Namib Desert soil microbial community diversity, assembly and function along a natural xeric gradient

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Abstract

The hyperarid Namib Desert is a coastal desert in southwestern Africa and one of the oldest and driest deserts on the planet. It is characterized by a west/east increasing precipitation gradient and by regular fog events (up to 75km inland) that can also provide moisture. In this study, we aimed to evaluate the role of this natural aridity and xeric gradient on edaphic microbial community structure and function in the Namib Desert. A total of 80 individual soil samples were collected at 10 km intervals along a 190 km transect from the fog-dominated western coastal region to the eastern desert boundary. Seventeen physicochemical parameters were measured for each soil sample. Soil parameters reflected the three *a priori* defined climatic/xeric zones along the transect ('Fog', 'Low Rain', and 'High Rain'). Microbial community structures were characterized by T-RFLP fingerprinting and shotgun metaviromics and their functional capacities were determined by extracellular enzyme activity assays. Both microbial community structures and functional capacities differed significantly between the three xeric zones. The deep sequencing of surface soil metavirome libraries also showed shifts in viral composition along the xeric transect. While bacterial community assembly was influenced by soil chemistry and stochasticity along the transect, their functional capacity rather appear to be by xeric stress.

Keywords: Aridity gradient, Xeric stress, Edaphic desert microbial communities, Extracellular enzyme activities, Dryland

1. Introduction

Deserts cover more than one-third of the Earth's total land surface, representing the largest terrestrial ecosystem (Laity, 2009). Worldwide, 5.2 billion hectares of desert lands are used for agriculture, of which an estimated 69% are either degraded or undergoing desertification as a consequence of climatic variation and intensive human activity (Gilbert, 2011). Because desert environments contain a limited range of higher plants and animals, soil microbial communities are considered to be the most productive components of these ecosystems as well as the dominant drivers of biogeochemical cycling (Pointing and Belnap, 2012; Makhalanyane *et al.*, 2015).

Compared to more productive ecosystems, desert microbial communities display a generally lower diversity (Lynch *et al.*, 2012; Neilson *et al.*, 2012; Fierer et al., 2012), which may limit their resistance and resilience to environmental changes (Van Horn *et al.*, 2014). As such, deserts systems may be particularly vulnerable to disturbances such as those linked to global climate change (Seager *et al.*, 2007). Global change effects are predicted to induce significant variability in annual precipitation levels in hot desert, both in time and intensity (Tsonis et al., 2005). Such changes will substantially impact the structures and functions of indigenous microbial communities, as water availability is the

main factor limiting their biological processes in arid ecosystems. This observation has led to the theoretical 'microbial-centric' TTRP (trigger-transfer-reserve-pulse) framework (Belnap et al., 2005), where precipitation events act as a trigger to transfer nutrients to the soil microbial communities (the reserve) and lead to pulses in biogeochemical activities (e.g., C/N dynamics; Belnap et al., 2005). The Namib Desert of southwestern Africa is among the oldest and driest deserts on the planet and its central section has sustained hyperarid conditions for at least the last 5 million years (Seely and Pallet, 2008). Rainfall in the Namib Desert is spatially and temporally highly variable, usually of low intensity, seasonally regulated but increasing gradually from the coast towards inland (mean values of 15 to 185 mm per annum for the western and eastern desert margins, respectively; Figure 1; Lancaster et al., 1984; Eckardt et al., 2013). Due to the cold Benguela Atlantic current, the coast of the Namib Desert is also influenced by regular fog events that can reach as far as 75 km inland and provide up to 183 mm (mean annual) moisture (Figure 1; Lancaster et al., 1984; Eckardt et al., 2013). This climatic specificity has led to a high level of faunal and floral endemism in the Namib Desert, including fog-harvesting beetles (*Onymacris, Stenocara* and *Physasterna* spp.; Hamilton and Seely, 1976; Nørgaard and Dacke, 2010) and dune grasses (*S. sabulicola*) (Ebner et al., 2011).

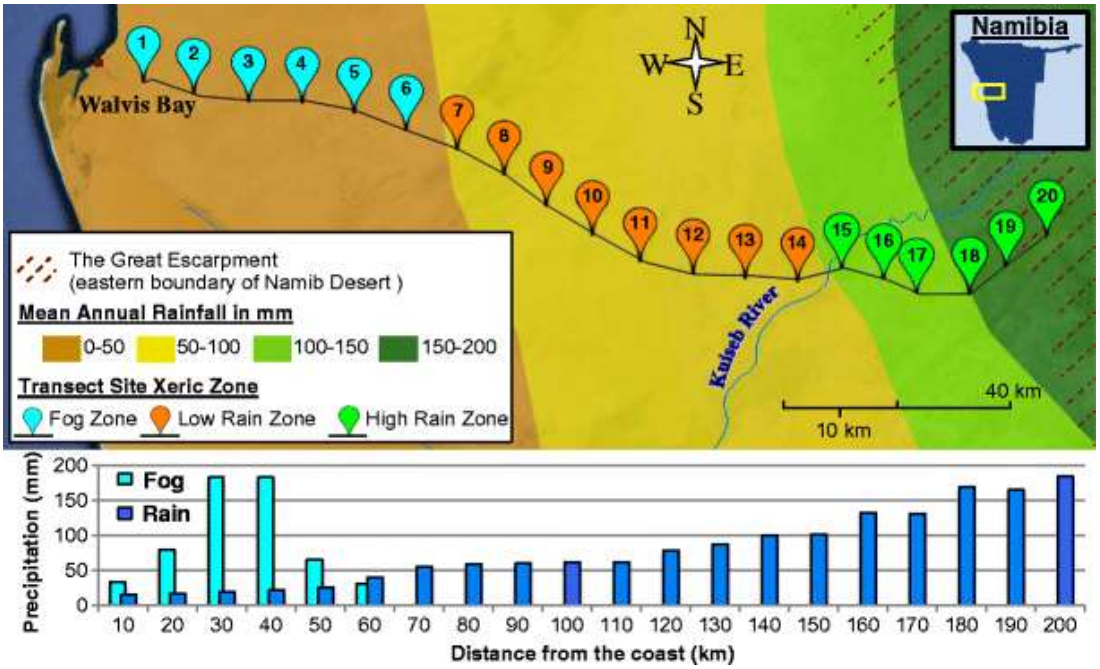

Fig. 1. Map showing the distribution of sampling sites in the Namib desert across the longitudinal west/east xeric gradient. Adapted from [13, 14, 22]. Image produced using Google Earth, © 2016 DigitalGlobe

The contribution of these two water sources (i.e. rainfall and fog) has led to a well-defined gradient of xeric stress across the Namib Desert (Figure 1; Lancaster et al, 1984; Eckardt et al, 2013). Moisture source has previously been shown to influence Namib Desert hypolithic microbial community structures, assembly and colonization (Stomeo *et al.*, 2013; Warren-Rhodes *et al.*, 2013; Valverde *et al.*, 2015), but studies on the effect of water/moisture source on Namib Desert edaphic community diversity and function are limited: In an V-shaped transect, with no inter-site replication, Namib Desert edaphic bacterial community structures were found influenced by water source (i.e. fog vs rain; Stomeo *et al.*, 2013), and a more recent microcosm experiment established that water regime history was a critical factor in driving bacterial and fungal community structures as well as their adaptation to water stresses (Frossard *et al.*, 2015).

In this study, we established a high resolution 190 km west–east transect across the Namib Desert. Twenty sampling sites were established at 10 km intervals. Based on a large body of climatic data (Lancaster et al, 1984; Directorate of Environmental Affairs, 2002; Henschel and Seely, 2008; Eckardt et al., 2013), we defined three distinct 'xeric zones': a fog-dominated coastal zone (the 'fog zone'; sites 1 to 6), an intermediate 'low rainfall' zone (the 'Low Rain' zone; sites 7 to 14), and an inland region of higher rainfall (the 'High Rain' zone; sites 15 to 20) (Figure 1). Our working hypothesis was that climate and soil parameters across the xeric gradient should correlate with Namib Desert edaphic microbial community structures, as assessed by T-RFLP fingerprinting (Johnson et al., 2017) and shotgun metaviromics (Zablocki et al 2017). Similarly, gross functional capacities, as measured by extracellular enzymatic assays (Frossard et al., 2015), were also expected to respond quantitatively to water availability from the coast to the inland desert margin.

2. Materials and methods

2.1. Soil sampling strategy and storage

Twenty sites were sampled at 10 km spacing across a west-east transect in the central Namib Desert in April 2013. The transect spanned the three xeric zones defined by long-term climatic data (Figure

1; Lancaster *et al.*, 1984; Directorate of Environmental Affairs, 2002; Eckardt *et al.*, 2013): the 'Fog' zone (F; sites 1 to 6; 15-40 mm precipitation per annum), the 'Low Rain' zone (LR; sites 7 to 14; 55-100 mm precipitation per annum), and the 'High Rain' zone (HR; sites 15 to 20; 101-185 mm precipitation per annum).

