Physical ecology of hypolithic communities in the central Namib Desert: The role of fog, rain, rock habitat, and light

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[1] Hypolithic microbial communities are productive niches in deserts worldwide, but many facets of their basic ecology remain unknown. The Namib Desert is an important site for hypolith study because it has abundant quartz rocks suitable for colonization and extends west to east across a transition from fog- to rain-dominated moisture sources. We show that fog sustains and impacts hypolithic ecology in several ways, as follows: (1) fog effectively replaces rainfall in the western zone of the central Namib to enable high (≥95%) hypolithic abundance at landscape (1–10 km) and larger scales; and (2) high water availability, through fog (western zone) and/or rainfall (eastern zone), results in smaller size-class rocks being colonized (mean 6.3 ± 1.2 cm) at higher proportions (e.g., 98% versus approximately 3%) than in previously studied hyperarid deserts. We measured 0.1% of incident sunlight as the lower limit for hypolithic growth on quartz rocks in the Namib and found that uncolonized ventral rock surfaces were limited by light rather than moisture. In situ monitoring showed that although rainfall supplied more liquid water (36 h) per event than fog (mean 4 h), on an equivalent annual basis, fog provided nearly twice as much liquid water as rainfall to the hypolithic zone. Hypolithic abundance reaches 100% at a mean annual precipitation (MAP) of approximately 40–60 mm, but at a much lower MAP (approximately 25 mm) when moisture from fog is available.

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1. Introduction

[2] Hypolithic microbial communities are cooccurring phototrophic and heterotrophic consortia inhabiting the undersides of translucent rocks (quartz, granite, limestone, and gypsum) in the world's major deserts [*Cameron and Blank*, 1965; *Friedmann and Galun*, 1974; *Cockell and Stokes*, 2004; *Warren-Rhodes et al.*, 2006, 2007b; *Pointing et al.*, 2009; *Cary et al.*, 2010; *Tracy et al.*, 2010; *Wong et al.*, 2010; *Khan et al.*, 2011; *Chan et al.*, 2012; *Pointing and Belnap*, 2012]. The rock substrate provides a stable refuge against wide temperature fluctuations, strong winds, high ultraviolet radiation, and moisture loss in hyperarid [≤25 mm mean annual precipitation (MAP)] and arid (>25–200 mm MAP) deserts [*Vogel*, 1955; *Friedmann et al.*, 1967; *Berner and Evanari*, 1978; *Büdel and Wessels*, 1991; *Cockell et al.*, 2008; *Cowan et al.*, 2010; *Wong et al.*, 2010]. These rock habitats shield moisture from excess evaporation by reducing the surface in direct contact with the atmosphere [*Vogel*, 1955; *Danalatos et al.*, 1995; *Li et al.*, 2009; *Kaseke et al.*, 2012; *Stomeo et al.*, 2013]. In extreme cold and hot deserts, hypolithic cyanobacterial communities play an important role in primary production and nitrogen fixation [*Allen*, 1997; *Cockell and Stokes*, 2004; *Warren-Rhodes et al.*, 2006; *Pointing et al.*, 2007; *Cowan et al.*, 2011] and serve as hot spots of biodiversity

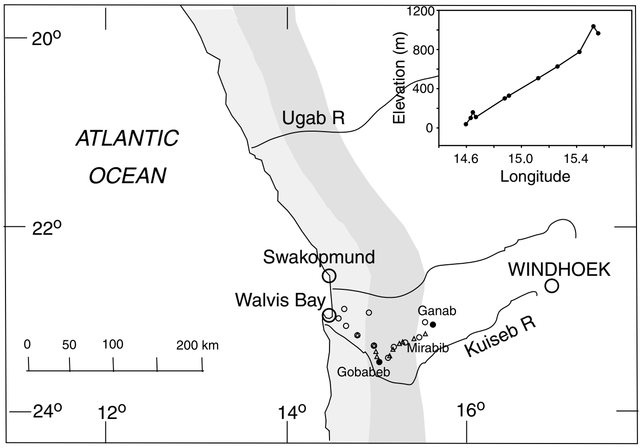

Figure 1. Map of central Namib Desert, with sampling sites shown: this study (open circles) and *Stomeo et al.* [2013] (open triangles). The light grey shaded region roughly indicates the fog-dominated zone. The dark grey shaded region indicates the rainfall-dominated zone.

amidst relatively depauperate open soil habitats [*Stomeo et al.*, 2013]. Previous studies suggest that these communities are clearly distinct from those of bare soil [*Smith et al.*, 2000; *Warren-Rhodes et al.*, 2006; *Pointing et al.*, 2007, 2009; *Cowan et al.*, 2010; *Wong et al.*, 2010; *Khan et al.*, 2011; *Makhalanyane et al.*, 2013; *Stomeo et al.*, 2013]. The advantages of hypolithic systems as functional models for landscape ecology and biogeography have been increasingly recognized [*Bahl et al.*, 2011; *Caruso et al.*, 2011; *Chan et al.*, 2012]. Indeed, a recent study of functional ecology in Antarctic hypoliths has revealed significant plasticity in photoautotrophic and heterotrophic pathways, including evidence for complete nitrogen cycling [*Chan et al.*, 2013]. In addition, the study has shown a range of novel stress response pathways among individual phyla that were postulated to confer adaptive benefits at the community level [*Chan et al.*, 2013].

[3] While hypolithic ecosystems have been studied in detail [*Friedmann et al.*, 1967; *Schlesinger et al.*, 2003; *Cockell and Stokes*, 2004; *Pointing et al.*, 2007; *Tracy et al.*, 2010; *Khan et al.*, 2011; for a review, see *Chan et al.*, 2012], relatively few desert-wide investigations of relative abundance and diversity have been undertaken [*Warren-Rhodes et al.*, 2006, 2007b; *Bahl et al.*, 2011; *Caruso et al.*, 2011]. Indeed, for most deserts, many basic ecological-climate questions have yet to be examined: For example, “How are hypolithic communities distributed at landscape scales?”; “Are different moisture sources equally effective in supporting hypolithic abundance?”; or “Is there a water availability threshold above which hypolithic communities colonize virtually all available habitat?” In answering these and other ecological questions, significant opportunities exist to broaden our understanding of hypolithic systems [*Chan et al.*, 2012], including in relatively well-studied areas, such as the Namib Desert.

