



The effect of the water source on niche partitioning of chlorolichens and cyanobacteria—implications for resilience?

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Abstract

Main conclusion Microclimate determines lichens and cyanobacteria distribution in the Negev, with lichens and cyanobacteria inhabit dewy and dewless habitats, respectively. Lichens experiences more frequent and extensive environmental fluctuations than cyanobacteria.

Abstract The spatial partitioning of chlorolichens (eukaryotes) and cyanobacteria (prokaryotes) are intriguing, especially following recent intense search for extraterrestrial life. This is especially relevant for deserts, where both lithobionts are thought to use rain and dew but may differ in their resilience to environmental extremes and fluctuations. Following the different spatial distribution of lithobionts in a south-facing slope of the Negev Highlands (with cyanobacteria-inhabiting rocks and chlorolichen-inhabiting cobbles), measurements of temperature, non-rainfall water (NRW) and biomass were carried out within the drainage basin aiming to test the hypotheses that (i) cobble-inhabiting lichens may access more water (through NRW) and may be subjected to more extensive environmental fluctuations of temperature and water than bedrock-inhabiting cyanobacteria, and (ii) will therefore have a greater contribution to the ecosystem productivity. In contrast to cyanobacteria, cobble-inhabiting chlorolichens were found to access NRW (up to 0.20 mm of daily amounts in comparison to < 0.04 mm of the cyanobacteria) and to experience higher fluctuations of temperatures (up to 4.1 °C higher and 5.3 °C lower). With lichens and cyanobacteria inhabiting dewy and dewless habitats, respectively, NRW was found responsible for contributing 6.8-fold higher organic carbon to the lithobiontic community. At this site, chlorolichens experience more extensive environmental fluctuations than cyanobacteria, possibly indicating a higher tolerance for environmental fluctuations. These observations may assist in the interpretation of the abiotic conditions responsible for past or present lithobiontic life on Mars.

Keywords Dew · Lithobionts · Negev Desert · Non-rainfall water

Abbreviations

CRB Carbohydrates
NF North-facing

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NFS	North-facing slope
NRW	Non-rainfall water
OC	Organic carbon
SF	South-facing
SFS	South-facing slope

Introduction

Studying the ecological thresholds or constraints of organisms is of importance in order to understand ecosystem ecology (Groffman et al. 2006). This is especially the case in extreme ecosystems, where microorganisms, whether prokaryotes or eukaryotes exist. This is also of prime importance to scientists engaged in either interpreting paleo environmental conditions thought to sustain extraterrestrial life (e.g., Mars; McKay and Davis 1991; Squyers et al. 2004) or concepts for a search for molecular signatures of extraterrestrial life (e.g. Avnir 2021).

Of special interest is the spatial distribution of the rock-dwelling photoautotrophic eukaryotes and prokaryotes (lithobionts). The fundamental question addressed in this paper is the relative abundance of chlorolichens and cyanobacteria in arid and fluctuating environments. We focus on a site in the Negev Desert where these organisms are found in close proximity but in distinct micro-environments.

Both domains (prokaryotes, eukaryotes) exhibit fundamental physiological differences, such as the eukaryote ability to activate their photosynthesis apparatus also at high relative humidity (Lange et al. 1986). This trait implies adaptation to a different suite of environmental conditions, for which our knowledge is still limited.

The findings that under controlled growth conditions excessive water and nutrients break the symbiosis within the lichen into its components, the photobiont (alga or cyanobacteria) and mycobiont (fungi) (Scott 1960; Ahmadjian 1993), led to the suggestion that lichens may be better adapted to cope with more xeric and nutrient-poor conditions than free-living microorganisms (Smith 1962; Hale 1967; Friedmann and Galun 1974). Lichens were therefore postulated to inhabit arid habitats unsuitable for the proliferation of the free-living components, such as cyanobacteria and green-algae (Smith 1962; Friedmann and Galun 1974; Armstrong 2017). Conversely, lichens were also reported from more mesic environments, as is for instance the case with biocrusts (Kidron et al. 2009; Young et al. 2016). Whether stemming from the clear spatial partitioning between cyanobacteria and lichens (Friedmann and Galun 1974) or from the notion expressed by some scholars that in comparison to prokaryotes (Bell 1993; Sterflinger et al. 2012), chlorolichens (i.e., lichens with green algae as photobionts) may abound in less xeric environments (Cockell et al. 2002; Nienow 2009). It was hypothesized that chlorolichens

may be vulnerable to frequent and extensive environmental fluctuations. It was assumed that frequent fluctuation of temperatures and moisture (Friedmann and Galun 1974; Friedmann 1982; Potts 1999; Nienow 2009), known to pose a heavy physiological burden on the cell (Smith 1962), may explain the lower proliferation of lichens in certain arid regions. Thus, the microclimate factors that control the distribution of these two contrasting groups of organisms, lichens and cyanobacteria, warrant further investigation.

Both groups of lithobionts, prokaryotes (cyanobacteria) and chlorolichens (endolithic and epilithic) inhabit the most extreme deserts, the Atacama (Wierzbos et al. 2011) and Antarctica (Friedmann 1982). Both groups of lithobionts also abound on the rocky terrain of the Negev Desert, Israel (Lange et al. 1970; Evenari et al. 1971; Friedmann and Galun 1974; Kappen et al. 1980; Danin and Garty 1983; Kidron 2000). Chlorolichens can be found sharing the same drainage basin with endolithic cyanobacteria (Danin and Garty 1983). As previously shown, while endolithic lichens prevail at sun-exposed habitats, epilithic lichens predominate on sun-shaded aspects (Kidron et al. 2011). As for cyanobacteria, they are confined to sun-exposed bedrocks of the south-facing (SF) and east-facing (EF) midslopes. Alternatively, north-facing (NF) and west-facing (WF) bedrocks, as well as the cobbles at all aspects, are predominately covered by chlorolichens (> 90%).

The Negev is regarded as a dew desert. It receives an average annual amount of dew and fog of 33 mm forming during 195 days a year (Evenari et al. 1971). Dew and fog were assumed to be a major water source for both lithobiontic groups, cyanobacteria and chlorolichens in the Negev (Friedmann and Galun 1974) and in other deserts (Smith et al. 2000; DiRuggiero et al. 2013; Gauslaa 2014; Bernhard et al. 2018). While net photosynthesis of rock-dwelling chlorolichen following dew (Lange et al. 1970; Kappen et al. 1979, 1980), and even high relative humidity (Lange et al. 1986) was reported from the Negev, net photosynthesis by rock-dwelling cyanobacteria following dew was not recorded, and yet, the notion that dew and fog can benefit cyanobacteria is widely accepted (Warren-Rhodes et al. 2013; Bernhard et al. 2018).

