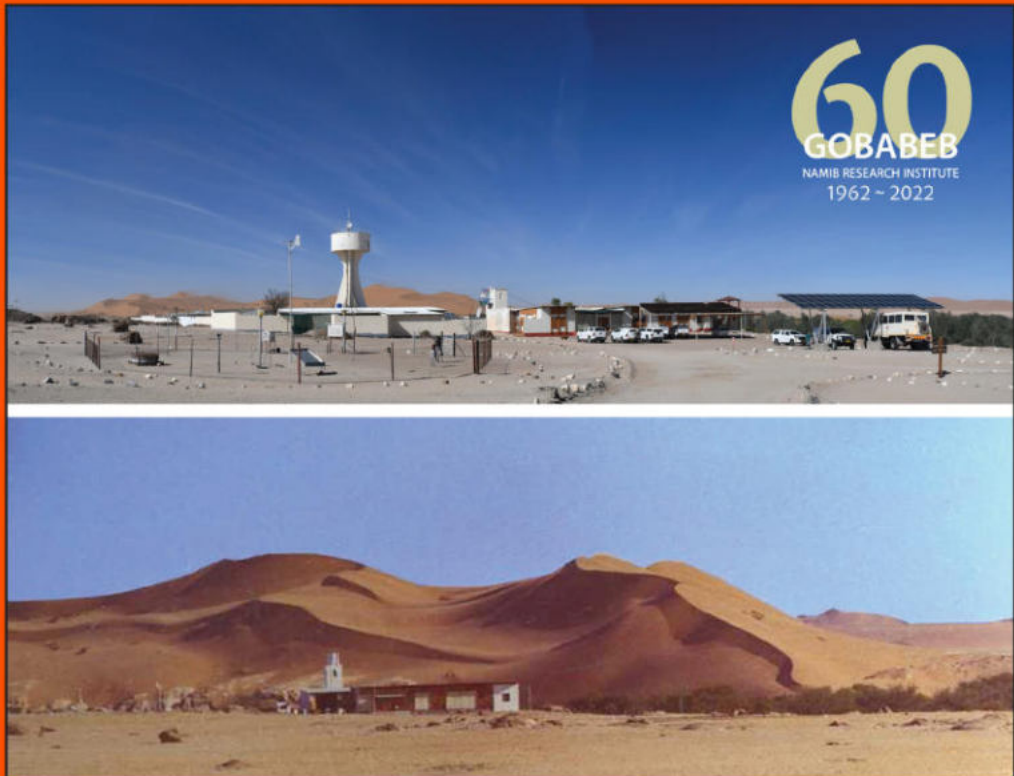


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A Decade of Microbiome Research in the Namib Desert

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Key words: Namib Desert, Soil; Microbiomics, Microbial ecology, Aridity.

Introduction

The Namib Desert, one of the oldest drylands on Earth with an estimated age of 43 million years, lies along the entire coast of Namibia, from the Kunene River and the Angolan border in the north (S 17.27°) to the Orange River and the South African border in the south (S 28.64°). This coastal desert is a land of two halves. Much of the northern sector, from the Kuiseb River (S 23.11°) to the Angolan border, is a flat calcrete gravel desert (Eckardt et al. 2013). The southern sector, from the Kuiseb River to the South African border, is largely sand dunes (the Namib ‘Sand-Sea’, a UNESCO World Heritage Site).

The climate of the Namib Desert, in terms of water relations, is distinctive (Eckardt et al. 2013). The Atlantic coastal regions, which are strongly influenced by the coastal upwelling of the cold southern Atlantic Benguela current, receive minimal rainfall, but are regularly inundated with fog which rolls in from the sea overnight and can penetrate inland for up to 60 km. Many of the coastal species, both plants and animals, are specially adapted to capture fog water. The interior hyper-arid regions of the Namib Desert receive no fog and little rain, while the eastern zone receives ‘regular’ seasonal rainfall. Although a strong driver of plant and insect species diversity, the effect of water-input zonation on the microbiology of the desert soils remained largely unknown until teams of researchers led by Prof. Don Cowan, initially from the University of the Western Cape (2009 to 2012) and subsequently from the University of Pretoria (2013 to 2022), undertook annual research expeditions to the Gobabeb Research Station (now, Gobabeb-Namib Research Institute; <https://gobabeb.org/>) to unravel the microbial ecology of the Namib Desert.

