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# Microbiomics of Namib Desert habitats

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## Abstract

The Namib Desert is the world's only truly coastal desert ecosystem. Until the end of the first decade of the 21st Century, very little was known of the microbiology of this south-western African desert, with the few reported studies being based solely on culture-dependent approaches. However, from 2010, an intense research program undertaken by researchers from the University of the Western Cape Institute for Microbial Biotechnology and Metagenomics, and subsequently the University of Pretoria Centre for Microbial Ecology and Genomics, and their collaborators, led to a more detailed understanding of the ecology of the indigenous microbial communities in many Namib Desert biotopes. Namib Desert soils and the associated specialised niche communities are inhabited by a wide array of prokaryotic, lower eukaryotic and virus/phage taxa. These communities are highly heterogeneous on both small and large spatial scales, with community composition impacted by a range of macro- and micro-environmental factors, from water regime to soil particle size. Community functionality is also surprisingly non-homogeneous, with some taxa retaining functionality even under hyper-arid soil conditions, and with subtle changes in gene expression and phylotype abundances even on diel timescales.

Despite the growing understanding of the structure and function of Namib Desert microbiomes, there remain enormous gaps in our knowledge. We have yet to quantify many of the processes in these soil communities, from regional nutrient cycling to community growth rates. Despite the progress that has been made, we still have little knowledge of either the role of phages in microbial community dynamics, or inter-species interactions. Furthermore, the intense research efforts of the past decade have highlighted the immense scope for future microbiological research in this dynamic, enigmatic and charismatic region of Africa remains vast.

## Introduction

The hyper-arid Namib Desert is located along the South Atlantic Ocean shore on the western side of southern Africa. It is an isolated, cool, coastal desert of less than 140 km wide that stretches longitudinally for over 2000km from northern South Africa to southern Angola (Figure 1). The Central Namib is characterized by extensive gravel plains, which are separated by the ephemeral Kuiseb River from the Namib Sand Sea, a UNESCO World Heritage site, to the south. Edaphic conditions in these two desert systems are very different, with the gravel plains characterised by relatively stable surfaces with rock outcrops and pebbly 'desert armour', while the Sand Sea consists of vast expanses of wind-blown sand and active aeolian dunes. Deserts are characterised as water pulse-system driven environments (Noy-Meir, 1973; Belnap et al, 2005). However, and despite being one of the driest places on Earth, the Namib Desert presents a near-unique hydroclimatology that is largely influenced by the cold coastal waters from upwelling caused by the Benguela Current. At the coast, where almost no rainfall occurs during most years, fog precipitation is high. The incidence of fog and moisture derived from advected fog rapidly decreases towards the interior and, at the most, reaches about 60km inland. In contrast, mean annual rainfall increases inland towards the eastern margins of the Namib Desert. While rainfall events are spatially and temporally variable, fog water input is more consistent, with over 125 foggy days near the coast annually. This has led to a high degree of plant and animal endemism in the Namib Desert, particularly in the fog-influenced coastal zone (Seely and Pallet, 2008).

Hyper-arid deserts, such as the Namib, exert polyextreme conditions on indigenous (micro)biota; these typically include high xeric stress (with associated oxidative stress), high temperatures, large daily temperature fluctuations and low levels of available nutrients (Pointing and Belnap, 2012). In consequence, microorganisms (and, of course, higher organisms) exhibit multiple physiological and colonization strategies to cope with these stresses (Pointing and Belnap, 2012; Makhalanyane et al, 2015; Lebre et al, 2017). Furthermore, given the relative scarcity of macroorganisms in desert ecosystems (compared to temperate and water sufficient terrestrial soils), microbial communities are considered to be the dominant drivers of nutrient cycling in these environments, and are consequently crucial for their productivity.

In this review, we summarize the body of microbiological and microbial ecological research that has been reported from many of the different niches that constitute the Namib Desert microbiome (Figures 2.1 to 2.7), and we highlight current gaps in our knowledge of the structure and function of Namib Desert edaphic communities.

## Edaphic systems

Edaphic ('open soil') systems have received, by far, the most attention in past research on Namib Desert microbial ecology. Many of the core studies of this microbiome have involved basic molecular phylogenetic surveys of microbial, particularly bacterial, diversity. When comparing microbial assemblages in various Namib Desert soils, the dominant phyla are those that are typically found in most soil environments (Actinobacteria, Proteobacteria, Bacteroidetes, Acidobacteria, Cyanobacteria) with Chloroflexi, Deinococcus-Thermus and Firmicutes as more minor but significant contributors to the diversity (Ronca et al, 2015; Armstrong et al, 2016; van der Walt et al, 2016; Valverde et al, 2016; Unc et al, 2019). Actinobacteria and Proteobacteria consistently dominated the active fraction of the bacterial communities (Gunnigle et al., 2017; León-Sobrino et al, 2019), while other numerically dominant taxa (such as Bacteriodetes) appeared to be largely dormant (i.e., not active, as determined by transcript analysis) in desiccated soils (León-Sobrino et al, 2019).

