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Biocrust heterogeneity drives water balance in the topsoil of temperate sandy post-mining ecosystem

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Abstract

Purpose Sandy habitats in temperate regions include a range of anthropogenic and semi-natural ecosystems, such as post-mining areas. Such environments face severe ecological constraints due to coarse soil texture, low nutrient content, and poor water retention. Among natural recovery processes, biological soil crusts (biocrusts) play a key role in shaping soil hydrology and surface stability.

Methods In this study, we investigated water-related traits and functional parameters of three biocrust types: algae-, moss-, and lichen-dominated, developing in temperate sandy post-mining ecosystem.

Results Our findings revealed significant ecohydrological differences between biocrusts dominated by various photoautotrophs. Lichen-dominated biocrusts showed high water-holding capacity (145.93%), vapor adsorption (0.197 mm) and evaporation cumulative amounts (4.768 mm), together with elevated dehydrogenase activity (284.23 µg TPF g^{-1} DW), total exopolysaccharide concentration (3.83 mg g^{-1} DW) and total chlorophyll content (156.63 µg g^{-1} DW). Their high evaporation rate (0.984 mm h^{-1}) may intensify short-term water fluctuations in sandy topsoils. In contrast, algae-dominated biocrusts showed consistently low values across studied water-related traits (e.g. vapor adsorption 0.02 mm), as well as low evaporation rate (0.294 mm h^{-1}) indicating prolonged surface moisture retention. Moss-dominated biocrusts showed moderate vapor adsorption (0.051 mm) and intermediate evaporation (0.859 mm h^{-1}), offering a more balanced hydrological profile.

Conclusions Our findings showed that different biocrust types spontaneously developing in post-mining sandy ecosystem contribute to maintaining the heterogeneity of the topsoil in terms of water holding capacity and the ability to absorb and evaporate water. This functional heterogeneity can help stabilize soil water dynamics, mitigate extreme fluctuations, and support more resilient vegetation development over time, and may be key to enhancing ecosystem resilience in temperate sandy soils.

Keywords Biological soil crust · Temperate climate · Water balance · Ecosystem resilience · Post-mining ecosystem

1 Introduction

Sandy soils, which span approximately 900 million hectares globally, are especially prevalent in arid and semi-arid regions but are also found across all climate zones (Yost and Hartemink 2019). These soils are defined by their high permeability, low water and nutrient retention capacity, and generally low organic carbon content (Osman 2018). In temperate regions, sandy habitats represent different anthropogenic and semi-natural ecosystems that may remain mobile or become partially stabilized by vegetation. However, the dominance of coarse-textured sand with large pore spaces creates dry, nutrient-poor conditions that limit plant establishment. The high infiltration and leaching rates typical of sandy substrates strengthened the nutrient loss through washout (Tsoar 2005; Xiao et al. 2019).

Former sand mines present a range of ecological challenges that significantly hinder natural ecosystem development due to the severe alteration of soil, hydrology, and landscape structure. These areas are typically left in

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a degraded state after mining operations cease, and without active restoration efforts, their ecological recovery is severely impeded (Favas et al. 2018). Water conditions in former sand mines, particularly at the soil surface, are critically important for maintaining soil condition and supporting vegetation development (Benigno et al. 2013). Moist conditions on the soil surface contribute to biological activity, including microbial processes that break down organic matter and release nutrients. In former sand mines, where nutrient levels are extremely low (Yost and Hartemink 2019), any enhancement of microbial activity helps initiate nutrient cycling and improves soil fertility over time. Dry, loose sand is highly prone to wind and water erosion, while maintaining adequate surface moisture helps bind soil particles together, reducing erosion and improving physical soil structure (Wiggs et al. 2004; Holz et al. 2015). This stability is essential for long-term vegetation growth and habitat restoration. In former sand mines, where traditional plant-based restoration can be difficult due to extreme soil and water limitations, biological soil crusts (biocrusts) developing spontaneously in temperate sandy habitats could support initiating ecological recovery and act as a foundational layer for future ecosystem development (Antoninka et al. 2020; Szafrańska et al. 2026).

Biocrusts form a cohesive layer within the uppermost millimeters of the soil surface, composed of photoautotrophic organisms, including cyanobacteria, algae, lichens, and mosses, as well as heterotrophic bacteria and microfungi, and are associated with soil particles (Weber et al. 2022). They perform several important ecological functions in ecosystems by contributing to carbon and nitrogen fixation (Maestre et al. 2011), enhancing microbial activity (Liu et al. 2017), initiating soil formation processes (Chamizo et al. 2012), and facilitating the establishment of vascular plants (Zhang et al. 2016). Biocrusts influence also key hydrological processes, including surface evaporation (e.g., Kidron and Tal 2012), runoff generation (e.g., Lázaro et al. 2015), infiltration (e.g., Chamizo et al. 2016a), and non-rainfall water deposition (e.g., Li et al. 2021). Regarding these several roles, biocrusts are often described as ecosystem engineers (Ferrenberg et al. 2017). Although most extensively studied in drylands of arid climates, biocrusts also occur in temperate regions, particularly in habitats where environmental constraints limit vascular plant development (Corbin and Thiet 2020). In more humid climates, biocrusts are typically found in semi-natural grasslands, sandy environments, or anthropogenically disturbed areas such as post-industrial landscapes (Szyja et al. 2018). A notable example includes former sand mining sites, where the extraction of sand from open pits leads to substantial alterations in geological structure, topography, hydrology, soil conditions, vegetation cover, and microclimate (Dulias 2010). Following such disturbances, biocrust communities are often among the earliest colonizers, as increased light availability and reduced plant competition create favorable conditions for their development (Bowker 2007).

Evaporation, vapor diffusion, and subsequent vapor condensation or adsorption near the soil surface represent fundamental processes governing water movement in the upper soil layers (Deb et al. 2011). Soil evaporation is often separated into three stages: high rate (stage I), falling rate (stage II), and low and constant rate stage (stage III) (Sun et al. 2024). While soil water vapor adsorption generally proceeds in three stages: monolayer adsorption at relative humidity (RH) from near 0 to 0.2, multilayer adsorption at RH 0.2–0.6, and capillary condensation at RH above approximately 0.6 (Quirk and Murray 1999; Arthur et al. 2016). Soil water transport is shaped by factors such as soil texture, porosity, structure, and particularly surface cover (Arthur et al. 2015), all of which are directly affected by biocrusts. By influencing soil retention, infiltration, evaporation, and surface runoff, biocrusts significantly alter the movement and availability of water in the soil profile (Eldridge et al. 2020; Li et al. 2022). As such, they act as important regulators of ecohydrological fluxes and mediate key biological and biogeochemical processes in the upper soil layers (Li et al. 2022; Xiao et al. 2022). The mechanisms by which biocrusts influence hydrological processes are complex and vary with environmental context, largely depending on their coverage and species composition (Chamizo et al. 2016b; Baldauf et al. 2023; Kidron 2021; Li et al. 2022). For example, on sandy soils, biocrusts often reduce infiltration relative to bare surfaces, while their effects on finer-textured soils proved to be more variable or even reversed (e.g. Eldridge et al. 2020). Additionally, biocrusts indirectly influence water dynamics by modifying soil characteristics like porosity, aggregation, and surface water retention (Chamizo et al. 2016b). These effects are directly linked to the functional traits of the biocrusts (Mallen-Cooper et al. 2020). Exopolysaccharides (EPS), produced mainly by cyanobacteria and algae, form a sponge-like matrix that enhances soil water retention and promotes aggregation, thereby increasing porosity and creating viable pathways for water flow (Rossi et al. 2012; Costa et al. 2018). Microbial activity, commonly assessed through dehydrogenase activity (DHA), indicates both the population size and metabolic capacity of soil microorganisms, which play a crucial role in biochemical processes affecting water and energy flow near the soil surface (Quilchano and Marañon 2002; Berdugo et al. 2020). Furthermore, the chlorophyll content of biocrusts serves as an indicator of photosynthetic biomass, linking the presence of photoautotrophic organisms such as cyanobacteria, algae, lichens, and mosses to the accumulation of organic matter (Beymer and Klopatek 1991). This