Despite the Namib Desert having been an intense focus of research for nearly 70 years (Seely & Pallett 2012; Henschel & Lancaster 2013), prior to 2010 very little was known of



Plate 1: The quartz-rich gravel plains of the hyper-arid central Namib Desert



*Plate 2: Dunes of the Namib Sand-Sea. The vegetated hummocks in the inter-dune valleys are clumps of speargrass (*Stipagrostis sabulicola*).*

any aspect of the region's microbiology. The Namib Desert lichens have received the most attention (Wessels & Van Vuuren 1986; Wessels 1989; Schieferstein & Loris 1992; Büdel et al. 2011; Hinchcliffe et al. 2017). There have been a few early studies of fungal diversity and physiology (Jacobson et al. 1993; Jacobson 1997; Jacobson & Jacobson 1998; Stutz et al. 2000). These, and a single study of soil viral diversity (Prestel et al. 2008), represent the totality of 'microbial knowledge' of the region.

In 2010, we initiated an intensive (and extensive) program to fill out this sparse knowledge. We began using modern molecular phylogenetic methods. Initially based on 16S rRNA gene (prokaryote diversity) and ITS (lower eukaryote diversity) molecular fingerprinting and amplicon sequencing, our work subsequently expanded to include deep shotgun metagenome sequence analysis (yielding both phylogenetic and functional diversity data), total DNA-metavirome sequencing and metatranscriptome sequencing (sequencing of cDNA libraries from extracted and purified total mRNA, yielding high volumes of data on gene expression). One of the many factors that helped to drive this research program was the knowledge that, in desert ecosystems where the higher plants are sparsely distributed and/or very transitory, the soil microbial populations are disproportionately important in supporting essential ecosystem services such as carbon and nitrogen cycling.



Plate 3: The 2019 multi-national research team at Gobabeb. The authors are first on left, front row (DAC), hidden in the middle, middle row (J-BR).

Microbiology of Gravel Soils and Sand Dunes

Diversity

Over the past 12 years, we have performed a large number of phylogenetic surveys aimed at clarifying the microbial diversity of Namib Desert surface soils, in the context of spatial scales, geology and geomorphology, soil chemistry and soil-water relations. Much of this work is detailed in recent reviews and chapters (Cowan et al. 2015; Makhalanyaane et al. 2015; Lebre et al. 2017; Ramond et al. 2019; Lebre et al. 2021; Cowan et al. 2020).

The dominant bacterial taxa of the Namib are those found in soils around the world: Actinomycetota, Pseudomonadota, Bacteroidota, Acidobacteriota and Cyanobacteria. Members of the phyla Chloroflexota, Deinococcota and Bacillota are more minor but significant contributors to the total bacterial diversity (Ronca et al. 2015; Armstrong et al. 2016; van der Walt et al. 2016; Gunnigle et al. 2017; Marasco et al. 2018; Leon-Sobrinho et al. 2019). The presence of cosmopolitan phyla contrasts with analyses performed at higher taxonomic resolution (family, genus), which show large numbers of novel phylogenotypes, some of which cannot be assigned phylogenetically.

Edaphic fungal communities in the Namib desert are typically dominated by Ascomycota. The class Dothideomycetes was 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; Vikram et al., manuscript submitted).

Of the archaea, members of Euryarchaeota, Thermoproteota and Nitrososphaerota phyla composed a large majority of all archaeal sequences identified, ranging from 2% to 25% of the total prokaryotic communities. This makes the Namib Desert soils among the most archaea-rich of all desert soils worldwide (van der Walt et al. 2016). Members of the dominant archaeal taxon (Nitrososphaerota) are involved in nitrogen turnover, particularly ammonia oxidation.

Edaphic metaviromes were strongly dominated by sequences belonging to the most common soil dsDNA phage order, the Caudovirales, and representing the families *Siphoviridia*, *Myoviridae* and *Podoviridae* (Adriaenssens et al. 2015; Zablocki et al. 2016, 2017; Scola et al. 2018). This distribution is typical of soils worldwide.

