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RESEARCH ARTICLE

Water inputs across the Namib Desert: implications for dryland edaphic microbiology

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Abstract

Microbes have a dominant role in nutrient cycling processes in the world's deserts, where growth and activity are limited by the availability of water. In order to understand the dynamics of water availability in a desert system and how it may affect the soil microbiome, we analysed soil temperature and relative humidity fluctuations recorded between April 2018 and April 2020 across a precipitation gradient in the Namib Desert and compared them with recorded data from satellites and nearby weather stations. This allowed us to assess the possible impact of fog and rain events in terms of biologically-available water. Using published literature on the water activity limits for various physiological processes in microorganisms, we were able to infer the annual 'metabolic windows' for desert microbial communities across the longitudinal precipitation gradient. Specifically, soil surface microbial communities were estimated to have the capacity for active growth for an average of 184-363 hours per year with the duration heavily dependent on intermittent rainfall events. During the relatively wet period of April 2018 - March 2019, the maximum growth window was found in the hyper-arid central region of the transect (approximately 100 km from the coast). During the dryer 2019-2020 period, there was almost no predicted growth capacity in the hyper-arid region but substantial metabolic windows both near the coast and for the eastern inland areas, where water input comes in the form of fog and moist coastal air, and higher rainfall, respectively. As the first detailed study of the temperature and relative humidity characteristics of Namib Desert near-surface soils, this study provides valuable insights into the biogeography of microbial communities. In addition, the estimates for organismal functionality calculated in this study offer a baseline for future quantitation of the impacts of climate change on the functional capacity of desert soil microbiomes.

Highlights

- Remote sensing approaches are reliable for soil surface temperature but not for soil relative humidity.

- Rainfall events raise the relative humidity of the soil for an average of 6.5 days.

- With the absence of rain, the window for active microbial growth in the soil is dramatically increased for communities in the fog zone compared to those further inland. This might be attributable to water acquisition by the soil microbiome from moist airflows as well as fog events.

- Namib Desert shallow sub-surface soil microbial communities have enough moisture for active growth for only 184-363 hours per year.

Introduction

The Namib Desert is a hyper-arid desert, approximately 2000 km long and 140 km wide, positioned in the southwestern corner of Africa, on the west coast of Namibia. Drylands (areas with a ratio of average annual precipitation to potential evapotranspiration of less 0.65), including deserts such as the Namib, occupy 46.2% of the global land area, making them the largest terrestrial biome (Mirzabaev et al. 2019). Due to the extreme environmental conditions, there are generally few plant or animal species present in deserts and therefore microbial communities play a larger role in nutrient cycling and shaping the environment (Belnap 2006, Pointing and Belnap 2012, Ramond et al. 2018).

Water is the dominant limiting resource in hyper-arid regions and is the primary driver of the ecology of desert ecosystems (Warren-Rhodes et al. 2006, McCrackin et al. 2008). The Namib Desert has a near-unique water input regime, dominated by longitudinal gradients of rainfall and fog. The coastal regions of Namibia, up to approximately 60 km inland, receive moisture from regular fog events (Lancaster et al. 1984, Olivier 1995, Eckardt et al. 2013, Spirig et al. 2019). In contrast, the eastern margins of the Namib receive regular rainfall inputs, decreasing in intensity and frequency towards the west, i.e., towards its coastal margins (Lancaster et al. 1984, Eckardt et al. 2013). Many organisms living in the Namib Desert have evolved to take advantage of the regular fog-water inputs, including the plant *Stipagrostis sabulicola* (Ebner et al. 2011), Tenebrionid beetles (Mary Seely et al. 2005) and the coastal lichen communities (Lange et al. 1994, Lange et al. 2006, Lange et al. 2007). There is also a growing body of evidence that fog water inputs can influence the structure and function of desert soil (Scola et al. 2018) and hypolithic microbiomes (Stomeo et al. 2013, Ramond et al. 2018).

Water inputs have been shown to dramatically alter the composition of Namib Desert soil microbial communities over the short term, both in *ex-situ* microcosm experiments (Frossard et al. 2015) and in *in-situ* field studies (Jacobson 1997, Armstrong et al. 2016, León-Sobrino et al. 2021). Similarly, exposure to wetting alters both the activity (Jacobson and Jacobson 1998, Rajeev et al. 2013, Jordaan et al. 2020) and spatial organisation (Garcia-Pichel and Pringault 2001) of desert soil microbial communities globally. The central Namib Desert soil microbiome has been shown to respond very rapidly to the addition of liquid water, with substantial up-regulation of key functional genes (particularly motility and transport process genes) within minutes of water addition (León-Sobrino et al. 2021). However, the sporadic and erratic nature of rain-water input in desert regions inevitably means that desert soils are, for a very large part of any annual cycle, fully desiccated (i.e., have gravimetric water content values of 0.5-2%) as seen in both the Negev (Agam (Ninari) and Berliner 2004) and Namib (Li et al. 2018) deserts. In addition, disturbances have been shown to affect the ability of biological soil crusts to respond to water inputs (Steven et al. 2018), suggesting that

studies on undisturbed soil may not fully reflect the situation in relatively heavily-trafficked areas such as game trails or roads.

The extent to which microbial communities remain active and the extent to which microbially-mediated ecosystem services are maintained during these long periods of soil desiccation are, in part, unknown. There is an extensive literature on the quantitation of desert soil respiration rates (Sponseller 2007, Sponseller and Fisher 2008, Cable et al. 2011, Ball and Virginia 2014, Wang et al. 2014, Fa et al. 2018, Throop et al. 2020), most focussing on the effects of water addition. For example, a study in the Namib Desert found an average soil respiration rate of 0.53 ± 0.031 µmol CO_2 m^{-2} s^{-1} with no water input, increasing to 0.74 ± 0.031 µmol CO_2 m^{-2} s^{-1} after the addition of 5 mm of water and 0.92 ± 0.032 µmol CO_2 m^{-2} s^{-1} after the addition of 10 mm of water (Throop et al. 2020). The non-zero respiration of dry soils is assumed to be mostly of biotic origin with the caveat that soil respiration in arid environments actually may be underestimated due to abiotic CO_2 fixation (Fa et al. 2018). There is also strong molecular evidence for continued microbial functionality in desiccated soils, based on transcriptomic and proteomic analyses (Gunnigle et al. 2014, Gunnigle et al. 2017, Schulze-Makuch et al. 2018, León-Sobrino et al. 2021).