Chlorolichens were found to have a substantially lower water threshold for net photosynthesis (Lange et al. 1986), also shown to be influenced by the photobiont type (Phinney et al. 2019). Chlorolichens were reported to begin respiration at relative humidity (RH) of 70% (Lange 1969), which corresponds to 0.03 mm (Kappen et al. 1979), while requiring RH of 80% for net photosynthesis (Lange 1969), corresponding to 0.05 mm of water (Kidron and Starinsky 2019). Conversely, prokaryotes such as cyanobacteria necessitate liquid water for net photosynthesis. While they may initiate respiration already at high RH (Lange et al. 1986), a minimum amount of 0.1 mm is necessary for net photosynthesis

(Lange et al. 1992), which is also the threshold for liquid water (Lange et al. 1992). One may safely assume that the spatial distribution of lithobionts may reflect the water requirements of the different groups of lithobionts.

Recent investigations conducted in the Negev shed some light on the spatial distribution of lithobionts. Thus, for instance, no significant differences in rainfall amounts were recorded on the north-facing slope (NFS) and the south-facing slope (SFS) of a first-order drainage basin near Sede Boqer (heart of the Negev Highlands) during 4 years of measurements, explained by the channeling effect of the rain-carrying westerly winds, which evenly distributed the rain at both sides of the narrow wadi (Kidron et al. 2011, 2014). Conversely, sharp differences characterized the irradiance with maximum irradiance, as recorded during the fall at SFS being 1.8-fold higher than that of NFS (Kidron et al. 2014). High variability characterized also the amounts of dew and fog at 10 stations along NFS and SFS, as determined by the cloth-plate method, CPM (Kidron 1998). While high amounts were obtained at NFS, substantially lower amounts characterized the SFS (Kidron et al. 2000).

The differences were substantially higher once the cloths, which serve as the depositional substrates, were directly attached to the rock surfaces. While dew formed on the NF bedrocks, it failed to form on the SF bedrocks. In fact, surface temperature of the SF bedrocks only rarely reached the dewpoint temperature, a necessary condition for vapor condensation (Beysens 2018). This is explained by the high daylight irradiance received at the sun-exposed SF bedrocks, and the subsequent higher nocturnal temperatures there. As a result, vapor condensation was never recorded during > 60 days of measurements that took place during the dewy period (Kidron et al. 2014). Similar results were also obtained on bedrocks at the east-facing (EF) midslopes, which were also inhabited by cyanobacteria. It was therefore concluded that cyanobacteria do not inhabit the dewy habitats of the drainage basin.

With bedrocks inhabited by cyanobacteria at SFS while adjacent cobbles are inhabited by chlorolichens (hereafter lichens), concomitant measurements of the abiotic conditions at both habitats are called for. Based on previous findings that showed frequent vapor condensation and net photosynthesis of these cobble-inhabiting lichens (Lange et al. 1970), we hypothesized that as far as the microclimate is concerned, dew formation at the lichen habitat may be reflected by high fluctuation of temperature and surface wetness, and that these fluctuations should be especially pronounced for the lichens growing on cobbles. We also hypothesized that by comparing SF lichens growing on cobbles (which receive rain and dew) and adjacent bedrocks (which only receive rain), the contribution of NRW to the lithobiont's organic carbon may be assessed. Supporting evidence for these hypotheses was sought by examining the

spatial distribution of sky-facing lithobiontic autotrophs in other extreme deserts.

Materials and methods

The research site

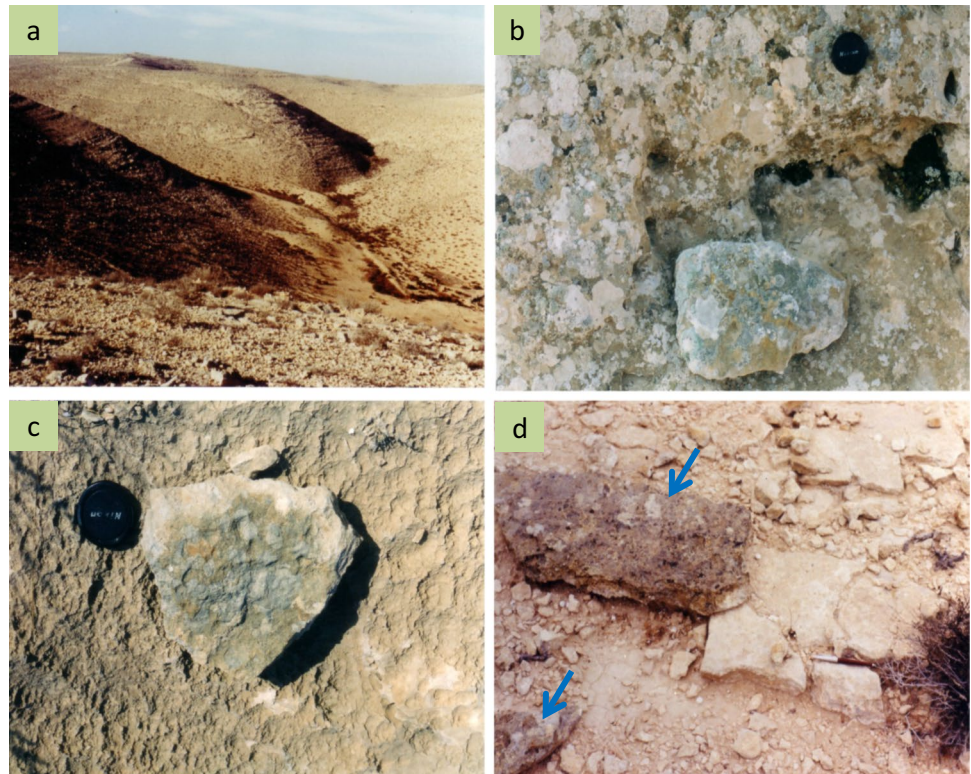
The research site is located near Kibbutz Sede Boqer, the Negev Desert Highlands, Israel, approximately 500 m above sea level (34°46' E, 30°56' N). Rain precipitation is limited to the winter months (November–April). Long-term mean annual rain precipitation (1950–1980) in the Negev Highlands is 95 mm (Rosenan and Gilad 1985), while being slightly lower (87.6 mm) during 1990–2020 (www.ims.data.gov.il/ims/7). As for dew, while 195 dewy days were reported during the 1960s (Evenari et al. 1971), 4 year-study during the early 1990s resulted in a similar number (194) of dewy days (Zangvil 1996). Average annual temperature is 17.9 °C; it is 24.7 °C during the hottest month (July) and 9.3 °C during the coldest month (January) (Rosenan and Gilad 1985). Annual pan evaporation is 2600 mm.