Drivers of diversity and community assembly

The deterministic drivers of edaphic community assembly include historical water regime history (i.e., gravel plain vs riverbed and/or fog vs rain; Frossard et al. 2015; Scola et al. 2018; Naidoo et al. 2021), the presence and the influence of plant (Marasco et al. 2018) or soil origin (i.e., dune vs gravel plain vs riverbed; Gombeer et al. 2015) and soil physico-chemistries (e.g., Johnson et al. 2017; Scola et al. 2018). It is worth noting that Namib archaeal, bacterial and fungal communities were influenced by different physico-chemical

variables (Johnson et al. 2017). In the fog zone, for example, salt concentration of the soil had a significant influence on edaphic communities (Stomeo et al. 2013; Scola et al. 2018).

Stochasticity¹ was also identified as an important driver of community assembly (Scola et al. 2018). Co-occurrence network analyses of soils and plant-associated soil niches suggest that biotic interactions (i.e. between different microbial taxa) also play an important role (Gunnigle et al. 2017; Marasco et al. 2018).

Functionality

While phylogenetic marker surveys provide comprehensive data on the presence and diversity of microorganisms, they yield no information on either the activity or functional capacity of the community. A range of methods, such as *in situ* enzyme assays, soil respirometry, metatranscriptomics (for functionality) or metagenomics (for a measure of the functional potential of a community) are used to assess community functions or functional potential.

Our studies of Namib gravel plain soils challenge the paradigm that desert soil microbial communities are completely dormant during long periods of drought. For example, 16S rRNA gene cDNA metabarcoding demonstrated that the dynamics of soil bacterial communities vary throughout the day. The Ascomycota were the most active fungal taxa, particularly during the cooler night hours (Gunnigle et al., 2107). A recent metatranscriptomic study also showed active nutrient cycling (C, N and P) in desiccated Namib soils (Leon-Sobrinho et al. 2019). Under dry conditions, photoautotrophic carbon fixation was very limited, while chemoheterotrophic carbon acquisition pathways dominated. 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, suggesting that nitrate was the primary source of metabolic nitrogen in desiccated gravel plain soils (Leon-Sobrinho et al. 2019).

A new paradigm for desert soil microbial energetics has emerged in the past 5 years. Following the discovery that carbon and energy acquisition in Antarctic soils was driven by Trace Gas Chemotrophy; i.e., assimilation and oxidation of atmospheric H₂ and CO driving high affinity CO₂ fixation (Ji et al. 2017), we demonstrated that Namib Desert soils also have this capability, as do other hot desert soils (Leung et al. 2020; Jordaan et al. 2020). Given that aerobic H₂ oxidation is hydro-genic (water-generating), this process may provide a hitherto unsuspected source of metabolic water for desert soil microbiomes (Bosch et al. 2021).

¹ Stochasticity: randomness, not affected by measurable factors such as rainfall, soil pH etc.

Cryptic Microbial Community Niches

Most microbial life is microscopic and invisible to the naked eye. In particular favoured niches, however, microbial consortia can form visible macroscopic structures. In the moister areas of the Namib, for example, biological soil crusts (BSCs) form on the soil surface. BSCs are complex assemblages of lichens, green algae and cyanobacteria (green photosynthetic filamentous bacteria). In the more arid areas of the Namib, conditions are too extreme for BSCs to survive. Life moves to the under-surfaces of quartz rocks and pebbles, forming microbial communities known as *hypolithons* (hypo-‘under’, lith-‘rock’). These microbial communities are abundant across the geologically complex Namib Desert, but are generally invisible from the surface. Hypolithons are visible as black/green crusts adhering to the under-surfaces of rocks and at the rock-soil interface. Hypolithic communities are dominated by photosynthetic bacteria (mostly cyanobacteria), but include many other species of bacteria, fungi, viruses and phage, and even invertebrate ‘grazers’ such as springtails.

The hypoliths are the ‘tropical rain-forests’ of the Namib Desert. The hypolithic niche is a less extreme environment than the exposed soil surface. The overlying quartz is translucent, allowing light to penetrate and support cyanobacterial photosynthesis. This, in turn, supports all the other species in the community. The overlying rock also protects the hypolithon community from the extreme midday temperatures (the surface soil in the Namib can reach over 60°C), and from the desiccating effects of the very low humidity atmosphere (Bosch et al. 2022). The quartz rock also filters out potentially damaging short-wavelength solar radiation (Gwidzala et al. 2021).