Together, these observations highlight the need to further understand the dynamics of water input and loss in desert soils, as a basis for assessing longer-term soil microbiome functionality, its contribution to ecosystem services over spatial and temporal scales and how it will be affected by anthropogenic climate change (Thuiller et al. 2006, Jansson and Hofmockel 2020). Here, we use soil temperature and relative humidity data, coupled with remote sensing data, to explore how fog and rain events might affect the microbial communities in the Namib Desert. We interpret these data in the context of biologically-available water and metabolic functionality, both of which are directly relevant to ecosystem servicing by the most dominant surface microbial communities in desert ecosystems: biological soil crusts and hypolithic communities (Büdel et al. 2009, Cowan et al. 2019).

Materials and Methods

Study sites

The study was conducted along a 220 km longitudinal transect, running west-to-east, along the C-14 road and traversing the Namib-Naukluft National Park in western Namibia. One iButton (DS1923-F5# Hygrochron, iButtonLink, LLC, Whitewater, USA) was placed at each of 10 GPS-located sites, positioned at 20 km intervals, at a depth of 1.0-2.0 cm below the soil surface (C14-02 to C14-20; Fig. 1). All of the iButtons, which had been calibrated by the manufacturer, were placed horizontally with the humidity pore facing upwards. We observed no alterations in the desert pavement at the iButton location sites over time and are confident that the iButton depths remained
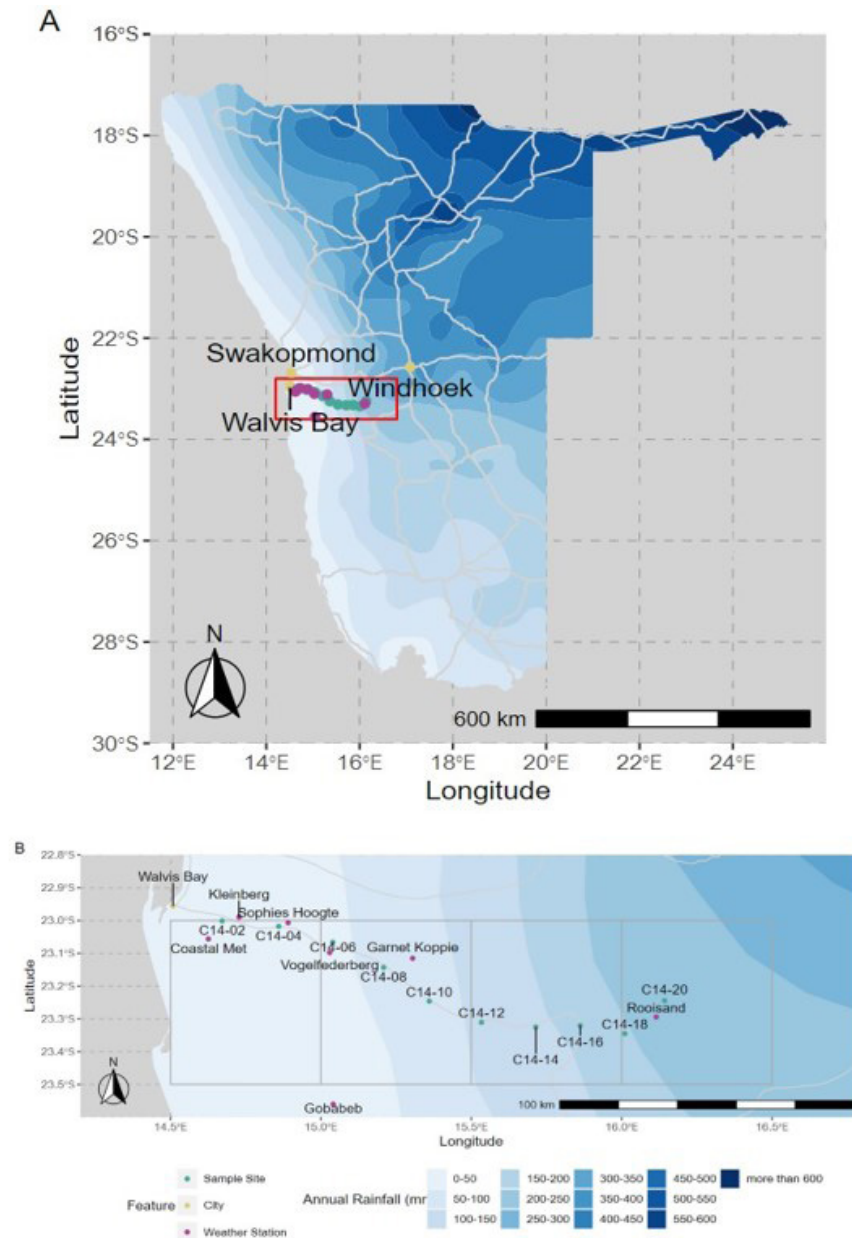
Fig. 1. Map of Namibia (A) and of the sampled transect (B). The red box in A represents the region which is shown in B. The sites where iButtons were buried are labelled as C14-XX and shown as green points, major cities are shown as orange points and weather stations are shown as purple points. The grey blocks show the areas covered by the NASA Power dataset. The mean annual rainfall is shown as different shades of blue with the data taken from the Digital Atlas of Namibia (https://www.uni-koeln.de/sfb389/e/e1/download/atlas_namibia/index_e.htm). Grey lines display major roads.

constant during the experiment. The iButtons were programmed to record temperature (°C) and relative humidity (%) data at 4-hour intervals at high resolution with no rollover. The first set of iButtons were placed in April 2018 and recorded data until March 2019, at which point their internal memory was full. The first set of iButtons were collected in May 2019 and replaced with a second set of iButtons which recorded data from May 2019 until April 2020. All iButtons, except that for site C14-14 during the 2019-2020 period, were successfully retrieved. While the use of iButtons has been criticised in environments where the soil may

become saturated (Fawcett et al. 2019), they have been used extensively in both hot (Frossard et al. 2015, Day et al. 2018) and cold (McGaughran et al. 2009, Stomeo et al. 2012) desert systems to monitor relative humidity. Soil physicochemical properties along this transect have been previously reported (Scola et al. 2018) and will not be further discussed in this paper.