A first order drainage basin, with relatively steep slopes of up to 24° and 31° (but with inclined rock 'terraces' of up to 60°–70°) at the NF and SF midslope, respectively, was chosen (Fig. 1a). The bedrocks consist of Turonian limestone, with three formations: Netzer (at the upper slopes), Shivta (at the midslopes) and Drorim (at the bottom slopes). The bedrocks are covered by numerous limestone cobbles. Vegetation cover is low, 15–25%, usually below 50 cm in height. Over 94% of all rocky formations, whether rock outcrops or cobbles, are covered by lithobionts (Kidron and Temina 2013).

A sharp contrast in the lithobiont population characterizes the Shivta formation at the NF and SF midslopes. While endolithic cyanobacteria (*Gloeocapsa* sp.) inhabit the bedrocks of SFS (Friedmann and Galun 1974), endolithic and especially epilithic lichens, both with green algae as photobionts, i.e., chlorolichens, inhabit the bedrocks of NFS. Endolithic chlorolichens inhabit the SF cobbles while endolithic and epilithic chlorolichens inhabit the NF cobbles. Thus for instance, epilithic lichens cover only 0.4% of the cobbles of the SF midslope but 42.6% of the cobbles of the NF midslope (Kidron et al. 2011). The cover of epilithic lichens was however substantially higher at the NF bedrocks—96.5% (Temina and Kidron, data not shown).

All lithobionts have a distinct appearance. Whereas the epilithic lichens form a relatively smooth-faced surface (Fig. 1b), cyanobacteria render the surface a ragged micro-relief caused by weathering pits. Adjacent cobbles are inhabited by endolithic lichens, which render the surface a jigsaw-puzzle pattern of weathering (Fig. 1c; Danin and Garty 1983). These cobbles may be visibly wetted following

Fig. 1 General view of the research site (a), epilithic lichens covering the north-facing bedrock and cobbles (b), cyanobacteria covering the south-facing bedrock with endolithic lichens inhabiting the cobbles (c), and preferential wetting of stones and cobbles by dew (arrows) while the bedrock remains dry (d)



heavy dew while at the same time the bedrocks remain dry (Fig. 1d).

Among the endolithic lichens, *Pyrenodesmia alociza* (A. Mass.) Arnold (= *Caloplaca alociza*) predominates. Among the epilithic lichens, *Variospora aurantia* (Pers.) Arup, Frödén & Söchting (= *Caloplaca aurantia*), *Caloplaca circumalbata* (Delile) Wunder var. *circumalbata* (= *Caloplaca aegyptiaca*), *C. circumalbata* var. *bicolor* (Müll. Arg.) Wunder, *Diplotomma epipolium* (Ach.) Arnold (= *Buellia epipolia*), *Lobothallia farinosa* (Flörke) A. Nordin, Savić & Tibell (= *Lecanora farinosa*), *Myriolecis albescens* (Hoffm.) Śliwa, Zhao Xin & Lumbsch (= *Lecanora albescens*), and *Tephromela atra* (Huds.) Hafellner (= *Lecanora atra*) predominate (Lange et al. 1970; Friedmann and Galun 1974; Danin and Garty 1983). As for the midslopes, whereas the epilithic lichens *M. albescens* and *C. circumalbata* var. *bicolor* predominate at the north-facing bedrocks, *C. circumalbata* var. *bicolor* predominate at the cobbles, with epilithic lichens covering <5% and 43% of the south-facing and north-facing cobbles, respectively. Noteworthy is the low cover of endolithic lichens at the bedrocks of the north-facing midslope, <5%.

Microclimate

A pair of plots, 2 × 2 m, and 30 m apart was demarcated at the middle of NFS and SFS. At each plot, temperatures were measured by thermistors that were placed on randomly

chosen surface bedrock and two randomly chosen cobbles, ~ 15 cm × 15 cm × 5 cm each, within each plot. We used 3 cm-long and 0.5 cm-diameter TMC6-HD thermistors (Onset Computer Corporation, Bourne, MA, USA), which were calibrated prior to the experiment (± 0.05 °C) and were connected to U-12 Hobo (Onset Computer Corporation) data loggers. The thermistors were shielded from direct sun radiation with 4 cm × 1 cm × 0.5 cm polyurethane sheets. Temperatures were recorded and stored in 20 min intervals. Measurements were carried out for 30 days between August 22nd and September 20th, 2008.

Following the similar amounts of rain that were measured in both midslopes, our measurements were confined to NRW, mainly to dew and fog. Fog (defined as vapor condensation in the air that limits the visibility to less than one kilometer and which lasts at least half an hour; WMO 1992) was visually observed. Measurements were periodically undertaken during the years 2008–2010 using synthetic velvet-like 6 cm × 6 cm × 0.1 cm cloths (Vileda company, Weinheim, Germany), directly attached to the rock and the cobble surfaces with four adhesive stickers at their four corners. The cloths were attached in the afternoon and collected around sunrise during the following morning, during which condensation was maximal (Kidron et al. 2000). The cloths were placed into pre-weighed flasks that were immediately sealed. The flasks were then taken to a nearby lab, weighed, oven-dried at 70 °C until reaching a constant weight and then re-weighed in order to determine their water

content. The amount of water absorbed by the cloths was then divided by the surface area of the cloth. It included the weight of the liquid water following vapor condensation, but also the weight of vapor during mornings during which the relative humidity was not high enough to result in condensation (Kappen et al. 1979). The amount of water (in millimeters) was then calculated according to Kidron and Kronenfeld (2020):

$$NRW \left(\frac{\text{mm}}{\text{day}} \right) = 10 \frac{WC_{wet} - WC_{dry}}{A\rho} \quad (1)$$

where NRW is the measured non-rainfall water (mm); WC_{wet} and WC_{dry} are the wet and dry weight of the cloths (g), respectively; A is the surface area (cm^2); and ρ is the density of water (g cm^{-3}) at a given temperature.

The applicability of using cloths to evaluate the water regime of lichens was confirmed by simultaneous measurements of cloths and the lichen thalli of *Ramalina maciformis* (Delise) Bory. These measurements showed that vapor accumulation, whether on the cloths or the thalli, when placed on the same substratum yielded similar values, supporting the use of cloths as a reliable mean for NRW measurements (Kidron et al. 2014). Yet, as thoroughly discussed (Kidron and Kronenfeld 2022a), while adequately mimicking above-surface lichens, the cloths may overestimate the amount of NRW relevant for cyanobacteria, which inhabiting the 1–3 mm-deep subsurface. Cyanobacteria may therefore experience higher nocturnal temperatures and as such lower amounts of NRW than those recorded by the cloths (Kidron and Kronenfeld 2022a).