Hypolithic communities are complex structural systems. Their composition is influenced by local aridity (Stomeo et al. 2013) and by selective recruitment of microbial taxa from the edaphic community (Makhalanyane et al. 2012). These communities are intimately associated with the surfaces of the quartz rock, penetrate into cracks and interstices (endolithy), are embedded in matrices of EPS (Extracellular Polysaccharide Substances) and are often lichenised, forming structured associations of filamentous fungi with cyanobacteria or green algae (de los Rios et al. 2021).

Hypolithons are thought to represent both biodiversity- and functional-hotspots in desert pavements (Vikram et al. 2016; Le et al. 2016; Ramond et al. 2022). Stable isotope analyses (Ramond et al. 2018) show that hypolithons were the major drivers of nitrogen fixation in Namib Desert soils, and that hypolithic cyanobacteria support entire sub-lithic food-webs (Valverde et al. 2015). Furthermore, hypolithic communities exhibited strongly mutualistic properties, with taxa belonging to the Cyanobacteria and α -Proteobacteria that have been identified as keystone species (Van Goethem et al. 2017).

We have sought to answer two simple questions about Namib hypolithic communities: how fast do hypolithic communities grow, and how does the growing community develop? We used artificial hypolithon arrays consisting of tiles and rocks to answer these questions. Arrays sited in the eastern rainfall zone showed hypolithic cyanobacterial biofilm growth



Plate 4: Uprturned quartz rock, showing the green mat of microbial life on the underside and the soil below the rock

after just two years under the translucent rocks, and adhesion to the rock under-surface after three years. Conversely, a hypolithon array sited in the hyper-arid soils near Gobabeb showed no visual evidence of hypolithon growth even after seven years, although phylogenetic data suggested some enrichment of cyanobacteria in the soil after five years. We conclude that many decades are required for development into mature hypolithic communities, particularly in the more arid regions of the Namib Desert. Local soil aridity plays a significant role.

One of the many intriguing questions about hypolithic communities is whether the filtering of light by the overlying translucent rock has led to special genetic or physiological adaptations in the cyanobacterial phototrophs? For example, do hypolithic photoautotrophs have photosynthetic pigments which preferentially adsorb at the red-end of the PAR spectrum, or do they have photosystems adapted to work efficiently at very low light levels? A recent study using a range of fluorimetric and spectroscopic methods showed that chlorophyll contents were not light-adapted, but that stress-linked adaptations, such as the presence of helical carotenoid proteins, were characteristic of these communities (Gwidzala et al. 2021).

Other cryptic niches colonised by desert microbial communities include the pores (cryptoendolithic) or the cracks/fissures (chasmoendolithic) of various rocks types (e.g.,



Plate 5: An artificial hypolithon array

sandstone, granite and limestone). Endolith communities in central Namib Desert sandstones were dominated by the cyanobacterial genus *Chroococidiopsis*, but community composition varied along an east-west precipitation gradient and was dependent upon substrate (Qu et al 2020).

Desert Plant-associated Microbiology

All plants have associated microbiomes, on leaf surfaces (epiphytes), inside cells and tissues (endophytes), and associated with root systems (the rhizosphere). The rhizospheric microbiome is thought to play key roles in supporting the plant host, while the microbiome benefits nutritionally from plant root exudates, making the rhizobiome a genuinely mutualistic association. Desert-adapted plants may harbour unique microbial populations, which may contribute to the host plant's resistance to drought.

We have investigated the microbiomes of one of the Namib's iconic inhabitants, the welwitschia (*Welwitschia mirabilis*, the only species within the Welwitschiaceae order). These slow-growing plants are endemic to the Namib Desert, and are ancient relatives of

the pine-tree. They are dotted across barren and rocky landscapes, surviving extremes of heat and desiccation with apparent ease.

We found that very few microbial taxa were shared between the *Welwitschia* rhizosphere and the surrounding bulk soil (Valverde et al. 2016). The welwitschia root system therefore possesses its own unique microbial community, which almost certainly contributes to the survival of this unique plant. In contrast, foliar fungal distributions were cosmopolitan, with little evidence of adaptation to their host species (Kemmler et al. 2021).

