bacteria. *Environ Microbiol* 2006;**8**:514–25.

Chater KF, Chandra G. The evolution of development in Streptomyces analysed by genome comparisons. *FEMS Microbiol Rev* 2006;**30**:651–72.

Chen L, Deng S, De Philippis R, *et al*. UV-B resistance as a criterion for the selection of desert microalgae to be utilized for inoculating desert soils. *J Appl Phycol* 2013;**25**:1009–15.

Chen WM, Moulin L, Bontemps C, *et al*. Legume symbiotic nitrogen fixation by beta-proteobacteria is widespread in nature. *J Bacteriol* 2003;**185**:7266–72.

Cheng L, Booker FL, Tu C, *et al*. Arbuscular mycorrhizal fungi increase organic carbon decomposition under elevated CO_2. *Science* 2012;**337**:1084–7.

Cho H, Winans SC. VirA and VirG activate the Ti plasmid repABC operon, elevating plasmid copy number in response to wound-released chemical signals. *P Natl Acad Sci USA* 2005;**102**:14843–8.

Clark JS, Campbell JH, Grizzle H, *et al*. Soil microbial community response to drought and precipitation variability in the Chihuahuan Desert. *Microbial Ecol* 2009;**57**:248–60.

Cockell CS, Knowland J. Ultraviolet radiation screening compounds. *Biol Rev Camb Philos* 1999;**74**:311–45.

Conley CA, Ishkhanova G, Mckay CP, *et al*. A preliminary survey of non-lichenized fungi cultured from the hyperarid Atacama Desert of Chile. *Astrobiology* 2006;**6**:521–6.

Connon SA, Lester ED, Shafaat HS, *et al*. Bacterial diversity in hyperarid Atacama Desert soils. *J Geophys Res-Biogeo* 2007;**112**:G04S17.

Cowan DA, Pointing SB, Stevens MI, *et al*. Distribution and abiotic influences on hypolithic microbial communities in an Antarctic Dry Valley. *Polar Biol* 2010;**34**:307–11.

Crenshaw CL, Lauber C, Sinsabaugh RL, *et al*. Fungal control of nitrous oxide production in semiarid grassland. *Biogeochemistry* 2008;**87**:17–27.

Crits-Christoph A, Robinson CK, Barnum T, *et al*. Colonization patterns of soil microbial communities in the Atacama Desert. *Microbiome* 2013;**1**:28.

Darby BJ, Neher DA, Belnap J. Soil nematode communities are ecologically more mature beneath late- than early-successional stage biological soil crusts. *Appl Soil Ecol* 2007;**35**:203–12.

de los Ríos A, Cary C, Cowan D. The spatial structures of hypolithic communities in the Dry Valleys of East Antarctica. *Polar Biol*, 2014;**37**:1823–33.

de Vries FT, Liiri ME, Bjornlund L, *et al*. Land use alters the resistance and resilience of soil food webs to drought. *Nat Clim Change* 2012;**2**:276–80.

Dean W, Milton S, Jeltsch F. Large trees, fertile islands, and birds in arid savanna. *J Arid Environ* 1999;**41**:61–78.

DeBruyn JM, Nixon LT, Fawaz MN, *et al*. Global biogeography and quantitative seasonal dynamics of Gemmatimonadetes in soil. *Appl Environ Microb* 2011;**77**:6295–300.

Delgado-Baquerizo M, Maestre FT, Gallardo A, *et al*. Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature* 2013;**502**:672–6.

Delmont TO, Malandain C, Prestat E, *et al*. Metagenomic mining for microbiologists. *ISME J* 2011;**5**:1837–43.

Dojani S, Kauff F, Weber B, *et al*. Genotypic and phenotypic diversity of cyanobacteria in biological soil crusts of the Succulent Karoo and Nama Karoo of Southern Africa. *Microb Ecol* 2013;**67**:286–301.

Dommergues Y, Ganry F. Biological nitrogen fixation and soil fertility maintenance. In: Uzo Mokwunye A, Vlek Paul LG (eds) *Management of Nitrogen and Phosphorus Fertilizers in Sub-Saharan Africa, Vol. 24*. The Netherlands: Springer, 1986, 95–115.

Drahorad S, Felix-Henningsen P, Eckhardt K-U, *et al*. Spatial carbon and nitrogen distribution and organic matter characteristics of biological soil crusts in the Negev desert (Israel) along a rainfall gradient. *J Arid Environ* 2013;**94**:18–26.

Drees KP, Neilson JW, Betancourt JL, *et al*. Bacterial community structure in the hyperarid core of the Atacama Desert, Chile. *Appl Environ Microb* 2006;**72**:7902–8.

Duncan FD, Dickman CR. Respiratory patterns and metabolism in tenebrionid and carabid beetles from the Simpson Desert, Australia. *Oecologia* 2001;**129**:509–17.