[4] The Namib Desert (hereafter Namib) stretches nearly 2000 km south from Angola along the western coast of Namibia to South Africa (Figure 1). In the central Namib, where the current study was focused, a well-established west-east climate gradient exists [*Lancaster et al.*, 1984; *Eckardt et al.*, 2013]. Along this inverse fog-rainfall gradient, coastal stratus clouds penetrate 100–120 km inland from the coast, and fog predominates in the western 60 km (“fog-dominated” zone), where rainfall is relatively scarce (~10–20 mm yr^{-1}). Conversely, at roughly 50 km inland (near Gobabeb), inputs from fog sharply decline [*Lancaster et al.*, 1984; *Mendelsohn et al.*, 2009], but rainfall increases from 21 mm yr^{-1} at Gobabeb [*Eckardt et al.*, 2013] to 87 mm yr^{-1} at Ganab, located 120 km inland within the eastern, “rainfall-dominated” zone. At Ganab, the contribution from fog is effectively zero. As in other deserts, rainfall in the Namib is highly variable both interannually and intraannually, occurring as erratic and localized convective summer storms [*Besler*, 1972; *Gamble*, 1980; *Hachfeld and Jürgens*, 2000; *Eckardt et al.*, 2013].

[5] In the Namib, with its unique climate gradient, many fog-adapted fauna and flora exist, including beetles and succulent shrubs that glean moisture from fog and dew [*Louw*, 1972; *Hamilton and Seely*, 1976; *Louw and Seely*, 1980; *Polis and Seely*, 1990; *Henschel et al.*, 2001; *Henschel and Seely*, 2008]. Lichens and biological soil crusts also thrive in the fog-dominated zone [*Hachfeld and Jürgens*, 2000; *Lalley et al.*, 2006; *Büdel et al.*, 2009]. In contrast to these well-studied ecosystems, relatively few systematic surveys of hypolithic community ecology have been done in the region [*Vogel*, 1955; *Büdel et al.*, 2009; *Stomeo et al.*, 2013]. This is especially true for the fog-dominated zone of the Namib’s quartz-abundant gravel plains [*Logan*, 1960; *Eckardt et al.*, 2001; *Miller*, 2008; *Makhalanyane et al.*, 2013], which are known to harbor hypolithic microbial communities [*Vogel*, 1955; *Kappen*, 1982; *Büdel and Wessels*, 1991; *Schmiedel and Jürgens*, 1999; *Büdel et al.*, 2009]. Indeed, with the exception of a single coastal site in the Chilean Atacama Desert [*Azua-Bustos et al.*, 2011], the effect of fog on hypolithic abundance is just beginning to be broadly examined for any desert.

[6] The central Namib is an ideal environment to study basic physical features of hypolithic ecology. The widespread occurrence of gravel plains with an abundant distribution of quartz, from small pebbles to large rocks, makes this location valuable for examining the effects of rock size on colonization and enables comparison with similar studies elsewhere, in the Atacama (Chile), Taklimakan (China), and Mojave (U.S.) Deserts. Furthermore, the presence of the well-documented fog-rainfall gradient [*Henschel*, 1999; *Eckardt et al.*, 2013] facilitates a systematic examination of the effects of varying dominant water sources on hypolithic colonization. For this study, we established a research transect that followed the central Namib’s natural climate gradient, centered about the Gobabeb research station. Along the transect, *Stomeo et al.* [2013] analyzed the composition of microbial soil and hypolithic communities at multiple sites. They found variations in microbial community structure between open soil and hypolithic communities and suggested that the latter exhibited a fog-related distribution. Soil salinity was also determined to be an environmental factor influencing both soil and hypolithic community composition.

[7] Here we report on hypolithic abundance and physical ecology parameters, moisture, rock size, and light, particularly along the same transect (Figure 1). In addition to sites surveyed by *Stomeo et al.* [2013], we included additional

sites spanning the fog and rainfall zones to address colonization on a landscape scale. Furthermore, we collected regional and in situ microclimate environmental data at several sites to gauge the role of fog (and rainfall) at multiple spatial scales. Our results are examined within the context of other deserts to ascertain patterns observed for rock size and water abundance relationships.

2. Methods

2.1. Field Sites

[8] Eleven experimental sites (six in the fog-rich zone and five in the rainfall-dominated zone) were surveyed between April 2010 and April 2012 along a west-east transect of the central Namib [*Logan*, 1960; *Eckardt et al*., 2001; *Kaseke et al*., 2012] (Figure 1). To minimize geological variation, study sites of similar rock and soil type (i.e., quartz gravels) were selected along a tight latitudinal transect (22.7–23.6°S), which also minimized among-site mean annual temperature variations [*Lancaster et al*., 1984]. Previous geochemical analyses revealed that the total soil carbon, nitrogen, sodium, potassium, and magnesium contents varied across the transect (for further detailed descriptions of surficial geology and mineralogy, see *Makhalanyane et al*. [2013] and *Stomeo et al*. [2013]), but only soil salinity played a role in hypolithic and soil bacterial community diversity, and its effect was localized to coastal zones (~30 km from the coast). Two of the 11 sites exhibited moderate to heavy mechanical disturbance by vehicles and/or animals, which resulted in loose soils and overturned rocks. In order to ensure consistent comparison, disturbed sites were excluded from the present analysis.