Many desert plants have unusual modifications to their roots systems, such as cylindrical sheaths of mineral sand particles around the major roots (termed rhizosheaths). The rhizosheath is held in place by root hairs and cemented by extracellular polysaccharide ‘glue’ secreted by bacteria. *Stipagrostis* (the dominant grass of the gravel plains) rhizosheath microbiomes were about 1000-fold enriched compared with the surrounding sand, and were more organized: sand microbial community compositions were driven more by sand properties, and less by the plant species (Marasco et al. 2018).



Plate 6: Mature *Welwitschia* plants: male (front) and female (behind)



Plate 7: *Stipagrostis* (speargrass) rhizosheaths

Microbiology of Fairy Circles

For centuries, the enigmatic *fairy circles* of the Namib Desert have been the cause of wonder and argument. The indigenous peoples of the Namib thought that they were the work of dragons. In more recent times, theories of their origins have included the actions of UFOs, dancing fairies, radioactive hot-spots, natural gas seepages, poisonous residues of dead *Euphorbia* plants, the presence of colonies of sand termites or pathogenic fungi, or the result of natural plant self-organization processes. Scientific papers claiming to have discovered the true origins of fairy circles appear quite regularly, but with no real resolution of their origins. They remain a tantalizing enigma.

We have pursued the hypothesis that fairy circles are the result of microbial phytopathogenic processes. It has long been known that the abundance of culturable microorganisms differs within and at the edges of fairy circles (Theron 1979). Our own studies have focussed on the microbiology of the fairy circles that can be found in the gravel plains near the Gobabeb-Namib Research Institute. We demonstrated, using molecular fingerprinting, that soils from the centres and margins of the fairy circle had different bacterial and fungal communities compared to the “vegetated” surrounding soils (Ramond et al. 2014).



Plate 8: Fairy Circles scattered across the sands of the eastern Namib Desert

Fairy circles are found in both the gravel plains and on the margins of sand-dunes. If fairy circles are formed by microorganisms that prevent plant growth inside the circles, these microorganisms should be found in both habitats, irrespective of the geographical distance between them (~200 km, in this study). Even though the microbial communities from fairy circles in sand-dunes differed significantly from fairy circles in the gravel plains, we identified one archaeal, nine bacterial, and 57 fungal phylotypes that were consistently detected in all fairy circle soils throughout the Namib. These microbial taxa constitute putative candidates as the causative agents behind these enigmatic landscape features. We note that some of the identified taxa are closely related to well-known phytopathogens; i.e., microorganisms that are harmful to plants. However, proof of a phytopathogenic origin of fairy circles still requires the well-known Koch's postulates² to be fulfilled: in particular, we need to isolate the target microorganisms and prove in pot- and field-trials that they are toxic to plant growth.

² (i) The microorganism must be found in abundance in all organisms suffering from the disease, but should not be found in healthy organisms.

(ii) The microorganism must be isolated from a diseased organism and grown in pure culture.

(iii) The cultured microorganism should cause disease when introduced into a healthy organism.

(iv) The microorganism must be re-isolated from the inoculated, diseased experimental host and identified as being identical to the original specific causative agent.

Microbiology and Virology of Saline Springs, Salt Pans and Playas

The Namib Desert has numerous saline springs and salt pans with halite evaporates (often termed *playas*), located mostly near the coast (Eckardt & Drake 2010). These are caused by groundwater flowing westwards tens or hundreds of meters below the surface, until encountering a geological sill or dyke (Eckardt et al. 2022) which forces the water to emerge at the surface. Gradual mineral solubilisation and evaporative processes in the groundwater stream increase the salt concentrations, and the waters emerge as saline springs.

The emergent spring waters typically flow a few tens or hundreds of meters before sinking back into the sands. Before disappearing, and as the water evaporates, these saline streams support extensive salt crystallisation and hypersaline conditions in marginal pools. The result is a wide range of different saline water and soil habitats, which support a wide diversity of salt-adapted microorganisms (Johnson et al. 2017). These saline springs can also serve as essential water sources for local wildlife.