At each site, four true replicate soil samples were collected 100 m apart, resulting in a total of 80 individual samples. Vegetation and rocks larger than 1 cm were avoided during collection, as well as disturbed areas such as footprints. Surface soils (0 to 5 cm) were aseptically collected by pooling 8 pseudo-replicates from within a 1 m^2 quadrat into separate sterile Whirl-Pak® plastic bags (Nasco, Fort Atkinson, U.S.A.). Soil samples were stored at 4°C for soil physicochemical analyses, at −80°C for molecular analysis and at −20°C for enzymatic activity assays.

2.2. Soil physicochemical analyses

Seventeen physicochemical properties were measured for each of the 80 soil samples (Supplementary Table S1). Soils were 2mm-sieved and dried at 60°C overnight prior to analysis. Soil texture (i.e., Very Coarse Sand [VCS], Coarse Sand [CS], Medium Sand [MS], Fine Sand [FS], Very Fine Sand [VFS], silt and clay contents) was determined as described by the American Society for Testing and Materials (ASTM D, 2007) and by the Bouyoucos (Bouyoucos, 1962) protocols. Soil pH was determined in a soil slurry at a 1:2.5 soil to deionized water ratio (pH meter Crison Basic +20, Barcelona, Spain). Total soil carbon content was determined using the Walkley–Black acid digestion method (Walkley, 1947) and soil organic matter content using the weight loss-on-ignition method (360°C for 2 h; with a 2 h/150°C pre-treatment to remove the soils gypsum crystallized water; Schulte and Hopkins, 1996). Soil ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were determined using the steam distillation and titration method (Keeney and Nelson, 1982) and soil phosphorus (P) was estimated using the Bray-1 method (Bray and Kurtz, 1945). Cation exchange capacity (CEC) was determined by ammonium acetate extraction of exchangeable and water-soluble cations (Rhoades, 1982). Soil calcium (Ca^+), potassium (K^+), magnesium (Mg^+), sodium (Na^+), and sulfur (S) were

extracted with ammonium acetate and the concentrations measured by inductively coupled plasma optical emission spectroscopy (ICP-OES) (SPECTRO Genesis, Ametek, Kleve, Germany) (Rhoades, 1982).

2.3. Enzymatic assays

The extracellular activity of five enzymes was assessed with chromogenic substrate analogues as described in Frossard et al (2015): β-glucosidase (BG; involved in C biogeochemical cycling through cellulose degradation), β-N-acetylglucosaminidase (NAG; involved in N cycling through the degradation of chitin), leucine aminopeptidase (LAP; involved in N cycle through protein degradation), alkaline phosphatase (AP; involved in the P cycle through the hydrolusis of phosphodiester bonds under alkaline conditions) and phenol oxidase (PO; involved the oxidation of the phenolic humics and lignin). Assays were performed by combining 3 g of soil and 100 mL 50 mM Tris-HCl buffer. Under constant agitation, 200 µL of this soil-buffer slurry was transferred to a 96-well plate. Four replicate wells were used for each sample and controls for both substrate analogue and soil background absorbance were prepared. Plates were incubated at 43°C (the average daytime soil temperature of the sampling site on collection days) in the dark under constant agitation. After 4h, 10 µl of 0.5 M NaOH was added to each well to terminate the enzymatic activity and the enzymatically induced absorbance changes were measured using a Multiskan™ GO Microplate spectrophotometer (Thermo Scientific, Waltham, U.S.A.). Extracellular enzyme activities were calculated as absorbance change 'per g dry soil' (gDS).h^{-1}, under the stated reaction conditions, which is accepted as an ecosystem-level measure of microbial activity and allows for direct comparison of activities between samples (Boerner *et al.*, 2005; Cunha *et al.*, 2010).

Carbon and nutrient ratios (C:N, C:P, and N:P) were calculated across the transect. In order to normalize the variance, all enzyme activities were calculated per gOM and log transformed (ln[x + 1]) prior to analysis. The C:N enzyme activity ratios were calculated as the ratio of BG activity to the combined activity of NAG and LAP (BG:[NAG + LAP]); the C:P one as the ratio of BG activity to AP

activity (BG:AP); and the N:P one as the combined activity of NAG and LAP to AP activity ([NAG + LAP]:AP) (Sinsabaugh *et al.*, 2008).

Fluorescein diacetate (FDA) hydrolysis assay, used as a proxy of total microbial activity (e.g., Ronca et al., 2015) was performed as previously described (Green *et al.*, 2006). Briefly, 0.5 g of soil was combined with 12.5 mL of 1 × PBS buffer (pH 7.4) and 0.25 mL 4.9 mM FDA dissolved in acetone, and incubated at 43°C for 2 h under constant agitation. After incubation, FDA hydrolysis was halted by adding 40 µl of acetone to 1 ml of soil slurry. Samples were then centrifuged at 8800g for 5 min, and fluorescence (490 nm) was measured with a portable fluorometer (Quantifluor™, Promega, Madison, USA).

2.4. Bacterial community structure analysis

2.4.1. Metagenomic DNA Extraction, 16S rRNA gene PCR amplification and purification

Metagenomic DNA (mDNA) was extracted from 0.5 g soil using the PowerSoil® DNA Isolation Kit (MO BIO, Carlsbad, U.S.A.), with minor modifications (MO BIO Laboratories, 2013). Soils from the coastal/fog sites (i.e. sites 1 to 6) were pretreated due to their high salt concentrations and low biomass (Supplementary Table S1) (Bickley *et al.*, 1996). The pretreatment included three washes with TE buffer (10 mM Tris-EDTA, pH 5.0) centrifuged for 10 min at 7200g prior to mDNA extraction (Emmerich *et al.*, 2012). Six parallel mDNA extractions were performed for the TE buffer washed soils using the MoBio PowerSoil kit (MO BIO, Carlsbad, U.S.A.) with a modified elution step: the eluate from the first spin column was used as the eluent for the next spin column as previously described (Fierer *et al.*, 2012). The extracted DNA was stored at -80°C.

PCR amplification targeting the bacterial 16S rRNA gene was performed using a T100 Thermo Cycler (Bio-Rad, Hercules, U.S.A.). A standard 50 µL reaction volume was used: 0.75% formamide, 0.1 mg/mL bovine serum albumin (BSA), 1 X DreamTaq™ buffer (Thermo Scientific, Waltham, U.S.A.), 0.2 mM of each dNTP, 0.5 µM of fluorescent-labeled forward primer 341F (Ishii and Fukui, 2001) (5'-CCTACGGGAGGCAGCAG-3'), 0.5 µM of reverse primer 908R (Lane *et al.*, 1985)

(5'-CCGTCAATTCCTTTRAG-TTT-3'), 0.005 U/µL DreamTaq™ DNA polymerase (Thermo Scientific, Waltham, U.S.A.) and 1 µL of metagenomic DNA as template. The cycling conditions consisted of an initial denaturation step of 5 min at 95°C; 20 amplification cycles of 95°C for 30s, 55°C for 30s, and 72°C for 90s; and a final extension step at 72°C for 10 min. PCR products were purified using the NucleoSpin® Gel and PCR Clean-up kit (Macherey-Nagel, Duren, Germany) in accordance with the manufacturer's protocol.

2.4.2. Terminal restriction fragment length polymorphism (T-RFLP)

Purified PCR amplicons (400 ng) were digested using the FastDigest® *Msp*I restriction endonuclease (restriction site C^CGG) (Thermo Scientific, Waltham, U.S.A.) for 15 min at 37°C. Digested products were purified using the NucleoSpin® Gel and PCR Clean-up kit (Macherey-Nagel, Duren, Germany) prior to capillary electrophoresis at the DNA Sequencing Facility of the University of Pretoria (South Africa) using an ABI 3500 XL Genetic Analyzer (Applied Biosystems, Foster City, U.S.A.).