Chlorophyll, carbohydrates and organic carbon

Measurements of chlorophyll a (Chl), total carbohydrates (CRB) and organic carbon (OC) were performed in order to determine the lithobiont biomass. Being aware of the possible effect of slope angle upon the results, preliminary measurements were conducted on the inclined and relatively flat surfaces of the bedrocks. While significantly higher biomass was obtained by the inclined (and therefore shaded) NF bedrocks (Kidron et al. 2014), non-significant differences characterized the sun-exposed inclined and relatively flat surfaces of the SF bedrocks. In agreement with the general characteristics of these habitats (with > 80% of the surfaces being inclined), sampling was confined to the inclined surfaces of the bedrocks. As for the cobbles, the sampled communities were only slightly inclined, reflecting the location of most cobbles at the relatively flat (and therefore stable) sections of the slope terraces.

The surfaces of all samples were brushed to eliminate, as much as possible, dust particles and other sources of contamination. For Chl and CRB measurements, 15 samples, 1

cm^2 each and approximately 1.0 cm thick, were randomly taken from the bedrock and cobbles of each plot during the fall of 2008 (total of 30 samples for each habitat). The rock samples were immersed in water for 5 min to soften the substrate, and the top 5 mm of the rock was scraped for Chl and CRB determination. Chlorophyll was extracted by 5 ml of hot methanol (70°C, 20 min) in the presence of MgCO_3 (0.1% w/v) in sealed test tubes and assayed according to Wetzel and Westlake (1969) using the equation:

$$\text{Chl } a \left(\mu\text{g l}^{-1} \text{cm}^{-2} \right) = (A_{665} - A_{645}) \times 13.9 \times 5. \quad (2)$$

Following the Chl extraction, total carbohydrates was determined by the anthrone method, during which the blue-green color formed between the carbohydrates and the anthrone reagent (a tricyclic aromatic ketone) was measured spectrophotometrically and the concentration was calculated from a standard curve (Hassid and Abraham 1957). As for organic carbon (OC), it was determined by loss of ignition. For OC, twelve rock samples, approximately 6 cm × 4 cm × 0.5 cm, were randomly taken from the bedrock and cobbles of each plot (total of 24 samples for each habitat), weighed and then ignited at 450 °C for 8 h and then reweighed.

Statistics

For all variables, a normal distribution was tested and the assumption of homogeneity of variance was examined via the Levene's test statistic. We ascertained that the variables were normally distributed and that the homogeneity of variance was not violated. We executed thereafter one-way ANOVA (using SPSS 11.0 for Windows; SPSS, Chicago, IL) with habitat as the dependent variable and Chl, CRB, OC, minimum temperatures (TEMP_{\min}), maximum temperatures (TEMP_{\max}) and NRW as the independent variables. Once significant, post-hoc tests were performed, using the least significant difference (LSD) for Chl, CRB and OC, and paired t -test for TEMP_{\min} , TEMP_{\max} and NRW. Differences were regarded significant at $P < 0.05$.

Results

A total of 22 dewy mornings and 4 foggy mornings were measured. Fogs commonly exhibited higher amounts of NRW than dew. Examination of the habitat properties showed high variability, as verified by one-way ANOVA (Table 1). When post-hoc tests were performed for Chl, significant differences characterized all habitats. As for CRB, apart from the bedrocks and the SF cobbles that exhibited marginal significant differences ($P = 0.087$), all other habitats exhibited significant differences. Significant

Table 1 One-way ANOVA tests for chlorophyll (Chl), organic carbon (OC), maximum temperature (TEMP_{max}), minimum temperature (TEMP_{min}), and non-rainfall water (NRW)

Variable	Category	df	SS	MS	F	P
Chl	Between groups	3	232,087.6	77,362.5	31.39	<0.001
	Within groups	116	285,932.7	2464.9		
	Total	119	518,020.2			
OC	Between groups	3	10,303,916	3,434,638.5	74.95	<0.001
	Within groups	116	5,315,490	45,823.2		
	Total	119	15,619,405			
TEMP _{max}	Between groups	3	2659.7	886.6	269.3	<0.001
	Within groups	116	381.9	3.3		
	Total	119	3041.6			
TEMP _{min}	Between groups	3	298.4	99.5	21.48	<0.001
	Within groups	116	537.2	4.6		
	Total	119	835.6			
NRW	Between groups	3	0.231	0.077	14.7	<0.001
	Within groups	100	0.522	0.005		
	Total	103	0.753			

differences also characterized the OC of all habitats, as well as the TEMP_{max} and TEMP_{min} (paired *t*-test). As for NRW, except for the cobbles at both aspects ($P=0.606$), all other habitats exhibited significant differences.

The average values of Chl, CRB and OC are shown in Fig. 2a–c, respectively. Expectedly, both variables exhibited substantially higher values at NFS than SFS, with Chl, CRB and OC being 1.5-, 3.5-, and 2.4-folds higher at the NF cobbles than at the SF cobbles, respectively. The differences were substantially higher for the bedrocks, 11.5-, 31.9-, and 47.2-fold higher for Chl, CRB and OC at the NF bedrocks in comparison to the SF bedrocks, respectively. Significant differences also characterized these variables within each aspect. All variables were higher for the NF bedrocks. In comparison to the cobbles, Chl, CRB and OC were 1.5-, 1.6-, and 2.9-fold higher for the NF bedrocks. Contrasting findings were found for SFS where the cobbles exhibited higher values than the bedrock. In comparison to the bedrock, Chl, CRB and OC were respectively 5.0-, 5.9-, and 6.8-folds higher at the cobbles. Generally, all these variables followed the pattern: Rock NF > cobble NF > cobble SF > rock SF.

Surface temperatures exhibited high variability. Average hourly temperatures during daytime and nighttime are shown in Fig: 3a and 3b, respectively. While the SF cobbles exhibited higher maximum temperatures, SF bedrocks exhibited higher minimum temperatures. As one may expect, and clearly evident during simultaneous measurements (Fig. 3c), the high variability in the minimum temperatures also resulted in high variability in the NRW amounts. Yet, while minimum temperatures followed the pattern: rock SF > rock NF > cobble SF > cobble NF, the amounts of NRW followed the pattern: cobble NF > cobble SF \approx rock NF > > rock SF.

Expectedly, average temperatures of the cobble and rock surfaces at SFS showed higher daytime temperatures than the rock and the cobble at NFS, respectively (Fig. 4a). Maximum temperatures of the SF bedrocks were on average 10.3 °C higher than the NF bedrocks. Within the SFS, average maximum temperatures of the SF cobbles were 1.9 °C higher than at the SF bedrocks (with the maximum recorded difference being up to 4.1 °C); however the average minimum temperature of the SF cobbles was 3.4 °C cooler (with the maximum recorded difference being 5.3 °C) than the SF bedrocks (Fig. 4b). When the average nocturnal cooling rate (between 20:00 and 05:00) was calculated, the highest cooling rates were exhibited by the cobbles. Interestingly, the cooling rate of the NF bedrocks was the lowest, explained by its low maximum temperatures (Fig. 4c).