Durant S, Pettorelli N, Bashir S, *et al*. Forgotten biodiversity in desert ecosystems. *Science* 2012;**336**:1379–80.

Dvorak P, Hasler P, Poulickova A. Phylogeography of the microcoleus vaginatus (Cyanobacteria) from three continents—a spatial and temporal characterization. *PloS One* 2012;**7**: e40153.

Eckardt FD, Soderberg K, Coop LJ, *et al*. The nature of moisture at Gobabeb, in the central Namib Desert. *J Arid Environ* 2013;**93**:7–19.

Elbert W, Weber B, Burrows S, *et al*. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nat Geosci* 2012;**5**:459–62.

Ensign JC. Formation, properties, and germination of actinomycete spores. *Annu Rev Microbiol* 1978;**32**:185–219.

Escolar C, Martinez I, Bowker MA, *et al*. Warming reduces the growth and diversity of biological soil crusts in a semi-arid environment: implications for ecosystem structure and functioning. *Philos T R Soc B* 2012;**367**:3087–99.

Evenari M. Adaptations of plants and animals to the desert environment. In: Evenari M, Noy-Meir I, Goodall D (eds) *Ecosystems of the World:Hot Deserts and Arid Shrublands*, **Vol. 12A**, Amsterdam, Netherlands: Elsevier, 1985, 79–92.

Ffolliott PF, Dawson JO, Fisher JT, *et al*. *International Arid Lands Consortium: A Synopsis of Accomplishments*. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, 2003, 154–6.

Fierer N, Bradford MA, Jackson RB. Toward an ecological classification of soil bacteria. *Ecology* 2007a;**88**:1354–64.

Fierer N, Leff JW, Adams BJ, *et al*. Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. *P Natl Acad Sci USA* 2012;**109**:21390–5.

Fierer N, Strickland MS, Liptzin D, *et al*. Global patterns in below-ground communities. *Ecol Lett* 2009;**12**:1238–49.

Finkel OM, Burch AY, Elad T, *et al*. Distance-decay relationships partially determine diversity patterns of phyllosphere bacteria on Tamarix trees across the Sonoran Desert. *Appl Environ Microb* 2012;**78**:6187–93.

Finkel OM, Burch AY, Lindow SE, *et al*. Geographical location determines the population structure in phyllosphere microbial communities of a salt-excreting desert tree. *Appl Environ Microb* 2011;**77**:7647–55.

Free CL, Baxter GS, Dickman CR, *et al*. Resource pulses in desert river habitats: productivity-biodiversity hotspots, or mirages? *PLoS One* 2013;**8**:e72690.

Gallardo A, Schlesinger WH. Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems. *Biogeochemistry* 1992;**18**:1–17.

Gao Q, Garcia-Pichel F. Microbial ultraviolet sunscreens. *Nat Rev Microbiol* 2011;**9**:791–802.

Garcia-Pichel F, Johnson SL, Youngkin D, *et al*. Small-scale vertical distribution of bacterial biomass and diversity in biological soil crusts from arid lands in the Colorado Plateau. *Microbial Ecol* 2003;**46**:312–21.

Garcia-Pichel F, Loza V, Marusenko Y, *et al*. Temperature drives the continental-scale distribution of key microbes in topsoil communities. *Science* 2013;**340**:1574–7.

Garcia-Pichel F, Pringault O. Cyanobacteria track water in desert soils. *Nature* 2001;**413**:380–1.

Gelsomino A, Azzellino A. Multivariate analysis of soils: microbial biomass, metabolic activity, and bacterial-community structure and their relationships with soil depth and type. *J Plant Nutr Soil Sc* 2011;**174**:381–94.

Gommeaux M, Barakat M, Montagnac G, *et al.* Mineral and bacterial diversities of desert sand grains from south-east Morocco. *Geomicrobiol J* 2010;**27**:76–92.

Gorbushina AA. Life on the rocks. *Environ Microbiol* 2007;**9**:1613–31.

Goswami D, Pithwa S, Dhandhukia P, *et al.* Delineating Kocuria turfanensis 2M4 as a credible PGPR: a novel IAA producing bacteria isolated from saline desert. *J Plant Interact* 2013;**9**:566–76.

Grace PR, Post WM, Hennessy K. The potential impact of climate change on Australia's soil organic carbon resources. *Carbon Balance Manag* 2006;**1**:14.

Grigg AM, Veneklaas EJ, Lambers H. Water relations and mineral nutrition of closely related woody plant species on desert dunes and interdunes. *Aust J Bot* 2008;**56**:27–43.

Grainger A. The role of science in implementing international environmental agreements: the case of desertification. *Land Degrad Dev* 2009;**20**:410–30.

Green JL, Bohannan BJM, Whitaker RJ. Microbial biogeography: from taxonomy to traits. *Science* 2008;**320**:1039–43.