organic matter acts as a natural cementing agent that stabilizes soil aggregates, enhancing soil structure and facilitating faster water vapor diffusion (Gao et al. 2010; Yang et al. 2022). Biocrusts influence soil evaporation through their biological composition and altered surface properties like roughness, porosity, and hydrophobicity (Chamizo et al. 2016b). However, their effect remains debated, with studies reporting both increased (Li and Xiao 2022) and reduced evaporation (Kakeh et al. 2021). Some studies highlighted their moisture-retention benefits due to high biomass, EPS, organic matter, and fine particle content (e.g., Xiao et al. 2010), whereas others suggested that biocrusts may increase evaporation by darkening the soil surface and promoting heat adsorption (e.g., Qin et al. 2002).

Biocrust ability to influence water dynamics has been extensively documented in arid and semi-arid regions, where water scarcity critically limits vegetation growth and ecosystem functioning (e.g., Sun et al. 2024; Kidron et al. 2022). However, there is a significant knowledge gap concerning the hydrological characteristics of biocrusts in temperate climates. In contrast to arid and semi-arid regions, temperate ecosystems have received far less attention. Although, in temperate climates high precipitation and competition from vascular plants restrict cryptogams primarily to edaphically dry sites, such as open grasslands and sand dunes, biocrusts, together with mosses and lichens, readily colonize open habitats and open-canopy forests (Corbin and Thiet 2020; Rieser et al. 2021). To date, no comprehensive studies have examined or compared the water-related traits of different biocrust types under mesic conditions. Moreover, the majority of studies focused on the changes of evaporation and adsorption induced by biocrusts compared to bare soils (e.g., Chamizo et al. 2016a; Sun et al. 2024). Thus, we consider this effect to be well-established. Consequently, in the present study, instead of focusing on the general impact of biocrusts on hydrological effects, we compared water-related traits between three specific biocrust types occurring in temperate climate, i.e., algae-, moss- and lichen-dominated biocrusts. This study offers the first in-depth comparison of different biocrust types under mesic conditions, shifting the focus from their general impact to a more type-specific perspective. Finally, we analyzed key functional parameters of particular biocrust types to better elucidate the differences in their water-related traits. We hypothesized that: (1) Moss-dominated biocrust, similar to those from arid habitats, would exhibit higher water adsorption and evaporation rates compared to other biocrust types; (2) Moss-dominated biocrust would have higher total EPS level, while algae-dominated would exhibit the lowest total EPS level; (3) Lichen-dominated biocrust would exhibit the highest dehydrogenase activity.

2 Materials and methods

2.1 Study site

The study was conducted in the area of the former Szczakowa sand mine (50° 15′ 17.69″ N, 19° 24′ 28.20″ E), located in the town of Bukowno in southern Poland. Spanning approximately 32 km², this open-pit mine is among the largest mining sites in both Poland and Europe (Dulias 2013). Since the 1950s, the Szczakowa mine has been used to extract large deposits of Quaternary sands. The mined areas typically feature geometric outlines, steep side slopes, and flat bottoms. Major excavations reached an average depth of 15–20 m (Dulias 2005). Between 1960 and 2005, around 29.64 km² of the site were reclaimed through afforestation efforts (Pełka-Gościniak 2011). However, in some parts of the area, after mining operations ceased, no reclamation measures were undertaken, allowing natural succession to take place. Aeolian processes became active in these areas, creating small accumulative and deflation forms on the pits slopes and bottoms (Pełka-Gościniak 2007). Subsequently, early soil development and vegetation succession took place, leading to the formation of initial Arenosols (Pietrzykowski and Krzaklewski 2006). For this study, we selected sites located on the flat bottom areas of the sand mine that had not undergone reclamation. They represent plant communities of poor Spergulo-Corynephoretum association with a predominance of *Corynephorus canescens*, *Polytrichum piliferum*, and *Cladonia* sp. with single seedlings of *Pinus sylvestris*, *Betula pendula*, and *Populus tremula*. The climate in the sampling area is categorized as a warm-summer humid continental climate (Dfb), according to the Köppen–Geiger classification system (Beck et al. 2018). The detailed climatic features are presented in Fig. S1 (prepared for the years 1951–2024 based on records from the local meteorological station IMGW code: 250190390, raw data were obtained from the Institute of Meteorology and Water Management – National Research Institute, Poland).

2.2 Field study and sample collection

The study sites represent different stages of vegetation succession from 6 to 24 years after the cessation of sand extraction (Bednarczyk et al. 2015). For purpose of this study, we selected three different biocrust types (Fig. 1): (1) Algae-dominated crust with the dominance of *Zygogonium* sp., (2) Moss-dominated crust with dominance of *Polytrichum piliferum* Hedw. (3) Lichen-dominated crust with dominance of *C. cervicornis* subsp. *verticillata* (Hoffm.) Ahti. This open-pit sand mine area is characterized by the occurrence of different types of biocrusts simultaneously (Chowaniec

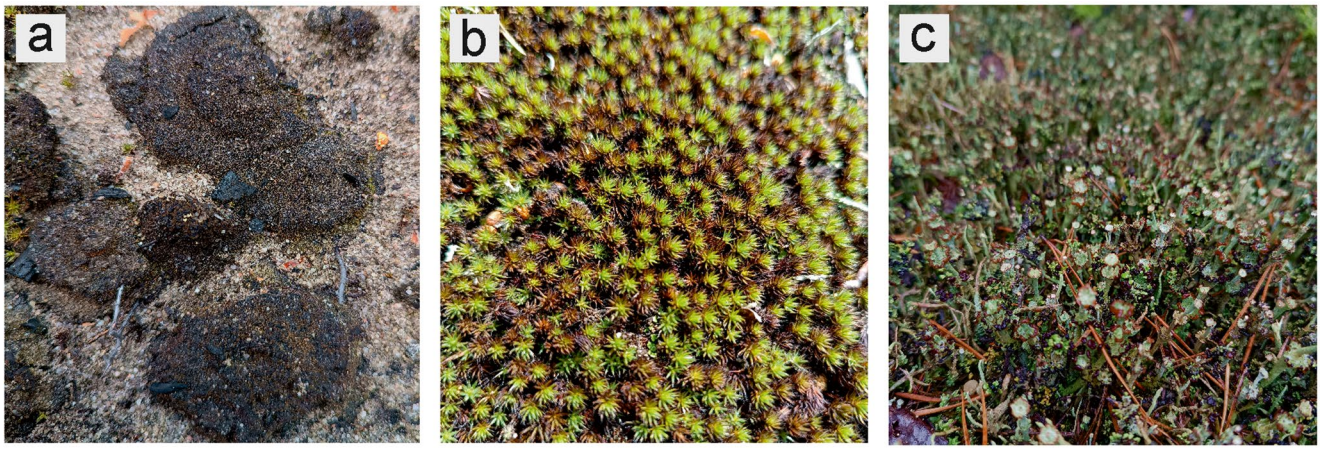


Fig. 1 The types of biocrust considered in the present study: (**a**) algae-dominated crust, (**b**) moss-dominated crust, (**c**) lichen-dominated crust