To a large extent, the surface temperatures were reflected in the amount of NRW. While the NF and SF cobbles and the NF bedrocks showed the highest average daily amounts (0.10–0.17 mm), bedrocks at SFS showed the lowest amounts, 0.020 mm (Fig. 4d). One may note that even during foggy mornings, maximum daily NRW at the SFS bedrock was <0.04 mm (Fig. 3c).

Discussion

Interrelation between abiotic and biotic variables

The high differences in the amounts of Chl, CRB and OC in all habitats could not have been attributed to rock properties. Being a few tens of meters apart and located at the same geological formation, no differences were disclosed by scanning electron microscope with energy-dispersive analysis of elements (ESEM-EDS) or thin section examination as

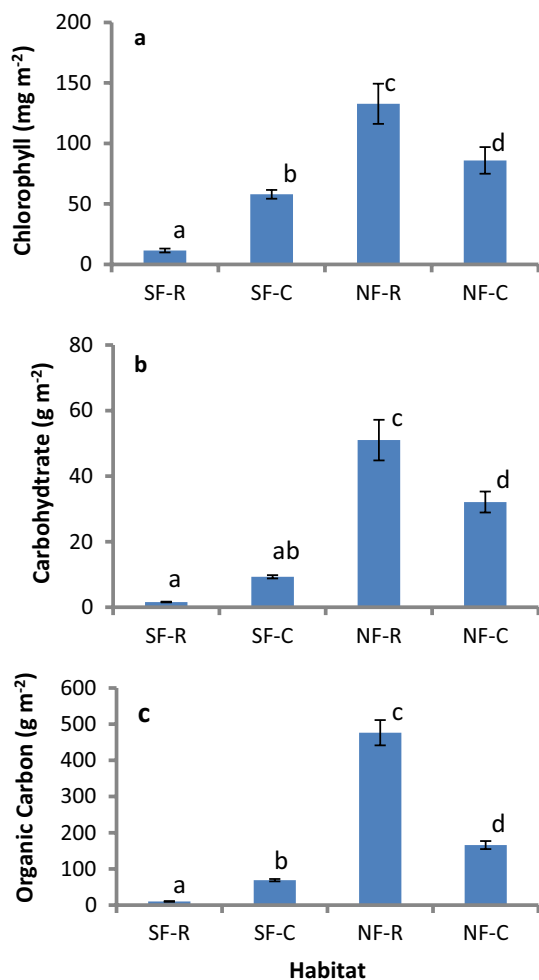


Fig. 2 Chlorophyll *a* (a), total carbohydrates (CRB) (b) and organic carbon (OC) content (c) of lithobionts inhabiting north-facing bedrocks (NF-R) and cobbles (NF-C) and south-facing bedrocks (SF-R) and cobbles (SF-C). Bars represent one standard error ($n=30$ for Chl and CRB and 24 for OC). Different letters denote significant differences ($P<0.05$)

previously reported (Kidron et al. 2014). The data thus suggest that environmental rather than lithological factors are responsible for the differences observed. Also, with both slopes receiving similar rain amounts (Kidron et al. 2011, 2014), the differences observed could not have been attributed to rain, leaving NRW as the only possible source of water that could have explained the different species composition at these habitats.

High differences in surface temperatures characterized both slopes, an expected outcome following the 1.8-fold higher maximum radiation at SFS (Kidron et al. 2014). However, while the higher maximum temperatures at the SF bedrocks in comparison to the NF bedrocks and the higher maximum temperatures at the SF cobbles in comparison to the NF cobbles are expected, the higher maximum temperatures of the cobbles in each aspect in comparison to

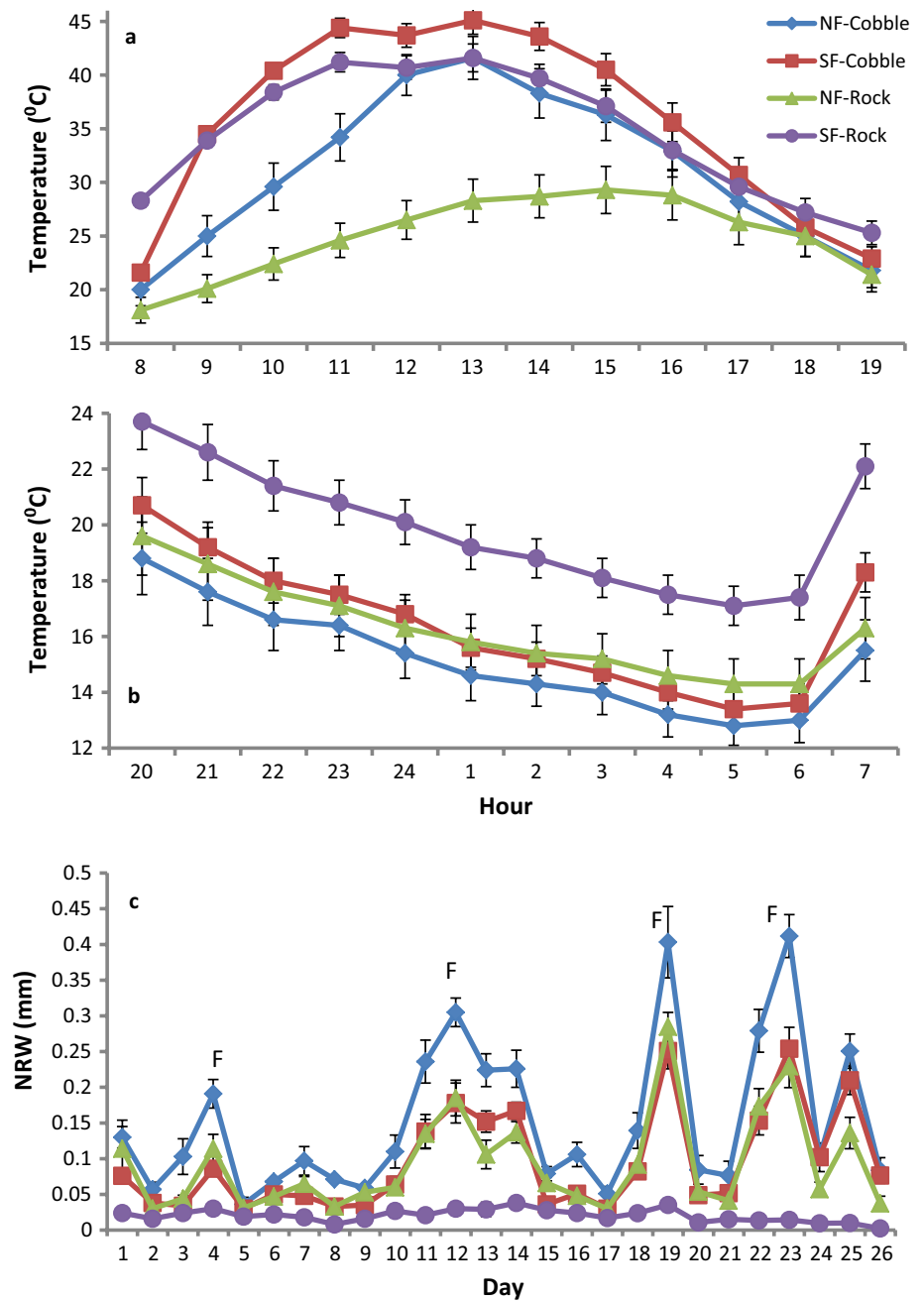
the bedrocks (1.9 °C for the SF slope and 9.7 °C for the NFS) deserve explanation. This is also the case regarding the lower minimum temperatures (2.8–3.4 °C on average) of the cobbles in comparison to the bedrocks.