2.2. Hypolithic Abundance

[9] Macroscopic hypolithic assemblages were visually identified on upturned quartz rocks as light to dark adherent biofilm [*Cockell and Stokes*, 2006; *Büdel et al*., 2009; *Pointing et al*., 2009; *Lacap et al*., 2011]. Visual assessment of hypolithic colonization has been shown as a robust method in landscape ecology studies [*Warren-Rhodes et al*., 2006, 2007b, 2007c; *Pointing et al*., 2009; *Wong et al*., 2010]. The cyanobacteria-dominated biofilms are clearly visible with the naked eye [*Vogel*, 1955], and in assessments of thousands of colonized versus uncolonized rocks, this observation has been correlated with cyanobacterial biofilms in 100% of cases [*Warren-Rhodes et al*., 2006, 2007b, 2007c; *Pointing et al*., 2009; *Wong et al*., 2010] and reviewed in *Chan et al*. [2012]. Detailed hypolithic and soil community biodiversity results for sites across the west-east transect are reported elsewhere [*Stomeo et al*., 2013].

[10] Hypolithic abundance is defined herein as percent colonization (no. of colonized rocks/total quartz rocks × 100). Sampling design and field methods from plant and animal landscape ecology were used to measure percent colonization [*Andrew and Mapstone*, 1987; *Krebs*, 1999; *Warren-Rhodes et al*., 2007b]. A pilot study (April 2010) was conducted at Mirabib (Figure 1) to optimize the sampling method. The pilot study was carried out by randomly placing a single 1 m × 20 m transect within the site. All quartz rocks ≥5 cm in the transect were counted, visually inspected, and measured (maximum length, nearest 0.5 cm). (The 5 cm size cutoff for the main study was chosen from the results of a separate study of 100 small rocks at Mirabib showing that 100% of rocks in the 2–5 cm size class were colonized.)

[11] Mirabib pilot study results showed 100% hypolithic colonization in the transect; thus, the sampling protocol was simplified (compared to previous deserts, e.g., see *Warren-Rhodes et al*. [2007b]) by using a random walk method [*Krebs*, 1999], which provided identical results to the transect method. A minimum sample size of 100 rocks per study site was chosen to achieve a ±10% ($\sqrt{n}/n$) sampling error. In addition to site colonization studies, detailed spatial investigations of colonization patterns of a large quartz rock cluster (144 m^2, Figure 2a) were also completed at Mirabib (E15.42°, S23.44°), with methods identical to those used in the Atacama Desert [*Warren-Rhodes et al*., 2007c]. Briefly, at Mirabib, a 1 m^2 quadrat grid (1 cm × 1 cm smallest mesh grid size) was used to examine all quartz rocks within the cluster and map rock (colonized and uncolonized) spatial distribution (i.e., *x–y* orientation). Within the quadrat, all quartz rocks ≥5 cm were counted, sized (maximum length, vertical thickness/height), and recorded spatially.

[12] Macroscopic colonization patterns and microclimate (see below) of individual rocks were also examined at Mirabib and Gobabeb (Figures 2b-2d). For colonized rocks, general rock parameters (vertical height, maximum length) and specific facets of colonization [rock face/directional orientation; vertical depth of colonized zone from the soil surface/rock interface and/or the rock bottom (nearest 0.1 cm); thickness of the colonization zone] were measured [see *Warren-Rhodes et al*., 2007c].

2.3. Regional Climate Data and Hypolithic Community Microclimate Field Measurements

[13] Long-term mean annual rainfall and fog data were obtained from the historical literature [*Lancaster et al*., 1984; *Henschel et al*., 2001; *Eckardt et al*., 2013] and from the Namibia Meteorological Service. For the period 28 April to 31 July 2010, in situ rainfall, fog (vertical 1 m^2 Standard Fog Collectors), and dew (1 m^2 Polycarbonate Standard Dew Collector; OPUR foil, *Eckardt et al*. [2013]; collector designed and provided by Simon Berkowicz, Hebrew University, Jerusalem) values were obtained from the Gobabeb meteorological station [*Seely and Henschel*, 1998; *Seely et al*., 1998]. Detailed microclimate studies of the hypolithic community habitat, i.e., the quartz-soil interface, were completed at two sites: the Gobabeb meteorological station (E15.05°, S23.57°) and Mirabib (E15.42°, S23.44°), ~25 km northeast of the Gobabeb station. A single, large quartz rock at each site was instrumented with miniature (16 mm diameter × 6 mm height) iButton® data loggers (DS 1923: temperature sensor operating range −20°C to +85°C, ±0.5°C accuracy; and relative humidity (RH) sensor operating range 0–100% RH, ±5% accuracy; Maxim Integrated Products, Sunnyvale, CA). The data loggers recorded at 90 min intervals and were placed directly in the soil on the sides and bottoms of rocks (Figure 2b), taking care not to disturb adherent hypolithic biomass. Sensors were placed both in proximity to colonized and uncolonized areas and at various depths and rock face orientations. To test the RH sensors, 50 ml of water was applied to each side (~60 cm^2 area per side) of a quartz rock at the Gobabeb station (hereafter "Gobabeb rock"), equivalent to ~5 mm rainfall (Figure S1 in the supporting information).