et al. 2026). Macroscopic components (lichens and bryophytes) of biocrust samples intended for the study were determined using identification keys (Smith et al. 2009; Hodgetts 2024). Biocrust types were assigned based on the clear visual dominance of the main surface component during sample selection. Samples were classified as lichen- or moss-dominated when lichens or bryophytes, respectively, clearly constituted the dominant macroscopic component visible on the sample surface. For algae-dominated biocrusts, where the dominant photosynthetic component could not be reliably distinguished macroscopically from other cryptogamic components, algal dominance was confirmed by microscopic observations of slides prepared from each collected sample using microscope (Nikon Eclipse 80i light microscope). The sampling was done in the June of 2025, under stable, dry weather condition. The study area constituted the flat area of 1×1 km^2, at the bottom of the sand mine characterized by the presence of a uniform substrate over the entire surface. Biocrust samples representing each type (algae-, moss- and lichen-dominated biocrust) were collected from ten study plots of 2m × 2m. The plots were randomly distributed across the study area. The minimum distance between individual plots was approximately 50 m. At each study plot, metal ring with a diameter of 14 mm was used to randomly collect biocrust samples for laboratory analyses; samples were weighed with accuracy to 0.001 g before analyses. To avoid contamination, the sampling ring was thoroughly cleaned of debris and sterilized with 70% ethanol before and after each use, and sterile gloves were worn throughout the process. The collected biocrust samples were placed in paper bags for transport to the laboratory. Once in the lab, each sample was carefully cleaned of loose soil particles by gently tapping with a brush. Ten biological replicates of each biocrust type were intended for each analysis of biocrust traits.

2.3 Measurements of water holding capacity

The procedure for determining water holding capacity (WHC) was based on the method described by Kidron et al. (2020), with minor modifications. The biocrust samples with a constant surface area were submerged in distilled water for 1 h to ensure full saturation. Following saturation, the samples were weighed and transferred to petri dishes and dried in an oven at 105 °C for 6 h. They were then weighed and returned to the oven for an additional 2 h. If no further weight loss was observed after this period, the samples were considered completely dry, and the final weight was used for calculation. The water holding capacity was determined using the following formula:

$$WHC\ (\%) = \left(\frac{(Wsp - Ws)}{Ws}\right) \times\ 100\%$$

where.

Wsp = weight of the biocrust in the fully saturated state (g), Ws = weight of the dry biocrust after drying in 105 °C (g).

2.4 Measurements of water evaporation

The calculation of evaporation rate and cumulative evaporation amount measurement procedure were adapted from Sun et al. (2024). The biocrust samples of known surface area were placed in a climatic chamber (KK 115, POL-EKO) for 24 h at 20 °C and 90% relative humidity (RH). After this period, the wet samples were weighed and placed again in the climatic chamber at 20 °C and 50% RH. After specified time intervals (respectively 0.75 h, 1.25 h, 1.75 h, 2.5 h, 4 h, 6 h, 24 h, 48 h and 72 h), the samples were weighed. The time intervals were selected based on the protocol described

by Sun et al. (2024) and were further adjusted to ensure adequate temporal resolution. At the start of the experiment, the time intervals between measurements were shorter to capture the rapid initial changes in soil evaporation. As the process progressed and the evaporation process gradually approached equilibrium, the evaporation rate declined. As a result of this slowdown, the time intervals between measurements were extended to match the decreasing rate of change. The evaporation rate was calculated from the formula:

$$E = \frac{10\Delta m}{\rho \pi r^2 \triangle t}$$

where:

E is the water evaporation rate (mm h^{-1}); 10 is conversion factor used to convert centimeters (cm) to millimeters (mm); Δ m is the difference between mass (g) measured every time interval Δ t (h), r is inner radius of biocrust sample (cm), ρ is the density of water (g cm^{-3}) which is 1.0.

2.5 Measurements of vapor adsorption

The cumulative adsorption measurement method was adapted from Sun et al. (2024). The biocrust samples of known surface area were placed in a climatic chamber for 24 h at 20 °C and 30% relative humidity (RH). After this period, the dry samples were weighed and placed again in the climatic chamber at 20 °C and 90% RH. After specified time intervals (respectively 0.75 h, 1.25 h, 1.75 h, 2.5 h, 4 h, 6 h, 24 h, 48 h and 72 h), the samples were weighed. The cumulative vapor adsorption was calculated from the formula:

$$W = \frac{10\triangle m}{\rho \pi r^2}$$

where:

W is the cumulative vapor adsorption (mm); 10 is conversion factor used to convert centimeters (cm) to millimeters (mm); Δ m is difference between mass at particular time interval and the initial mass (g), r is inner radius of biocrust sample (cm), ρ is the density of water (g cm^{-3}) which is 1.0.

2.6 Extracting and quantifying of exopolysaccharides

The EPS extraction procedure was adopted from Rossi et al. (2018) with slight modifications. Approximately 50 mg of biocrust material was homogenized using a mortar, transferred into test tubes, and vortexed with 1 ml of distilled water for 30 s. After 20 min, they were centrifuged at 4000 × *g* for 15 min using a MIKRO 200 centrifuge (Hettich, Germany). The supernatant containing LB-EPS was carefully separated. Subsequently, 1 ml of 0.1 M Na_2EDTA was added to the remaining pellet containing TB-EPS and G-EPS. The samples were then incubated in the dark at 8 °C for 12 h. After incubation, they were vortexed and centrifuged at 4000 × g for 15 min. The resulting supernatant, containing TB-EPS, was transferred to a new tube, while the remaining pellet, containing G-EPS, was washed with a 1.5% NaCl solution. The pellet was subsequently rinsed with distilled water to eliminate any residual NaCl. Then, 1 ml of distilled water was added to each tube, and the samples were incubated in a water bath (JWE 357, Elpin-Plus, Poland) at 80 °C for 1 h. Following incubation, the samples were centrifuged again, and the supernatant containing G-EPS was collected. The carbohydrate content was then determined using the phenol-sulfuric acid method, as described by Dubois et al. (1956). The absorbance was measured using a UV–Vis spectrophotometer (Shimadzu UV-1900i, Shimadzu Corporation, Japan) at 490 nm. The concentration of each exopolysaccharide fraction was determined using a glucose standard curve, and the total concentration was calculated by summing the concentrations of the three EPS fractions.

2.7 Dehydrogenase activity assessment

Dehydrogenase activity (DHA) was determined following the procedure of Casida et al. (1964), with minor modification. The collected samples were transferred into glass test tubes, and 2 ml of a 3% triphenyl tetrazolium chloride (TTC) solution prepared in 50 mM sodium phosphate buffer (pH 6.8) was added. Afterward, the tubes were covered with aluminum foil and kept in the dark at 25 °C for 24 h. Once the incubation period ended, the samples were gently vortexed and then centrifuged at 3000 × g for 10 min. After discarding the supernatant, 2 ml of 99.9% methanol was added to each sample to extract the formed triphenyl formazan (TPF). Next, the samples were placed in a water bath at 60 °C for 30 min. The extraction process was then repeated by adding an additional 2 ml of methanol, followed by another 30-minute incubation at 60 °C in the water bath. Finally, the samples underwent a second centrifugation at 3000 × g for 10 min. The resulting supernatants were collected, and their absorbance was measured at 485 nm using a UV–Vis spectrophotometer. The TPF concentrations in the samples were determined based on a calibration curve prepared according to the standard procedure.