Green PN. Methylobacterium. In: Dworkin M (ed) *The Prokaryotes*. New York: Springer, 2006, 257–65.

Griffiths A, McCormick L. Effects of soil acidity on nodulation of Alnus glutinosa and viability ofFrankia. *Plant Soil* 1984;**79**:429–34.

Grishkan I, Nevo E. Spatiotemporal distribution of soil microfungi in the Makhtesh Ramon area, central Negev desert, Israel. *Fungal Ecol* 2010;**3**:326–37.

Grote EE, Belnap J, Housman DC, *et al.* Carbon exchange in biological soil crust communities under differential temperatures and soil water contents: implications for global change. *Global Change Biol* 2010;**16**:2763–74.

Gundlapally SR, Garcia-Pichel F. The community and phylogenetic diversity of biological soil crusts in the Colorado Plateau studied by molecular fingerprinting and intensive cultivation. *Microb Ecol* 2006;**52**:345–57.

Haki G, Rakshit S. Developments in industrially important thermostable enzymes: a review. *Bioresource Technol* 2003;**89**:17–34.

Hall-Stoodley L, Costerton JW, Stoodley P. Bacterial biofilms: from the natural environment to infectious diseases. *Nat Rev Microbiol* 2004;**2**:95–108.

Harel Y, Ohad I, Kaplan A. Activation of photosynthesis and resistance to photoinhibition in cyanobacteria within biological desert crust. *Plant Physiol* 2004;**136**:3070–9.

Hatzenpichler R, Lebedeva EV, Spieck E, *et al.* A moderately thermophilic ammonia-oxidizing crenarchaeote from a hot spring. *P Natl Acad Sci USA* 2008;**105**:2134–9.

Hawkes CV, Flechtner VR. Biological soil crusts in a xeric Florida shrubland: composition, abundance, and spatial heterogeneity of crusts with different disturbance histories. *Microbial Ecol* 2002;**43**:1–12.

He Z, Gentry TJ, Schadt CW, *et al.* GeoChip: a comprehensive microarray for investigating biogeochemical, ecological and environmental processes. *ISME J* 2007;**1**:67–77.

Hereford R, Webb R, Longpre C. Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert region, 1893–2001. *J Arid Environ* 2006;**67**:13–34.

Herman R, Provencio KR, Herrera-Matos J, *et al.* Resource islands predict the distribution of heterotrophic bacteria in chihuahuan desert soils. *Appl Environ Microb* 1995;**61**:1816–21.

Hooper DU, Adair EC, Cardinale BJ, *et al.* A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 2012;**486**:105–8.

Housman DC, Yeager CM, Darby BJ, *et al.* Heterogeneity of soil nutrients and subsurface biota in a dryland ecosystem. *Soil Biol Biochem* 2007;**39**:2138–49.

Islam K, McBratney A, Singh B. Rapid estimation of soil variability from the convex hull biplot area of topsoil ultra-violet, visible and near-infrared diffuse reflectance spectra. *Geoderma* 2005;**128**:249–57.

Jin VL, Evans RD. Microbial ^{13}C utilization patterns via stable isotope probing of phospholipid biomarkers in Mojave Desert soils exposed to ambient and elevated atmospheric CO_2. *Global Change Biol* 2010;**16**:2334–44.

Johnson NC, Angelard C, Sanders IR, *et al.* Predicting community and ecosystem outcomes of mycorrhizal responses to global change. *Ecol Lett* 2013;**16**:140–53.

Jones CG, Lawton JH, Shachak M. Organisms as ecosystem engineers. *Oikos* 1994;**69**:373–86.

Jorquera MA, Shaharoona B, Nadeem SM, *et al.* Plant growth-promoting rhizobacteria associated with ancient clones of creosote bush (Larrea tridentata). *Microb Ecol* 2012;**64**:1008–17.

Kendrick MG, Kral TA. Survival of methanogens during desiccation: implications for life on Mars. *Astrobiology* 2006;**6**:546–51.

Klejdus B, Kopecký J, Benešová L, *et al.* Solid-phase/supercritical-fluid extraction for liquid chromatography of phenolic compounds in freshwater microalgae and selected cyanobacterial species. *J Chromatogr A* 2009;**1216**:763–71.

Köberl M, Müller H, Ramadan EM, *et al.* Desert farming benefits from microbial potential in arid soils and promotes diversity and plant health. *PLoS One* 2011;**6**:e24452.

Kouskoumvekaki I, Shublaq N, Brunak S. Facilitating the use of large-scale biological data and tools in the era of translational bioinformatics. *Brief Bioinform* 2013;**15**:942–52.

Krumbein WE, Jens K. Biogenic rock varnishes of the Negev Desert (Israel) an ecological study of iron and manganese transformation by cyanobacteria and fungi. *Oecologia* 1981;**50**:25–38.