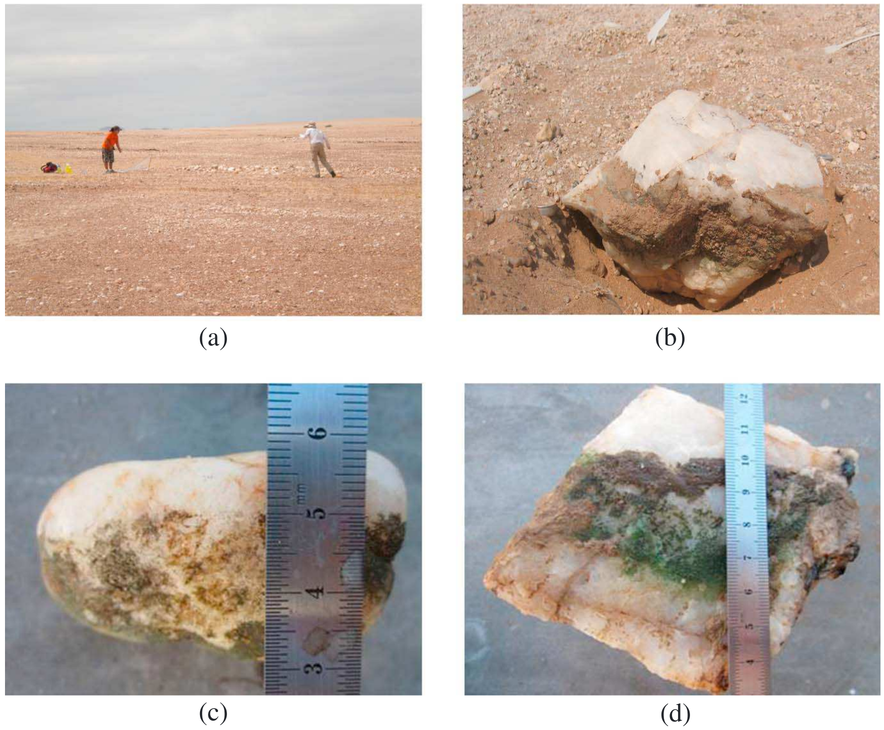

Figure 2. (a) Rock cluster in foreground at Mirabib site. (b) Quartz "microsensor" rock at Gobabeb with iButton sensors (~16 mm diameter × 6 mm thickness) seen in the left and right foreground. Shown is the northwest rock orientation heavily colonized by green-colored hypolithic communities. (c) Quartz rock with visible green hypolithic colonization from the soil/rock surface down to and on the rock bottom. (d) Visible green hypolithic band on the quartz rock, with the uncolonized zone at the deepest part of the rock.

Based on previous studies [*Schlesinger et al*., 2003; *Warren-Rhodes et al*., 2007a], liquid water was assumed present when the soil RH sensors reached ≥95%, as corroborated by field trials, including those at the Gobabeb field station. Although lichen communities can initiate photosynthesis at approximately 70% RH, our choice of the 95% RH cutoff reflects the predominantly cyanobacterial component of hypolithic communities, which require a higher %RH or liquid water to initiate photosynthesis [*Potts and Friedmann*, 1981; *Palmer and Friedmann*, 1990; *Lange et al*., 1994; *Schlesinger et al*., 2003; *Tracy et al*., 2010].

[14] The abundant quartz substrate near the Gobabeb station also provided an ideal setting to examine the impacts of light levels on hypolithic community physical ecology and to test whether light or water constraints limit hypolithic colonization on individual rocks. Light measurements were conducted on 24 rocks colonized by hypoliths collected from the gravel plains about a kilometer northwest of the Gobabeb station. Twelve of the rocks, ranging from 2 to 5 cm in total vertical thickness (or "height") were colonized by visible green biomass from the soil/rock surface to the deepest part of the rock and on the rock bottom (Figure 2c). The other 12 rocks, ranging from 7 to 12 cm in total vertical thickness, were colonized from the soil/rock surface to varying rock depths (i.e., "bathtub" ring of colonization, Figure 2d) but had uncolonized rock bottoms. For each rock, the total vertical height, the thickness of the colonized zone, and the thickness from the uncolonized zone to the bottom of the rock were measured to the nearest centimeter. The visible hypolithic community on each colonized rock was removed with a brush and paper towels. A Li-Cor model LI-185A quantum photometer (photon flux detection range 0.05–30,000 μmol m^{-2} s^{-1}, calibration error ±5%, and 8 mm sensor diameter) was pointed directly to the Sun, and the photon flux of direct midday sunlight [photosynthetically active radiation (PAR), 400–700 nm] was measured in μmol m^{-2} s^{-1}. The light sensor was then placed against the rock's ventral surface and black putty applied to eliminate ambient light at the rock-sensor juncture. Aluminum foil was wrapped around the sensor and rock to the soil line, and a measurement was made of the photon flux passing through the rock. Every effort was made to place the sensor in a representative area near the center of the ventral surface. Percent transmittance was calculated from light transmission through the rock divided by the average strength of direct sunlight, measured before and after the rock measurement, and multiplying by 100.

2.4. Statistical Analyses

[15] Chi-square analyses were performed to examine the null hypothesis that the proportion of colonized rocks by size and across Namib sites is the same. The chi-square analyses were also used to compare the proportion of colonized rocks in the Namib to other deserts [Atacama (Chile), Taklimakan (China), and Mojave (U.S.) Deserts]. The proportions were computed from the number of colonized quartz rocks for each size class divided by the total number of sampled quartz rocks for each size class within each region. All analyses were conducted using statistical software R (version 2.14.0). The chi-square analyses across the class sizes are reported based on 3 degrees of freedom,

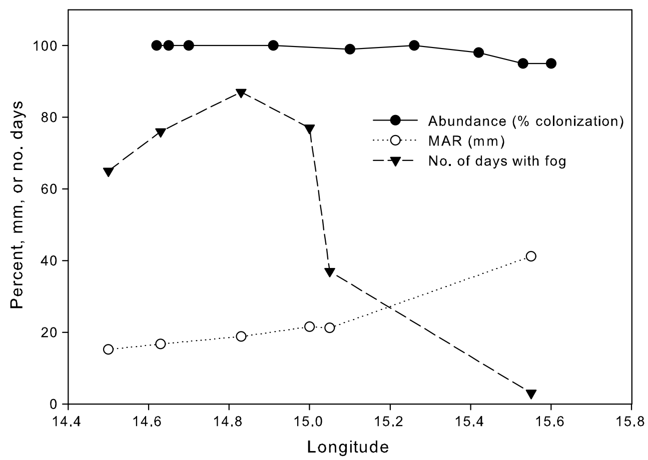

Figure 3. Hypolithic abundance measured as percent colonization at nine study sites along the fog-rainfall gradient. Two disturbed sites are excluded. The mean annual rainfall (mm) and the mean annual number of days with fog for the central Namib's major meteorological stations are from *Lancaster et al*. [1984].

and statistical significance was assessed at $\alpha < 0.05$. The degrees of freedom across regions was dependent on the number of regions examined for each research question and is reported within the corresponding results.