2.5. Viral DNA extraction, amplification and sequencing

The metaviromic DNA of soil samples from 4 sites (4, 7, 10 and 13; Figure 1) was extracted according to Williamson et al. (2005), with slight modifications. Five grams of soil (pooled from the 4 true replicates collected at each site) were added to 15 ml of 1% potassium citrate buffer and vortexed at full speed for 15 seconds. The mixture was incubated on ice for 25 min, followed by three cycles (30% amplitude for 59 sec) of sonication with an ultrasonic processor using a 1/16" probe tip. Samples were centrifuged at 3000g at 4°C for 30 minutes. The supernatant was decanted, transferred to a new tube and passed through a 0.20 µm cellulose acetate sterile syringe filter (GVS). Viruses and virus-like particles were concentrated by adding 25% PEG8000 (in 1M NaCl) to the filtrate to a final concentration of 10% (w/v) and incubated overnight at 4°C. Concentrates were centrifuged for 30 minutes at 32000g at 4°C. The supernatant was decanted and the viral pellet re-suspended in 300 µl phage buffer (10mM Tris-HCl, 10 Mm Mg SO4, 150 mM NaCl, pH 7.5). Viral concentrates were

treated with DNase I (Thermo Scientific, cat#EN0523) and RNase A (Thermo Scientific, #EN0531) according to the manufacturer's instructions. Viral DNA was purified using the Quick-gDNA MiniPrep kit (Zymo Research, cat# D3025) according to the manufacturer's instructions and randomly amplified using the REPLI-g Midi kit (Qiagen, cat# 150043) according to the manufacturer's instructions. Amplified DNA was precipitated with isopropanol, washed with 70% ethanol and re-suspended in 25µl milli-Q water.

The amplified metaviromes were checked for bacterial contamination by assessing the presence of the 16S rRNA gene by PCR amplification as described above. Library building for sequencing was done using the Ion Xpress™ Plus and Ion Plus Library Preparation for the AB Library Builder™ System (Publication Number MAN0006946). Template amplification was done using the Ion OneTouch™ 2 System (OT2) Ion PI™ Hi-Q™ OT2 200 Kit (Number MAN0010857). The metavirome libraries were multiplexed and sequenced using the Ion PI™ Hi-Q™ Sequencing 200 Kit (Number MAN0010947) using the Ion PI™ Chip Kit v3. Sequencing was performed on the Ion Proton platform, located at the Central Analytical Facilities, Stellenbosch University, South Africa.

2.6. Data Analyses

Physicochemical data were normalized in Primer6 and visualized using a correlation-based principal component analysis (PCA) to determine the dominant environmental gradients of the transect samples (Primer-E Ltd, Devon, UK) (Clarke and Warwick, 2001). Functional data were Hellinger-transformed (Legendre and Gallagher, 2001), and combined with the environmental parameters measured, were visualized in a redundancy analysis (RDA) plot with Bray-Curtis dissimilarity matrices (Bray and Curtis, 1957) in Primer6 (Primer-E Ltd, Devon, UK). Significant environmental parameters were calculated by *envfit* ($p < 0.05$; 999 permutations; vegan package R; Oksanen *et al.*, 2007) and fitted as vectors on the respective NMDS plots.

T-RFLP profiles were analyzed using Gene Mapper® software (Applied Biosystems, Foster City, U.S.A.). Terminal restriction fragments (T-RFs) smaller than 50 bp and greater than 600 bp were eliminated,

and a baseline threshold of 20 fluorescence units was used to delineate background noise. Peaks were then binned into Operational Taxonomic Units (OTUs) with custom scripts (standard deviation 1.5) using R (Abdo *et al.*, 2006; RCD Team, 2013). OTU relative abundances were Hellinger-transformed (Legendre and Gallagher, 2001) and were also combined with the edaphic parameters measured in a RDA. Mantel tests for correlations between environmental parameters, community activities and community structures were calculated using R (999 permutations) (Oksanen *et al.*, 2007). Variation partitioning and co-occurrence null model analyses were performed as previously described (Johnson et al 2017).

(PERM)ANOVA ([Permutational] analysis of variance) was used to identify significant differences between groups of samples using R. Using the PAST v3.14 software package, we tested for relationships between the 'distance to coast' (km) and the different soil enzyme activities. The latter were ln(x+0.5) transformed to achieve near normal distribution. Ordinary Least Square (OLS) was first used to evaluate linear relationships between 'distance to coast' (km) and the soil enzymatic activities. If unsuccessful, we tested for nonlinear relationships by using polynomial regression.

2.7. Metavirome sequence analyses

Metavirome sequence reads were curated for quality and adapter trimmed using CLC Genomics version 6.0.1 (CLC, Denmark), using the default parameters. *De novo* assembly for each read dataset was performed with the CLC Genomics assembler suite using the default parameters. Contigs were uploaded to and are available for analysis from the following online pipeline: the MetaVir version 2 server (Roux et al., 2014; http://metavir-meb.univ-bpclermont.fr/). The four metavirome read datasets are also available from the Sequence Read Archive of NCBI under the accession no. ERX1230691 to ERX1230694 (Zablocki et al. 2017). Taxonomic composition by MetaVir was computed from a BLASTp comparison with the Refseq complete viral genomes protein sequences database from NCBI (release of 2015-01-05) with an E-value threshold of 10^{-5}. Unique and shared virus hits were determined by recording the occurrence of all virus isolate hits (contig best blast hit

number, E-value threshold 10^{-5}, MetaVir) in each soil sample dataset, and visualized using the Venn diagram online tool, available from the Bioinformatics and Evolutionary Genomics group website (http://bioinformatics.psb.be/webtools/Venn/). The term "viral operational taxonomic unit" ("vOTU") is used here to describe contigs with a taxonomic assignment based on the best BLAST hit (BLASTp query against the RefSeq database, 10^{-5} threshold on the E-value).

3. Results and Discussion

Aridity in drylands have been shown to influence soil microbial communities although results are often contradictory. At the global scale (80 sites located on 5 continents), bacterial and fungal diversities and abundances increased with decreasing aridity (Maestre et al, 2015) while, at the local scale (within the country of Israel), soil bacterial abundances also decreased with aridity but their diversity remained constant (Bachar et al 2010). In terms of desert ecosystem functioning, water and nutrient availability limit desert productivity (Cleveland et al 1999), and thus their (microbial) biogeochemical activities (Delgado-Baquerizo et al, 2013), and arid land extracellular enzyme distribution is generally influenced by soil pH (Collins et al., 2008; Sinsabaugh et al, 2008) which is strongly affected by aridity (Maestre et al, 2015). However, Namib Desert soils presenting different water regime histories (riverbed vs gravel plain) but with similar pH were shown to present alternative nutrient acquisition capacities (Frossard et al, 2015).

These contradictions show that our knowledge on arid land microbial ecology must be improved, most particularly as (i) the vast majority of drylands' ecosystem processes are microbially-mediated (Pointing and Belnap, 2012; Makhalanyane et al, 2015) and (ii) predictive modeling shows that global surface area of arid land will increase (Huang et al, 2015). This experiment was therefore designed to study the structure and function of edaphic microbial communities across a naturally occurring xeric stress gradient (Figure 1).

3.1 Soil physico-chemical properties

A principal component analysis (PCA) plot based on the 17 soil parameters measured (Figure 2; Supplementary Table 1) showed that the soils from the three *a priori* defined xeric zones ('Fog', 'Low Rain', and 'High Rain' zones) were clearly separated along PCA axis 1 (which explains 30.6% of the sample variation; Figure 2a) which was strongly correlated with soil pH, 'coarse sand' content and Ca^{+}, S, Na^{+} and NO_3^{-} concentrations (Figure 2b,c). PERMANOVA confirmed that the soil physicochemistries of each zone were significantly different (PERMANOVA p = 0.001; Table 1), supporting a previous study which observed that within the Namib Desert gravel plains, multiple lithologies (e.g., schist, granite, surficial cover and salt crusts) and geological units (e.g., Kuiseb, Salem, Surficial cover, Saline spring) can be found (Gombeer et al, 2015). In general, the ionic (Ca^{2+}, K^{+}, S^{2-}, Mg^{2+}, Na^{+} and NO_3^{-}) content of the fog zone soils was higher than in those of the rain zones (Supplementary Tables 1 and 2). We attribute this effect to the transport and deposition of marine aerosols (Gustafsson and Franzèn, 1996; Liang et al, 2016) rather than fog input: the low ionic content of fog precipitation suggests that fog events have little impact on the soil chemistry (Eckardt and Schemenauer, 1998), other than the presence of gypsum deposits ($CaSO_4.2H_2O$) which originate from the combination of marine S and Ca^{2+} from secondary calcrete deposits (Eckardt et al, 2001). The 'High Rain zone' soils were characterized by significantly higher soil organic matter than all other transect soils (ANOVA $p < 0.05$; Supplementary Tables 1 and 2). We attribute this to the generally higher plant productivity in this region, as compared to those of the Fog and Low Rain zones (Mendelsohn, 2002).