Kurapova A, Zenova G, Sudnitsyn I, *et al.* Thermotolerant and thermophilic actinomycetes from soils of Mongolia desert steppe zone. *Microbiology* 2012;**81**:98–108.

Kuske CR, Ticknor LO, Miller ME, *et al.* Comparison of soil bacterial communities in rhizospheres of three plant species and the interspaces in an arid grassland. *Appl Environ Microb* 2002;**68**:1854–63.

Kuske CR, Yeager CM, Johnson S, *et al.* Response and resilience of soil biocrust bacterial communities to chronic physical disturbance in arid shrublands. *ISME J* 2012;**6**:886–97.

Lacap DC, Warren-Rhodes KA, McKay CP, *et al.* Cyanobacteria and chloroflexi-dominated hypolithic colonization of quartz at the hyper-arid core of the Atacama Desert, Chile. *Extremophiles* 2011;**15**:31–8.

Laity JJ. *Deserts and Desert Environments*. Chichester, UK: Wiley-Blackwell, 2009.

Langenheder S, Bulling MT, Solan M, *et al.* Bacterial biodiversity-ecosystem functioning relations are modified by environmental complexity. *PLoS One* 2010;**5**:e10834.

Langille MGI, Zaneveld J, Caporaso JG, *et al.* Predictive functional profiling of microbial communities using 16S rRNA marker gene sequences. *Nat Biotechnol* 2013;**31**:814–21.

Lauber CL, Hamady M, Knight R, et al. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. *Appl Environ Microb* 2009;**75**:5111–20.

Lawson M, Thomas D. Late Quaternary lunette dune sedimentation in the southwestern Kalahari desert, South Africa: luminescence based chronologies of aeolian activity. *Quaternary Sci Rev* 2002;**21**:825–36.

Le Houérou HN. Climate change, drought and desertification. *J Arid Environ* 1996;**34**:133–85.

LeRomancer M, Gaillard M, Geslin C, Viruses in extreme environments. In: Amils R, Ellis-Evans C, Hinghofer-Szalkay HG, et al. (eds) *Life in Extreme Environments*. Dordrecht, The Netherlands: Springer, 2007, 99–113.

Lefèvre CT, Viloria N, Schmidt ML, et al. Novel magnetite-producing magnetotactic bacteria belonging to the Gammaproteobacteria. *ISME J* 2012;**6**:440–50.

Lester ED, Satomi M, Ponce A. Microflora of extreme arid Atacama Desert soils. *Soil Biol Biochem* 2007;**39**:704–8.

Lester RE, Close PG, Barton JL, et al. Predicting the likely response of data-poor ecosystems to climate change using space-for-time substitution across domains. *Global Change Biol* 2014;**20**:3471–81.

Li W-J, Chen H-H, Zhang Y-Q, et al. Citricoccus alkalitolerans sp. nov., a novel actinobacterium isolated from a desert soil in Egypt. *Int J Syst Evol Micr* 2005;**55**:87–90.

Li W-J, Zhang Y-Q, Schumann P, et al. Kocuria aegyptia sp. nov., a novel actinobacterium isolated from a saline, alkaline desert soil in Egypt. *Int J Syst Evol Micr* 2006;**56**:733–7.

Liu M, Peng F, Wang Y, et al. Kineococcus xinjiangensis sp. nov., isolated from desert sand. *Int J Syst Evol Micr* 2009;**59**: 1090–3.

Lopez BR, Bashan Y, Trejo A, et al. Amendment of degraded desert soil with wastewater debris containing immobilized Chlorella sorokiniana and Azospirillum brasilense significantly modifies soil bacterial community structure, diversity, and richness. *Biol Fert Soils* 2013;**49**:1053–63.

Luo X, Wang J, Zeng X-C, et al. Mycetocola manganoxydans sp. nov., an actinobacterium isolated from the Taklamakan desert. *Int J Syst Evol Micr* 2012;**62**:2967–70.

McCarthy AJ, Williams ST. Actinomycetes as agents of biodegradation in the environment—a review. *Gene* 1992;**115**:189–92.

Mace GM, Norris K, Fitter AH. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol Evol* 2012;**27**: 19–26.

McKenna A, Hanna M, Banks E, et al. The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Res* 2010;**20**: 1297–303.

Maestre FT, Escolar C, de Guevara ML, et al. Changes in biocrust cover drive carbon cycle responses to climate change in drylands. *Global Change Biol* 2013;**19**:3835–47.

Makhalanyane TP, Valverde A, Birkeland N-K, et al. Evidence for successional development in Antarctic hypolithic bacterial communities. *ISME J* 2013b;**7**:2080–90.

Makhalanyane TP, Valverde A, Lacap DC, et al. Evidence of species recruitment and development of hot desert hypolithic communities. *Environ Microbiol Rep* 2013a;**5**:219–24.

Manzoni S, Schimel JP, Porporato A. Responses of soil microbial communities to water stress: results from a meta-analysis. *Ecology* 2012;**93**:930–8.