3. Results

3.1. Hypolithic Abundance, Regional Climate, and Abiotic Soil Data

[16] The mean percent colonization for all undisturbed sites was 98% and did not vary between fog- versus rainfall-dominated zones (Figure 3), despite a fourfold disparity in mean annual rainfall [*Lancaster et al*., 1984; *Eckardt et al*., 2013]. [In contrast, disturbed sites, which were excluded from the study, had substantially lower percent colonization: 50% (heavily disturbed site) to 70% (moderately disturbed site) colonization.]

[17] Soil salinity varied significantly across the sites and played a role in hypolithic and soil bacterial community diversity across the transect [*Stomeo et al*., 2013], but in the current study, it showed no statistically significant relationship to colonization. The mean colonized rock size was 6.3 ± 0.1 (SE) cm, simply reflecting the size of available quartz rocks. Unlike for previously studied hyperarid deserts (Figure 4), the percentage of rocks colonized did not vary by size class ($\chi^2(3) = 0.98$, $P = 0.807$) or across sites within the Namib ($P > 0.50$ for all rock classes).

3.2. Quartz Cluster Colonization and Rock Characteristics

[18] Detailed studies of the Mirabib site cluster (Figure 2a) showed 98% colonization of available quartz rocks and a mean colonized rock size of 8.8 ± 0.3 cm. Colonized rocks in the cluster were firmly cemented in the gravel pavement, while uncolonized rocks were generally lying loose on the soil surface. Of the 269 rocks in the cluster, only six (all in the 5.1–7 cm size class) were uncolonized. Colonized rocks in the cluster had a mean height of 4.8 ± 0.3 cm and ranged from 5 to 50 cm in length.

3.3. Hypolithic Community Rock Microclimates at the Gobabeb and Mirabib Sites

3.3.1. Light in the Hypolithic Habitat

[19] Small colonized rocks (2–5 cm in height/total vertical thickness) transmitted 0.1%–8% of incident sunlight to colonized rock bottom surfaces (Table 1a). In contrast, large rocks (7–12 cm in height) transmitted 0%–0.07% of incident light to bottom surfaces, where hypoliths were absent (i.e., below the zone of colonization) (Table 1b), indicating that uncolonized zones are light limited. Thus, the minimal quantity of light needed for hypolithic growth in Namib appears to be at or above 0.1% of direct sunlight.

3.3.2. Colonization Pattern

[20] The Gobabeb rock outfitted with microclimate sensors measured 13 cm (length) × 12 cm (width) × 12 cm (height or thickness). A band of colonization (Figure 2b), ranging from 1 to 7 cm in thickness, extended around the rock's perimeter. From visual observations, the band appeared thickest (5–7 cm) on the northwest rock orientation (G1–G3 iButton® sensors). Sparsest visible colonization was on the south-southwest orientation (G6–G7 sensors). Colonization was not observed at depths ≥7 cm from the soil surface at any orientation, including the rock bottom (G1 sensor). The Mirabib rock outfitted with microclimate sensors measured 14 cm (length) × 9 cm (width) × 8 cm (height). A thick colonization band was present on all sides of the rock from the rock-soil surface interface to the rock bottom (5 cm from the soil surface, M8 sensor; or 8 cm from the top of the rock).

3.3.3. Rainfall, Fog, and Dew at Gobabeb and Mirabib

[21] Free water (rainfall, fog, and dew) is present on soil/rock surfaces at Gobabeb for ~40% of d yr^{-1} [*Henschel and Seely*, 2008]. Prevailing winds transport cool moist sea air inland to Gobabeb, and stratocumulus fogs ("high fog") form frequently (37–67 d yr^{-1}), with a strong northerly/northeasterly flow associated to them [*Lancaster et al*., 1984; *Seely and Henschel*, 1998; *Henschel and Seely*, 2008; *Eckardt et al*., 2013]. When present, these fog events are associated with relative humidity to saturation levels. Radiation or ground fogs rarely develop at Gobabeb on calm

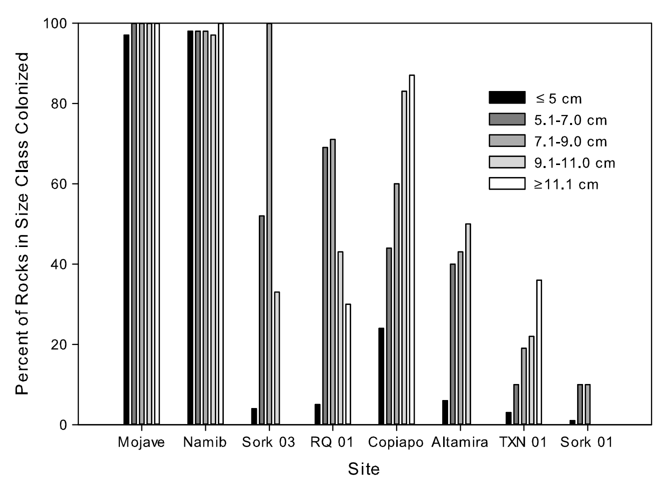

Figure 4. Percent of rocks in a size class that are colonized in deserts around the world, including the Mojave, Namib, Atacama (Copiapo, Altamira), and western China (Sork 01, RQ 01, Sork 03, TXN 01).