We have investigated several aspects of the microbiomics of saline spring ecosystems at Hosabes (near the Gobabeb-Namib Research Institute) and Eisfeld (east of Swakopmund), with a particular focus on the viral and phage communities. A survey of ssDNA viruses (Adriaenssens et al. 2016) demonstrated that a substantial majority of the



Plate 9: Hosabes saline spring and stream, with extensive crystalline evaporites

sequences identified were completely novel (i.e., not found in any of the public virome sequence databases). More recently, shotgun metagenomics identified host and viral taxa (Martinez-Alvarez et al. 2022), and characterised the functional potential of these organisms. Halite samples were dominated by extremely halophilic Euryarchaeota and Bacteriodota (*Salinibacter* species), with highly novel lineages of the Caudovirales phage. We also identified a potentially novel clade of Type II CRISPR-Cas genes, suggesting that these saline spring communities are involved in intense host-virus competition.

Microbial Community Responses to Water

Water, or rather the lack of it, is what makes a desert. The aridity of a desert is determined by the ratio of precipitation to potential evapotranspiration (P/PET). Very low precipitation (an average of a few mm of rain per year) and very high evapotranspiration qualifies the central Namib as *hyper-arid* (P/PET < 0.05).

Most microorganisms, when desiccated, transition into a dormant state, where residual metabolism (termed *anhydrobiosis*) is restricted to minimal (basal) metabolic processes necessary for the production of maintenance energy (Bosch et al. 2021). The extent of dormancy in desert soil microbiomes has never been resolved. Using metatranscriptomics methods, we were able to assess microbiome dormancy in Namib soils. While many of the major clades of bacteria show little or no gene expression in dry conditions (i.e., near or complete dormancy), a small fraction of the microbial species in dry desert soils retained metabolic activity (Gunnigle et al. 2017; Leon-Sobrino et al. 2019). Those ‘active’ species were part of the rare bacterial community, while the dormant fraction comprised the dominant taxa. We also showed that the magnitude of the microbiome response to precipitation depended on the water regime history of their environment of origin (riverbed vs gravel plain soils; Frossard et al. 2015).

Community gene transcription profiles (Leon-Sobrino et al. 2019) show that the active metabolic processes in microbiomes of desiccated soil were predominantly heterotrophic carbon acquisition (metabolizing fixed carbon from degrading lipids) and nitrogen acquisition by nitrate reduction (nitrate is often present at quite high concentrations in the driest desert soils). There was little evidence for the energy-expensive acquisition of atmospheric CO₂ assimilation (catalysed by RUBISCO) or atmospheric N₂ fixation (driven by nitrogenase).

In a desert, water changes everything! Heavy rains in the summer of 2011 triggered massive plant germination across the Namib, and for a while the depauperate desert became a prairie. This dramatic change in the landscape (and the desert biology) stimulated us to ask questions of how the addition of water (and the carbon rich plant biomass) might influence the soil microbiomes. A year-long field study (Armstrong et al. 2016) yielded some salutary lessons in experimental design. The single rain event (in month 11) triggered a massive shift in soil microbial community composition, coinciding with a

dramatic increase in soil respiration as newly expanded microbial populations accessed previously dry and inaccessible organic substrates.

This study did not tell us how quickly a dry soil microbiome can respond to water inputs. We prepared several hundred litres of DNA-free artificial rainwater, and applied this to a 5m² area of desert soil, taking soils samples prior to the addition and at increasing intervals after the artificial ‘rain event’ and analysing them using metatranscriptomics methods. The results were dramatic! Just 10 minutes after water addition (our first sample), the metatranscriptome changed dramatically (Leon-Sobrino et al. 2021). Up-regulated genes included those for cellular motility, substrate import and export, and cell division, all changes which might be expected for a microbial community with sudden access to a liquid continuum and a newly available supply of energy rich organic substrates. The most prominently down-regulated genes were those encoding stress response elements, as cells transitioned from a high stress (desiccation stress, energy limitation and oxidative stress) environment to a more favourable habitat.

Desert Insects and Micro-arthropods

The Namib Desert has provided many famous examples of the unique diversity and physiology of its insects (Seely & Pallett 2012; Henschel & Lancaster 2013), particularly the iconic fog-harvesting beetles (Hamilton and Seely 1976). While insects have not been the primary focus of our desert ecology studies, we have always been aware that they are core components of the Namib’s structured desert communities. At the urging of our New Zealand colleague, Professor Ian Hogg, we undertook a molecular bar-coding study of the Namib Desert’s Collembola (Springtails).