Data analysis

The soil temperature and relative humidity measurements from the iButtons were combined with data from nearby weather stations, supplied by the

Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL) Open Access Data Centre (Kaspar et al. 2015), and satellite readings, retrieved through the NASA Langley Research Center (LaRC) POWER Project. Weather stations were assigned to the nearest site: an average of the Kleinberg and Coastal Met weather station data was assigned to site C14-02, the Sophies Hoogte station data to site C14-04 and the Vogelfederberg station data to site C14-06. Due to limited weather stations further east, data from Garnet Koppie was assigned to sites C14-08, C14-10 and C14-12 and the data from Rooisand was assigned to sites C14-14, C14-16, C14-18 and C14-20. The Rooisand station stopped reporting humidity values in October 2018.

The NASA Power data has a resolution of 0.5° x 0.5° (roughly 50 km x 50 km), such that the entire transect was covered by four blocks of data and all sites within the same block shared the same data (Fig. 1). Due to the temporal resolution of the NASA data (daily), comparisons that involved data from multiple sources were converted to daily values by taking the mean of all observations.

Data were analysed in R 4.1.1 (R Core Team 2021) using the packages ggplot2 3.3.5 (Wickham 2016), gridExtra 2.3 (Auguie 2017), ggsignif 0.6.2 (Ahlmann-Eltze 2019), lubridate 1.7.10 (Grolemund and Wickham 2011), nasapower 4.0.0 (Sparks 2018), stringr 1.4.0 (Wickham 2019), vegan 2.5-7 (Oksanen et al. 2019), ggrepel 0.9.1 (Slowikowski 2021), ggpubfigs 0.0.1 (Steenwyk 2021), sf 1.0-2 (Pebesma 2018), rgdal 1.5-23 (Bivand et al. 2021), broom 0.7.9 (Robinson et al. 2021), RcolorBrewer 1.1-2 (Neuwirth 2014), ggspatial 1.1.5 (Dunnington 2021), rnaturalearth 0.1.0 (South 2017) and associated dependencies.

Results and Discussion

Soil conditions in the Namib Desert

The iButtons recorded soil relative humidity and temperature for both the April 2018 – March 2019 (Fig. S1) and May 2019 – April 2020 (Fig. S2) periods. The summarised data (Fig. 2) shows a clear trend of decreasing relative humidity and increasing temperature with distance from the coast. The mean soil temperature in the coastal fog 'zone,' during the 2018-2019 period, was just below 25 °C but increased to 29.9 °C at the most inland site, with a maximum recorded temperature over 64.0 °C. While the average temperature in the 2019-2020 period was slightly higher than in the preceding year, there was little sign of major variations in temperature between years either in the mean or the extremes.

Mean near-surface soil relative humidity values ranged from 49.3% at the coastal sites C14-02 to 31.6% at the inland site C14-20 during the 2018-2019 period. By comparison, the 2019-2020 period was characterised by very low water inputs into the system; the mean relative humidity at the midpoint of the transect (centre of the hyper-arid 'zone') was 44.6% in 2018-2019 compared to 24.5% in 2019-2020. The differences in relative humidity values between the 2018-2019 and 2019-2020 datasets were lowest in the coastal fog zone, where there is regular water input in the form of fog, and at the eastern, inland portion of the transect, where rainfall in early 2020 resulted in an increased soil relative humidity.

We used Principal Coordinates Analysis (PCA) to compare daily temperature and relative humidity values at each site (Fig. 3A+D), as well as PCA loadings of different temperature and relative humidity
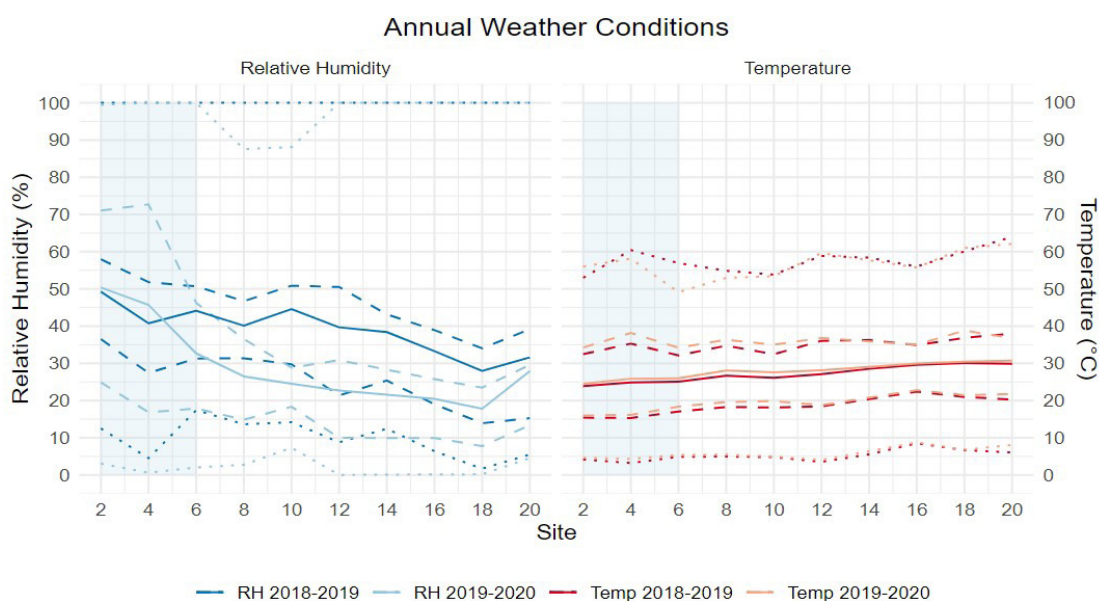

Fig. 2. Annual Weather Conditions. Average temperature and relative humidity data for the 1-2 cm depth Namib Desert soil horizon. The solid line represents the mean, the dashed lines represent the 1st and 3rd quartiles and the dotted lines represent the maximum and minimum recorded values. The blue-shaded portion of the graph depicts the fog zone.

measurements (Fig. 3C+F). As expected, the PCA plots showed that the sample sites were distributed across a gradient that follows the availability of moisture, with sites closer to the coast having higher moisture availability. Sample sites could be clustered according to their primary water input mechanism; sites 2, 4 and 6 receive most water input from fog while sites 8, 10, 12, 14, 16, 18 and 20 receive water input from rainfall. The clustering between the fog zone and the rainfall zone was statistically significant in both the 2018-2019 (MANOVA: p = 0.001, R^2 = 0.12) and 2019-2020 (MANOVA: p = 0.001, R^2 = 0.15) periods. The coastal fog and inland rainfall zones were used in the subsequent analysis of the effects of rainfall in the Namib Desert.