2.8 Determination of chlorophyll concentrations

Prior to chlorophyll extraction, the dry weight of each biocrust sample was recorded. The samples were then lightly moistened with distilled water to activate the organisms and facilitate pigment extraction, following the approach of Caesar et al. (2018). Each sample was transferred to a glass tube, wrapped in aluminum foil, and treated with 3 ml of DMSO (≥99.9%, Sigma-Aldrich) containing $CaCO_3$ (≥99.0%, Sigma-Aldrich). The tubes were incubated in a water bath at 65 °C for 90 min. After incubation, the samples were vortexed for 30 s, and an additional 3 ml of fresh DMSO was added to each tube to begin a second extraction cycle, also conducted in the water bath for 90 min. Following the extraction, the samples were centrifuged at 3000 × g for 10 min. The absorbance of the resulting supernatants was then measured at 648 nm, 665 nm, and 700 nm using a UV–Vis spectrophotometer. To minimize chlorophyll degradation, all steps of the extraction process were conducted under semi-dark conditions. Chlorophyll concentrations were calculated according to the method described by Caesar et al. (2018).

2.9 Determination of biocrust thickness

The biocrust thickness was determined according to the procedure described in Mallen-Cooper et al. (2020) by measurement using a digital caliper of the shortest distance between the uppermost living tissue (excluding reproductive structures, such as sporophytes, as well as podetia) and the mineral soil surface.

2.10 Determination of biocrust roughness

Surface roughness was assessed using the chain method (Saleh 1993). A tight-linked metal chain was carefully draped over the soil surface so that it closely followed the microtopography of the biocrust. The horizontal distance between the chain endpoints (L_2) and the length of the chain required to cover that distance on the surface (L_1) were measured. The roughness index (R) was calculated using the formula:

$$R = 100 \cdot \left(1 - \frac{L2}{L1}\right)$$

2.11 Statistical analysis

One-way analysis of variance (ANOVA; $p<0.05$) followed by Tukey's HSD test was used to test the significance of differences in particular parameters among different biocrust types. Prior to analyses, the distribution normality was verified with Kolmogorov–Smirnov test, and Levene's test was performed to assess the homogeneity of variance across groups. When assumptions were not met, either Welch's ANOVA or the nonparametric Kruskal–Wallis test was applied. Principal component analysis was applied to visualize differences between biocrust types in terms of water-related and other functional traits. To account for the different units and scales of the variables, all data were standardized using Z-score transformation prior to the analysis. The PCA was subsequently based on the correlation matrix. The suitability of the data for PCA and the assumption of linearity were verified through a visual inspection of a scatterplot matrix. The relationships between variables were found to be predominantly linear. Moreover, prior to PCA, the suitability of the dataset was assessed using the Kaiser–Meyer–Olkin measure of sampling adequacy and Bartlett's test of sphericity. The KMO value was 0.775, indicating good sampling adequacy, and Bartlett's test was significant ($\chi^2 = 1049.09$, $df = 66$, $p<0.001$), confirming that the correlation matrix was suitable for PCA. Pearson correlation coefficients were calculated to assess relationships among the studied parameters. For both PCA and Pearson correlations, for water-related parameters, values after 72 h were used. Statistical analyses were performed using STATISTICA 13 (TIBCO Software Inc., USA) and Statgraphic Centurion 19 (Statgraphics Technologies, Inc., USA).

3 Results

3.1 Effect of biocrust type on water-related parameters

Regarding the evaporation rate across all biocrust types, the highest values were observed at the beginning of the measurement period, followed by a gradual decline over the first six h (Fig. 2a, b). After that, all samples reached consistently low and stable levels (Fig. 2a, b). During the first two time intervals, the lichen-dominated biocrust exhibited the highest evaporation rate. However, from 1.75 to 6 h, this rate became comparable to or even lower than that of the moss-dominated biocrust (Fig. 2a, b). The algae-dominated biocrust showed the most stable and consistently low evaporation rate throughout the measurement period, in contrast to both the moss- and lichen-dominated biocrusts (Fig. 2a, b). Average values of evaporation rate for the lichen- and moss-dominated biocrust were 0.984 mm h^{-1} and 0.859 mm h^{-1} respectively, which was 235% and 192% higher, respectively, compared to the algae-dominated biocrust (0.294 mm