Being of low volume and detached, loose cobbles experience efficient longwave radiative cooling. In comparison to the bedrocks, the relatively isolated and low-volume cobbles warm up quickly during the day, while they also cool off quickly during the night. The amount of NRW, particularly dew, is closely linked to the temperature of the substratum (T_s), and therefore lower minimum temperatures within a given site should result in higher NRW (Beysens 2018). Minimum temperatures of the NF cobbles were lower than those of the NF bedrocks, and subsequently higher NRW were obtained by the cobbles. Nevertheless, higher biomass characterized the lichen-inhabiting bedrocks. This may be explained by the apparent younger community of the cobbles due to the unstable position of the cobbles, which may be dislocated, especially on relatively steep slopes, and by the more inclined and therefore shaded position of the bedrocks, which facilitate longer hours of activity following rain and NRW. This was also evident during occasional measurements that exhibited 20–25% of longer wetness duration on inclined north-facing surfaces in comparison to flat surfaces (Kidron, data not shown). With wetness duration principally dictating lithobiont growth and biomass (Kappen et al. 1980; Kidron et al. 2011), longer wetness duration at the high-angle NF bedrocks may thus explain longer activity and subsequently higher biomass at the bedrock-inhabiting lichens.

In light of the minimum amounts of water required for lithobiont activity, the amounts recorded on the SF bedrocks shed light on the lithobiont distribution in the Negev. The minimum amount required for net photosynthesis by cyanobacteria (0.1 mm; Lange et al. 1992) exclude the possible growth of cyanobacteria at the SF bedrocks following dew or fog. Also, the minimum amount found to allow for net photosynthesis for chlorolichens (0.05 mm; Kidron and Starinsky 2019) also excludes the possible growth of chlorolichens at the SF bedrocks, pointing out that rain serves as the sole source of water for the cyanobacteria growth at the SF bedrocks (Kidron et al. 2014; Kidron and Kronenfeld 2022a).

This however is not the case with endolithic chlorolichens dwelling on cobbles (or stones) at SFS. Due to efficient outgoing longwave radiative cooling, the cobbles are occasionally wetted by dew while the bedrocks at the same time remain dry (Fig. 1d). These differences in water sources are indeed reflected in the lithobiont biomass, which is substantially higher at the SF cobbles, with Chl, CRB and OC being 5.0-, 5.8-, and 6.8-fold higher at the SF cobbles than the SF-bedrocks. With photobionts occupying only a small percentage of the lichen thalli (< 10%; Ahmadjian 1993), and with OC also reflecting the heterotrophic component (fungi) of the cobble-dwelling lichens, the higher differences

Fig. 3 Average hourly daytime (a) and nighttime (b) temperatures as measured concomitantly during the fall of 2008 (August 22nd to September 20th), and the daily amount of dew and fog as measured concomitantly during 26 days on the north- and south-facing bedrocks and cobbles (c). Fogs are denoted by the letter F. Bars represent one standard error



that characterize OC (in comparison to Chl) are expected. Experiencing similar irradiation, rain and evaporation, the significantly higher biomass of the lichens at the SF cobbles can be solely explained by the contribution of NRW to the cobble-inhabiting lichens.

Calculating lithobiont activity and NRW contribution

Multiplying the daily average amount of dew at the four habitats by the amount of dewy events (195 days), the relationships between the total annual rain and dew amounts and

the lithobiont biomass (Chl, CRB, OC) can be calculated (Table 2; Fig. 5a). Similarly, taking the length of time as estimated for the dew and rain duration for NFS and SFS (Kidron et al. 2011), the relationships between the annual time duration and the OC of the lithobionts can be calculated (Table 2; Fig. 5b). Except for CRB, no significant relationships characterize the combined *amount* of rain and NRW and the amount of Chl and OC. Significant relationships characterized however the combined *wetness duration* of rain and NRW and the amount of Chl, CRB and OC with $r^2 > 0.95$. The findings pointed to the overwhelming effect of wetness duration (rather than the amount of NRW and rain)

Fig. 4 Average maximum and minimum temperatures as measured during 30 days (August 22nd to September 20th) (a), the average cooling rate of all habitats (b), and the average daily dew and fog amounts during 26 days of dew and fog measurements on the north-facing bedrocks (NF-R) and cobbles (NF-C) and south-facing bedrocks (SF-R) and cobbles (SF-C) (c). Bars represent one standard error. Different letters denote significant differences ($P < 0.05$)

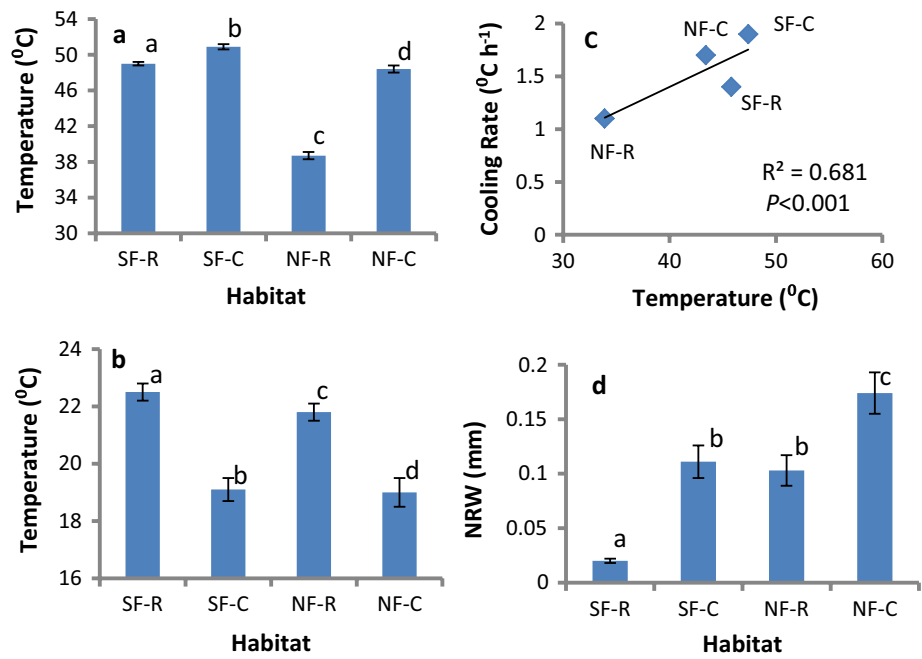


Table 2 Calculation of the wetness duration of rain during periodical measurements of rock wetness duration following variable-size rain events (a) and calculation of the amount and duration of NRW and the total amount and duration for the north-facing (NF) and south-facing (SF) bedrocks (R) and cobbles (C) (b) (after Kidron et al. 2011)