Clustering data according to month allowed a broad division between two seasonal groups (Fig. 3B + E). The 'summer' group covered a period from the beginning of
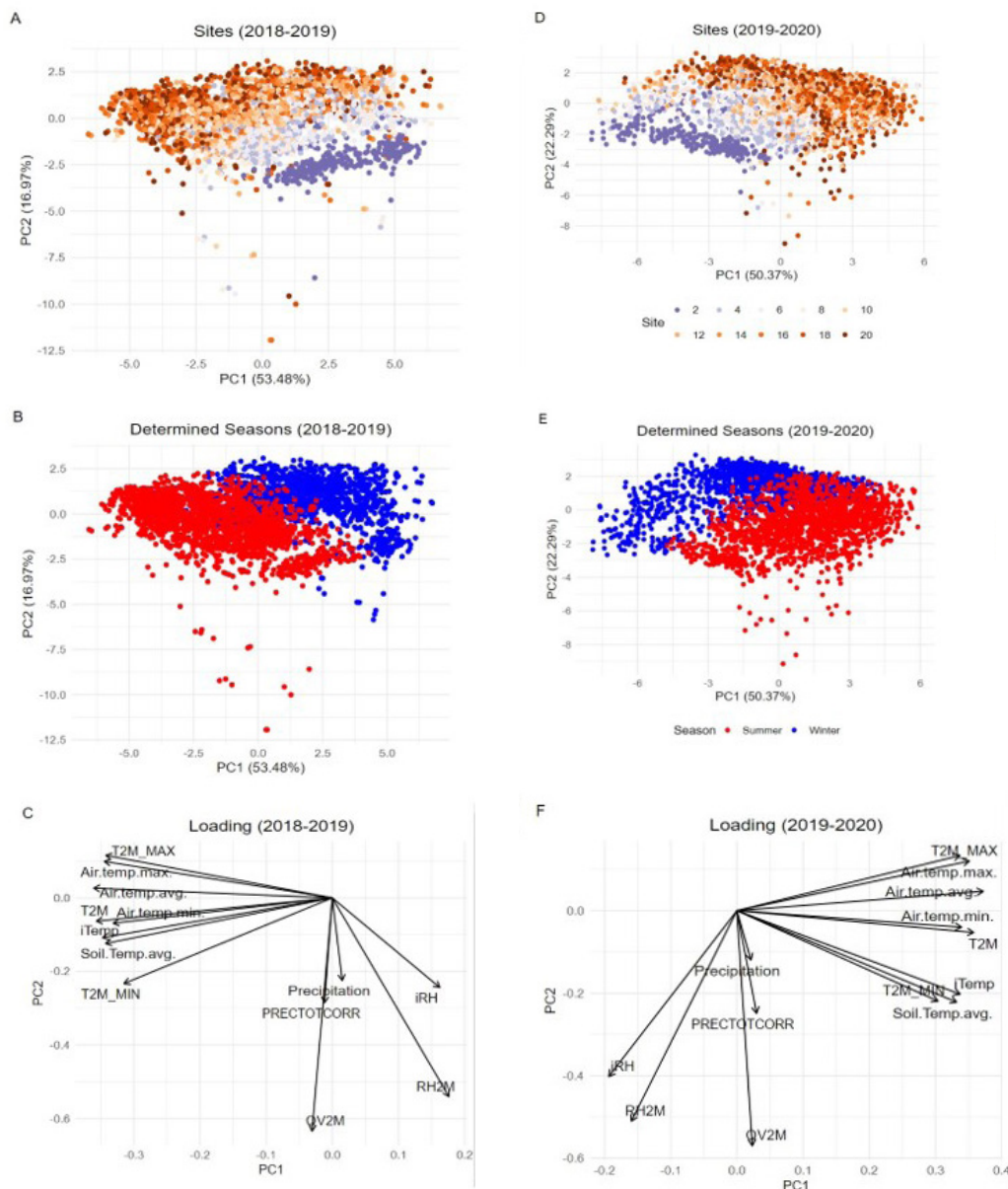

Fig. 3. PCA comparison of groupings. Plots on the top row use the 2018-2019 data and those on the bottom row, the 2019-2020 data. Each point represents the data of a single site on a particular day, coloured according to site (A + D) or determined season (B +E). The contribution of each variable to the position in the PCA is shown in panels C + F. In panels A + D, sites which occur in the fog zone are coloured in purple and those which occur in the rain zone are coloured in orange. The following variables were used: soil temperature (iTemp) and soil relative humidity (iRH) from the iButtons; total precipitation (PRECTOT), absolute humidity of air at 2 m altitude (QV2M), relative humidity of air at 2 m (RH2M), average air temperature at 2 m (T2M), maximum air temperature at 2 m (T2M_MAX) and minimum air temperature at 2 m (T2M_MIN) from NASA; average air temperature (Air.temp.avg.), minimum air temperature (Air.temp.min.), maximum air temperature (Air.temp.max.), precipitation (Precipitation) and average soil temperature at a depth of 10 cm (Soil.Temp.avg) from SASSCAL weather stations.

October until the end of April, with the 'winter' group continuing from the beginning of May until the end of September. This clustering is statistically significant and explained a large proportion of variation for both the 2018-2019 (MANOVA: p = 0.001, R^2 = 0.34) and 2019-2020 (MANOVA: p = 0.001, R^2 = 0.26) periods, with temperature being the main driver. Over the entire length of the sampling transect, the mean summer soil temperature, as measured by the iButtons, was 31.4 °C in both the 2018-2019 and 2019-2020 periods, compared to a mean winter soil temperature of 22.0 °C in 2018-2019 and 23.6 °C in 2019-2020.