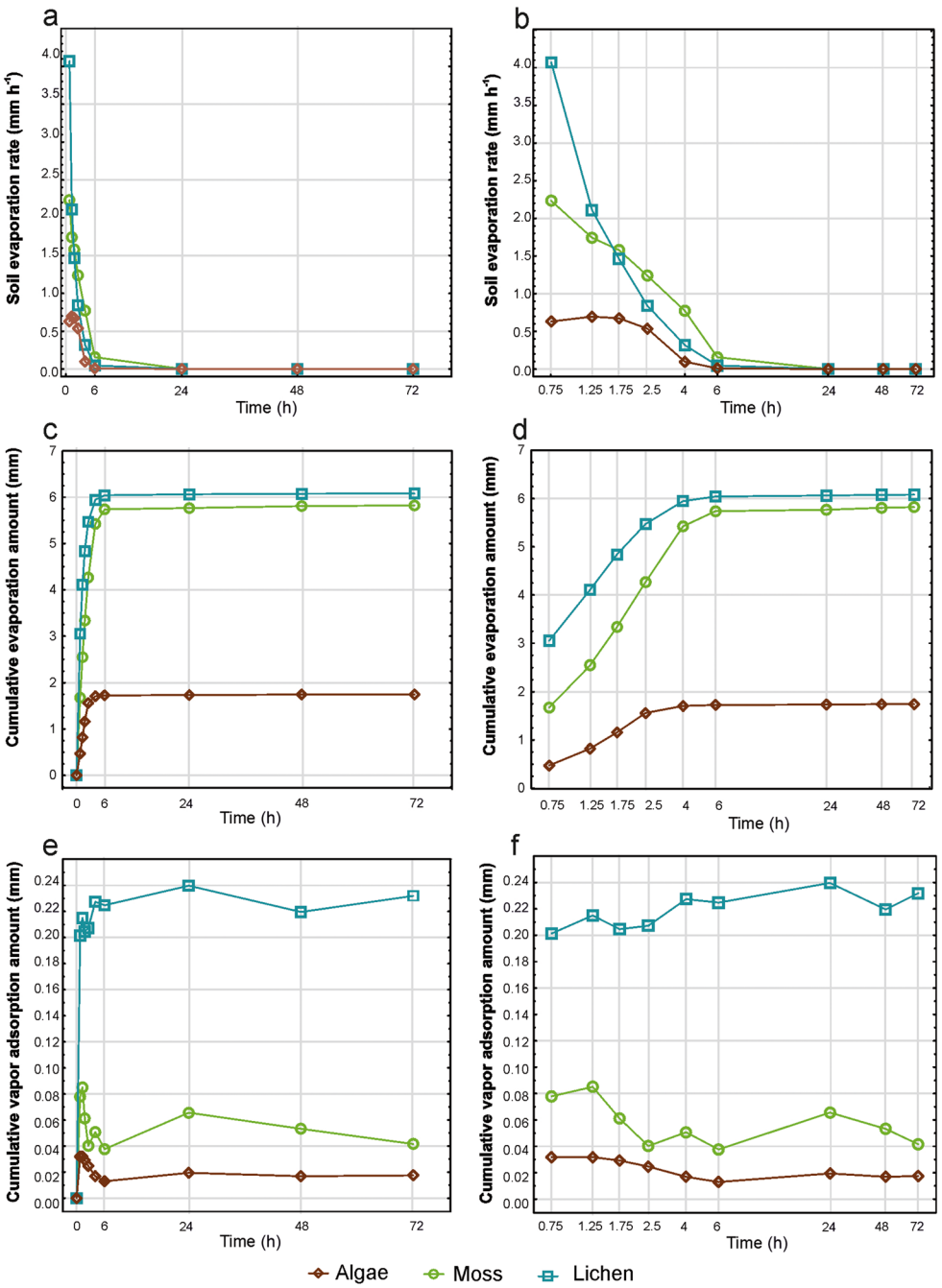


Fig. 2 Water-related parameters in three biocrusts types (dots indicate mean values, $n = 10$): algae, moss, and lichen-dominated. (**a**, **b**) soil evaporation rate (mm h^{-1}), (**c**, **d**) cumulative evaporation amount (mm), (**e**, **f**) cumulative vapor adsorption amount (mm). We used logarithmic scale to better visualise the rapid initial changes and later stabilisation. For detailed results see Table S1

h^{-1}). The greatest increase in cumulative evaporation amount occurred during the first 6 h in all biocrust types, after which stabilization was observed (Fig. 2c, d). Specifically, the lichen-dominated biocrust showed the highest cumulative evaporation amount increase, followed by the moss-dominated biocrust (Fig. 2c, d). In contrast, the algae-dominated biocrust exhibited the lowest cumulative evaporation amount that was considerably lower than in the lichen- and moss-dominated types (Fig. 2c, d). Average values of cumulative evaporation amount for lichen- and moss-dominated biocrust were 4.768 mm and 4.039 mm respectively, which was 276% and 219% higher, respectively, compared to the algae-dominated biocrust (1.268 mm). Regarding the cumulative vapor adsorption amount, the largest increase occurred during the first time interval (0.75 h) across all biocrust types (Fig. 2e). In the following intervals, the values within each group remained relatively stable, with some deviations (Fig. 2e, f). The lichen-dominated biocrust consistently showed the highest cumulative adsorption amount, followed by the moss-dominated biocrust, while the algae-dominated biocrust exhibited the lowest

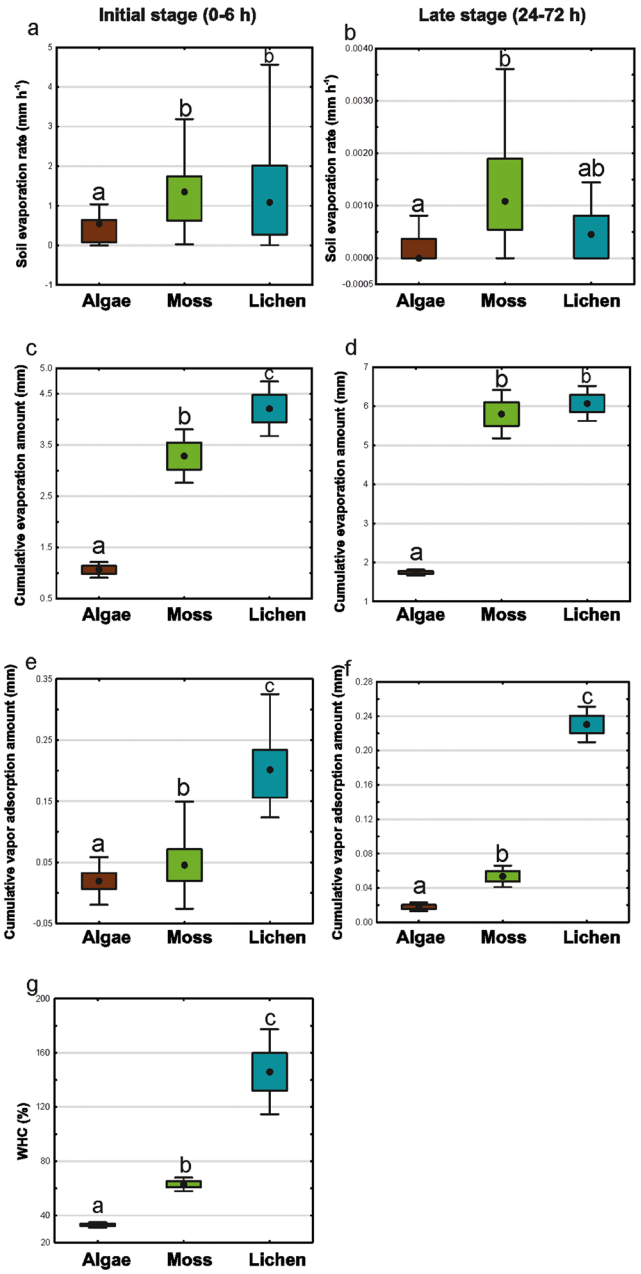


Fig. 3 Water-related parameters in three biocrusts types, algae, moss, and lichen-dominated: Initial stage (0–6 h) and Late stage (24–72 h), and water holding capacity of samples: (**a**, **b**) soil evaporation rate (mm h^{-1}) during initial stage, (**c**, **d**) cumulative evaporation amount (mm), (**e**, **f**) cumulative vapor adsorption amount, (**g**) water holding capacity (%). The results of post-hoc test Tukey's HSD or Gomes-Howell test after one-way ANOVA ($p<0.05$; dots indicate mean values, boxes indicate SE, whiskers indicate 95% confidence interval) or multiple comparisons of mean ranks after the Kruskal-Wallis test ($p<0.05$; dots indicate median, boxes indicate 25th to 75th percentiles, whiskers indicate Non-Outlier Range) are presented graphically. For detailed results see Tables S1

values (Fig. 2e, f). Average values of cumulative vapor adsorption amount for lichen- and moss-dominated biocrust were 0.197 mm and 0.051 mm respectively, which was 885% and 155% higher, respectively, compared to the algae-dominated biocrust (0.020 mm). For detailed results see Table S1.

Regarding the evaporation rate during Initial stage (0–6 h), significant differences were observed between biocrust types (Fig. 3a, Table S1). Higher values were observed in lichen- and moss-dominated biocrust, and these groups differ significantly from algae-dominated biocrust (Fig. 3a). During Late stage (24–72 h) also significant differences were observed (Fig. 3b, Table S1). In detail, the highest values were observed in the moss-dominated biocrust, and the lowest in the algae-dominated biocrust (Fig. 3b). As regards the cumulative evaporation amount, significant differences between biocrust types were found in both stages (Fig. 3c, d, Table S1). During the Initial stage, the highest cumulative evaporation was recorded in the lichen-dominated biocrust, while the lowest was observed in the algae-dominated biocrust; the moss-dominated biocrust did differ significantly from the other groups (Fig. 3c). In Late stage, significant differences were observed, with the moss- and lichen-dominated biocrusts showing the highest values and the algae-dominated biocrust the lowest (Fig. 3d). For cumulative water adsorption amount in both Initial and Late stage, all biocrust types differed significantly from one another, with the lichen-dominated biocrust exhibiting the highest values, and algae-dominated the lowest (Fig. 3e, f, Table S1). Regarding water holding capacity, significant differences between the biocrust types were observed (Fig. 3g, Table S1). The highest values were found in the lichen-dominated biocrust, while the lowest in the algae-dominated biocrust (Fig. 3g).