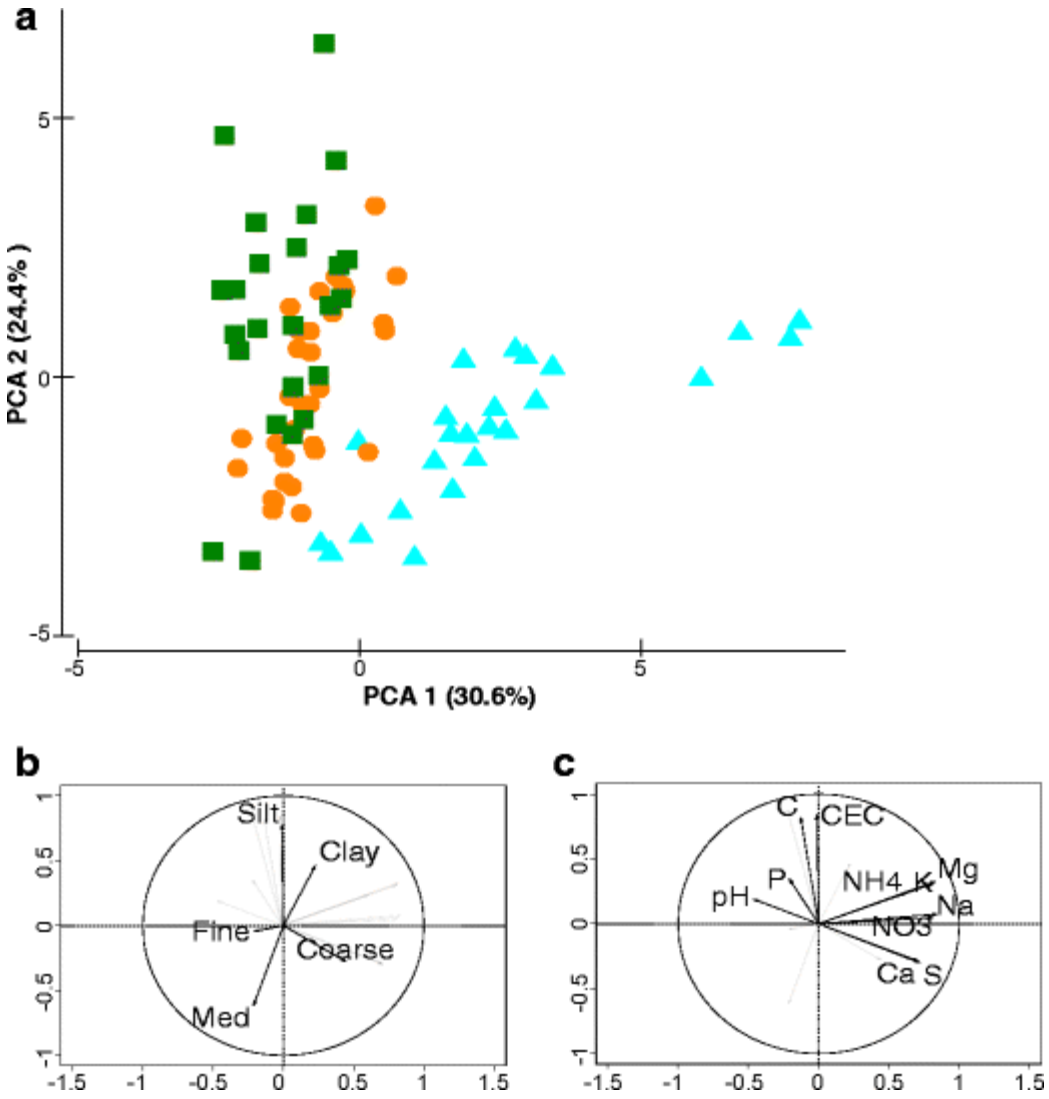

Fig. 2. Results of the principle component analyses (PCAs) using the 17 Namib desert soil variable recorded. **a** PCA ordination plot. Correlation circles showing the relationships between the environmental variables and the first two PCA axes: the soil particle sizes (**b**) and the chemical descriptors (**b**). The descriptors were separated in two separate correlation circles for clarity. Variables that are correlated with the first two axes of the PCA plot are the most important in explaining the variability in the dataset. Vectors indicate the strength (length) and direction (arrow orientation) of the variables in the ordination. *Coarse, Med, Fine* coarse, medium, fine sand content, respectively; *C* carbon; *CEC* cation exchange capacity; Ca^{+} calcium; K^{+} potassium, Mg^{+} magnesium; Na^{+} sodium; NH_4^{+} ammonium; NO_3^{-} nitrate; *OrgMatter* organic matter content; *Phos* phosphorus; *S* sulfur. *Light blue square* = "fog zone," *orange square* = "light rain zone," and *green square* = "high rain zone"

Table 1: PERMANOVA results showing differences in environmental and biological characteristics between the *a priori* defined xeric zones.

Soil Physicochemistries	PERMANOVA		
	Df	F	P
Global Test	2,77	17.52	**0.001***
Fog – Low Rain	1,54	18.57	**0.001***
Fog – High Rain	1,46	21.35	**0.001***
Low Rain – High Rain	1,54	7.57	**0.001***
Global Microbial activity			
Global Test	2,77	13.547	**0.001***
Fog – Low Rain	1,54	22.113	**0.001***
Fog – High Rain	1,46	12.89	**0.001***
Low Rain – High Rain	1,54	3.225	**0.022***
Microbial Community structures			
Global Test	2,69	10.930	**0.001***
Fog – Low Rain	1,46	12.518	**0.001***
Fog – High Rain	1,38	13.268	**0.001***
Low Rain – High Rain	1,54	5.348	**0.001***

Significant values ($p < 0.05$) are designated in bold and by an asterisk. (Df = degree of freedom, F = F value, and p = p value).

3.2 Namib Desert Microbial Community

Each xeric zone showed significantly different microbial structures (Figure 3A) and bacterial community functional capacities (Figure 3B) (PERMANOVA, $p < 0.05$; Table 1). In particular, the soil samples from the fog zone were clearly separated from the other samples in terms of bacterial community structure (Figure 3A) and, to a lesser extent, for extracellular enzymes activities (Figure 3B). This was essentially due to the higher salt, particularly cation, contents in the soils of the fog zone (Figure 3). These parameters are well-known environmental filters (Lozupone and Knight, 2007).

3.3 Bacterial Community Structure and Assembly

The bacterial communities in the low and high rain zones also presented higher α- and lower β-diversities than those of the fog zone (Table 2). However, we acknowledge the accepted limitation that T-RFLP-derived diversity indexes, as they typically reflect differences in community composition and not in 'true' diversity (Blackwood et al, 2007). We used variation partitioning and co-occurrence

null model analyses to evaluate the assembly of the bacterial communities in the different xeric zones (Table 2; Stomeo et al, 2013; Johnson et al, 2017). The combination of spatial (xeric zone) and environmental (soil chemistry) parameters explained 37.5% of the variation of the assembly of bacterial communities along the transect. This result strongly suggests that stochasticity plays a major role in Namib Desert bacterial community assembly (Hubbell, 2001). Furthermore, only 7% (0.06/0.375; Table 2) of the variation of the bacterial community's assembly in the transect was