(a)

Rain amount (mm)	Average number of events	Average wetness duration (h) ^a			
		Per Event		Per Annum	
		NFS	SFS	NFS	SFS
< 1	10.8	0.75	0.5	8.1	5.4
1–4	8.2	3.4	2.6	27.9	21.3
4–10	5.0	11.3	9.2	56.5	46.0
> 10	2.1	12	8.5	25.2	17.9
Total				117.7	90.6

(b)

Habitat	Dew amount per dewy morning (mm)	Calculated annual amount of dew ^b (mm)	Calculated annual amount of rain and dew ^c (mm)	Dew duration per dewy morning ^d (h)	Calculated annual duration of dew ^b (h)	Calculated annual duration of rain and dew (h)
R-SF	0.022	4.3	99.3	0	0	90.6
C-SF	0.087	17.0	112.0	2.25	438.8	529.4
R-NF	0.092	17.9	112.9	4.3	838.5	956.2
C-NF	0.127	24.8	119.8	3.8	741	858.7

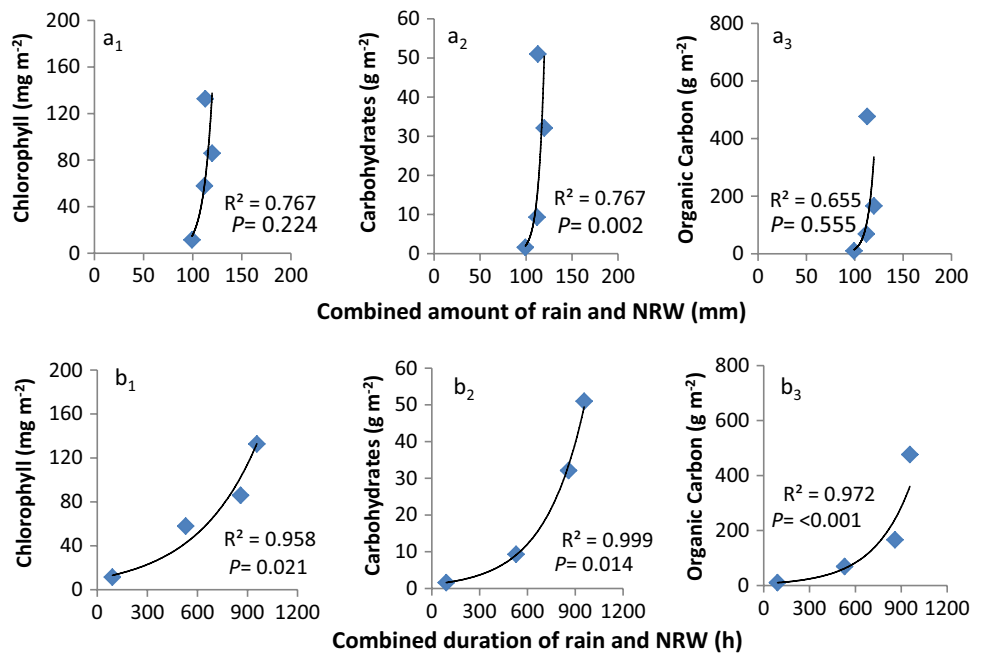
^aWe assume similar duration of rain for bedrocks and cobbles within the same aspect. We figure that while evaporation from the bedrock may be higher due to higher surface temperatures, the more efficient cooling of the cobbles by wind may compensate for the higher evaporation at the bedrock due to higher surface temperatures

^bBased on 195 days of NRW (Evenari et al. 1971)

^cSince non-significant differences characterized the amount of rain in both aspects, the long-term mean of 95 mm was added to the amount of dew

^dBased on Kidron et al. (2000)

Fig. 5 The relationship between the combined amount (a) and duration (b) of non-rainfall water and rain and the lithobiont chlorophyll (a₁, b₁), carbohydrates (a₂, b₂) and organic carbon (a₃, b₃)



on the lithobiont biomass, similar to the relationships found for soil biocrusts (Kidron et al. 2009).

Whether on rocks or soil, a thick film of water impedes CO₂ diffusion into the carboxylation sites (Lange and Tenhunen 1981), which may explain in turn the lack of a clear relationship between the amount of water and biomass. Wetness duration rather than the water amount (depth) may therefore principally dictate the microorganism activity and subsequently growth.

By comparing the lithobionts at the SF aspect, the current findings allow estimation of the NRW contribution to lithobiont productivity. Based on the current analysis, the contribution of NRW to the lithobiont Chl, CRB and OC is substantial: 5.0-, 5.8-, and 6.8-fold higher than that of rain, respectively. The contribution of NRW is remarkable given the fact that the amount of the annual dew is ~ 1/3 of that of rain. But as already noted above, it is not the amount but rather the wetness duration that counts. As can be seen in Table 2, the 5.8-fold longer wetness duration at the SF cobbles (529.4 h) in comparison to the SF bedrock (90 h) is closely linked to the 5.0–6.8-fold increase in the lithobiont biomass.

With lichens serving as a food source for snails (Shachak et al. 1987), the entire food chain is impacted, affecting in turn the entire ecosystem productivity. With cobbles triggering dew formation and due to the fact that dew is largely enriched with nutrients (with potassium, nitrate and ammonium being 7.6-, 7.7- and 2.6-fold higher in comparison to rain; Kidron and Starinsky 2012), productivity should also be indirectly enhanced at the cobbles through additional fertilization. Total productivity of a dew desert such as

the Negev is therefore expected to be substantially higher than for a non-dewy desert with the same long-term mean precipitation.