3.2 Changes in EPS production depending on biocrust type

Regarding the concentrations of LB-EPS fraction, significant differences between the biocrusts types were observed (Fig. 4a, Table S2). The highest values were observed in the moss- and lichen-dominated biocrust, while the lowest in the algae-dominated biocrust (Fig. 4a). In the case of the other two fractions, as well as total EPS concentration, the particular biocrust types differ significantly from each other (Fig. 4b, c, d, Table S2). In each case, the highest concentrations were observed in the lichen-dominated biocrust, while the lowest in algae-dominated biocrust (Fig. 4b, c, d).

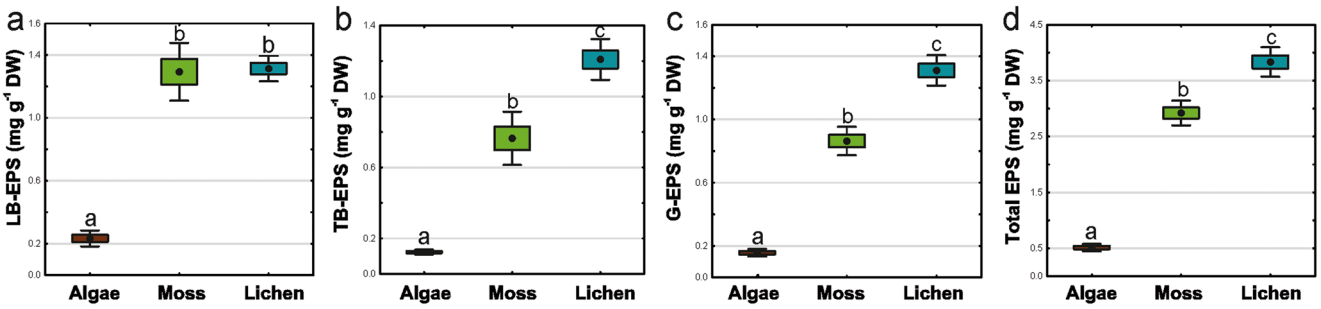


Fig. 4 Exopolysaccharide concentrations in three biocrusts types: algae, moss, and lichen-dominated (dot indicate mean values, box indicate SE, whisker indicate 95% confidence interval): (**a**) LB-EPS (mg g^{-1} DW), (**b**) TB-EPS (mg g^{-1} DW), (**c**) G-EPS (mg g^{-1} DW) and (**d**) total EPS (mg g^{-1} DW). The results of one-way ANOVA ($p<0.05$) are presented graphically. The different letters above the bars indicate significant differences between biocrust types (see Table S2 for detailed results)

3.3 Changes in overall microbial activity and photosynthetic biomass in biocrusts

Regarding dehydrogenase activity defined as triphenylformazan (TPF) expressed on dry weight, significantly the highest values were observed in the lichen-dominated biocrust, while the algae- and moss-dominated biocrust had similar, lower level of TPF (Fig. 5a, Table S2). However, when interpolated into the surface area, the values differed significantly between the biocrust types, with the highest level in lichen-dominated biocrust, and lowest in the algae-dominated biocrust (Fig. 5b). With regard to the chlorophyll *a* concentrations and chlorophyll *b* concentrations on dry weight, chlorophyll $a+b$ concentration on dry weight and interpolated into the surface, significant differences between the particular biocrust types were recorded (Fig. 5c-f, Table S2). For all these parameters, the highest concentrations were observed in the lichen-dominated biocrust, while the lowest in the algae-dominated biocrust (Fig. 5c-f). By contrast, the algae-dominated biocrust reached significantly the highest levels of chlorophyll *a/b* ratio, while the moss- and lichen-dominated biocrust had lower levels, and did not differ significantly from each other (Fig. 5g, Table S2). Biocrust types differ significantly in terms of the thickness (Fig. 5h, Table S2), and the highest thickness was observed in the lichen-dominated biocrust, while the lowest in the algae-dominated biocrust (Fig. 5h). The same trend was observed for biocrust roughness (Fig. 5i).

3.4 Relationships between water-related and functional traits in different biocrust types

Principal component analysis (PCA) showed the variation in water-related and functional parameters and effectively differentiated the three biocrust types (Fig. 6). Principal component 1 explained 76.35% of the variation, and all studied parameters, except for the chlorophyll *a/b* ratio, were positively correlated with this axis. Along the first axis, there was a clear gradient related to the biocrust type, going from the left, where the samples of the algae-dominated biocrust were grouped, then in the middle characteristic for the moss-dominated biocrust, to the right, where the lichen-dominated biocrust samples are grouped. Lichen-dominated biocrusts were related to high DHA, cumulative vapor adsorption amount, chlorophyll $a+b$, WHC, roughness, thickness, TB-EPS, and G-EPS, while the moss-dominated biocrusts were associated with high cumulative evaporation amount and LB-EPS. Chlorophyll *a/b* ratio showed the highest negative loading with axis 1 and was related to the algae-dominated biocrust. Most of the analyzed variables were significantly correlated ($p<0.05$), except for TPF and cumulative evaporation amount (Fig. S2).

4 Discussion

The movement of water vapor within soil significantly influences the water and energy dynamics of near-surface layers, thereby affecting key ecosystem processes such as microbial activity, plant growth, and nutrient availability (Berdugo et al. 2020). Future climate projections suggest that continued global warming will lead to increased temperatures and aridity in dryland regions by the late 21st century, potentially intensifying soil vapor transport processes (IPCC 2021). Moreover, the increasing frequency, intensity, and duration of droughts are projected not only for arid and semi-arid regions but also for temperate areas, particularly during summer months with unprecedented increases in soil drought (Samaniego et al. 2018). This will have profound effects on biocrusts in temperate sandy post-mining habitats, which, as the living skin, play a pivotal role in modulating soil water dynamics and act as key regulators of ecohydrological, biological, and geochemical processes (Xiao et al. 2022).

Our results showed that the algae, moss- and lichen-dominated biocrust types differed significantly in terms of both

