

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 fraction 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 topology that is essentially barren, with a limited range of higher plants and animals. In consequence, 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.

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 $33.7 \times 10^6 \text{ km}^2$) (Figure 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 *et al.*, 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 *et al.*, 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 sub-classification. 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: sub-humid (P/PET = 0.5 - 0.65), semi-arid (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 Ultra-Violet (UV) radiation and strong winds (Lester *et al.*, 2007, Chamizo *et al.*, 2012, Stomeo *et al.*, 2013) (Table 1).

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 & Bjorkman, 1980, Evenari, 1985). One consequence of the extremes of the desert environment is that the diversity of macrofauna is often 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 adaptation in hot desert ecosystems. To date, much of the research 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 & 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 system services.

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. Current thinking is that the impact of environmental conditions on desert soil ecosystems results in reduced levels of microbial diversity (Fierer *et al.*, 2012, Neilson *et al.*, 2012), and a consequent reduction of soil system functionality (i.e., ecosystem services). While the diversity of higher eukaryotic species has been directly related to system functionality, in particular the efficiency of resource utilization (Naeem *et al.*, 1994, Tilman *et al.*, 1996, Naeem *et al.*, 2012), the effects of accelerated rates of species extinction on community functionality remain unclear. 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 *et al.*, 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, adaptation 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). 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 dominate desert soil phylogenetic surveys (Liu *et al.*, 2009, Goswami *et al.*, 2013, Makhalanyane *et al.*, 2013). For example, Namib Desert soils (Figure 2A) were dominated by actinobacterial phylotypes (44%) with high homology to *Rubrobacter*, *Arthrobacter*, *Thermopolyspora* and *Streptomyces* spp. (Drees *et al.*, 2006, Makhalanyane *et al.*, 2013, Santhanam *et al.*, 2013). Many Actinobacteria isolated from deserts soils appear to be novel species (Li *et al.*, 2005, Li *et al.*, 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.*, 2013). The presence of the pioneer genus *Frankia* may be vital in depauperate environments as significant contributors to soil fertility (Griffiths & McCormick, 1984, Dommergues & 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 & Williams, 1992, Chater & Chandra, 2006, Gao & Garcia-Pichel, 2011).

Bacteroidetes are also common in desert soils and are dominated by the classes of *Flavobacteria* and *Sphingobacteria* (Prestel *et al.*, 2008, Prestel *et al.*, 2013). 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 *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 are prominent members of desert soil bacterial communities (Chen *et al.*, 2003, Lester *et al.*, 2007, Spain *et al.*, 2009, Bachar *et al.*, 2012, Lefèvre *et al.*, 2012), although desert soils often have a lower abundance of proteobacteria compared to other biomes (Fierer *et al.*, 2012). *Alpha-*, *Beta-* and *Gammaproteobacteria* are often associated with soils receiving higher rates of organic carbon inputs (Fierer *et al.*, 2007, Lopez *et al.*, 2013). 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.*, 2013, Richer *et al.*, 2014), and these phyla may be comparatively more abundant in desert soils than in other biomes (Fierer *et al.*, 2012). Although Gemmatimonadetes are ubiquitously distributed in soils, virtually nothing is known of their physiology or ecology (DeBruyn *et al.*, 2011). To date, only 6 arid soil Gemmatimonadetes isolates have been described (Ludwig *et al.*, 2008, DeBruyn *et al.*, 2011). Despite the paucity of functional information, 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 *et al.*, 2008, Gommeaux *et al.*, 2010). 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 desert soils (Cary *et al.*, 2010, Whitton & 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). For instance, these taxa contribute significantly to desert soil nutrient status through improving soil stability, moisture retention and fertility (Belnap & Gardner, 1993). The ability of members of this phylum to withstand high levels of UV irradiation, desiccation and water stress (Cockell & Knowland, 1999, Starkenburg *et al.*, 2011) is likely to provide a significant competitive advantage. Despite these advantages, cyanobacteria in the most extreme hyperarid deserts are generally restricted to protected sub-lithic 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 *Chroococidiopsis*, 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 *et al.*, 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 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 & 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 *et al.*, 1976, Titus *et al.*, 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 & Steinberger, 2008). A detailed overview of hot and cold desert fungi has been published by Sterflinger and colleagues (Sterflinger *et al.*, 2012).