Namib Desert edaphic fungal communities are typically dominated by Ascomycota (van der Walt et al, 2016; Valverde et al, 2016; Marasco et al, 2018). Interestingly, the class Dothideomycetes was found to be significantly more abundant in gravel plain soils than in dune soils, while Agaricostilbomycetes, Chytridiomycota and Sordariomycetes classes showed the opposite trend (van der Walt et al, 2016). Other possible examples of niche selection have been observed, where fungi of the Eurotiomycetes and Sordariomycetes classes (Ascomycota) dominated the rhizosphere of the endemic desert specialist plant, *Welwitschia mirabilis* (Valverde et al, 2016), while these taxa and members of the Dothideomycete class dominated in the different compartments of the rhizosheath structures of dune speargrass plants (Marasco et al, 2018). Shotgun metatranscriptomics of dry Namib Desert gravel plain soils suggested that the Ascomycota were the most active fungal taxa, particularly during the cooler night hours (León-Sobrino et al, 2019).

Numerous *Glomus* species (*G. aggregatum*, *G. eburneum*, *G. etunicatum*, *G. intraradices*, *G. microaggregatum*, *G. mosseae*, *G. occultum*, *G. spurcum*, *G.* AZ112, *G.* AZ123, *G.* TX106 and *G.* NB118), together with *Acaulospora morrowiae* and *Acaulospora trappei,* have been isolated from various

Namib Desert soils (Uhlmann *et al*., 2006; Stutz *et al*., 2000), although molecular phylogenetic surveys do not suggest that these are dominant taxa. A range of mycorrhizal *Glomus* species associated with the desert plants *Stipagrostis* spp., *Centropodia glauca*, *Cladoraphis spinosa* and *Welwitschia mirabilis* have also been isolated (Jacobson, 1993, 1997). Interestingly, Cooper-Driver and colleagues (2000) observed that 82% of 616 female *W. mirabilis* plants surveyed were infected by the phytopathogenic fungus *Aspergillus welwitschiae,* formerly known as *Aspergillus niger* var*. phoencis*. However, no obvious evidence of pathogenic physiology in the adult host plant was reported.

In Namib Desert soils, Crenarchaeota/Thaumarchaeota comprised from 2% to 25% of the total the prokaryotic communities (van der Walt et al, 2016; Armstrong et al, 2016), making these soils among the most archaea-rich of all desert soils studies (Bates et al, 2011). Based on 16S rRNA transcript numbers, Thaumarchaeota was the most active archaeal phylum in desiccated soils, followed by Euryarchaeota and Crenarchaeota (León-Sobrino et al, 2019). Interestingly, Euryarchaeota, most particularly methanogens, represented a substantial proportion of a Namib Desert gravel plain metaproteome (Gunnigle et al, 2014), supporting the view that dryland soils participate in the global methane cycle, despite the fact that the soils are almost always aerobic (Angel et al, 2011, 2012).

Viral sequences belonging to the common soil dsDNA phage, of the order Caudovirales and representing the families *Siphoviridia*, *Myoviridae* and *Podoviridae*, dominated Namib Desert edaphic metaviromes (Zablocki et al, 2017; Scola et al, 2018). The metaviromic results confirmed earlier transmission electron microscopy analyses (Prestel et al, 2008). As observed in Namib Desert salt pan samples, lysogenic viruses were highly prevalent in Namib Desert soils (Prestel et al, 2008). This observation is consistent with the suggestion that phage play a limited role in host community dynamics and gene flow in dry soils (Zablocki et al, 2017), probably reflecting the limited capacity for communication between microbial biofilms associated with individual soil particles or sand grains, in the absence of a liquid water continuum (Zablocki et al, 2016).

Edaphic microbial community assembly was found to be mostly deterministically driven over both short and long spatial scales (e.g., Ramond et al, 2014; Ronca et al, 2015; Gombeer et al, 2015; Johnson et al, 2017; Marasco et al, 2018). Among the deterministic drivers of edaphic community assembly, water regime history (i.e., gravel plain vs riverbed; Frossard et al, 2015), long-term climatic conditions (i.e., fog vs rain; Scola et al, 2018; Unc et al, 2019), plant cover (van der Walt et al, 2016; Unc et al, 2019) or soil origin (i.e., soils vs rhizospheric vs rhizosheath soils / dune vs gravel plain; van der Walt et al, 2016; Marasco et al, 2018) and soil physico-chemistries (Gombeer et al, 2015; Ronca et al, 2015; Scola et al, 2018) have been identified. The salt concentration of the soil was also identified as an important environmental filter of microbial community structures in the fog zone (Scola et al, 2018; Unc et al, 2019). Similarly, 'distance-to-coast' (i.e., a proxy of long term climatic conditions, particular water availability) and water regime history were found to significantly influence the functionality of soil communities, as evaluated by the activities of extracellular enzymes (Scola et al, 2018; Frossard et al, 2015). However, along a 190 km longitudinal gradient in the central Namib Desert gravel plains where four replicate samples were collected at 10 km intervals, stochasticity was also identified as a dominant driver of community assembly (Scola et al, 2018). Similarly, community composition of the rhizosheath-root system of three speargrass species (*Stipagrostis sabulicola*, *Stipagrostis seelyae* and *Cladoraphis spinosa*) was, independent of the plant host, principally driven by neutral assembly processes (Marasco et al, 2018). Furthermore, co-occurrence network analyses of soils and plant-associated soil niches have suggested that biotic interactions also play an important role (Gunnigle et al, 2017; Marasco et al, 2018; León-Sobrino et al, 2019).