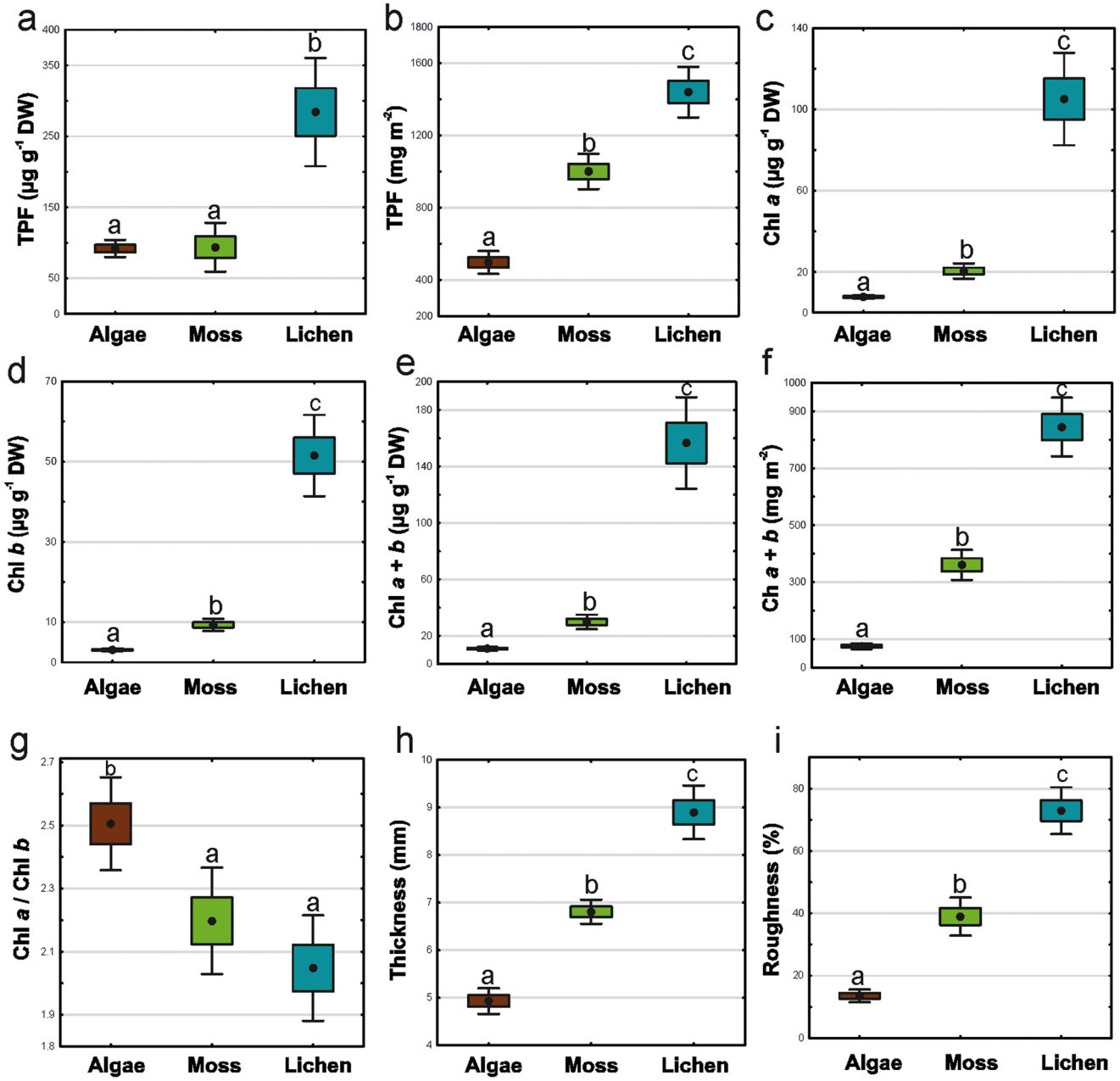


Fig. 5 Functional parameters related to three biocrusts types: algae-, moss-, and lichen-dominated (dot indicate mean values, box indicate SE, whisker indicate 95% confidence interval): (**a**) triphenylformazan (TPF) (µg g^{-1} DW), (**b**) triphenylformazan (TPF) (mg m^{-2}), (**c**) chlorophyll *a* (µg g^{-1} DW), (**d**) chlorophyll *b* (µg g^{-1} DW), (**e**) chlorophyll *a*+*b* (µg g^{-1} DW), (**f**) chlorophyll *a*+*b* (mg m^{-2}), (**g**) chlorophyll *a*/*b* ratio, (**h**) thickness (mm), (**i**) roughness (%). The results of one-way ANOVA ($p<0.05$) are presented graphically. The different letters above the bars indicate significant differences between biocrust types (see Table S2 for detailed results)

water-related and other functional parameters despite all being common in the early stages of ecological succession. The lichen-dominated biocrusts exhibited the highest vapor adsorption and evaporation cumulative amounts, and the greatest water-holding capacity along with the highest dehydrogenase activity, EPS content, and chlorophyll concentrations among the three studied biocrust types. Lichens are known for their ability to rapidly absorb water from vapor, and this trait is associated with several key anatomical and biochemical features. When exposed to high humidity, they can rehydrate rapidly, restoring their metabolic functions through passive absorption (Canali et al. 2025). The highest capacity of the lichen-dominated biocrust to absorb vapor is related to different surface-to-volume ratios of studied biocrust types that likely explain contrasting patterns of vapor adsorption and evaporative loss. In our study, the dominant

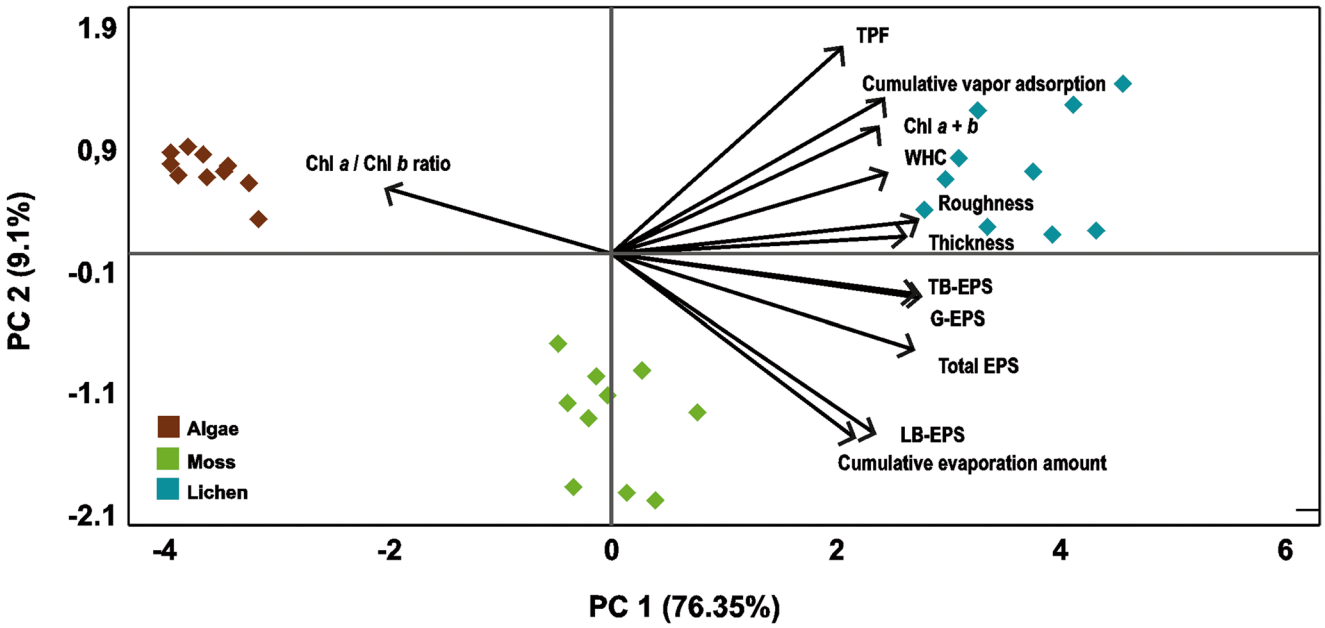


Fig. 6 Principal component analysis ordination diagram (PC 1 vs. PC 2) of the samples represented by different biocrust types in terms of water-related and physiological parameters. The percentage of the total variance explained by each axis is shown on the graph