Archaeal Communities

Archaeal taxa are relatively rare across many biomes but seem to be more abundant in desert soils (Fierer *et al.*, 2012), with *Thaumarchaeota* being the principal archaeal group. All known organisms of this lineage are chemolithoautotrophic ammonia-oxidizers and may play important roles in biogeochemical cycling (Brochier-Armanet *et al.*, 2008). An earlier 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 (Figure 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 & 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 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.*, 2007, Prestel *et al.*, 2008, Fierer *et al.*, 2012, Prestel *et al.*, 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 bacteriophages. 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 and colleagues (2008) suggest that the environmental conditions in deserts may prevent the induction of these putative lysogens through UV exposure.

Fierer and colleagues (Fierer *et al.*, 2007) 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., Figure 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.*, 2007), 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.*, 2007).

Microbial functionality in desert soils

We know surprisingly little about microbial functionality in desert soils. Metagenome data from a cross biome study showed that functional diversity, as represented by the abundances of genes implicated in nitrogen, potassium and sulfur 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 commonly been measured in desert soil micro-ecology, despite its importance when interpreting the

diversity and distribution of genes across communities (Petchey & Gaston, 2002, Green *et al.*, 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.*, 2007, Fierer *et al.*, 2012, Manzoni *et al.*, 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 (Demergasso *et al.*, 2004, Angel *et al.*, 2010, Fierer *et al.*, 2012, Stomeo *et al.*, 2012, Garcia-Pichel *et al.*, 2013, Sher *et al.*, 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.*, 2013) and may facilitate the persistence of other groups through the production of exopolysaccharides (EPS) which may aid in water uptake and retention (Hall-Stoodley *et al.*, 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.

Localised, cryptic and refuge niches

Microbial populations are inhomogeneously distributed in arid soil systems, particularly in the more ‘extreme’ hyper-arid 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.*, 2013, 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.*, 2013).

Biological soil crusts

Biological soil crusts are complex microbial communities colonizing interspace soil surfaces between patchily distributed plants and are widely distributed in both hot and cold deserts (Pointing & 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 *et al.*, 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 harbour abundant populations of Actinobacteria (Garcia-Pichel *et al.*, 2003, Steven *et al.*, 2012, Steven *et al.*, 2012), 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 harbour 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 & Flechtner, 2002, Gundlapally & Garcia-Pichel, 2006, Housman *et al.*, 2007, Strauss *et al.*, 2012). Biogeographic patterns in BSCs have also been investigated at a continental scale (Dvorak *et al.*, 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 (Dvořák *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 *et al.*, 1994). For instance, these communities fix large amounts of atmospheric carbon dioxide (CO₂) (over 2.6 pg of C per year globally) (Elbert *et al.*, 2012), regulate the temporal dynamics of soil CO₂ efflux and net CO₂ 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 sub-crust soils also stimulates increases in heterotrophic microbial and invertebrate populations, including bacteria, fungi, and nematodes (Darby *et al.*, 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 & 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, Caruso *et al.*, 2011). Such hypolithic communities may represent a sub-lithic 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 hyper-arid Atacama Desert, the rate of quartz rock hypolithic colonization is as low as approx. 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 hyper-arid 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).

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.*, 2013). 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 *Gleocapsis* lineages also form a significant portion of hypolithic communities (Azua-Bustos *et al.*, 2013, Makhalanyane *et al.*, 2013).

The dominance of cyanobacteria emphasises the important role played by hypoliths in hot desert soils where, for example, unicellular N₂-fixing *Gloeotheca* (*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.*, 2013). Actinobacterial phylotypes include a number of radiation tolerant taxa, such as *Rubrobacter* sp. (Lacap *et al.*, 2011, Makhalanyane *et al.*, 2013). 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 & Winans, 2005). Interestingly, cyanobacteria are known to produce phenolic compounds which may protect them from oxidative stressors (Pintero Estrada *et al.*, 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.*, 2013). 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.*, 2013). *Methylobacterium* spp. which have been found, for instance, in Atacama (Azua-Bustos *et al.*, 2011) and Namib desert (Makhalanyane *et al.*, 2013) 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.*, 2013). 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). A field experiment with artificial (glass) hypolithic substrates suggests that initial colonisation events (in the form of adherent ventral cyanobacterial films) can occur in a 2 to 3 year time-scale (Wing, McKay and Cowan, unpublished results).