A year-long soil study of a site in the Namib Desert gravel plains suggested that edaphic community structures were stable over time in the absence of rainfall but, as expected (Belnap et al, 2005), a single rainfall event (of 38mm) could trigger substantial functional responses in the soil microbiome, with increasing respiration rates, increased chlorophyll a concentrations (a proxy for photosynthetic capacity) and fluorescein diacetate degradation (proxy for soil microbial activity) (Armstrong et al, 2016). In parallel, bacterial communities were also significantly altered by the rain event but, after a month, largely recovered their pre-rain structure, demonstrating the structural resilience of edaphic communities to stochastic environmental changes. Moisture addition also activated fungal-dependent litter decomposition (Jacobson and Jacobson, 1998; Jacobson et al, 2015), and it was noted that the intensity of a water event rather than the frequency of water events was the principal driver of structural changes in edaphic bacterial and fungal communities (Frossard et al, 2015).

The multi-omics *in situ* studies of dry Namib gravel plain soils (Gunnigle et al, 2014, 2017; Leon-Sobrino et al, 2019) challenged the paradigm that desert soil microbial communities are only active when stimulated by moisture addition (Belnap et al, 2005; Shade et al, 2013). 16S rRNA gene cDNA metabarcoding demonstrated that a highly diverse bacterial community displayed short-term diel dynamicity (Gunnigle et al, 2017), while a recent shotgun metatranscriptomic study (León-Sobrino et al, 2019) also showed that microbial communities were fully capable of C, N and P nutrient cycling in desiccated soils. Most notably, under dry conditions photoautotrophic carbon fixation was relatively limited (as indicated by the low number of RUBISCO transcripts), while chemoautotrophic C fixation pathways apparently dominated (Leon-Sobrino et al, 2019). Furthermore, transcripts for key dinitrogen fixation genes (*nifH*) were detected in very low numbers, while genes for nitrate and nitrite reduction enzymes (*nar* and *nir* genes, respectively) were abundantly expressed, strongly suggesting that nitrate is the primary source of metabolic nitrogen in desiccated Namib Desert gravel plain soils (León-Sobrino et al, 2019).

### Microalgae (Diatoms)

Very little is known of the existence of microalgae, of which diatoms are probably the most abundant taxa, in the Namib Desert. A microscopic survey of diatoms, conducted by Rumrich et al (1989), showed that hypolithic communities in various regions of Namibia (including the coastal areas around Henties Bay, Luderitz, Diaz-Point, the Erongo Mountains in the central-west part of the country, and Grunau in the south-west) contained high abundances of diatoms and a range of different diatom taxa. It was speculated that diatoms would benefit from the presence of cyanobacteria and other organisms that significantly improve the water retention capacity of the hypolithon (Rumrich et al, 1989; Adessi et al, 2018). Interestingly, diatom assemblages found in the vicinity of the coast were dominated by freshwater taxa rather than aerophilic or typically soil-associated species, whereas terrestrial (aerophilic) diatoms prevailed in hypolithic samples collected farther from the coast (Rumrich et al, 1992).

Notably, many freshwater diatom forms were found in samples collected from Namibian plants and lichens (*Arthraerua leubnitziae, Zygophyllum stapffii, Z. simplex, Xanthoparmelia walteri,* and *Teloschistes capensis*) growing within the 2 km-wide coastal zone (Rumrich et al, 1991). The authors concluded that freshwater diatoms can survive in these almost rainless areas due to the frequent fog event that regularly deposit water on the surfaces of plants and rocks. The apparent lack of host or even substratum specificity observed in the communities analysed further suggests that the presence (or absence) of moisture is the primary factor affecting the development of local diatom colonies (Rumrich et al, 1991). Contrary to the previous assumptions (Rumrich et al, 1989), sea spray and salt water did not seem to affect hypolith diatom community compositions and only a few (most likely non-viable) marine forms were found in the studied material (Rumrich et al, 1991). This also indicates that despite the strong prevailing westerly winds, marine diatom remnants (i.e., empty siliceous frustules) did not constitute a significant source of contamination. Altogether 147 diatom taxa were found in hypolithon and soil samples during the survey conducted by Rumrich et al (1992), and the average number of taxa per sample decreased inland.