Applicability of large scale data to local conditions in assessing water availability for environmental edaphic communities

While data sources such as the SASSCAL weather stations and NASA satellite measurements serve as invaluable sources of macro-scale climatic data, there are concerns that conditions at the micro-scale can differ substantially from macro-scale measurements of air conditions (Pincebourde and Salle 2020). This study offered an excellent opportunity to compare data on the same variables from different sources and at different scales.

Relative humidity measured in the air showed peaks that corresponded with rainfall events but which rapidly returned to basal levels after rain events, whereas the soil relative humidity remained high for days to weeks, presumably due to liquid water held in the soil (Fig. 4, Table S2). The NASA and SASSCAL data for relative humidity were similar (r2 = 0.63), although NASA estimates were consistently lower. These data suggest that remote sensing of atmospheric relative humidity is reliable for the Namib Desert region but that atmospheric relative humidity cannot be used to predict the relative humidity of the soil where the effects of water input may be long-lived.

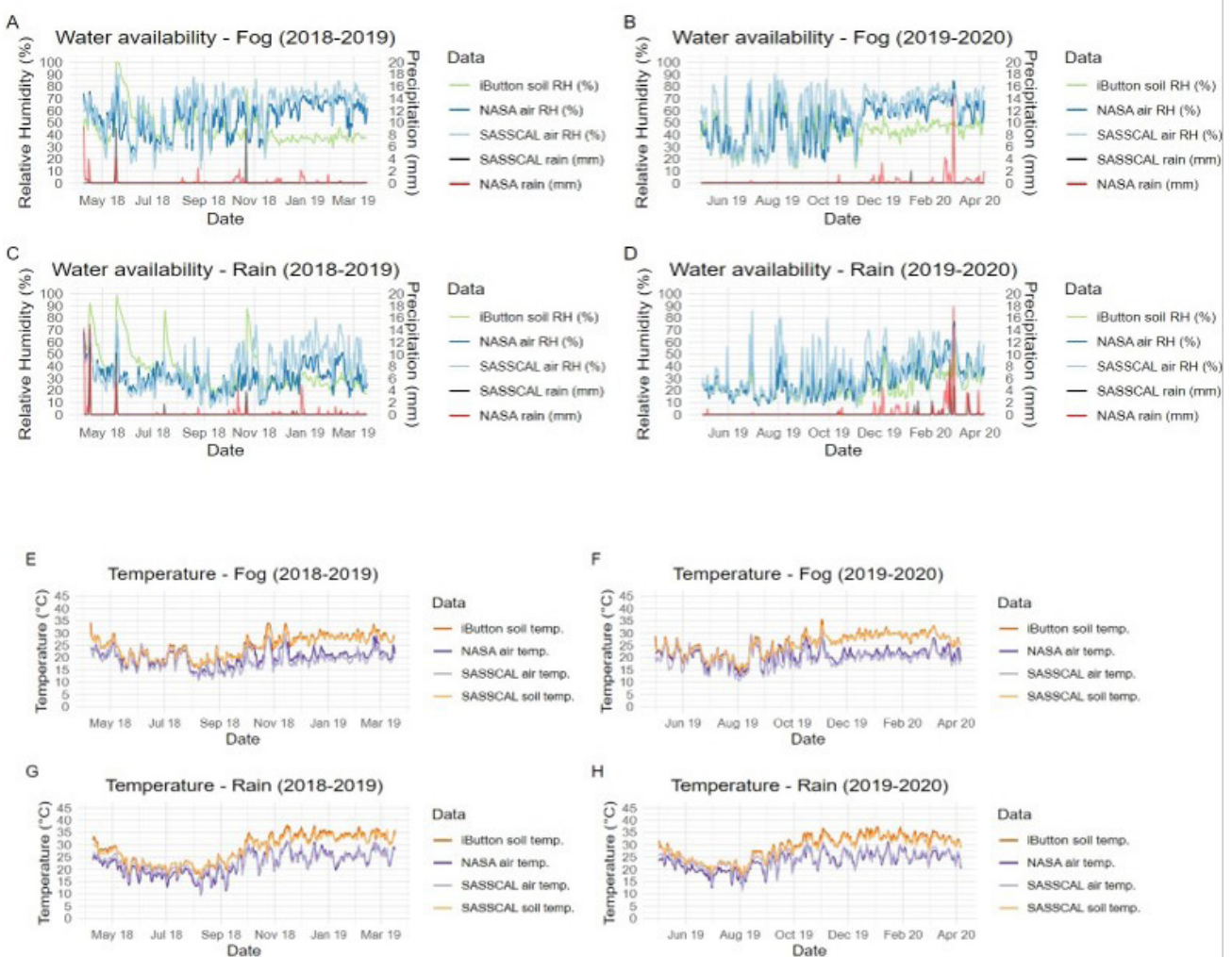**Fig. 4.** Comparison of data sources. Relative humidity (%) and precipitation (mm) versus time for the fog (A + B) and rain (C + D) zones for both the 2018-2019 (A + C) and 2019-2020 (B + D) periods as recorded by different data sources. Temperature (°C) versus time for the fog (E + F) and rain (G + H) zones for both the 2018-2019 (E + G) and 2019-2020 (F + H) periods as recorded by different data sources.

Precipitation events measured by SASSCAL weather stations ('Precipitation') better matched the peaks of the iButton soil relative humidity ('iRH') than precipitation measured by NASA's remote sensing ('PRECTOTCORR') and had a higher correlation with the iButton data (iRH vs Precipitation r^2 = 0.03, iRH vs PRECTOTCORR r^2 = 0.01; Fig. 4 and Table S1). This is perhaps unsurprising since SASSCAL rainfall data come from direct physical measurements and should therefore have a degree of higher accuracy. Conversely, discrepancies between the NASA data and the iButton relative humidity measurements may arise due to the limited spatial resolution of the satellite data (roughly 50 km x 50 km). During the 2019-2020 period, the correlation between iButton relative humidity and precipitation measured by NASA was stronger (Table S1) but may be due to the lack of rainfall inputs in this period; the correlation between iButton relative humidity and SASSCAL precipitation remained constant between the periods.