Maphangwa KW, Musil CF, Raitt L, et al. Experimental climate warming decreases photosynthetic efficiency of lichens in an arid South African ecosystem. *Oecologia* 2012;**169**:257–68.

Martirosyan V, Steinberger Y. Microbial functional diversity in the phyllosphere and laimosphere of different desert plants. *J Arid Environ* 2014;**107**:26–33.

Maupin-Furlow JA, Humbard MA, Kirkland PA. Extreme challenges and advances in archaeal proteomics. *Curr Opin Microbiol* 2012;**15**:351–6.

Mayilraj S, Krishnamurthi S, Saha P, et al. Rhodococcus kroppenstedtii sp. nov., a novel actinobacterium isolated from a cold desert of the Himalayas, India. *Int J Syst Evol Micr* 2006;**56**: 979–82.

Meehl GA, Stocker TF, Collins WD, et al. Global climate projections. *Climate Change* 2007;**3495**:747–845.

Miralles I, Trasar-Cepeda C, Leiros MC, et al. Labile carbon in biological soil crusts in the Tabernas desert, SE Spain. *Soil Biol Biochem* 2013;**58**:1–8.

Monge ME, Harris GA, Dwivedi P, et al. Mass spectrometry: recent advances in direct open air surface sampling/ionization. *Chem Rev* 2013;**113**:2269–308.

Mosweu S, Munyati C, Kabanda T. Modification of soil properties by Prosopis L. in the Kalahari Desert, South-Western Botswana. *Open J Ecol* 2013;**3**:145.

Moustafa A, Sharkas M, Kamel SM. Thermophilic and thermotolerant fungi in the desert and salt marsh soils of Kuwait. *Norw J Bot* 1976;**23**:213–20.

Naeem S, Duffy JE, Zavaleta E. The functions of biological diversity in an age of extinction. *Science* 2012;**336**:1401–6.

Naeem S, Thompson LJ, Lawler SP, et al. Declining biodiversity can. *Nature* 1994;**368**:21.

Nano CE, Pavey CR. Refining the 'pulse-reserve' model for arid central Australia: seasonal rainfall, soil moisture and plant productivity in sand ridge and stony plain habitats of the Simpson Desert. *Aust Ecol* 2013;**38**:741–53.

Neilson J, Quade J, Ortiz M, et al. Life at the hyperarid margin: novel bacterial diversity in arid soils of the Atacama Desert, Chile. *Extremophiles* 2012;**16**:553–66.

Oren A, Steinberger Y. Catabolic profiles of soil fungal communities along a geographic climatic gradient in Israel. *Soil Biol Biochem* 2008;**40**:2578–87.

Osborne PL. *Tropical Ecosystems and Ecological Concepts*. Cambridge: Cambridge University Press, 2000.

Paltridge R, Southgate R. The effect of habitat type and seasonal conditions on fauna in two areas of the Tanami Desert. *Wildlife Res* 2001;**28**:247–60.

Pandey A, Purohit R, Rokad M. Soil aggregates and stabilization of sand dunes in the Thar desert of India. *Environ Conserv* 1995;**22**:69–71.

Pandit A, Joshi M, Bhargava P, et al. Metagenomes from the saline desert of Kutch. *Genome Announcements* 2014;**2**:e00439–14.

Pankova E. Environmental conditions and soils of natural oases in the Alashan Gobi Desert, Mongolia. *Eurasian Soil Sci* 2008;**41**:827–36.

Parker KC. Topography, substrate, and vegetation patterns in the northern Sonoran Desert. *J Biogeogr* 1991;**18**:151–63.

Parniske M. Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nat Rev Microbiol* 2008;**6**:763–75.

Pell S, Chivas A, Williams I. Great Victoria Desert: development and sand provenance. *Aust J Earth Sci* 1999;**46**:289–99.

Petchey OL, Gaston KJ. Functional diversity (FD), species richness and community composition. *Ecol Lett* 2002;**5**:402–11.

Philippot L, Spor A, Henault C, et al. Loss in microbial diversity affects nitrogen cycling in soil. *ISME J* 2013;**7**:1609–19.

Pinero Estrada J, Bermejo Bescos P, Villar del Fresno A. Antioxidant activity of different fractions of Spirulina platensis protean extract. *Farmaco* 2001;**56**:497–500.

Placella SA, Brodie EL, Firestone MK. Rainfall-induced carbon dioxide pulses result from sequential resuscitation of phylogenetically clustered microbial groups. *P Natl Acad Sci USA* 2012;**109**:10931–6.

Pointing SB, Belnap J. Microbial colonization and controls in dryland systems. *Nat Rev Microbiol* 2012;**10**:551–62.

Pointing SB, Belnap J. Disturbance to desert soil ecosystems contributes to dust-mediated impacts at regional scales. *Biodivers Conserv* 2014;**23**:1659–67.