A variety of Namib Desert sites within a 50 km radius of the Gobabeb-Namib Research Institute (S 23.5523$^{o}$ E 15.0410$^{o}$) and substrates (including cyanobacterial mats, salt crystals, rocks and soil) were sampled for diatom diversity analysis during a 2017 field expedition (R Majewska, unpublished results). All samples contained diatoms, with *Achnanthidium exiguum* dominating in almost all terrestrial habitats and *Nitzschia* sp. prevailing in the salt pans (Figure 3). As previously observed (Rumrich et al, 1989), the majority of the taxa found in the Namib Desert samples are known from various European habitats and locations. This could suggest that desert diatom communities are dominated by eurytopic and highly resistant cosmopolitan species. However, recent studies indicate that an exceptionally high level of cryptic (or pseudo-cryptic) diversity may exist in common diatoms such as *Pinnularia borealis* (Pinseel et al, 2019), and more extensive studies are required to reliably assess the true diversity of desert-inhabiting diatoms, the range of their phenotypic plasticity, ecological preferences and phylogenetic relationships.

## Fairy Circles

The Namib Desert, together with some regions of the Australian outback (Getzin et al, 2016), is home to the mysterious "Fairy Circle" phenomenon. Fairy Circles are circular, barren patches of soil within an otherwise grass-covered matrix, occurring both on the Namib gravel plains and vegetated dune sands (Figure 2.6), and with a limited range distribution around the 50/150mm isohyet (Van Rooyen et al, 2004). Multiple hypotheses have been proposed to explain their aetiology (Van Rooyen et al, 2004; Ramond et al, 2014; Tschinkel, 2015; and references therein). However, given the scope of this review, we will limit this discussion to the microbial phytopathogenesis hypothesis (Ramond et al, 2014).

This hypothesis was originally based on culture-dependent studies (Theron, 1979), demonstrating that anaerobic bacteria were enriched in Fairy Circle centres when compared to the margins, and that fungi displayed the opposite trend. The first study to use a molecular-based approach to study Namib Desert Fairy Circles, comparing the fungal and bacterial community fingerprints of the gravel plain Fairy Circle centres, margins and grass matrix (Ramond et al, 2014), showed that the barren soil communities were significantly different and more variable (i.e., less stable) than those from the external grass matrix.

More recently, amplicon sequencing was used to compare the prokaryotic and fungal communities of Namib Desert dune and gravel plain Fairy Circles (van der Walt et al, 2016). The study concluded that niche partitioning was a significant driving factor in the Fairy Circle soil community composition, and identified 1 archaeal, 9 bacterial and 57 fungal Fairy Circle-specific OTUs; i.e., OTUs exclusively present in Fairy Circle soils and common to both the gravel plain and dune sites (which are ~100 km apart). Among these, 10 phylotypes belonged to well-known phytopathogenic clades: *Periconia* sp., *Curvularia* sp., and *Aspergillus* sp, the fungal order Pleosporales, the fungal family Chaetomiaceae and the bacterial class γ-Proteobacteria. These phylotypes therefore constitute potential candidates in a phytopathogenic Fairy Circle aetiology. We note that their identification in Australian Fairy Circle soils would help to confirm the microbial phytopathogenesis hypothesis. The fundamentally important issue of whether these observations are '*cause*' or '*effect*' has, however, not been resolved, and will require completion of the Koch's Postulate cycle.

**Cryptic niche habitats**

Microorganisms in deserts often colonize and thrive in specialized, often cryptic, refuge niches, as a physical adaptation to the extreme conditions of the desert habitat (Pointing and Belnap, 2012). These refuge niches include the ventral surface of translucent rocks (hypoliths; Pointing, 2016) and the pores (cryptoendoliths) or cracks (chasmoliths) of weathered rocks. For these cyanobacterial-dominated communities to develop, the rock substrate must permit the transmission of sufficient PAR (photosynthetically active radiation) to support photoautotrophy. Suitable substrates include quartz, marble, agate and prehnite for hypoliths (Pointing, 2016), granite, limestone, marble, gneiss, gypsum, halite, evaporite, sandstone rocks for cryptoendoliths and granite, gypsum, anorthrosite, sandstone, marble and siliceous rocks for chasmoliths (Makhalanyane et al, 2015). Among these, only hypolithic communities in the central Namib Desert have been studied in any detail. There is, therefore, considerable scope for further studies focusing on Namib Desert lithic communities.