In contrast to relative humidity data, temperature measurements were highly similar for both the NASA ('T2M') and SASSCAL ('Air.temp.avg.') datasets across all zones ($r2$ = 0.67) (Fig. 4, Table S1) as well as being similar to the iButton ('iTemp') measurements taken from the soil (iTemp vs T2M $r2$ = 0.62, iTemp vs Air.temp.avg. $r2$ = 0.68). Soil temperatures were higher than the surrounding air during the summer months as, unlike the low density atmosphere, the high density mineral soils absorb and retain heat, as has been previously observed for Namib Desert rocks (Viles 2005). The SASSCAL soil temperature measurements were highly correlated with the iButton measurements ($r2$ = 0.94), even when there were large physical distances between the sites and weather stations, suggesting that soil temperature variation at the micro-scale is not very pronounced.

Impact of fog events on soil moisture availability

The mean soil relative humidity in the fog zone was 44.7% and 42.9% in the 2018-2019 and 2019-2020 periods respectively. In the rainfall zone, soil relative humidity was 36.5% and 23.0% in the 2018-2019 and 2019-2020 periods, respectively. The data also show that sites in the fog zone experienced larger variations in daily soil relative humidity than sites in the rainfall zone (Figs S1, S2).

While the soil relative humidity is undeniably higher in the fog zone, it is not clear that this is the direct result of fog events. Fog events occur regularly on the western coast of Namibia but their frequency changes according to the time of the year (Olivier 1995, Kaseke et al. 2018, Spirig et al. 2019). For instance, an average of 9 fog days per month can be expected from October to December but only 3 fog days per month from April to June (Spirig et al. 2019). Due to a lack of visibility measurements and the difficulties in reliable detection of fog via remote sensing (Olivier 1995, Bendix et al. 2005, Ebner et al. 2011, Spirig et al. 2019) or measurements of fog precipitation (Feigenwinter et al. 2020), it was not possible to determine the number of fog events

during the period of this study, but previous studies do not support the possibility of fog events being a daily occurrence for a full annual cycle.

Fog events are a known, documented and important water source for many species in the fog zone of the Namib Desert (Lange et al. 1994, Mary Seely et al. 2005, Lange et al. 2006, Lange et al. 2007, Ebner et al. 2011) and the presence of extensive epiphytic lichen growth in the area of the near-coastal sites (Lange et al. 1994, Lange et al. 2006, Lange et al. 2007, Hinchliffe et al. 2017) is a strong indication that this area receives regular fog water input. However, previous research has found that, at a depth of 2 cm, no change in soil moisture can be associated with visible fog events (Warren-Rhodes et al. 2006, Ebner et al. 2011, Li et al. 2018).

Taken together, this suggests that both the frequency and the magnitude of the changes in soil relative humidity in the fog zone are too great to be explained by fog events alone, and the amplitudes of the daily relative humidity values (Figs S1, S2) are too great to be explained by the inverse relationship between relative humidity and diurnal changes in soil temperature. While we argue that the intermittent fog events do contribute to shallow sub-surface soil moisture, we suggest that the frequent and high soil relative humidity values observed in the fog zone soil samples are the result of the effects of the moist (high relative humidity) onshore coastal air-flow (~60% in the fog zone according to data from SASSCAL weather stations).

Impact of rainfall events on soil moisture availability

Rainfall events were identified as peaks in a 4-day sliding window in the SASSCAL precipitation data and were analysed for the duration and magnitude of their effect on soil relative humidity (Fig. 5, Table S2). For each rainfall event, the mean soil relative humidity for the previous seven days was taken as the baseline; rain effect duration was defined as the number of days for the soil relative humidity to return to the baseline level after a rain event, and the magnitude of a rainfall event was the difference between the baseline and the maximum relative humidity during the rain event.

During the 2018-2019, there were 14 (22.0 mm total water input) rainfall events in the fog zone and 11 (36.0 mm) rainfall events in the rain zone. In the 2019-2020 observation period, there were 18 (4.0 mm) rainfall events in the fog zone and 12 (27.7 mm) rainfall events in the rain zone (Fig. 5, Table S2). This shows the stark difference in rainfall between the two study years, a difference which was even more pronounced as 26.5 mm of the rainfall recorded in the rain zone during the 2019-2020 period fell between 17 January 2020 and 30 March 2020. The majority of rainfall events were small with only 7/55 (13%) rainfall events recorded depositing more than 5 mm of rain. We note that these values are sums of averages across the different zones along the transect and there is no available record of the amount of rain at each sample site.
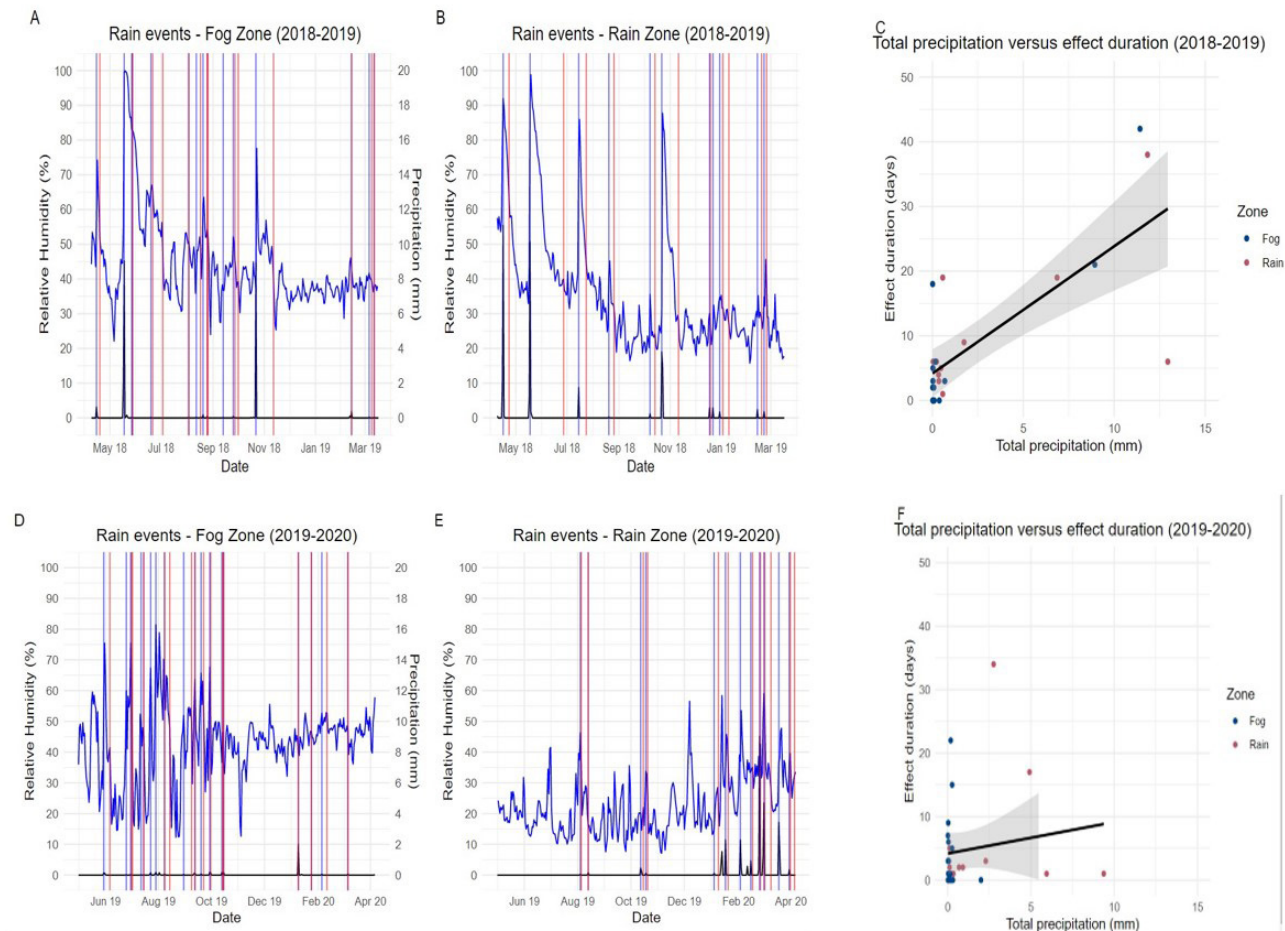
Fig. 5. Rainfall events. Mean soil relative humidity per day (blue), recorded by iButtons, and mean precipitation per day (black), recorded by SASSCAL weather stations, versus time for the fog (A + D) and rainfall (B + E) zones during both the 2018-2019 (A + B) and the 2019-2020 (D + E) periods. Blue vertical lines represent peaks in the measured precipitation while red vertical lines indicate the end of the effect of the rainfall event. Total precipitation is positively correlated with the duration of the effect of a rainfall event; both for the 2018-2019 (C) and the 2019-2020 (F) periods.