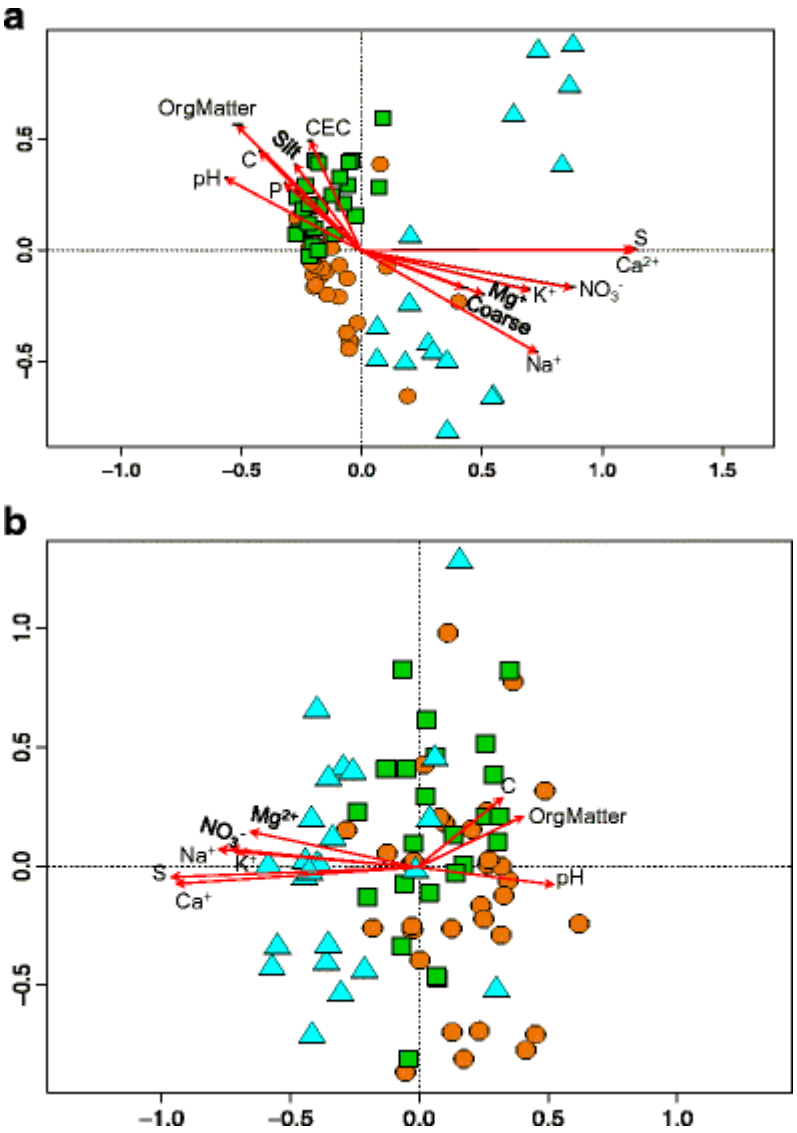

Fig. 3. Redundancy analysis (RDA) bi-plots displaying the influence of soil physicochemistries on Namib desert. **a** Edaphic bacterial community structures. **b** Global soil functional capacities. Only the environmental variables that significantly ($p < 0.05$) explained variability in microbial community structures are fitted to the ordination (*arrows*). The direction of the arrows indicates the direction of maximum change of that variable, whereas the length of the arrow is proportional to the rate of change. *Light blue square* = "fog zone," *orange square* = "light rain zone," and *green square* = "high rain zone"

Table 2. Namib Desert gravel plain bacterial community α-, β- and γ-diversities, and variation partitioning and co-occurrence null model analyses.

α-diversity	Fog	9.63 ± 2.80
	Low Rain	12.31 ± 2.31
	High Rain	13.38 ± 2.70
β-diversity	Fog	3.53
	Low Rain	2.76
	High Rain	2.54
γ-diversity	Fog	34
	Low Rain	34
	High Rain	34
Variation Partitioning	Total Explained Variation (R^2)	0.375
	Soil Chemistry (S)	0.2
	Xeric zone (X)	0.026
	Soil chemistry and water regime (SX)	0.15
	Unexplained Variation	0.625
	P-value	≤ 0.001
Co-occurrence null model analysis	Observed C-score	56.174
	Mean Simulated C-score	52.148
	Standardized Effect Size	15.497
	P-value	< 0.001

β-diversity was measured as the γ-diversity over the mean α-diversity: $\beta = \gamma / \bar{\alpha}$.

attributed to the xeric zonation which indicated that the historical nature and intensity of their precipitation (fog, light rain or high rain) is not a critical factor. However, null model analysis indicated that the co-occurrence of OTUs was non-random (Table 3), suggesting that a combination of deterministic and stochastic processes (Dumbrell et al, 2010; Vellend, 2010) are involved in microbial community assembly along the Namib Desert longitudinal transect. The high and positive standardized effect size (SES, Table 3), also suggested that biological interactions play a role (Nemergut et al. 2013) in the assembly of Namib Desert edaphic communities. This would appear to contradict the results obtain in our recent study (Johnson et al, 2017) which showed that Namib Desert edaphic communities assembled primarily by deterministic processes (e.g., niche speciation). However, in the latter study, communities from highly contrasted soil biotopes (dunes, gravel plains,

riverbeds, and salt pans) were included while, here, we focused on a single biotope: the Namib Desert gravel plains. This confirms that depending on the scale of observation, community dynamics can vary (e.g., metacommunity vs local community; Leibold et al, 2004).

3.4 Namib Desert Soil Extracellular Enzymatic Activities

We measured the extracellular activities of five enzymes commonly used as proxies for soil microbial nutrient demand (Frossard et al, 2015; 2012; Sinsabaugh et al, 2008}. Extracellular enzyme activities were calculated as absorbance change "per g dry soil" (gDS) h^{-1}, which is accepted as an ecosystem-level measure of microbial activity and allows for direct comparison of activities between samples (Boerner et al, 2005; Cunha et al, 2010).

Significant relationships between distance to the coast of the sampling sites and the activities of five of the six enzymes tested were also detected (Figure 4); namely, fluorescein diacetate (FDA) hydrolysis, β-glucosidase (BG), alkaline phosphatase (AP); leucine aminopeptidase (LAP) and phenol oxidase (PO) activities. Because of the strong and significantly positive linear relationships between the distance from the coast and the annual rain precipitation ($r^2 = 0.94$, $p < 0.001$; data not shown) along the transect, the role of long-term climate could not be excluded in explaining the Namib Desert's edaphic communities' functional diversity. Extracellular enzyme activities in the high rain zone were generally more important than in the low rain and fog zones (Figure 4; Supp. Table 3). However, only the activities of FDA (general activity), BG (C-acquiring) and LAP (N-acquiring) were higher in the Low Rain than in the Fog zone (Figure 4; Supp. Table 3). Soil enzyme activities have been found to respond to water events depending on their water regime histories (Frossard et al, 2015). Furthermore, soil moisture is known to directly influence the potential enzyme activities in drylands (Henry 2012) and their activities are simulated by the abundance of water availability following rainfall events (Ladwig et al., 2015).

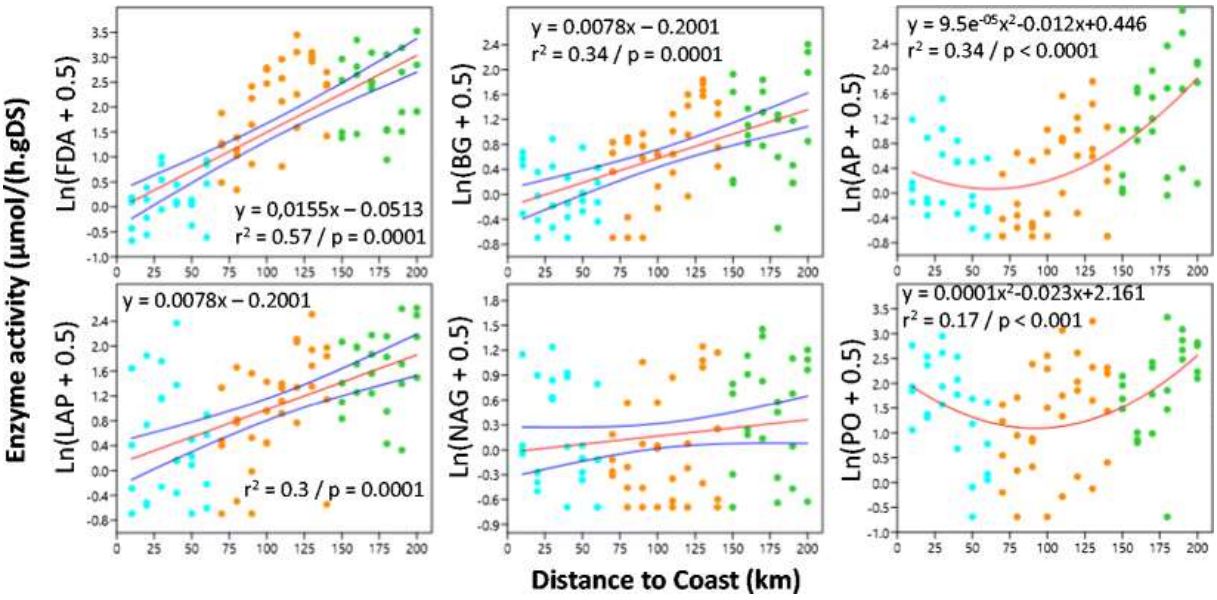

Fig. 4. Relationships between the Namib desert soil enzymatic activities and the distance to the coast. When significant, the linear or nonlinear relationships are indicated on the plot along with the equations and r^2 values. Bootstrapped 95% confidence intervals (1999 replicates) border the OLS linear regression lines. The enzymatic activities used were calculated as "per g dry soil" (gDS). *Light blue square* = "fog zone" activities, *orange square* = "light rain zone" activities, and *green square* = "high rain zone" activities