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 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 Rios, Cowan, unpublished results). 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 inter-shrub sites in arid and semi-arid 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 *et al.*, 2012), including high temperatures (Bowers & Wiegel, 2011) and desiccation (Kendrick & 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 *et al.*, 2013). A recent T-RFLP study of the microbial community composition of Namib Desert gravel soils through a full annual cycle (Armstrong, Ramond and Cowan, unpublished results) has shown that major changes in community structure can occur over relatively short (week-month) timescales.

The issue of whether desert plant root systems select for unique rhizospheric and rhizoplastic 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 (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 *H. 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 & 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 9 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 years 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 CO₂ efflux and reduced soil net CO₂ uptake, lessening the capacity of drylands to sequester atmospheric CO₂. 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 (*Microcoleus. 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 & Conrad, 2013); Actinomycetales were the dominant bacterial order in dry biocrusts but showed a massive reduction in occurrence after artificial hydration events (Angel & 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 *et al.*, 2012).

Elevated atmospheric CO₂ concentrations are expected to increase plant photosynthetic activity and the transfer of fixed carbon below-ground (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 CO₂ compared with ambient conditions (Jin & 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 1h, accompanied by upregulation of anabolic pathways. The beginning of desiccation was characterized by the induction of genes for oxidative and photo-oxidative 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 semi-arid) 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 CO₂ 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 & 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. For example, the physical structure of biocrust and hypoliths stabilizes the soil against wind and water erosion (Pointing & Belnap, 2012). Biocrusts and hypolithic communities have been shown to increase soil fertility and soil moisture retention (Pointing & 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. 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 CO₂ concentrations (Cheng *et al.*, 2012), these changes

may have major implications for below-ground 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 below-ground, compromising their ability to mitigate increased levels of atmospheric CO₂.

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 *et al.*, 2013, Subramanian *et al.*, 2013), mass spectrometry (Monge *et al.*, 2013, Segata *et al.*, 2013) and bioinformatics tools (McKenna *et al.*, 2010, Kouskoumvekaki *et al.*, 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 *et al.*, (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 & 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 time-scales. 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 under-studied arid environments.