All typical prokaryotic and lower eukaryote taxonomic groups (Bacteria, Fungi, Archaea, Viruses, Protista and Metazoans) have been detected in Namib Desert hypolithic communities (e.g., Adriaenssens et al, 2015; Valverde et al, 2015; Vikram et al, 2016). Recruited from the surrounding soils (Makhalanyane et al, 2013), these communities are cyanobacteria-dominated, particularly by organisms belonging to the genus *Chroococcidiopsis* (Order Chroococcidiopsidales) and the Oscillatoriales and Stigonematales orders (Valverde et al, 2015). A cDNA-based study suggested that members of the cyanobacterial orders Pseudanabaenales, Synechococcales, Oscillatoriales, Chroococcales and Nostocales dominated the active hypolithic community. Heterotrophic taxa were dominated by α-, β- and γ-Proteobacteria, Actinobacteria, Acidobacteria, Bacteroidetes and *Deinococcus-Thermus* (Valverde et al, 2015). Other bacterial phyla, each representing less than 2% of the total community, included Verrumicrobia, TM7, Planctomycetes, OD1, Nitrospira, Gemmatimonadetes, Firmicutes, δ-Proteobacteria, Chloroflexi and Armatimonadetes (Valverde et al, 2015). Sequences from the Thaumarchaeota, Euryarchaeota and Crenarchaeota archeal phyla were also detected in a shotgun metagenome (Vikram et al, 2015), with only the former two found to be active (Van Goethem et al, 2017). Fungal phylotypic signatures have been found to represent only a low proportion (5.6%) of reads in a Namib Desert shotgun metagenome (Vikram et al, 2016), and a detailed analysis of the fungal diversity in Namib Desert soils remains to be undertaken.

Viruses from the *Caudovirales* order and the *Microviridae* family were highly abundant in hypolithic biomass, while only a few cyanophage sequences could be detected, most probably due to current limitations of sequence databases, where the cyanobacterial sequence datasets are dominated by organisms of marine origin (Adriaenssens et al, 2015; Vikram et al, 2016).

Stable isotope analyses suggest that hypoliths are positioned at the base of the Namib Desert primary production web, particularly by being N-fixing hubs (Ramond et al, 2018). However, it must be noted that only five different cyanobacterial and α-proteobacterial *nifH* gene variants, encoding N-fixing nitrogenases, were detected in a hypolith shotgun metagenome (Vikram et al, 2015), despite putative N-fixing microorganisms (e.g., *Chroococcidiopsis* sp.) being commonly detected in amplicon based studies (Makhalanyane et al, 2015). Analysis of gene presence/absence in Namib Desert hypolithons also suggests that these communities do not have the capacity to perform the complete N cycle, and particularly lack anaerobic ammonium oxidation (Anammox) genes (Vikram et al, 2016). The presence of a full complement of key cyanobacterial and proteobacterial photosynthetic genes suggests that hypolithic communities have the capacity for photoautotrophic C fixation, and P and S chemolithotrophic metabolism (Vikram et al, 2016).

In a study of a longitudinal transect, from the fog-dominated coast to the rain-dominated eastern boundaries of the Namib Desert, it was observed that 98% of the quartz rocks over 5 cm in size were colonized (Warren-Rhodes et al, 2013). This suggested that water regime (fog *vs* rain) does not play a role in the *maintenance* of hypolithic communities. However, water regime is a significant driver of both hypolithic community assembly (that is, the taxonomic composition of the communities), and biotic interactions within the communities (Stomeo et al, 2013; Valverde et al, 2015; Van Geothem et al, 2017). Furthermore, cyanobacteria, and particularly an OTU from the GpI genus, were found to be major drivers of Namib Desert hypolithic food-web structures (Valverde et al, 2015).

**Saline Systems**

Numerous brackish springs are found on the gravel plains within 100 km of the coast which arise from a fracture zone lying roughly parallel to the coast (Day and Seely, 1988). The central Namib Desert north of the Kuiseb River has a drainage network of ephemeral channels that cross this ancient, highly eroded plain. A 1% east-west gradient maintains a persistent groundwater flow, which emerges in localised depressions as perennial springs and salt pans or playas. The springs emerge where northeast-southwest aligned Precambrian intrusions, e.g. dolerite dykes, form dams permitting the ponding of shallow groundwater (Eckardt and Drake, 2011; Eckardt et al, 2013). Typically, these form playas within poorly developed drainage systems or endorheic basins surrounded by hydromorphic gypsum ($CaSO_4 \cdot 2H_2O$), “puffy” soils, often less than 1 m deep (Day and Seely, 1988; Day, 1993; Eckardt and Drake, 2011). The springs are essentially freshwater or only slightly mineralised and exhibit moderate flow along short braided channels. However, in this hot, arid environment the water is subject to strong evaporative concentration and rapidly becomes hypersaline (Lancaster et al, 1984; Day and Seely, 1988). The waters are enriched in Na+ and Cl- due to the preferential precipitation of CaSO4.2H2O, any carbonates are similarly removed from solution, so that springs and seepages are typically surrounded by thick crusts of gypsum and halite (NaCl) (Day and Seely, 1988; Day, 1993). Other evaporite minerals including sylvite (KCl), humberstonite ($K_3Na_7Mg_2(SO_4)_6(NO_3)_2 \cdot 6H_2O$) (Eckardt et al, 2013) and perchlorate ($ClO_{4-}$) (Rao et al, 2010) have been recorded.