The relative abundance of extracellular enzymes involved in C, N, and P cycling, reflects the biogeochemical equilibrium between metabolic and nutrient requirement of microbial communities and nutrient availability from the environment (Sinsabaugh et al., 2009). Ratios of log values of activities for C-acquiring hydrolytic enzymes (BG) to N-acquiring (NAG and LAP) enzymes did not vary significantly across the transect (ANOVA p = 0.6) and averaged 0.84 (± 0.34) (Supplementary Figure S1a). With 16 of the 20 transect sites displaying C:N ratios below 1, Namib Desert soils are rather N-limited over C (Supplementary Figure S1a). Contrastingly, the ratio of C-acquiring (BG) to P-acquiring (AP) potential enzyme activities was significantly lower in the 'Fog Zone', averaging 0.89 (± 0.38) compared to the low and high rain zones where the ratio averaged X (±X) and X (±X) respectively (ANOVA; $p < 0.05$), indicating a higher P demand relative to C (Supplementary Figure S1b) from the Namib Desert soil microbiota. The N-acquiring to P-acquiring enzyme activity ratio did not differ significantly among the 3 xeric zones (ANOVA p = 0.4). It averaged 1.22 (± 0.30) which indicated that the demand for P was consistently higher relative to N (Supplementary Figure S1c). The nutrient acquisition ratios of Namib Desert soils are generally consistent with those observed in Chinese

steppes, where the C:N, C:P and N:P activity ratios of the desert samples were significantly higher than those of the temperate ones (Peng and Wang, 2016). However, in the Chihuahuan Desert, C:N:P stoichiometric ratio of extracellular enzymes averaged 1:1:1 (Tapia-Torres et al., 2015), similar to the global ecoenzymatic stoichiometry patterns (Sinsabaugh et al., 2009). The soil microbial communities in this desert appeared to be co-limited by C and by either N or P, depending of local soil resource limitations (Tapia-Torres et al., 2015). In the Namib Desert, however, N was observed to be the scarcer nutrient in which the microbial community must invest to maintain the elemental homeostasis across all the three xeric zones.

3.5 Viral Community Composition

Multiplexed sequencing of the viral communities from site 4 of the fog zone and sites 7, 10 and 13 of the light rain zone (Figures 1 and 5) produced 93,519,306 reads (~13.4 Gb), yielding approximately 22 million reads per metavirome. The mean read length was 142.5 bp and the mean GC content ranged from 54 to 62%. Bacterial contamination in the metaviromes was minimal, as no amplification of rDNA was observed and no rDNA sequences were identified by the MG-RAST pipeline. Across all soil samples, the ratio of taxonomically assigned to unassigned sequences ranged from 9.18 to 18.91%, indicating a highly uncharacterized pool of viral diversity and confirming that viral populations are still poorly characterized in arid environments (Zablocki et al, 2016). Rarefaction curves for all metaviromes remained linear (Supplementary Figure S2), indicating that each dataset did not represent the full viral diversity within each sample. In site 4 from the fog zone, the dominant hits were assigned to *Mycobacterium* phage Adler (6.5%) and *Rhyzobium* phage 16-3 (4.35%), both unclassified members of the *Siphoviridae* family of tailed phages (Order: *Caudovirales*). Members of the nucleocytoplasmic large DNA virus (NCLDV) families *Mimiviridae* and *Phycodnaviridae*, were also primarily identified in the fog zone site 4 (Figure 5A). Single-stranded DNA (ssDNA) viruses were only detected in the light rain sites (2.44% in site 7, 0.68% in site 10 and 6.78% in site 13) despite using a DNA amplification method biased towards the detection of circular ssDNA viruses (Figure 5A). This is

in stark contrast with salt pans located in the 'Fog' and 'Low Rain' zones which contained a high diversity of ssDNA viruses (Adriaenssens et al, 2016), leading to the hypothesis that these viruses are not well adapted to edaphic environments.

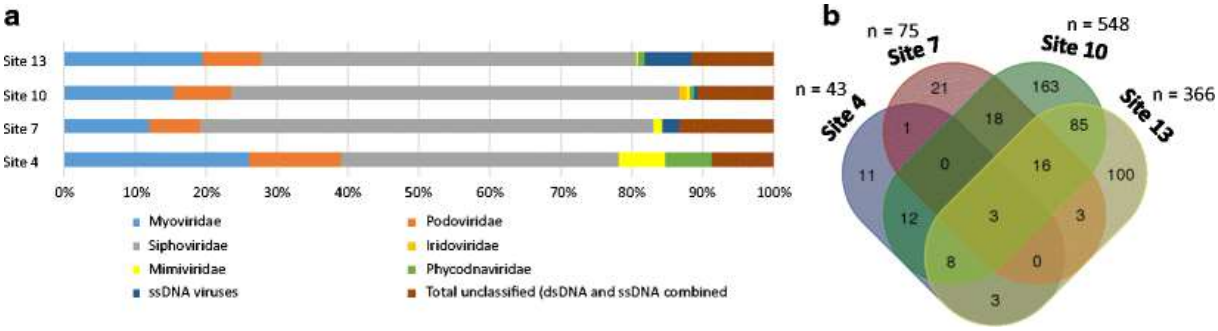

Fig. 5. Diversity of the Namib desert soil metaviromes in the four transect soil studied. **a** Family-level taxonomic compositions computed from a BLAST comparison with NCBI RefSeq complete viral genome proteins using BLASTp (threshold 10–5 on the *E*-value). Virus hit numbers were normalized and converted into ratios. The unclassified category includes all dsDNA and ssDNA viruses. **b** Venn diagram showing the distribution of unique and shared viral OTUs. "*n*" indicates the total number of vOTUs detected in each site

Of the 1032 individual vOTU detected, only 3 (0.3%) were observed in all 4 samples (Figure 5B), namely, *Streptomyces* phage mu1/6, *Yersinia* phage phiR1-37 and *Cellulophaga* phage phi19:1) while 295 vOTUs (66.44%) were exclusive to single sampling sites (Figure 5A). It is noteworthy that the 3 cosmopolitan vOTUs were assigned to viruses infecting bacterial phyla which are known to be dominating desert soils; i.e., Actinobacteria, Proteobacteria and Bacteroidetes (Makhalanyane et al, 2015). However, while *Streptomyces* sp. are common in Namib Desert soils (Makhalanyane et al, 2015) and *Yersina* phages have already been detected in desert soils (Prestel et al, 2013), the detection of the marine *Cellulophaga* phage phi19:1 (Sepulveda et al, 2016) throughout the transect was unexpected. Marine-phage sequences have recently been detected in a ~100km inland Namib metaviromic study (Hesse et al, 2017), and our result, therefore, tends to confirm their hypothesis that marine fog and wind play a role in the dispersal of (marine) phages in Namib Desert soils. Assuming that viral community composition mirror the host community structure (Thurber, 2009; Zablocki et al 2016), the observation of marine phage signals in inland desert soils is also in line with our finding that, stochasticity (here mainly through dispersal) in combination with determinism (e.g.,

niche partitioning) (Table 2) are involved in the assembly of Namib Desert gravel plain microbial communities.

Conclusions

As initially hypothesized, Namib Desert microbial community structures were significantly different in the three *a priori* defined xeric zones along the longitudinal desert transect (Figure 3). We also However, while soil physicochemistry was identified as a significant factor in microbial community assembly, long-term precipitation patterns were not (Table 2). This strongly suggests that adaptation to the immediate edaphic environment is a stronger environmental filter for soil communities than long term climatic patterns in desert ecosystems. This is most probably because microbial communities in Desert soils experience (hyper)arid conditions for much of any given time period, and that, while differences in precipitation in the xeric zones were significantly different in terms of volumetric loads, their biological impact was not (Table 2). Furthermore, precipitation events are generally highly localized in desert systems, particularly in the Namib Desert (Eckardt et al, 2013). Contrastingly, microbial community functional capacities increased from the coast towards inland as expected (Figure 4), confirming that long-term precipitation patterns (or different xeric stresses) play a role in the structuring of desert edaphic community functional potential (Frossard et al, 2015).

Overall, our study thus demonstrated that, while we observe different Namib Desert edaphic desert community structures with different functional capacities along a xeric stress gradient, the bacterial community structure is rather influenced by soil physicochemistries while its functional capacity more by long term precipitation patters, i.e., their xeric stress.

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Supplementary Table 1. Soil physico-chemical parameters of the 20 sampling sites along the xeric stress gradient of the Namib Desert gravel plains. Data are given as the mean ± standard error (n=4).