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Table 1: General characteristics (size, topography, physicochemical, pH, 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 Hyper-arid –Arid	pH: 7.6 – 7.9, OC ^a (%) ^a 0.1 – 1.2, N (%) 0.8 – 0.1	Osbourne, (2000) ,Badr El-Din <i>et al.</i> , (2006), Benslama & Boulahrouf, (2013)
Kalahari/ Southwestern Africa	520,000	Sand sheets, longitudinal dunes	-10 - 45	100 – 250 Arid– Semi-arid	pH: 7.7 - 8.7, OC (%) 0.1 - 0.5 N (%) 0.01 – 0.08	Lovegrove <i>et al.</i> , (1991), Dean <i>et al.</i> , (1999), Lawson & Thomas, (2002), Mosweu <i>et al.</i> (2013)
Namib/ Southwestern Africa	81,000	Gravel plains, sand plains, dunes	5 - 45	5 - 100 Hyper-arid – Arid	pH: 7.9 - 8.5, OC (%) 0.1 - 0.3 N (%) 0.03 – 0.05	Stomeo <i>et al.</i> (2013) , Eckardt <i>et al.</i> , (2013)
Karoo/ South Africa	395,000	Gravel plains, bush lands, savannah	2 - 40	50 - 200 Arid – Semi-arid	pH: 6.9 – 9, OC (%) 0.3 - 1.3 N (%) 0.02 – 0.06	Schmiedel & Jurgens, (1999), Burke, (2002)
Chihuahuan/ North Central Mexico – Southwestern USA	455,000	Numerous mountain ranges with shrub covered flat basins	10 - 40	70 – 400 Arid - Semi-arid	pH: 5.9 - 6.2, OC (%) 0.2 -1.9 N (%) 0.07 – 0.1	Gallardo & Schlesinger, (1992) Bell <i>et al.</i> , 2(008)
Mojave/ Southwestern USA	152,000.	Mountain chains, dry alkaline lake beds, calcium carbonate dunes	-10 - 50	30 - 300 Arid – Semi-arid	pH: 7.1 - 9.4, OC (%) 0.04 – 0.1, N (%) 0.03 – 0.09	Shaeffer <i>et al.</i> (2002), Titus <i>et al.</i> , (2002) Wood <i>et al.</i> , (2005), Hereford <i>et al.</i> ,(2006)
Sonoran/ Southwestern USA	312,000.	Basins and plains bordered by mountain ridges	-10 - 50	70 - 400 Arid – Semi-arid	pH: 5 – 8.6, OC (%) 0.4 – 2 N (%) 0.003 – 0.07	Parker, (1991), Weiss & Overpeck (2005) Andrew <i>et al.</i> , (2012)
Atacama-Sechura/ Chile-Peru	105,000	Salt basins, sand plains, lava fields	-5 - 40	0 - 20 Hyper-arid	pH – 6.6 – 9.2, OC (%) 0.1 – 2.6, N (%) 0.01 – 0.15	Barros <i>et al.</i> (2008), Lester <i>et al.</i> , (2009) Lecap <i>et al.</i> , (2011), Crits-Christoph <i>et al.</i> (2013)
Arabian/ Arabian Peninsula	2,300,000	Sand, gravel plains, rocky highlands	5 - 40	25 - 230 Arid – Semi-arid	pH: 7 – 7.5, OC (%) ,N (%) /	Abdel Hafez (1982) , Almazroui <i>et al.</i> , (2012)
Thar/ India and Pakistan	200,000	Rocky sand, dunes and saline soil	4 - 50	200 - 300 Semi-arid	pH: 7.9-8.1, OC (%) 0.3 - 0.4 N (%) 0.02 – 0.06	Pandey <i>et al.</i> , (1995), Bhatnagar & Bhatnagar, (2005), Tripathi <i>et al.</i> , (2007) Rafique <i>et al.</i> , (2008)
Gobi/ Southern Mongolia	53,000	Grasslands, rocky outcrops, 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 <i>et al.</i> , (2010) Kurapova <i>et al.</i> (2012)
Great Victoria/ Southwestern Australia	350,000	Dunes, gravel plains, grassland	18 - 40	150 – 230 Arid – Semi-arid	OC (%) 0.2	Pell <i>et al.</i> , (2009), Grace <i>et al.</i> , (2009)
Great Sandy/ Northwestern Australia	285,000	Linear dunes, wide plains, saline lakes	10 - 40	250– 370 Semi-arid	pH: 5.8 – 6, OC (%) 0.1 – 1.1 N (%) 0.05 – 0.09	Grigg <i>et al.</i> , (2008), Grace <i>et al.</i> , (2009)
Tanami/ Northern Australia	185,000	Sandy plains, grassland, shrubs	10 - 40	300 – 500 Semi-arid	pH: 4.9 – 6.7, OC (%) 0.1 – 1.4, N (%) 0.01 – 0.08	Paltridge & Southgate (2001), Reith <i>et al.</i> , (2012)
Simpson/ Central Australia	180,000	Extensive dune-fields	5 - 40	50 - 400 Semi-arid	pH: 6.5 – 7, OC (%) 0.1 – 0.3 N (%) 0.05 – 0.07	Duncan & Dickman, (2001), Islam & Singh, (2005), Free <i>et al.</i> (2013), Nano & Pavey, (2013)
Gibson/ Southern Australia	156,000	Sandy plains, rocky highlands, grassland	6 - 40	200– 400 Semi-arid	OC (%) 0.06, N (%) /	Grace <i>et al.</i> , (2009)
Negev/ Israel	13,000	Dunes, sandy soilm rocky highlands	5 - 40	100 – 300 Arid – Semi-arid	pH: 7.2 – 8, OC (%) 0.5 -0.7 N (%) 0.006 – 0.04	Angel <i>et al.</i> , (2010), Angel <i>et al.</i> , (2013) Drahorad <i>et al.</i> , (2013), Martirosyan & Steinberger, (2014)

^a organic carbon

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
<i>Aspergillus</i> sp., <i>Penicillium</i> sp., <i>Acrophialophora</i> sp., <i>Aleternaria</i> sp.	Arid soils of Western Rajasthan (India)	Release of bioavailable phosphorous from organic phosphorous compounds	Culturing	Tarafdar et al., 1988
<i>Acaulospora</i> sp., <i>Archaeospora</i> sp., <i>Entrophospora</i> sp., <i>Glomus</i> sp., <i>Paraglomus</i> 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., 2006
Phylotypes from the Ascomycota (mainly <i>Alternaria</i> sp. and <i>Acremonium</i> sp.) and Basidiomycota divisions	Biological soil crusts of the Colorado Plateau (USA)	The dark-pigmented <i>Alternaria</i> sp. may be involved in UV resistance of the BSC	DGGE	Bates & 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 & 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 contributes 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