Ecophysiological implications

The findings may have important ecophysiological consequences, supporting recent publications suggesting that eukaryotes may also have high resilience to desiccation and UV radiation (Gostinčar et al. 2009), such as the extremely high resilience exhibited by micro colonial fungi (Sterflinger et al. 2012) or yeasts (Pulschen et al. 2015). As far as the chlorolichens are concerned, the notion that chlorolichens are more vulnerable to wet-dry cycles or high temperature fluctuation (Potts 1999; Nienow 2009), as also reported in textbooks (Campbell et al. 1999; Raven et al. 2005) was not supported at this site. Chlorolichens, such as those dwelling on the SF cobbles were subjected to slightly higher temperature extremes. Although the differences in temperature fluctuations were not large, they had a high impact on moisture fluctuation, which, as found for various microorganisms, requires specific physiological adaptations (Rajeev et al. 2013).

The exposure of chlorolichens to frequent (and higher) temperature and moisture fluctuation can be also deduced from their location in other arid areas, for instance in the Arctic, and the Namib (Table 3). Chlorolichens abound in the islands and coasts of the Arctic (Cockell et al. 2002; Omelon et al. 2006), where they are subjected to frequent wet-dry cycles following dewfall or fog, or to the top of cobbles and stones in the Namib where they are subjected

Table 3 Preferential location of desert chlorolichens (eukaryotes) and cyanobacteria (prokaryotes)

Desert	Zone	Loci	References
(a) Eukaryotes			
Arctic	Coast	As epiliths on rocks	Cockell et al. (2002), Omelon et al. (2006)
Namib	Coast	As epiliths on rock particles	Wessels (1989), Hinchliffe et al. (2017)
Atacama		As epiliths on rocks and rock particles (grit)	Jung et al. (2020)
US deserts		On bedrocks	Nash et al. (1977)
Negev		On rock particles and bedrocks	Danin and Garty (1983), Kidron et al. (2011, 2014)
(b) Prokaryotes			
Arctic	Coast	As endoliths in rocks	Cockell et al. (2002)
Namib	Inland	As endoliths in sandstone	Weber et al. (1996)
Atacama		Within halite	Wierzchos et al. (2006), Davila et al. (2010), Wierzchos et al. (2011)
		Within gypsum	DiRuggiero et al. (2013)
		As chasmoendoliths	
US deserts		As endoliths on sandstones	Bell et al. (1986)
Negev		On sun-exposed bedrocks	Danin and Garty (1983), Kidron et al. (2011, 2014)

to frequent wet-dry cycles following fogs (Hinchliffe et al. 2017). Alternatively, and similarly to the SF cyanobacteria at our site, cyanobacteria in arid regions are mainly confined to habitats/microhabitats that receive liquid water (Table 3), whether within gypsum (Wierzchos et al. 2011) or halite (Davila et al. 2010) as is the case in Atacama.

The requirement of additional water by lichens is also evident for soil-dwelling lichens. It is evident in the lichen fields in the Namib (Schieferstein and Loris 1992) and the coast line near Salar Grande in the Atacama (Warren-Rhodes et al. 2007). While receiving negligible rain, whether in the Namib (Büdel et al. 2009) or the Atacama (Davila et al. 2015), heavy fogs provide the lichens with the required amount of water (Lange et al. 2006). However, in places where water is more scarce such as at the central valleys of the Atacama, e.g. the Yungay and similar sites southward (McKay et al. 2003), only cyanobacteria that colonize halite (Wierzchos et al. 2006; Davila et al. 2010), or gypsum (Wierzchos et al. 2015) can be found, explained by deliquescence. This corresponds to the model suggested by Kidron et al. (2014), and further supported by additional findings (Kidron and Kronenfeld 2022a, 2022b). Accordingly, while cyanobacteria are confined to habitats that receive liquid water, habitats with high relative humidity may support chlorolichens.

Based on the nature of dew formation (which exhibit a gradual increase in relative humidity until condensation; Beysens 1995), it is therefore postulated that chlorolichens, which can also utilize high relative humidity, may have a competition advantage over cyanobacteria in dewy and foggy habitats (Kidron and Kronenfeld 2022b), and may explain the dominance of chlorolichens in foggy coastal regions of extreme deserts like the Atacama and the Namib (Lange

et al. 2006). At the same time, scarcity of rain in the coastal Namib may explain the scarcity of cyanobacterial biocrusts there (Kidron 2019).

Our findings point to a completely different suite of environmental conditions required by each domain, implying that cyanobacteria and chlorolichens may serve as useful bioindicators for the prevailing water sources at the different sites. The findings may also have important consequences regarding global warming, and especially following a possible increase in nocturnal temperatures (Price et al. 1999), which may principally affect chlorolichen cover and biomass (Kidron and Kronenfeld 2022a). Our findings may also contribute to the reconstruction of the ecological setting of possible paleo life on Mars (McKay and Davis 1991; Squyers et al. 2004), and the development of approaches for the detection of biomarkers of extraterrestrial life (Avnir 2021).

Conclusions

We report an analysis of the growth patterns of cyanobacteria and lichens in a single drainage basin in the Negev Desert that has variations in the amount of dew across the site. Our results support previous work in the Negev Desert (Kidron et al. 2014) that concluded that lichens dominate at habitats where the principle water supply is dew and cyanobacteria are confined to habitats supplied by rain. We hypothesized that in some cases, chlorolichens (eukaryotes) may experience higher environmental fluctuation of temperature and NRW than cyanobacteria (prokaryotes). Subsequently, we carried out concomitant measurements of temperature and NRW on NF cobble-dwelling lichens and bedrocks, SF cobble-dwelling lichens and on SF rock-dwelling cyanobacteria

in the Negev Desert. Substantially higher fluctuations in temperatures and especially in NRW characterized the SF cobbles in comparison to the SF bedrocks. As a result of lower nocturnal temperatures (by 3.4 °C on average), higher daily NRW characterized the SF cobbles (averaging 0.11 mm) in comparison to the bedrocks (averaging 0.020 mm). The higher NRW was responsible in turn for the development and growth of chlorolichens on the cobbles. As also suggested by the spatial distribution of eukaryotes and prokaryotes in other arid regions, our findings do not support the occasionally-mentioned hypotheses that chlorolichens are adapted only to habitats of low water availability and that prokaryotes (cyanobacteria) abound in extreme deserts due to the eukaryote (chlorolichens) vulnerability to cope with high environmental fluctuations. As far as the lithobionts are concerned, the findings assess the contribution of NRW to the ecosystem productivity, with NRW contributing 6.8-fold the amount of OC in comparison to rain. Subsequently, global (especially nocturnal) warming may have a profound effect on the lithobiont distribution and thus on ecosystem productivity.

Author contribution statement GJK and AS conceived and designed the research; RK, SYT, MT and GJK conducted the experiments; GJK, AS, and CPM wrote and edited the manuscript.

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Data Availability Data will be available upon request.

Declarations

Conflict of interest The author declare no conflict of interest.

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