Table 1. Light Transmittance Measurements of Small (Colonized to the Bottom of Rocks) and Large (With Deep Uncolonized Zones) Quartz Rocks With Visible Hypolithic Biomass Near the Gobabeb Research Station[a]

(a) Small Colonized Rock Samples

Total Rock Thickness (cm)	Thickness of the Colonized Zone (cm)	Direct Sun Before Measurement	Light Level Below Rock	Direct Sun After Measurement	Percent Transmittance
5.0	1.0	1860	8.6	1860	0.46
2.5	1.0	1840	2.0	1840	0.11
4.0	2.0	1850	40	1860	2.2
3.0	2.0	1860	21	1860	1.1
4.5	0.5	1850	4.5	1850	0.24
3.0	2.0	1810	12	1800	0.66
3.5	1.5	1800	17	1800	0.94
2.0	1.0	1800	150	1810	8.3
4.5	2.0	1800	21	1760	1.2
4.0	1.5	1780	28	1780	1.6
4.0	1.0	1750	8.5	1790	0.48
2.5	0.5	1780	71	1800	4.0

(b) Large Rocks With Colonization Band and Uncolonized Zones at Depth

Total Rock Thickness (cm)	Thickness of the Colonized Zone (cm)	Thickness of the Uncolonized Zone (cm)	Direct Sun Before Measurement	Light Level Below Rock	Direct Sun After Measurement	Percent Transmittance
8.0	5.0	0.5	1790	0.10	1780	0.006
8.0	5.0	0.2	1750	0.25	1730	0.01
6.0	4.0	0.2	1750	0.5	1750	0.03
7.0	4.0	0.4	1740	0.21	1720	0.01
8.0	5.0	1.5	1730	0.02	1700	0.001
7.0	3.5	0.5	1680	1.15	1700	0.07
12	6.0	2.0	1670	0.01	1640	0.0006
6.0	3.0	1.5	1620	0.01	1640	0.003
8.0	4.0	2.0	1580	0.38	1580	0.024
6.0	4.5	0.5	1580	0.16	1580	0.01
6.0	3.5	1.0	1580	0.05	1580	0.003
7.0	5.0	0.5	1560	0.17	1570	0.011

[a]All light measurements are photon fluxes in μmol m^{-2} s^{-1}.

mornings, although advective high fogs coming with a northerly breeze are the major fog source in the Namib interior [*Seely and Henschel*, 1998].

[22] Microsensor data for the Gobabeb station (recorded as the number of hours of liquid water for each sensor position) show that during the 3 month monitoring period (April–July 2010), a 10 mm rainfall (1 May 2010) and multiple intermittent fog and dew events (Table 2) occurred. For the rocks outfitted with sensors at Gobabeb and Mirabib, in situ data revealed that both rainfall and fog events supplied liquid water to hypolithic communities (Table 2). At both sites, the 1 May rainfall event delivered 50.5–56.5 h (≥95% RH cutoff) liquid water to hypolithic communities at the surface to 2 cm depths. By comparison, each of five individual fog events supplied a mean of 6.2 h liquid water to these same depths (Table 2). Only liquid water from rainfall reached hypoliths at ≥5 cm depths.

Table 2. Number of Hours Liquid Water (≥95% RH) Provided by Moisture Events (First Two Left-Hand Columns) as Recorded by In Situ %RH Sensors (30 April to 29 July 2010) at Multiple Depths (Soil Surface to 10 cm) and Rock Face Orientations at Gobabeb (G) and Mirabib (M)[a]

Date	Gobabeb Station Data	G3, 1 cm[b]	G2, 5 cm[b]	G1, 10 cm[b]	G6, 3 cm[c]	G7, 2 cm[c]	G4, 2 cm[d]	G5, 2 cm[e]	M10, surface[f]	M9, 1 cm[f]	M8, 5 cm[f]
5/1/10	Rain	36	213	255	99	57	65	68	36	65	521
5/13/10	Fog	0	0	0	0	0	1.5	0	0	0	0
6/9/10	Dew	0	0	0	0	0	0	0	0	0	0
6/10/10	Fog	1.5	0	0	0	0	0	0	0	0	0
6/11/10	Dew	0	0	0	0	0	0	0	0	0	0
7/6/10	Fog	0	0	0	0	0	0	0	0	0	0
7/10/10	Fog	9	0	0	0	0	10.5	12	6	0	0
7/23/10	Fog	1.5	0	0	0	0	6	9	0	0	0
7/26/10	Fog	0	0	0	0	0	0	4.5	0	0	0
Total		47.5	213	255	99	57	83	93.5	42	65	521

[a]The source of liquid water is confirmed by the Gobabeb Meteorological Station fog, rain, and dew collectors for the same event period.
[b]NW face of the rock.
[c]W/SW face of the rock.
[d]NE face of the rock.
[e]SE face of the rock.
[f]North face of the rock.

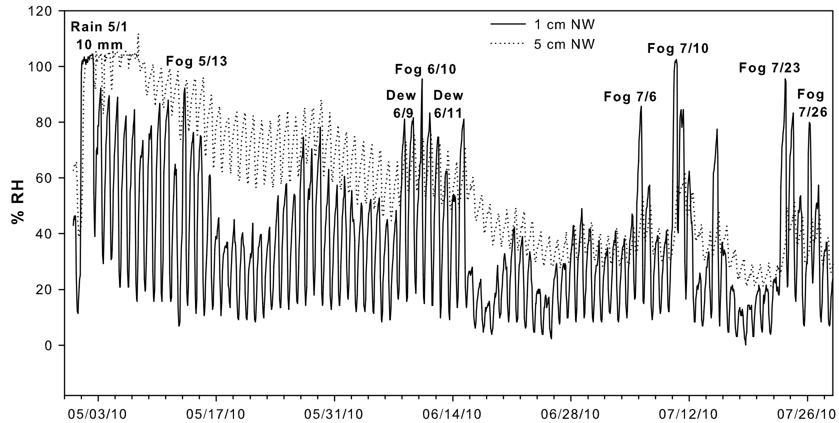

Figure 5. Relative humidity (RH) iButton sensor data (29 April to 30 July 2010) for the Gobabeb microsensor rock. Soil %RH sensors on the NW rock side (G1–G3 sensors, see Figure 2b and Table 2) at 1 cm and 5 cm depths near the green band of hypolithic colonization.

[23] It is very difficult to quantitatively relate fog to rain. Although fog is sometimes reported in terms of milliliters, this refers to the specific collection geometry and catching area of the collector and cannot directly be compared to millimeters of rain. In this study, wetting at depth of the soil-rock interface was measured and correlated to rain and fog events during the study's measurement interval. This method allowed a quantitative comparison of the efficacy of water provided to the hypolithic community habitat by fog or rain.