Pointing SB, Warren-Rhodes KA, Lacap DC, et al. Hypolithic community shifts occur as a result of liquid water availability along environmental gradients in China's hot and cold hyperarid deserts. *Environ Microbiol* 2007;**9**:414–24.

Prestel E, Regeard C, Salamitou S, et al. The bacteria and bacteriophages from a Mesquite Flats site of the Death Valley desert. *Anton Leeuw* 2013;**103**:1329–41.

Prestel E, Salamitou S, DuBow MS. An examination of the bacteriophages and bacteria of the Namib desert. *J Microbiol* 2008;**46**:364–72.

Prigent M, Leroy M, Confalonieri F, et al. A diversity of bacteriophage forms and genomes can be isolated from the surface sands of the Sahara Desert. *Extremophiles* 2005;**9**: 289–96.

Raes J, Letunic I, Yamada T, et al. Toward molecular trait-based ecology through integration of biogeochemical, geographical and metagenomic data. *Mol Syst Biol* 2011; **7**:473.

Rafique T, Naseem S, Bhanger MI, et al. Fluoride ion contamination in the groundwater of Mithi sub-district, the Thar Desert, Pakistan. *Environ Geol* 2008;**56**:317–26.

Rainey FA, Ray K, Ferreira M, et al. Extensive diversity of ionizing-radiation-resistant bacteria recovered from Sonoran Desert soil and description of nine new species of the genus Deinococcus obtained from a single soil sample. *Appl Environ Microb* 2005;**71**:5225–35.

Rajeev L, da Rocha UN, Klitgord N, et al. Dynamic cyanobacterial response to hydration and dehydration in a desert biological soil crust. *ISME J* 2013;**7**:2178–91.

Ranzoni FV. Fungi isolated in culture from soils of the Sonoran desert. *Mycologia* 1968;**60**:356.

Raymond J. Coloring in the tree of life. *Trends Microbiol* 2008;**16**:41–3.

Reed SC, Coe KK, Sparks JP, et al. Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nat Clim Change* 2012;**2**:752–5.

Reith F, Brugger J, Zammit CM, et al., Influence of geogenic factors on microbial communities in metallogenic Australian soils. *Isme J* 2012;**6**:2107–18.

Rice G, Stedman K, Snyder J, et al. Viruses from extreme thermal environments. *P Natl Acad Sci USA* 2001;**98**:13341–5.

Richer R, Banack SA, Metcalf JS, et al. The persistence of cyanobacterial toxins in desert soils. *J Arid Environ* 2015;**112**: Part B(0)134–9.

Rillig MC, Maestre FT, Lamit LJ. Microsite differences in fungal hyphal length, glomalin, and soil aggregate stability in semiarid Mediterranean steppes. *Soil Biol Biochem* 2003;**35**: 1257–60.

Rousk J, Bååth E, Brookes PC, et al. Soil bacterial and fungal communities across a pH gradient in an arable soil. *ISME J* 2010;**4**:1340–51.

Santhanam R, Rong X, Huang Y, et al. Streptomyces bullii sp. nov., isolated from a hyper-arid Atacama Desert soil. *Anton Leeuw* 2013;**103**:367–73.

Saul-Tcherkas V, Unc A, Steinberger Y. Soil microbial diversity in the vicinity of desert shrubs. *Microb Ecol* 2013;**65**:689–99.

Schaeffer S, Billings S, Evans R. Responses of soil nitrogen dynamics in a Mojave Desert ecosystem to manipulations in soil carbon and nitrogen availability. *Oecologia* 2003;**134**:547–53.

Schlesinger WH, Pippen JS, Wallenstein MD, et al. Community composition and photosynthesis by photoautotrophs under quartz pebbles, Southern Mojave Desert. *Ecology* 2003;**84**:3222–31.

Schlesinger WH, Reynolds JF, Cunningham GL, et al. Biological feedbacks in global desertification. *Science (Washington)* 1990;**247**:1043–8.

Schmidt SK, Nemergut DR, Darcy JL, et al. Do bacterial and fungal communities assemble differently during primary succession? *Mol Ecol* 2014;**23**:254–8.

Schmiedel U, Jürgens N. Community structure on unusual habitat islands: quartz-fields in the Succulent Karoo, South Africa. *Plant Ecol* 1999;**142**:57–69.

Segata N, Boernigen D, Tickle TL, et al. Computational meta'omics for microbial community studies. *Mol Syst Biol* 2013;**9**:666.

Shash SM. Molecular analysis of phenotypic diversity among four Frankia isolated from Casuarina nodules in Egypt. 1: some clonal variation among four Frankia isolates. *Aust J Basic Appl Sci* 2009;**3**:529–35.

Sher Y, Zaady E, Nejidat A. Spatial and temporal diversity and abundance of ammonia oxidizers in semi-arid and arid soils: indications for a differential seasonal effect on archaeal and bacterial ammonia oxidizers. *FEMS Microbiol Ecol* 2013;**86**:544–56.