While most rainfall events lasted for less than one day, one event in the fog zone was notable for a duration of six days, from 16 May 2018 to 22 May 2018, depositing 11.4 mm of rain (Fig. 5, Table S2). As a result, the soil relative humidity only returned to baseline levels after 42 days. Over the complete study period, this event was the longest recorded rainfall event, the third-highest amount of water deposited in a rainfall event and took the longest for the soil relative humidity to return to pre-rainfall levels. In contrast, the average rainfall event deposited a mean of 1.6 mm of rain (median: 0.2 mm) and had an effect on soil relative humidity levels lasting a mean of 6.5 days (median: 3 days) with higher average volumes and longer average durations recorded in 2018-2019 than in 2019-2020.

A natural rainfall event in the central Namib Desert was reported to cause a large shift in the soil microbial community composition, which reverted to its original 'dry' composition within 30 days (Armstrong et al. 2016). The results presented here indicate that rainfall

events seldom cause a change in soil relative humidity that persists for longer than 10 days (Fig. 5), in line with previous work showing that rainfall events of less than 4 mm did not wet Namib Desert soil at a depth of 10 cm and that the effects of even 46 mm of rain only lasted for 22 days (Jacobson and Jacobson 1998). This suggests that shorter time scales will be necessary to observe water-input related community dynamics.

Potential metabolic windows for edaphic microbial life in the central Namib Desert

Relative humidity is a measure of thermodynamic water activity (a_w; 100% relative humidity = a_w 1) and is assumed to be a measure of bioavailable water (Friedmann 1982). Using the known experimental limits of microbial life at various measured water activities, we estimated the windows during the year at which different microbial metabolic processes were likely to be functional.

Some gram-negative bacteria cease cell division at water activities below 0.95 (Fontana 2020), while

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many soil Actinobacteria continued to grow down to a water activity of 0.90 (Stevenson and Hallsworth 2014). Specific halophilic bacteria and archaea continue to divide in concentrated saline media (a_w < 0.64) (Stevenson et al. 2015) and the extreme xerophile *Aspergillus penicillioides* is capable of cell division at a water activity of only 0.59 (Stevenson et al. 2017). These extreme a_w values are obtained in media with high concentrations of osmolytes rather than an absolute molar water deficit.

Published data from mineral soils show that soil microbial community activity generally ceases at a water potential of -13.8 MPa (Manzoni et al. 2012), equivalent to -138 bar and >a_w 0.90 (Harris 1981). Taking this into account, and despite the paucity of relevant data, we assume here that growth (i.e., cell division) of the majority of members of the soil bacterial communities ceases below a_w 0.90 (Stevenson and Hallsworth 2014) and, while individual species may maintain growth and activity below this threshold, it may not be relevant at a community scale (Manzoni et al. 2012).

Cellular metabolic processes continue at water activities below those which prevent gross physiological processes such as cell division. Photosynthetic processes are generally considered to be very sensitive to desiccation, with some lichen photobionts losing photosynthetic capacity when the water activity drops below 0.80 (Bertsch 1966). Under certain conditions, such as association with hygroscopic salt crystals, photosynthesis has been observed even down to 70% relative humidity (Davila et al. 2013). However, some core metabolic processes continue to function at even lower water activities. For example, amino-acid biosynthesis (probably via transamination reactions from Citric Acid Cycle intermediates) was detectable

at water activities as low as 0.30 (Cowan et al. 1979). Transcriptomic studies of a desiccated soil community in the hyper-arid Namib Desert showed the unexpected presence of gene transcripts for enzymes driving inorganic nitrogen and organic carbon assimilation at soil relative humidity values between 13 and 28% (equivalent to a water activity of 0.13 to 0.28, assuming that cells of the soil microbiome were in equilibrium with the soil relative humidity) (León-Sobrino et al. 2019). These data suggest that even in an 'anhydrobiotic' state, some basal metabolic processing continues within desiccated microbial cells (Bosch et al. 2021), functionally consistent with the 'maintenance energy' concept (Leung et al. 2020).