[24] Specifically, at Gobabeb, both the simulated and the 1 May rainfall events provided ~3.3–3.6 h liquid water per millimeter rainfall to hypoliths at a 5 cm depth. By comparison, fog supplied approximately 1.1 mm of liquid water per event to hypoliths at the surface to 1 cm depths, similar to the 0.88–1.1 mm previously recorded for Gobabeb [*Kaseke*, 2009]. Assuming a fog frequency of 37 days annually [*Lancaster et al.*, 1984], the equivalent amount of liquid water is 41 mm yr^{-1}. Although this comparison is preliminary, fog appeared to provide nearly twice as much water as rainfall to the areas where hypolithic communities were present.

[25] For each rock at the two sites, the duration of liquid water from rainfall maximized at a subsurface depth, with the highest number of hours of liquid water at ≥5–10 cm (G1, M8, rock bottoms) (Table 2). Similar to the effects of the rock substrate above, upper soil surface layers can shield those below from excess evaporation and thus act as a buffer for deeper layers, hence the longer hours of wetness [*Li*, 2002; *Danalatos et al.*, 1995; *Kaseke et al.*, 2012]. As shown in Figure 5 (and Figure S1), in comparison to the upper soil surface layers (surface to 1 cm), where diurnal fluctuations are large and moisture loss is rapid following fog and rain events, the ≥2–5 cm depths consistently showed higher humidity and less fluctuation.

[26] Fog events at Gobabeb and Mirabib during the measurement period produced liquid water accounting for roughly 15–30% of the total hours of liquid water available to hypoliths at the soil-rock surface interface to 2 cm soil depths (Table 2). Fewer hours of liquid water from fog persisted when morning soil temperatures were higher (10 July versus 23 July events at Gobabeb). Dew events did not provide liquid water to the hypolithic habitat, although an increase in soil %RH at 1–5 cm depths to 83% RH was recorded on several occasions (Figure 5).

4. Discussion

4.1. Hypolithic Distribution and Regional Climate

[27] Hypolithic communities have been studied in many of the world's hot and cold deserts [*Cameron and Blank*, 1965; *Friedmann and Galun*, 1974; *Büdel and Wessels*, 1991; *Smith et al.*, 2000; *Cockell and Stokes*, 2004; *Warren-Rhodes et al.*, 2006, 2007b; *Pointing et al.*, 2009; *Cowan et al.*, 2010; *Tracy et al.*, 2010; *Wong et al.*, 2010; for a review, see *Chan et al.*, 2012]. Surprisingly, only recently has research begun to test landscape ecology hypotheses and identify generalizable relationships between hypolithic microbial systems and their environment over multiple scales [*Warren-Rhodes et al.*, 2007b; *Bahl et al.*, 2011; *Caruso et al.*, 2011; *Stomeo et al.*, 2013]. Identifying these relationships can be complex due to the inherent variability of the multiple factors affecting these communities across desert regions.

[28] In the current study, we took advantage of a natural, well-established climate gradient across the quartz gravel plains of the central Namib to examine the impact of fog and rainfall on hypolithic abundance. Our results show virtually 100% colonization of quartz substrate across the entirety of the gradient. Evidence from the current study clearly demonstrates for the first time that fog is as effective as rainfall in supporting hypolithic cyanobacterial communities across wide landscape scales. It also points to a specific water availability threshold (discussed below) that enables full colonization, if met, but which varies according to relative and absolute availability of specific water sources.

[29] In the western central Namib, if fog were excluded as a moisture source, colonization should be extremely low (approximately 20%), based on comparable data from earlier studies (Figure 6) [*Warren-Rhodes et al.*, 2006, 2007b]. Instead, persistent fog provides a predictable and reliable supply of moisture [*Vogel*, 1955; *Kappen*, 1982; *Pietruszka and Seely*, 1985; *Olivier*, 1993; *Henschel et al.*, 2001; *Shanyengana et al.*, 2002] that enables hypolithic colonization to approach 100% despite rainfall levels that would be hyperarid. Conversely, in the central Namib's eastern rainfall-dominated zone, rainfall (with little to no contribution from fog) is sufficiently high to support full colonization. Together, fog and rainfall sources combine across the central Namib to explain the abundant and homogeneous distribution

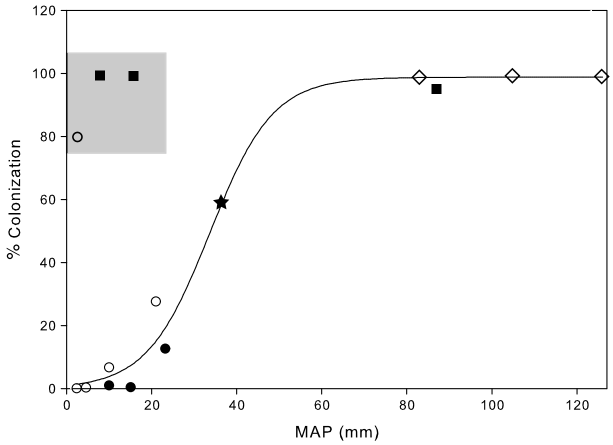

Figure 6. Hypolithic abundance versus MAP (mm). Open circles = Atacama Desert; filled circles = western China deserts; star = Gobi Desert [*Allen*, 1997]; open diamonds = Mojave Desert [*Schlesinger et al*., 2003] (K. Warren-Rhodes, unpublished data, 2012); filled squares = Namib Desert (representative sites, not all from the current study shown). The shaded grey area indicates sites with significant fog (coastal Atacama, *Azua-Bustos et al*. [2011]; Namib fog-zone sites).

of hypolithic communities. The results broaden findings from a single coastal Atacama location, where the presence of frequent coastal fog sustained high (80%) hypolithic abundance under otherwise hyperarid conditions [*Azua-Bustos et al*., 2011]. Interestingly, *Stomeo et al*. [2013] found variations in hypolithic community structure between fog- and rainfall-dominated sites in the central Namib. Taken together with our findings, this indicates that water availability dominates hypolithic abundance at landscape scales, whereas hypolithic community diversity is more sensitive to soil salinity and water source (fog versus rainfall).