Some of the desert springs have been well documented (Day and Seely, 1988; Brain and Koste, 1993; Day, 1993; Eckardt and Drake, 2011) most notably at Hosabes, situated in the sporadically functional Sout River about 7 km NNE of Gobabeb Research and Training Centre. However, these saline systems have received only limited attention in terms of their microbial ecology even though microbial life is evident to the casual observer. Green unicellular cyanobacteria can be seen on the underside of gypsum crusts and spring channels have benthic microbial mats having a spongy consistency, orange-brown coloured on the surface and green underside (Day and Seely, 1988; Jones, personal observations). Only three relevant studies have been published to date: (1) a microbial community (bacteria, archaea and fungi) fingerprinting (T-RFLP) study which compared Hosabes stream bed soils with those of the surrounding salt crusts (Johnson et al, 2017), (2) the metaviromes of the Eisfeld and Hosabes salt pan microbial mats (Adriaenssens et al, 2016), and (3) a study of archaeal, bacterial and cyanobacterial diversity using DGGE, T-RLFP and 16S rRNA clone library sequencing (Cloete, 2015).

T-RFLP analyses suggested that fungal α-diversity was higher than those of Archaea or Bacteria, and that among prokaryotes, the archaeal community was the richest. [Halo]Archaea are common in extremely saline environments (Ventosa et al, 2011) which may explain this higher diversity in the salt pan environment compared to Bacteria. Prokaryotic diversity was essentially shaped by ion concentrations and carbon content and non-stochastic processes influence community assembly in common with other niche environments in the Namib Desert (Johnson et al, 2017). Independently of the Domain examined, communities from the salt stream were significantly different from those of the salt crusts, probably due to higher ion concentrations in the latter (Johnson et al, 2017).

A metavirome study (Adriaenssens et al, 2016) illustrated the uniqueness of the Namib Desert salt pans. Despite deep sequencing efforts and extensive database enquiry, >92% of the reads and >79% of the contigs could not be assigned, suggesting largely unknown, possibly novel, viral communities. Network analysis provided some general taxonomic assignments. Despite being over 120 km apart the two salt pans, Hosabes and Eisfeld playas, had highly similar viral community structures with about

55% sequence similarity. The metaviromes from both playas were particularly abundant in ssDNA virus sequences of the *Gokushovirinae* subfamily (Family *Microviridae*). ssDNA *Circoviridae* sequences were prominent at Eisfeld while at Hosabes *Inoviridae*, *Microviridae* and *Geminiviridae* sequences formed the majority. The detection of viral contigs with a resemblance to haloarchaeal viruses known to infect *Haloarcula* (genus *Salterprovirus*) at Hosabes is in keeping with the known [halo]Archaea abundance at this site (Johnson et al, 2017). Finally, the identification of multiple phage integrase genes at both sites suggests that lysogeny is an important mode of infection in these saline systems.

The earliest study (Cloete, 2015) attempted to characterise the microbial diversity of soil, water and microbial mat material collected at Hosabes and Eisfeld playas using culture-independent methods. Despite extensive investigation, the full extent of diversity could not be established but communities of saline environment specialists were identified. A previous culture-based study of cyanobacteria (J-B. Ramond, unpublished) indicated the presence of *Leptolyngbya*, *Pseudoanabaena*, *Chroococcus* and *Halothece* species in the Namib Desert saline springs. Interestingly, the majority of 16S rRNA gene sequences recovered in the earliest study (Cloete, 2015) were related to uncultured microorganisms. The most common phylotypes identified were Proteobacteria and Bacteriodetes, with Firmicutes, Planctomycetes and Verrucomicrobia as minor components of the community. Some of the genera retrieved included known (marine) halophiles, such as *Haloanaerobium*, *Halocella*, *Salinibacter*, *Caulobacter*, *Sphingomonas* and *Idiomarina*, indicating a specialised halophile community within the Namib Desert saline environments. Independent culture-based studies using Hosabes spring water-based media confirmed the presence of *Idiomarina* sp., related to *I. zobellii* and *I. loiheinsis*, as confirmed by 16S rRNA gene sequencing of individual isolates (B.E. Jones, unpublished).

## Conclusions and Perspectives

The near-unique climatic regime of the Namib (i.e., a longitudinal water regime transition from coastal fog to inland rain; Eckardt et al, 2013) has been central to much of the local research effort, which has focused on the role of water regimes in organismal speciation and adaptation (Seely, 1990; Henschel and Lancaster, 2013). The Namib Desert has also proved to be a highly appropriate environment for studies of the distribution, adaptation and functioning of microbial communities. This ’research opportunity’ is enhanced by the fact that the Namib Desert offers a multitude of landscapes, geologies, lithologies and different microbial niches (Seely and Pallet, 2008).