Using our iButton soil relative humidity data, and making various assumptions based on the published water-related activity limits (Bertsch 1966, Cowan et al. 1979, Manzoni et al. 2012, Stevenson and Hallsworth 2014, León-Sobrino et al. 2019, Gomez et al. 2021), we estimated various 'metabolic windows' for soil microbial communities, at a depth of 1-2 cm, along a precipitation gradient in the Namib Desert (Fig. 6). Our analysis includes data from two years; 2018-2019 which showed a relatively high total volume of rainfall (57.9 mm total rainfall) and 2019-2020 which was much drier (31.6 mm total rainfall with 28.8 mm occurring in the final three months).

From the relative humidity data in this study, there was a clear decrease in the predicted metabolic windows with increasing distance from the coast that mirrors the decrease in available moisture described above. This trend was observed in both the 2018-2019 and 2019-2020 periods. According to the calculated data, active microbial growth was only possible for, on average, 363 hours during the 2018-2019 period and 184 hours during the 2019-2020 period (Fig 6).
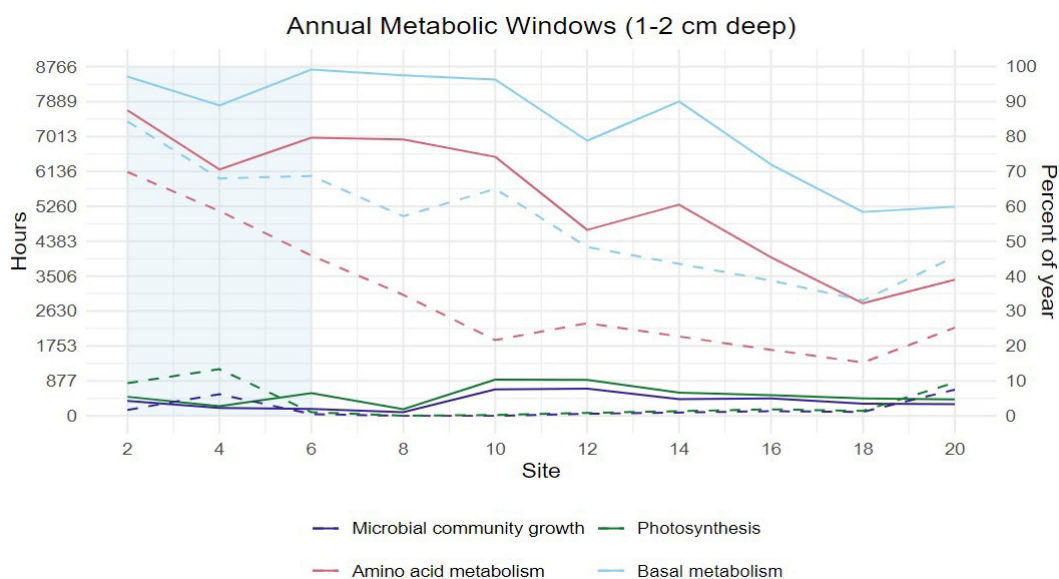

Fig. 6. Annual Metabolic Windows for Namib Desert soil microbial activities. The number of hours (left axis) and the percentage of the year (right axis) when there is sufficient soil moisture, at a depth of 1-2 cm, for various metabolic processes at each of the sites along the C14 transect (bottom axis) during either the 2018-2019 (solid lines) or the 2019-2020 period (dashed lines).

This is equivalent to between 8 and 15 full days, similar to the values calculated for the hyperarid Atacama Desert (Warren-Rhodes et al. 2006), though lower than previous measurements from Gobabeb in the Namib Desert, recorded between 1982 and 1989 (Jacobson et al. 2015). While basal metabolic processes, possibly sufficient for maintenance energy demands, were estimated to continue for a large proportion of the annual cycle, at some inland sites it is too dry to even support basal metabolism for between 40-60% of the year.

We note that low water activity and physical absence of bulk water are different stress parameters (Potts 1994, Billi and Potts 2002, Kieft 2003, Vriezen et al. 2007) and that physical limitations, such as a lack of a liquid medium for nutrient diffusion, will impose constraints on microbial functionality that differ from those imposed by low intracellular water activity (Dechesne et al. 2010, Manzoni et al. 2012). In addition, only limited data are available on the limits of metabolic processes in relation to water activity and, where available, often come from laboratory studies of single organisms. While acknowledging the weakness of extrapolating single-organism data to entire microbial communities, the implication from these estimates is that the capacity for microbial community growth is severely constrained in all Namib Desert soils and active growth may only occur during the brief, and intermittent, rain events and for relatively short periods thereafter (León-Sobrino et al. 2021).

It is evident that there is still much to understand about the quantitative and temporal relationships between water availability and microbial community functionality in desert soils. We suggest that a viable approach to quantification of this relationship would be the use of controlled relative humidity or water supplementation experiments coupled with a suite of functional assays (e.g., respiration rates (Throop et al. 2020), CO_2 and N_2 fixation), meta-proteomics and/or metatranscriptomics. Such approaches could help to define the functional limits of various cellular processes, and thus aid in an assessment of how critical microbiome functions, particularly those related to ecosystem services, might change in a future changing climate scenario. This work has focussed on the immediate sub-surface of the soil but the microbial communities, their functions and the conditions they experience at lower depths likely differs from the immediate sub-surface. There are still open questions regarding how deep the microbial community extends below the soil surface and the relative contribution to microbial metabolism from communities at different depths.

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Author Contributions

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Data Accessibility

The analysis scripts necessary to reproduce this study are available on Github (https://github.com/jasonbosch/Water-inputs-across-the-Namib-Desert-implications-for-dryland-edaphic-microbiology) and the raw data files have been deposited on Zenodo (https://doi.org/10.5281/zenodo.5577945).

Supplementary Material

This material is available as part of the online article from https://escholarship.org/uc/fb
Figure S1. Raw iButton data graphs (2018-2019).
Figure S2. Raw iButton data graphs (2018-2019).
Table S1. Correlations between measurements by different data sources.
Table S2. Table of rain events.

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