Site	Km	Altitude	Annual mean rain	Coarse Sand	Medium Sand	Fine Sand	Silt	Clay	pH	CEC	OM	Corg	P	Na^+	Ca_2^+	S	K^+	Mg_2^+	NH_4^+	NO_3^-
			mm	%	%	%	%	%		$cmol^+ kg^{-1}$	%	%	$mg\ kg^{-1}$	$mg\ kg^{-1}$	$g\ kg^{-1}$	$mg\ kg^{-1}$	$mg\ kg^{-1}$	$mg\ kg^{-1}$	$mg\ kg^{-1}$	$mg\ kg^{-1}$
1	10	21	15.2	16.4 ± 5.2	9.0 ± 1.8	59.8 ± 8.3	6.5 ± 1.0	8.3 ± 2.4	6.70 ± 0.04	5.13 ± 0.20	0.42 ± 0.09	0.25 ± 0.08	12.3 ± 5.3	11357 ± 4094	18.5 ± 7.1	12278 ± 6120	522 ± 71	460 ± 46	11.3 ± 3.0	54.1 ± 23.4
2	20	117	16.7	19.5 ± 3.8	10.4 ± 1.0	53.7 ± 2.4	4.0 ± 1.6	12.5 ± 3.7	7.07 ± 0.35	5.9 ± 0.26	0.41 ± 0.09	0.06 ± 0.02	17.6 ± 3.2	1465 ± 1821	26.5 ± 2.6	16101 ± 1288	299 ± 66	102 ± 49	5.2 ± 1.3	9.1 ± 5.6
3	30	237	18.8	18.4 ± 4.9	14.2 ± 3.6	45.6 ± 5.8	4.5 ± 1.0	17.3 ± 3.0	7.19 ± 0.09	6.61 ± 1.08	0.53 ± 0.12	0.21 ± 0.04	10.4 ± 7.3	1060 ± 1043	27.4 ± 1.2	16436 ± 618	332 ± 109	166 ± 100	3.9 ± 0.6	10.9 ± 8.3
4	40	311	21.5	11.7 ± 1.0	14.2 ± 0.6	52.5 ± 3.4	7.0 ± 2.6	14.6 ± 1.8	7.24 ± 0.23	7.2 ± 0.63	0.42 ± 0.08	0.07 ± 0.02	6.7 ± 3.9	622 ± 198	25.6 ± 2.1	15270 ± 1283	339 ± 63	169 ± 107	3.1 ± 0.8	21.5 ± 21.4
5	50	416	25.5	20.2 ± 2.7	23.0 ± 3.2	47.3 ± 2.6	5.5 ± 1.9	3.9 ± 1.8	6.91 ± 0.20	4.7 ± 0.54	0.12 ± 0.03	0.05 ± 0.05	9.83 ± 2.2	1589 ± 3107	9.8 ± 3.8	5637 ± 3039	181 ± 204	67.6 ± 75.5	3.1 ± 0.6	6.9 ± 12.7
6	60	525	40	23.7 ± 4.7	15.5 ± 1.7	46.5 ± 3.9	5.5 ± 1.9	8.8 ± 4.6	6.93 ± 0.12	4.65 ± 0.72	0.28 ± 0.15	0.05 ± 0.07	10.7 ± 3.0	151 ± 176	19.1 ± 8.7	11454 ± 5931	163 ± 65	40.5 ± 20.9	4.4 ± 1.0	5.1 ± 7.3
7	70	568	55.5	8.2 ± 1.6	13.0 ± 1.7	68.0 ± 2.7	5.5 ± 1.9	5.3 ± 1.9	7.57 ± 1.35	4.05 ± 0.37	0.22 ± 0.03	0.03 ± 0.01	12.9 ± 2.3	23.2 ± 3.4	4.7 ± 3.6	2375 ± 2315	80.8 ± 15.5	23.7 ± 3.7	4.0 ± 0.3	0.3 ± 0.0
8	80	613	59	10.7 ± 2.7	14.3 ± 1.9	64.5 ± 3.4	4.0 ± 0.0	6.6 ± 1.5	7.03 ± 0.21	3.78 ± 0.34	0.26 ± 0.15	0.08 ± 0.03	9.95 ± 3.1	437 ± 807	4.5 ± 2.4	1646 ± 1640	130 ± 84	65.1 ± 73.6	3.3 ± 0.4	4.0 ± 7.6
9	90	686	59.8	7.8 ± 3.2	15.1 ± 5.2	64.0 ± 5.3	4.0 ± 0.0	9.1 ± 4.2	7.80 ± 1.14	5.16 ± 0.89	0.32 ± 0.10	0.08 ± 0.03	10.6 ± 3.5	31.0 ± 9.4	2.0 ± 0.5	141 ± 120	130 ± 43	49.3 ± 9.5	3.5 ± 0.3	1.3 ± 0.2
10	100	749	62	12.6 ± 1.8	11.8 ± 1.7	49.8 ± 3.8	7.0 ± 1.2	18.9 ± 3.6	8.05 ± 0.98	7.59 ± 0.30	0.68 ± 0.08	0.28 ± 0.04	5.7 ± 2.2	19.6 ± 4.8	4.4 ± 0.1	10.9 ± 3.9	232 ± 25	76.0 ± 9.3	3.5 ± 0.3	1.1 ± 0.7
11	110	828	61.8	8.2 ± 2.7	18.7 ± 5.5	53.1 ± 3.2	5.0 ± 2.0	15.1 ± 5.2	7.50 ± 0.14	6.21 ± 1.03	0.54 ± 0.12	0.09 ± 0.05	11.3 ± 5.1	27.9 ± 2.9	1.7 ± 0.4	62.7 ± 26.2	209 ± 91	83.2 ± 16.4	4.5 ± 0.7	1.4 ± 0.5
12	120	938	78.8	14.5 ± 6.6	7.5 ± 1.0	58.1 ± 6.5	5.5 ± 1.9	14.4 ± 9.7	7.87 ± 0.95	6.79 ± 1.39	0.76 ± 0.16	0.21 ± 0.10	3.02 ± 3.1	36.8 ± 25.6	1.3 ± 0.2	72.0 ± 28.8	244 ± 155	70.9 ± 16.7	4.9 ± 2.0	1.5 ± 0.6
13	130	931	87.5	12.2 ± 3.2	6.9 ± 1.3	56.6 ± 6.6	7.0 ± 2.0	17.3 ± 2.2	7.44 ± 0.86	7.22 ± 0.69	0.83 ± 0.13	0.24 ± 0.07	10.2 ± 2.7	35.3 ± 10.1	1.3 ± 0.2	45.3 ± 11.7	284 ± 96	102 ± 8	4.5 ± 0.8	3.3 ± 2.2
14	140	884	100.5	16.3 ± 8.1	12.1 ± 2.0	54.5 ± 6.5	4.5 ± 1.0	12.6 ± 2.8	7.53 ± 0.31	5.66 ± 1.10	0.98 ± 0.18	0.35 ± 0.08	8.96 ± 3.5	48.9 ± 39.7	1.8 ± 0.1	50.3 ± 34.5	215 ± 29	155 ± 16	5.2 ± 1.7	4.2 ± 3.1
15	150	881	101.5	14.0 ± 4.8	9.6 ± 0.6	57.9 ± 4.1	4.5 ± 1.0	14.1 ± 4.0	7.99 ± 0.77	5.62 ± 1.24	0.73 ± 0.14	0.27 ± 0.14	14.1 ± 3.9	22.0 ± 3.8	2.1 ± 0.1	30.6 ± 7.1	143 ± 28	114 ± 8	4.3 ± 1.0	2.1 ± 0.7
16	160	962	133	16.1 ± 6.9	9.3 ± 3.2	45.6 ± 4.8	4.5 ± 1.0	24.5 ± 6.5	7.71 ± 1.70	7.78 ± 0.92	1.26 ± 0.13	0.51 ± 0.06	10.1 ± 5.3	23.9 ± 2.6	2.0 ± 0.7	19.6 ± 9.4	152 ± 18	200 ± 61	5.8 ± 0.9	2.7 ± 1.3
17	170	1023	131.5	9.4 ± 2.9	13.3 ± 4.1	65.4 ± 5.9	4.0 ± 0.0	7.8 ± 7.0	7.90 ± 0.57	6.61 ± 0.82	0.9 ± 0.41	0.3 ± 0.18	14.5 ± 10.0	23.3 ± 3.0	2.2 ± 0.4	11.3 ± 2.7	176 ± 18	82.2 ± 15.4	6.7 ± 2.3	3.7 ± 1.2
18	180	1085	169.3	67.0 ± 0.9	28.7 ± 14.0	49.7 ± 3.1	5.0 ± 1.2	9.5 ± 11.1	8.45 ± 0.91	5.09 ± 1.64	0.54 ± 0.36	0.18 ± 0.15	27.5 ± 23.9	18.8 ± 1.6	0.7 ± 0.3	2.5 ± 1.3	70.3 ± 31.6	41.2 ± 22.3	4.4 ± 1.4	2.6 ± 0.7
19	190	1078	165.3	6.4 ± 1.7	10.3 ± 1.8	60.3 ± 2.9	6.5 ± 1.0	16.5 ± 4.7	8.75 ± 0.24	6.76 ± 0.84	1.14 ± 0.38	0.58 ± 0.54	29.7 ± 7.1	14.6 ± 2.2	1.3 ± 0.3	2.7 ± 3.1	89.7 ± 26.7	55.0 ± 15.7	2.9 ± 0.5	2.1 ± 1.3
20	200	1255	184.8	9.6 ± 5.0	11.9 ± 1.7	56.8 ± 6.7	6.5 ± 1.0	15.2 ± 2.3	7.45 ± 0.29	8.23 ± 1.67	1.79 ± 0.78	0.71 ± 0.33	23.3 ± 14.1	2.6 ± 0.5	2.2 ± 1.1	0.1 ± 0.1	192 ± 104	83.1 ± 40.8	3.8 ± 0.6	4.4 ± 2.1