The Namib Desert Collembola had been long thought to consist of only 4 species. We collected over 400 springtail specimens from 77 pit-fall traps across the desert, extracted genomic DNA and analysed the CO1 gene locus. The results were spectacular: GMYC

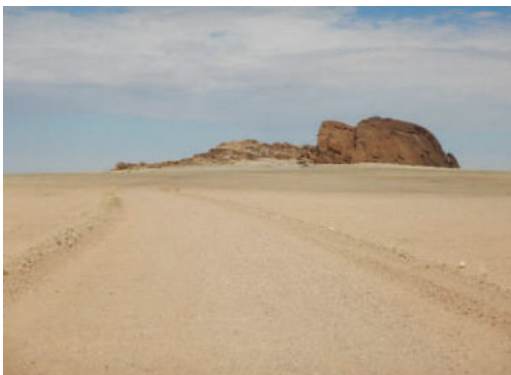


Plate 10: The central Namib Desert at Mirabebe, before and after the 2011 rains

(Generalized Mixed Yule Coalescent) analyses indicated a minimum of 30 putative species, 70% of which were found only at a single site (Collins et al. 2019). This study has raised many more questions than it has answered. Issues such as gene isolation and gene flow, distribution, dispersal and more all remain to be addressed and answered.

Conclusions

If there is a single lesson we can draw from a decade of microbiomics research in the Namib Desert, it is that, despite our extensive and intensive studies using state-of-the-art sequencing and bioinformatics technologies, our ignorance remains much greater than our knowledge. We have partially answered some of the simpler questions, particularly those relating to microbial community composition and compositional drivers. Yet, some of the results are contradictory, and some major taxonomic groups, such as the viruses, phages, and the microarthropods, remain grossly understudied. We know relatively little of the complex interactions within communities although we have exposed tantalizing hints suggesting that these interactions are critical elements of community function. We have barely scratched the surface of temporal effects on microbiome structure and function. We have very little kinetic data of any sort, from the functional rates of single taxa to the spatially integrated rates of key ecosystem services. We know little of the ways in which Namib Desert edaphic microbial communities may respond to changing climate parameters, over any timescale.

Our studies have also been spatially restricted: to an area of the central Namib Desert of less than 10,000 sq. km. and mostly at low spatial resolution (10 or 20 km sample site spacing). Given that the entire Namib Desert covers an area of approx. 81,000 sq. km, and microbial ecology studies of some major regions such as the Skeleton Coast National Park and the Namib Sand-Sea are almost completely non-existent, we can hardly claim to have comprehensively surveyed the microbial communities of the region.

This summary of our knowledge deficits is not intended to be pessimistic, but merely to highlight the potential for research over the next decade(s). The rapid development of sophisticated molecular and analytical tools can only accelerate the pace and value of such research, and the outcomes of such efforts are likely to be at least as exciting as those of the past decade, and probably much more so.

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We particularly thank Associate Professor Frank Eckardt (University of Cape Town) for introducing a team of microbial ecologists to the essential complexities of desert geomorphology, geology and soil science.

Throughout more than a decade of Namib Desert microbiomics research, we have used an open collaborative model. Our annual field expeditions to the Gobabeb-Namib Research Institutions have been multi-partner team efforts, with collaborators from all around the world joining our expeditions of up to 30 researchers. Many of these visitors have become sustained long-term collaborators.

Other collaborators deserve special mention and thanks: Dr Chris McKay (NASA, USA) for introducing Don Cowan to Gobabeb, back in 2008; Professor David Hopkins (Edinburgh, UK) for participating in many of our field expeditions and continuously guiding our research with his deep understanding of soil systems; Professor Daniel Daffonchio (KAUST, SA) for bringing his team of great researchers to many of our expeditions and for leading our thinking down new and exciting avenues; Professor Ian Hogg (University of Waikato, NZ) for reminding us that insects are important too; and Professor Marla Trindade (University of the Western Cape, Cape Town, RSA) for her role in all the early expeditions and for her subsequent inspired leadership of the UWC Institute for Microbial Biotechnology and Metagenomics, within which our Namib Desert studies were initiated.

We also extend our thanks to the superb postgraduate and postdoctoral researchers who have participated in this program from its inception: their names are now permanently embedded in the program through their publications.

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