The major focus of Namib Desert microbial ecology research has been on the bacterial, fungal and, to a lesser extent, archaeal communities (e.g., Johnson et al, 2017). Very little attention has been paid, to date, to the viruses (e.g., Adriaenssens et al, 2016) and even less to the microeukaryotes (e.g., André et al, 1997), both of which are likely to play critically important roles in the functioning (and maybe control) of desert soil microbial communities.

Culture-independent 'omics' technologies have contributed hugely to our understanding of the basic diversity of Bacteria, Archaea and fungi in Namib Desert soils. Meta-genomics, with molecular fingerprinting (e.g., Gombeer et al, 2015), barcoding (e.g., van der Walt et al, 2016) and shotgun (e.g., Vikram et al, 2016) sequencing [which also encompass metaviromics studies; e.g., Adriaenssens et al, 2016] studies, have now been applied extensively, while meta-proteomics (Gunnigle et al, 2014) and meta-transcriptomics (Gunnigle et al, 2017; León-Sobrino, 2019) approaches have, as yet, been used only to a limited extent. Metabolomics, a technique which has considerable potential for studies of adaptation (e.g., solute accumulation responses) and community carbon flow, has yet to be applied to Namib Desert microbial ecology.

Notwithstanding recent efforts to describe the viral diversity of the microbial communities in the Namib Desert (Adriaenssens et al, 2015, 2016; Zablocki et al, 2017; Scola et al, 2018), virtually nothing is known about the virus-host relationships, life cycles and viral population dynamics, or of the functional role of the viruses in this edaphic ecosystem. It has been proposed (Zablocki et al, 2015) that the discrete nature of desert soil microbial communities (i.e., in the absence of a liquid continuum, a discrete 'microbial community' may be considered the biofilm surrounding a single sand grain or soil particle) reduces the effective role of viruses and phage in controlling microbial population dynamics, as is well known from marine and aquatic systems (e.g., Bratbak et al, 1994; Rohwer and Thurber, 2009). This is a testable hypothesis, but requires a coordinated quantitative analysis of both the prokaryotic metagenome and the metavirome in the same samples under conditions which would stimulate host growth and viral response processes.

There is a particular opportunity, largely unencumbered by previous research, to investigate all aspects of the microinvertebrates (and other soil inhabiting species) of the Namib Desert. Apart from the cataloguing of different species (e.g., Marsh, 1987 (microarthropoda); Brain & Koste, 1993 (rotifers); André et al, 1997 (microarthropoda); Foissner et al, 2002 (cileates); Conti et al, 2019 (spiders)), virtually nothing is known of the diversity, biomass levels, and functional and wider roles of important soil organisms, particularly protists such as nematodes and Amoeba. Interestingly, a recent CO1 bar-coding survey of Namib Desert springtails (*Collembola*), the known diversity of which was limited to four genospecies (Collins et al, 2019 and references therein), identified up to 30 putative species, most of which were limited to a single sampling site (Collins et al, 2019). The scope for further studies on the biogeography of similar taxa is enormous!

Finally, little is yet known, in quantitative terms, of the role of Namib Desert soil microbial communities in ecosystem servicing. However, given that desert soil microbial communities are thought to be responsible for nutrient cycling for much of any annual cycle (in the absence of higher plants), and given that rising global temperatures, linked to Global Climate Change, are predicted by current climate models to increase the scale of drylands (IPCC 2014), we suggest that it is critical to understand the current contribution of microbial communities to nutrient cycling processes. We suggest that further efforts to determine microbial process rates in desert soils, and to integrate these rates on a landscape scale, would be a valuable baseline for further understanding the implications of climate change. Such experiments could be performed *in situ*, or *ex situ* (microcosm approach) with an appropriate range of analytical analyses, over extended timescales (seasonal to annual). For example, continual monitoring of carbon flux (fixation, respiration rates, coupled with in situ TOC analyses) would ultimately lead to a regional quantitative estimation of C cycling processes, and could more accurately revise the capacity of desert soil to sequester carbon (Cleverly et al, 2016).

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**Figure Legends**

Figure 1. Map of Namibia, showing the Namib Desert and Namib Sand-sea regions. Adapted from Li et al, 2016 and Kaseke et al, 2017.