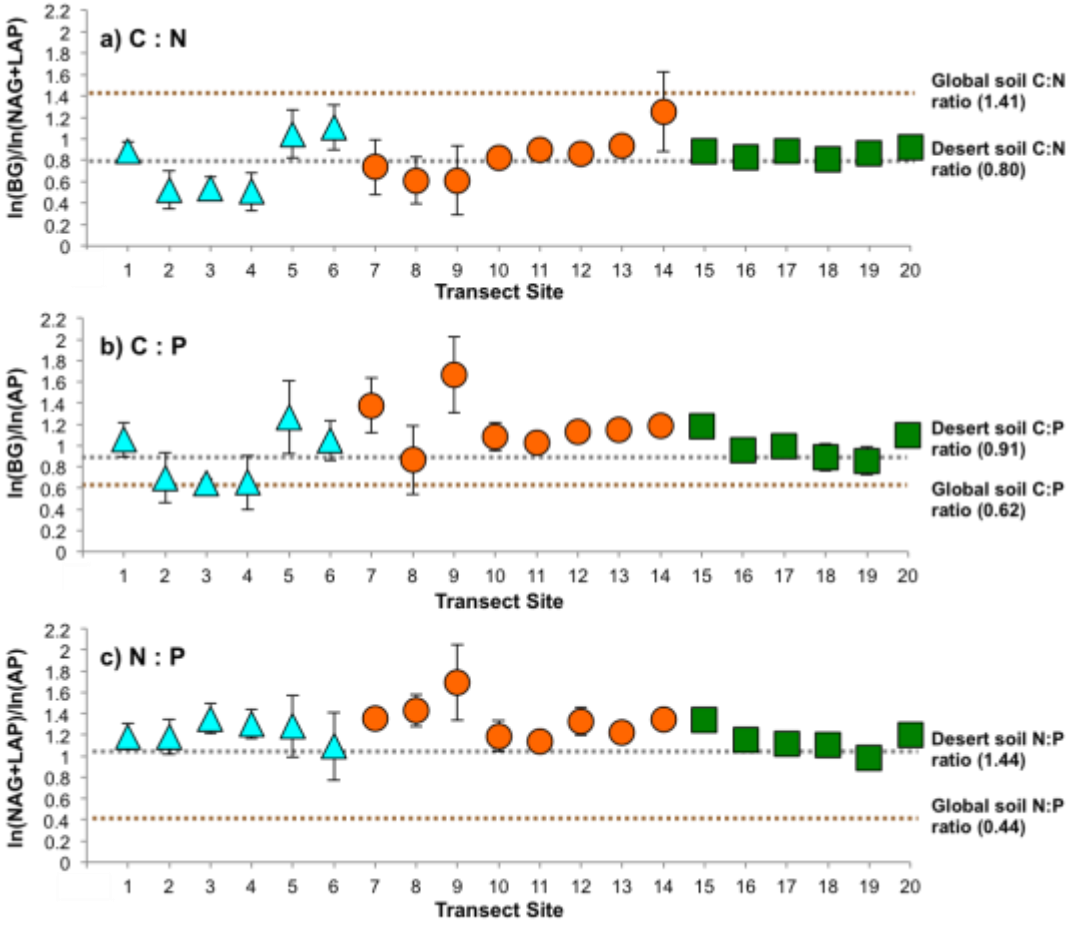
Supplementary Table 2: ANOVA results showing differences in the climatic and soil physicochemical properties overall, and between the three defined environmental zones. Significant values ($p < 0.05$) are designated in bold and by an asterisk. Df = degree of freedom, F = F value, and p = P value

		Organic Matter		Carbon		NH_4^+		NO_3^-		P		pH	
	Df	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Global Test	2,77	23.04	**<0.001***	17.12	**<0.001***	1.50	0.23	16.31	**<0.001***	11.47	**<0.001***	12.20	**<0.001***
Fog – Low Rain	1,54	9.98	**0.003***	3.40	0.071	2.61	0.11	19.51	**<0.001***	3.06	0.09	11.83	**0.001***
Fog – High Rain	1,46	34.79	**<0.001***	20.90	**<0.001***	0.57	0.45	13.46	**<0.001***	8.49	**0.006***	28.81	**<0.001***
Low Rain – High Rain	1,54	18.02	**<0.001***	17.06	**<0.001***	1.25	0.27	1.51	0.23	18.24	**<0.001***	3.70	0.060
		CEC		**Ca^{2+}**		**K^+**		**Mg^{2+}**		**Na^+**		**S**	
	Df	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Global Test	2,77	3.49	**0.035***	153.1	**<0.001***	14.95	**<0.001***	6.36	**0.003***	9.90	**<0.001***	159.47	**<0.001***
Fog – Low Rain	1,54	0.082	0.78	168.83	**<0.001***	11.75	**0.001***	9.51	**0.003***	11.09	**0.002***	175.65	**<0.001***
Fog – High Rain	1,46	6.19	**0.016***	150.42	**<0.001***	24.67	**<0.001***	4.39	**0.042***	8.73	**0.005***	154.25	**<0.001***
Low Rain – High Rain	1,54	4.38	**0.041***	5.06	**0.029***	5.56	**0.022***	1.60	0.21	1.23	0.27	4.48	**0.039***
		Coarse Sand		**Medium Sand**		**Fine Sand**		**Silt**		**Clay**			
	Df	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**		
Global Test	2,77	18.31	**<0.001***	0.76	0.47	7.52	**0.001***	1.97	0.15	2.41	0.79		
Fog – Low Rain	1,54	27.29	**<0.001***	2.37	0.13	15.97	**<0.001***	0.89	0.35	0.15	0.70		
Fog – High Rain	1,46	28.04	**<0.001***	0.06	0.81	5.68	**0.021***	3.66	0.06	0.51	0.48		
Low Rain – High Rain	1,54	0.43	0.51	0.64	0.43	1.64	0.21	1.39	0.24	0.12	0.73		

Supplementary Table 3. ANOVA results testing the differences in overall potential microbial activity and between xeric zones. Significant values ($p < 0.05$) are designated in bold and by an asterisk. Df = degree of freedom, F = F value, and p = p value; FDA = fluorescein diacetate hydrolysis, BG = β-glucosidase, NAG = β-N-acetylglucosaminidase, LAP = leucine aminopeptidase, AP = alkaline phosphatase, and PO = phenol oxidase

		FDA		BG		NAG		LAP		AP		PO	
	Df	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Overall	2,77	41.85	**<0.001***	12.93	**<0.001***	3.67	**0.030***	12.51	**<0.001***	16.28	**<0.001***	2.43	0.095
Fog – Low Rain	1,54	69.15	**<0.001***	13.26	**<0.001***	1.22	0.27	4.62	**0.036***	0.06	0.81	0.42	0.52
Fog – High Rain	1,46	92.90	**<0.001***	26.26	**<0.001***	2.31	0.14	25.51	**<0.001***	21.61	**<0.001***	2.25	0.14
Low Rain – High Rain	1,54	0.97	0.33	4.06	**0.049***	7.05	**0.01***	9.98	**0.003***	20.75	**<0.001***	4.45	**0.040***

Supplementary Figure S1. Carbon, Nitrogen and Phosphorous nutrient demands measured in the Namib Desert xeric transect. a) Potential C:N microbial nutrient demand estimated by the ratio of BG activity to the combined activities of NAG and LAP (BG:[NAG+LAP]). **b)** Potential C:P microbial nutrient demand estimated by the ratio of BG activity to AP activity (BG:AP). **c)** Potential N:P microbial nutrient demand estimated by the combined activities of NAG and LAP to AP activity ([NAG+LAP]:AP). The ratio of activities across 40 soil environments is denoted by a brown dashed line, and the ratio of activities across desert soils (n=3) is denoted with a gray dashed line (as measured by Sinsabaugh et al., 2009). ■ = 'Fog Zone' activities, ■ = 'Light Rain Zone' activities and ■ = 'High Rain Zone' activities.



Supplementary Figure S2. Rarefactions curves of Namib soil metaviromes. Rarefaction curves were generated based on a clustering of the predicted protein genes. Clustering (i.e. grouping) of predicted protein sequences was done through the detection of conserved domain (using the PFAM database) with a similarity threshold of 75%). The curve represents the number of different clusters created (y-axis) from a given number of sequences (x-axis).