4.2. Colonization and Rock Size

[30] The current study results showed no significant differences in rock size classes colonized by hypoliths in the fog-rich Namib [chi-square: $\chi^2(3) = 0.98$, $P = 0.807$ for all rock size classes], in contrast to results for other hyperarid deserts [Taklimakan: $\chi^2(3) = 437.4$, $P < 0.0001$; Atacama: $\chi^2(3) = 191.3$, $P < 0.0001$] [*Warren-Rhodes et al*., 2006, 2007b, 2007c; *Azua-Bustos et al*., 2011]. In the Namib, all rock size classes had nearly 100% colonization, whereas in the driest sites of the Atacama and China, colonization of abundant small rocks was rare (approximately 1–10%). This marked difference in habitability was especially evident for the clump study in both the Namib (Mirabib) and Atacama deserts (Aguas Calientes) (chi-square $P < 0.0001$ for all size classes). These findings are further reinforced by results from the driest part of the Mojave Desert, where both rainfall (MAP, ~200 mm yr^{-1}) and colonization are comparably high (K. Warren-Rhodes, unpublished data, Figure 4). These findings support the hypothesis that hypoliths in hyperarid deserts prefer large to small stones [*Warren-Rhodes et al*., 2006, 2007b]—likely due to the former's ability to redistribute, collect, and retain larger volumes of scarce moisture [*Vogel*, 1955; *Warren-Rhodes et al*., 2007c]. In deserts with greater water availability, such as the Namib or Mojave, hypolithic organisms exhibit no preference for rock size.

4.3. Microclimate, Water Availability, and Light in the Hypolithic Habitat

[31] In situ microclimate monitoring at Gobabeb and Mirabib captured both significant rain and fog events during the 3 month investigative period. Several important insights are evident, as follows: (1) microclimate conditions, namely, liquid water availability and light, satisfactorily accounted for colonization patterns on individual rocks, with the lower depth limit of colonization dictated by light penetration; (2) the heaviest colonization occurred at rock depths correlated with the most stable and abundant moisture environment down to the depth set by the limit of light availability; and (3) dew did not appear to be a significant source of liquid water to hypoliths during the period recorded. Given the short-term nature of the data, it will be necessary to further test these insights with long-term studies.

[32] Hypolithic colonization patterns of individual rocks reflect the microscale interplay of moisture availability, temperature, and light penetration [*Vogel*, 1955; *Warren-Rhodes et al*., 2007c]. Colonization of the Gobabeb rock was heaviest at ~2–5 cm—the depth where combined moisture from rainfall and fog was the most stable and most available. The stability of moisture at the 2–5 cm depth is supported by previous work [*Kaseke*, 2009] that suggests the creation of a vapor gradient at this depth, facilitating downward water movement into the soil following surface-level inputs. Moisture recharge to the 5 cm layer from below may be also occurring. In a recent study at Gobabeb, *Kaseke* [2009] has measured net average daily input into quartz gravel soils from nonrainfall sources (including water vapor adsorption, fog, and dew) to be 1.67–13.16 mm. In combination, these two gradients convey and concentrate water in the 2–5 cm layer, as reflected by the higher humidity and hypolithic colonization.

[33] Light measurement and rainfall data revealed that colonization is restricted by light rather than water limitations at depths >5 cm. In contrast to the 2–5 cm zone, colonization was absent at rock depths (≥7 cm for the Gobabeb rock) where light transmittance dropped to ≤0.1% of incident sunlight despite significant microsensor recorded inputs from rainfall (Table 2, G1 sensor).

[34] In our study, dew events were recorded by the Gobabeb station but did not provide liquid water to the hypolithic habitat. This result confirms that of *McKay et al*. [2003] for the Atacama Desert, where dew was present but did not provide moisture to the undersides of rocks, and that of *Kaseke* [2009] for the Namib, where minimal moisture contribution by dew to hypoliths at Gobabeb was found. Thus, although dew has been reported as a moisture source for soil crusts, lichens, and mosses [*Vogel*, 1955; *Kappen*, 1980; *Kidron et al*., 2002], its efficiency as a moisture source remains unclear [*Agam and Berliner*, 2006], and our results suggest that its importance to hypoliths in the Namib may be negligible.

5. Conclusions

[35] This landscape-scale study of the central Namib identifies water availability as a key element in determining hypolithic community abundance across large spatial scales.

As shown in Figure 6, empirical data for "high rainfall, 100% colonization" and "low rainfall, ≤20% colonization" are well represented, and full colonization likely occurs at a threshold of approximately 40–60 mm MAP when no other moisture inputs than rainfall are available. In contrast, when additional inputs from fog are available, such as in the Namib, the threshold for full colonization can be independent of rain. Moreover, as greater water availability occurs, physical habitat constraints that limit colonization elsewhere, such as rock size, become less relevant, including at landscape scales.

[36] At smaller scales, the responses of hypolithic communities to microclimate variations were also detectable. Hypolithic communities in the Namib sites colonized individual rocks at depths that reflected light limitations (0.1% of incident sunlight) and optimized water availability and duration, similar to those shown for lichens and biological soil crusts [*Bowker et al*., 2006; *Lalley et al*., 2006]. This highlights commonalities between desert microbial systems in some aspects of their adaptations to xeric conditions and warrants further study.

[37] Hypolithic communities represent one of the last refuges for photosynthetic biodiversity in the driest and coldest deserts on Earth and harbor unique radiation and desiccation resistant taxa [*Billi et al*., 2000; *Billi and Potts*, 2002; *Billi et al*., 2008; *Cockell et al*., 2011; *Chan et al*., 2012]. These systems therefore represent important Mars analogs, and the need for continued expansion of knowledge on how they adapt and function in extreme environments is important. Without an understanding of how hypolithic communities compare and contrast with other biological systems, as well as ongoing research to answer basic ecological-climate questions, the impact of climate change on these unique desert ecosystems will be difficult to predict.

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