Figure 2. Representative images of the dominant terrestrial and niche habitats in the Namib Desert region

Figure 3. Light (LM) and scanning electron micrographs (SEM) of diatoms from the Namib Desert. **3.1.** *Proschkinia hartii* (Cholnoky) Clavero & Hernández-Mariné (SEM). **3.2.** *Reimeria sinuata* (W.Gregory) Kociolek & Stoermer (SEM). **3.3.** *Proschkinia bulnheimii* (Grunow) Karayeva (SEM). **3.4.** *Achnanthidium exiguum* (Grunow) Czarnecki (SEM). **3.5.** *Brachysira aponina* Kützing (SEM). **3.6.** *Nitzschia* sp., two cells (LM). **3.7.** *Cyclotella meneghiniana* Kützing. **3.8.** Diatoms (*Nitzschia* spp. and *Halamphora* spp.) associated with cyanobacterial mats from the salt pans (LM). **3.9.** *Dorofeyukea kotschyi* (Grunow) Kulikovskiy, Kociolek, Tusset & T.Ludwig (SEM).

Scale bars: **3.8** – 20 µm; **3.1**, **3.3**, **3.5**, **3.6**, **3.9** – 10 µm; **3.2**, **3.4**, **3.7** – 5 µm

Figure 1. Map of Namibia, showing the Namib Desert and Namib Sand-sea regions. Adapted from Li et al, 2016 and Kaseke et al, 2017.

**Figure 2. Representative images of the different edaphic and niche habitats of the Namib Desert**


2.1 The hyper-arid gravel desert ‘open soil’ environments


2.2 The coastal ‘fog-impacted’ lichen fields

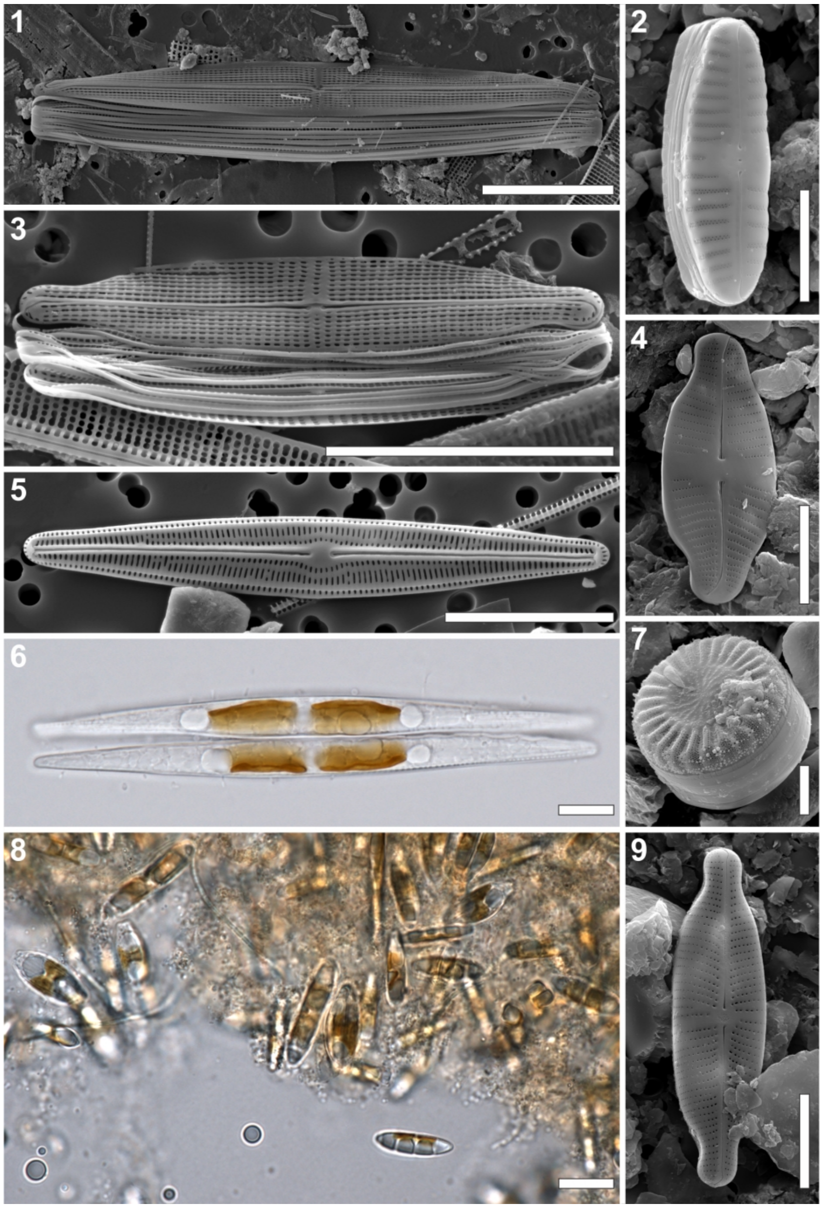

2.3 The ‘sand-sea’ dunes (dune, dune flank and inter-dune zones)

2.4 Saline springs and playas

2.5 Niche habitats: quartz hypolithic habitats

2.6 Fairy Circles (dune sand and gravel plain)

2.7 *Welwitchia mirabilis*



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