Figure Legends

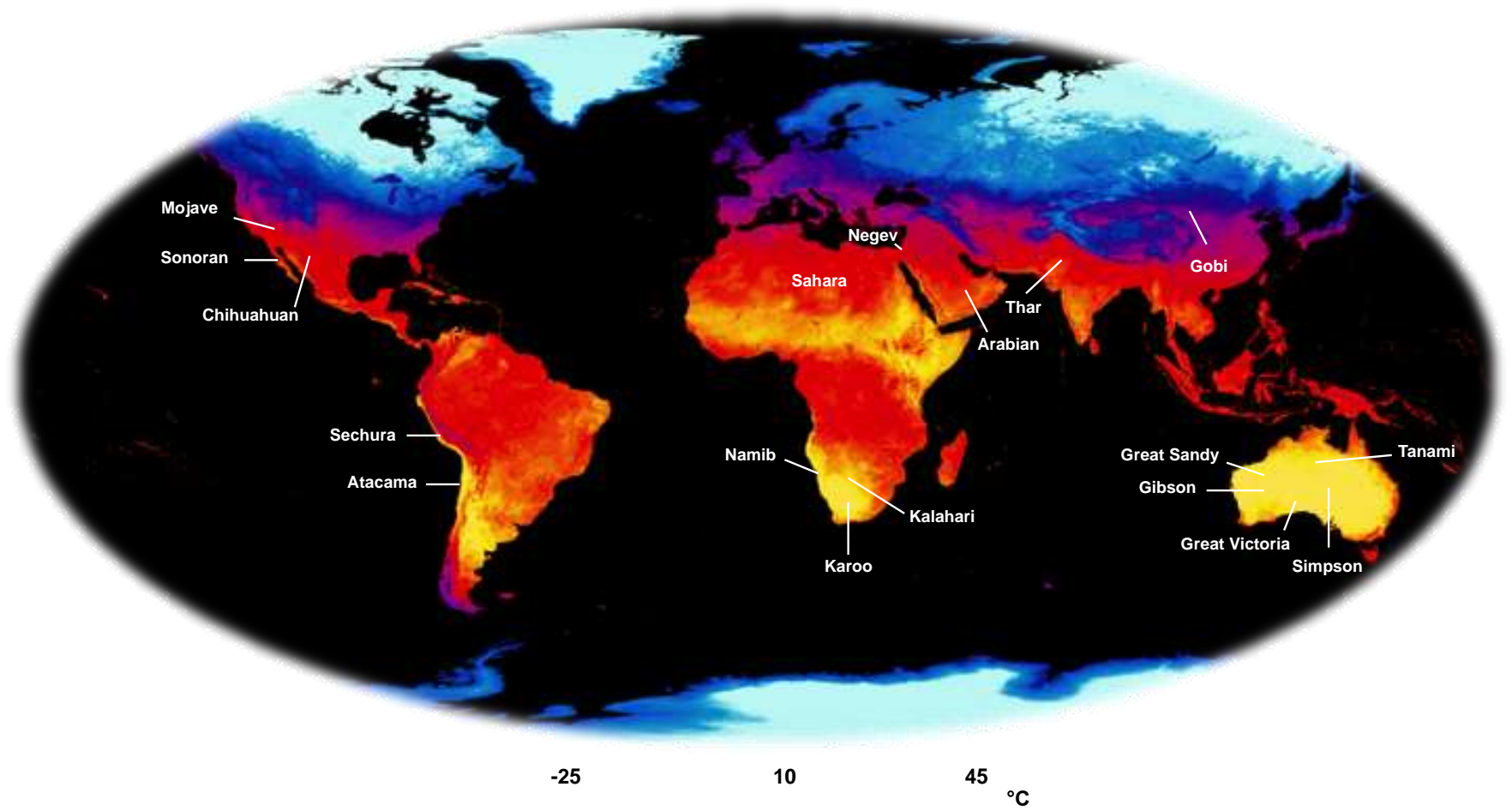
Figure 1: Global distribution of hot deserts with (A) land surface temperature (NEO, 2014) and (B) total precipitable water (NOAA, 2014) shown for January 2014.