Shi Z, Zhang L, Li X, et al. Diversity of arbuscular mycorrhizal fungi associated with desert ephemerals in plant communities of Junggar Basin, northwest China. *Appl Soil Ecol* 2007;**35**:10–20.

Singh H, Anurag K, Apte SK. High radiation and desiccation tolerance of nitrogen-fixing cultures of the cyanobacterium Anabaena sp. strain PCC 7120 emanates from genome/proteome repair capabilities. *Photosynth Res* 2013;**118**:71–81.

Singh H, Fernandes T, Apte SK. Unusual radioresistance of nitrogen-fixing cultures of Anabaena strains. *J Bioscience* 2010;**35**:427–34.

Singh SC, Sinha RP, Hader DP. Role of lipids and fatty acids in stress tolerance in cyanobacteria. *Acta Protozool* 2002;**41**: 297–308.

Solomon S, Qin D, Manning M, et al. *Climate change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Summary for Policymakers.* Cambridge, UK: Cambridge University Press, 2007.

Soon WW, Hariharan M, Snyder MP. High-throughput sequencing for biology and medicine. *Mol Syst Biol* 2013;**9**:640.

Sorrels CM, Proteau PJ, Gerwick WH. Organization, evolution, and expression analysis of the biosynthetic gene cluster for scytonemin, a cyanobacterial UV-absorbing pigment. *Appl Environ Microb* 2009;**75**:4861–9.

Spain AM, Krumholz LR, Elshahed MS. Abundance, composition, diversity and novelty of soil Proteobacteria. *ISME J* 2009;**3**:992–1000.

Starkenburg SR, Reitenga KG, Freitas T, et al. Genome of the cyanobacterium Microcoleus vaginatusFGP-2, a photosynthetic ecosystem engineer of arid land soil biocrusts worldwide. *J Bacteriol* 2011;**193**:4569–70.

Sterflinger K, Tesei D, Zakharova K. Fungi in hot and cold deserts with particular reference to microcolonial fungi. *Fungal Ecol* 2012;**5**:453–62.

Stetter KO. Extremophiles and their adaptation to hot environments. *FEBS Lett* 1999;**452**:22–5.

Steven B, Gallegos-Graves LV, Belnap J, *et al*. Dryland soil microbial communities display spatial biogeographic patterns associated with soil depth and soil parent material. *FEMS Microbiol Ecol* 2013;**86**:101–13.

Steven B, Gallegos-Graves LV, Starkenburg SR, *et al*. Targeted and shotgun metagenomic approaches provide different descriptions of dryland soil microbial communities in a manipulated field study. *Environ Microbiol Rep* 2012a;**4**:248–56.

Steven B, Gallegos-Graves LV, Yeager CM, *et al*. Dryland biological soil crust cyanobacteria show unexpected decreases in abundance under long-term elevated CO_2. *Environ Microbiol* 2012b;**14**:3247–58.

Stomeo F, Makhalanyane TP, Valverde A, *et al*. Abiotic factors influence microbial diversity in permanently cold soil horizons of a maritime-associated Antarctic Dry Valley. *FEMS Microbiol Ecol* 2012;**82**:326–40.

Stomeo F, Valverde A, Pointing SB, *et al*. Hypolithic and soil microbial community assembly along an aridity gradient in the Namib Desert. *Extremophiles* 2013;**17**:329–37.

Strauss SL, Day TA, Garcia-Pichel F. Nitrogen cycling in desert biological soil crusts across biogeographic regions in the Southwestern United States. *Biogeochemistry* 2012;**108**:171–82.

Subhash Y, Sasikala C, Ramana CV. *Pontibacter ruber* sp. nov. and *Pontibacter deserti* sp. nov., isolated from the desert. *Int J Syst Evol Micr* 2014;**64**:1006–11.

Subramanian S, Di Pierro V, Shah H, *et al*. MiST: a new approach to variant detection in deep sequencing datasets. *Nucleic Acids Res* 2013;**41**:e154.

Suttle CA. Marine viruses—major players in the global ecosystem. *Nat Rev Microbiol* 2007;**5**:801–12.

Tarafdar J, Rao A, Bala K. Production of phosphatates by fungi isolated from desert soils. *Folia Microbiol (Praha)* 1988;**33**:453–7.

Taylor DL, Bruns TD, Szaro TM, *et al*. Divergence in mycorrhizal specialization within Hexalectris spicata (Orchidaceae), a nonphotosynthetic desert orchid. *Am J Bot* 2003;**90**:1168–79.

Taylor-George S, Palmer F, Staley J, *et al*. Fungi and bacteria involved in desert varnish formation. *Microb Ecol* 1983;**9**:227–45.