Figure 2: Hot desert landscapes: A. Namib Desert gravel plains, B. The dune-interdune landscape of the central Namib sand-sea C: Vegetated landscape of the Mojave Desert D. The Negev Desert

Figure 3: Phylogenetic diversity of bacterial 16S rRNA gene sequences

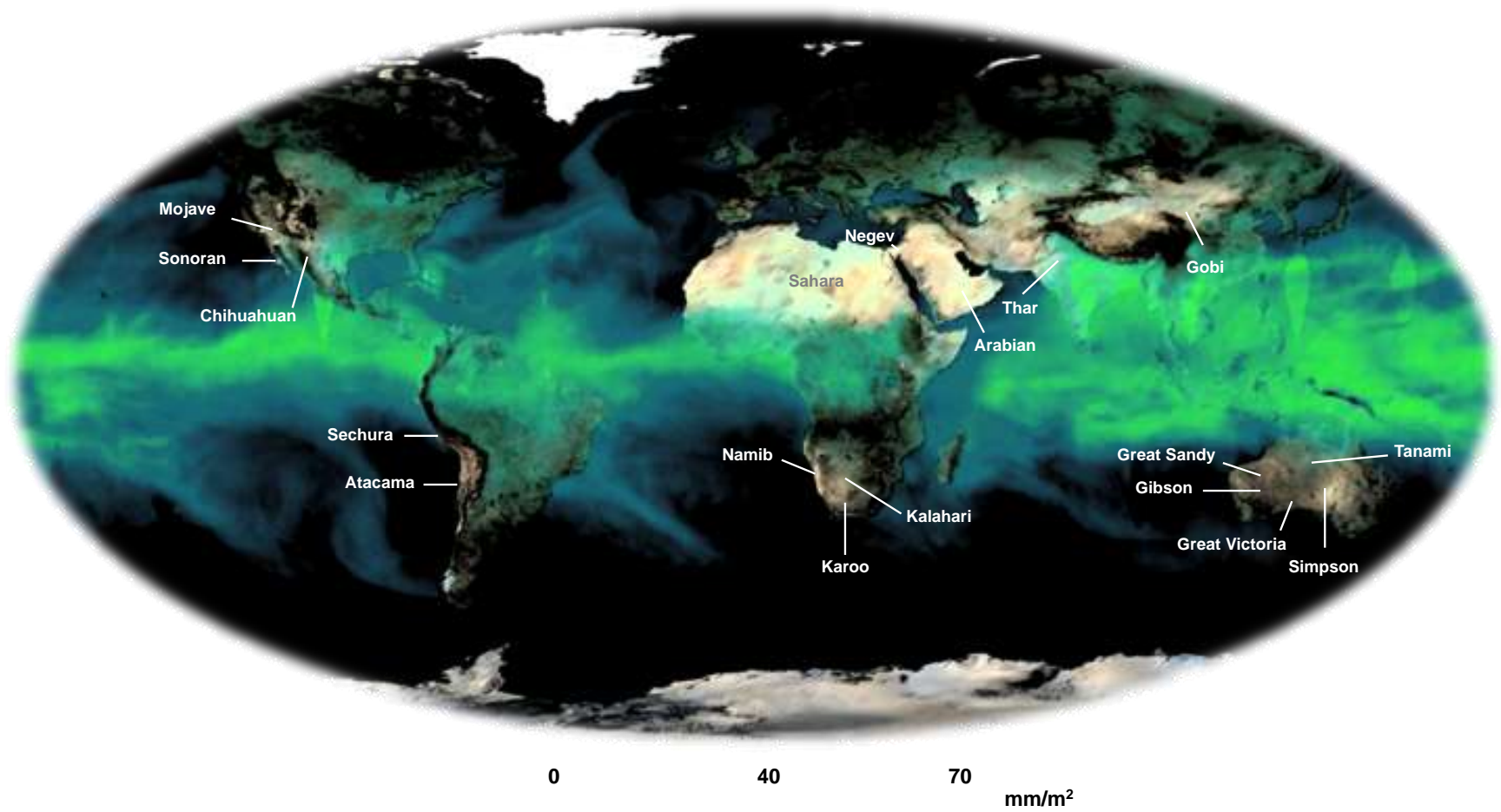
Figures

A



Hot desert microbial communities

B



Hot desert microbial communities



A.



B.



C.



D.

Hot desert microbial communities