Teixeira LCRS, Peixoto RS, Cury JC, *et al*. Bacterial diversity in rhizosphere soil from Antarctic vascular plants of Admiralty Bay, maritime Antarctica. *ISME J* 2010;**4**:989–1001.

Thomas AD. Impact of grazing intensity on seasonal variations in soil organic carbon and soil CO2 efflux in two semiarid grasslands in southern Botswana. *Philos T R Soc B* 2012;**367**:3076–86.

Tilman D, Wedin D, Knops J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 1996;**379**:718–20.

Titus JH, Nowak RS, Smith SD. Soil resource heterogeneity in the Mojave Desert. *J Arid Environ* 2002;**52**:269–92.

Tracy CR, Streten-Joyce C, Dalton R, *et al*. Microclimate and limits to photosynthesis in a diverse community of hypolithic cyanobacteria in northern Australia. *Environ Microbiol* 2010;**12**:592–607.

Tripathi G, Kumari R, Sharma B. Mesofaunal biodiversity and its importance in Thar desert. *J Environ Biol* 2007;**28**:503.

Trumper K, Ravilious C, Dickson B. Carbon in drylands: desertification, climate change and carbon finance.

A *UNEP-UNDPUNCCD Technical Note for Discussions at CRIC 7* Istanbul, Turkey, 2008, 1–12.

van der Heijden MGA, Horton TR. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *J Ecol* 2009;**97**:1139–50.

Waller F, Achatz B, Baltruschat H, *et al*. The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. *P Natl Acad Sci USA* 2005;**102**:13386–91.

Wang J, Shen J, Wu Y, *et al*. Phylogenetic beta diversity in bacterial assemblages across ecosystems: deterministic versus stochastic processes. *ISME J*. 2013;**7**:1310–21.

Wang X, Chen F, Dong Z. The relative role of climatic and human factors in desertification in semiarid China. *Global Environ Chang* 2006;**16**:48–57.

Warren-Rhodes KA, McKay CP, Boyle LN, *et al*. Physical ecology of hypolithic communities in the Central Namib Desert: The role of fog, rain, rock habitat and light. *J Geophys Res-Biogeo* 2013;**118**:1451–60.

Warren-Rhodes KA, Rhodes KL, Boyle LN, *et al*. Cyanobacterial ecology across environmental gradients and spatial scales in China's hot and cold deserts. *FEMS Microbiol Ecol* 2007;**61**:470–82.

Warren-Rhodes KA, Rhodes KL, Pointing SB, *et al*. Hypolithic cyanobacteria, dry limit of photosynthesis, and microbial ecology in the hyperarid Atacama Desert. *Microb Ecol* 2006;**52**:389–98.

Weinbauer MG. Ecology of prokaryotic viruses. *FEMS Microbiol Rev* 2004;**28**:127–81.

Weiss JL, Overpeck JT. Is the Sonoran Desert losing its cool? *Global Change Biol* 2005;**11**:2065–77.

Wesche K, Ronnenberg K, Retzer V, *et al*. Effects of large herbivore exclusion on southern Mongolian desert steppes. *Acta Oecologica* 2010;**36**:234–41.

Whitton BA, Potts M. Introduction to the cyanobacteria. In: Whitton BA (ed.) *Ecology of Cyanobacteria II*. Dordrecht, The Netherlands: Springer, 2012, 1-13.

Williams TJ, *et al*. Microbial ecology of an Antarctic hypersaline lake: genomic assessment of ecophysiology among dominant haloarchaea. *Isme J* 2014;**8(8)**:1645–58.

Wittebolle L, Marzorati M, Clement L, *et al*. Initial community evenness favours functionality under selective stress. *Nature* 2009;**458**:623–6.

Wong FK, Lacap DC, Lau MC, *et al*. Hypolithic microbial community of quartz pavement in the high-altitude tundra of central Tibet. *Microb Ecol* 2010;**60**:730–9.

Wood Y, Graham R, Wells S. Surface control of desert pavement pedologic process and landscape function, Cima Volcanic field, Mojave Desert, California. *Catena* 2005;**59**:205–30.

Xu L, Zeng X-C, Nie Y, *et al*. Pontibacter diazotrophicus sp. nov., a novel nitrogen-fixing bacterium of the family Cytophagaceae. *PLoS One* 2014;**9**:e92294.

Zeng Y, Feng F, Medová H, *et al*. Functional type 2 photosynthetic reaction centers found in the rare bacterial phylum Gemmatimonadetes. *P Natl Acad Sci USA* 2014;**111**:7795–800.

Zhang L, Dai J, Tang Y, *et al*. Hymenobacter deserti sp. nov., isolated from the desert of Xinjiang, China. *Int J Syst Evol Micr* 2009;**59**:77–82.

Zhou Y, Wang X, Liu H, *et al*. Pontibacter akesuensis sp. nov., isolated from a desert soil in China. *Int J Syst Evol Micr* 2007;**57**:321–5.