species in the lichen-dominated biocrust was *C. cervicornis* subsp. *verticillata*. This species has highly complex structure of fruticose thallus with tiers of cups stacked one on the other growing from the center of the cup below forming verticillate pattern, and this morphological trait is one of its most distinguishing characteristics (Nimis 2025). This is reflected in the highest surface roughness of the lichen-dominated biocrust (Fig. 5i), which could improve vapor adsorption from atmospheric sources as well as imply a higher evaporation rate. Previous studies also indicated that a high surface-to-volume ratio leads to relatively faster rates of both drying and rehydration in lichens (Esseen et al. 2015). Secondly, the increased vapor adsorption amount can be attributed to the high water-holding capacity of lichens, primarily due to the abundance of extracellular polymeric substances (Chock et al. 2019), and the highest biocrust thickness. Lichens are known to possess a well-developed EPS matrix with a multiorganismal composition in the thallus zone known as biofilm (Spribille 2018; Spribille et al. 2020). After hydration, EPS expands its volume within seconds (up to 70-fold its dry weight; Chenu 1993), which enhanced their water-holding capacity and leads to surface sealing and pore clogging (Guo et al. 2018). At the same time, the higher chlorophyll content and dehydrogenase activity observed in the lichen-dominated biocrusts indicate higher photosynthetic biomass and more intense microbial activity, which may create steeper water vapor gradients at the biocrust–air interface and thereby accelerate evaporation process. However, it should be remembered that the microbial activity may depends on many other factors such as water availability, substrate supply, aeration status and biocrust thickness (Goel et al. 1998; Brzezińska et al. 2001; Weaver et al. 2012; Youan and Yue 2012). Although an elevated evaporation rate may appear contrary to high water-holding capacity and vapor adsorption, these processes can coexist. The lichen-dominated biocrusts exhibit rapid water uptake, due to their poikilohydric nature and well-developed surface architecture (Green and Proctor 2016). Nevertheless, at the same time lichens are known to evaporate water very quickly, which creates low resistance to water loss from their surfaces (Larson 1979). Thus, structural complexity of the lichen-dominated biocrust likely contributed to accelerated water loss through evaporation in this biocrust type. Furthermore, the lichen-dominated biocrusts are characterized by the highest tightly bound EPS content (TB- and G-EPS). This indicates that tightly bound EPS primarily governs water storage through the formation of a highly hydrated hydrogel matrix capable of retaining substantial amounts of water (Mager and Thomas 2011; Rossi et al. 2018). The rapid initial evaporation observed in these biocrusts likely reflects their complex physical structure, including high surface area and porosity, which enhances vapor diffusion and facilitates fast exchange processes immediately after wetting. However, evaporation dynamics shifted over time. At later stages (after 24 h), evaporation rates in the lichen-dominated biocrusts decreased relative to the moss-dominated biocrusts, despite their initially higher evaporation rates. This pattern indicates a transition from surface-controlled to diffusion-limited evaporation. As drying progresses and easily accessible water

is depleted, evaporation becomes increasingly controlled by the availability and transport of water within the EPS matrix. Under these conditions, the higher TB- and G-EPS content in the lichen-dominated biocrusts likely promotes stronger water retention and reduces water mobility, thereby limiting the supply of water to the evaporating surface. In contrast, the moss-dominated biocrusts, with lower tightly bound EPS content, may retain water less strongly, allowing for more sustained evaporation at later stages. The comparable LB-EPS content in both crust types suggests that differences in late-stage evaporation are primarily related to water binding strength rather than differences in water redistribution capacity. Overall, the results support a conceptual framework in which tightly bound EPS controls the magnitude of water storage, whereas EPS-mediated water binding strength and biocrust structural properties regulate the kinetics of water exchange. Algal-dominated biocrusts, which exhibited the lowest concentrations of all EPS fractions, showed consistently reduced water retention and slower vapor exchange, highlighting the central role of total EPS content, particularly the tightly bound fractions, in determining hydrological functionality. These findings are consistent with previous studies demonstrating that EPS enhances water retention and modifies soil moisture dynamics by swelling upon hydration and altering pore structure (Mazor et al. 1996; Fischer et al. 2010; Rossi et al. 2018). However, the proposed links between the specific EPS fractions and evaporation dynamics represent a mechanistic interpretation supported by the observed relationships. Further targeted measurements, such as water retention curves or sorption isotherms for individual EPS fractions, would help to verify these mechanisms more conclusively.

Our previous studies demonstrated that biocrusts from middle- and late-successional stages in temperate climate (specifically pine forests developed after 10 to 30 years of succession from bare inland sand) showed increased photosynthetic biomass and overall microbial activity as succession progresses (Chowaniec et al. 2024, 2025; Skubała et al. 2025). However, biocrusts at different development stages could differ markedly in their physiological characteristics, primarily due to variations in their developmental maturity. In the present study, we focused on biocrusts from the early stages of succession, which were formed in a previously anthropogenically disturbed area and remained significantly less developed compared to those from later successional stages. Lower water holding capacity and cumulative evaporation and vapor adsorption amount in the moss-dominated biocrusts compared to the lichen-dominated ones could be linked with the small size and relatively low density of moss individuals in early colonizing mats. *Polytrichum piliferum*, which was a dominant species in the studied biocrusts, is a pioneer moss, capable of establishing on bare, nutrient-poor sandy substrates (Gypser et al. 2016). Moreover, this species is capable of penetrating and growing through annual sand layers of up to 2 cm in thickness (Ellenberg 1996). Unlike mosses developed in later successional stages, *P. piliferum* formed sparse, upright tufts with limited lateral spread and low tissue density in early colonization stages. Despite their lower vapor adsorption amount, the moss-dominated biocrusts also exhibit a lower evaporation rate, suggesting higher moisture retention over time. The lower structural complexity of these biocrusts manifested by significantly lower thickness and surface roughness compared to the lichen-dominated biocrusts may protect against rapid evaporation. Consequently, the moss biocrusts may serve a stabilizing hydrological function in temperate ecosystems, despite their lower ability to respond quickly to short-term rainfall.

Biocrust dominated by filamentous green algae are more compact, thinner and had a flat morphology (Fig. 5h, i), which certainly reduces the amount of water that can be stored or transported through capillary action compared to lichen- and moss-dominated crusts. Their structure limits surface area exposed to air, thus reducing both evaporation and adsorptive capacity. Moreover, unlike lichens (with abundant extracellular polysaccharides) or mosses (with capillary leaf and stem structures supporting extracellular water accumulation), filamentous algae lack specialized structures or compounds to retain or absorb large amounts of water. Previous studies reported also the lack of polysaccharide encapsulation or mucilaginous cover in the green algal genus *Zygogonium* (Hoppert et al. 2004; Gypser et al. 2016) that dominated the algae-dominated biocrusts in our study. Consequently, compact and smooth structure of the algae-dominated biocrust can protect against erosion but does not enhance soil moisture retention as much compared to the lichen- and moss-dominated crusts. Moreover, *Zygogonium ericetorum* is also known to form water repellent mats (Ettl and Gärtner 1995) and thus was found to decrease substrate wettability under temperate conditions (Fisher et al. 2012). This could be a second possible reason for reduced adsorption and retention of moisture in the algae-dominated biocrusts. Low water holding capacity, as well as low cumulative vapor adsorption and evaporation amount in the algae-dominated biocrust reflect a low-impact hydrological role of this biocrust type in sandy habitats of temperate climate and its negligible contribution to moisture dynamics. Higher water-holding capacity of the moss- and lichen-dominated biocrust compared to the algae-dominated ones could be also explained by the differences in the thickness of biocrust, higher photosynthetic biomass and consequent higher level of organic matter accumulation. Biocrusts fix atmospheric carbon through photosynthesis and deposit it into the soil, leading to an accumulation of organic matter

(Dümig et al. 2013, 2014; Kakeh et al. 2018). This organic matter not only improves soil structure but also enhances the water-holding capacity of the biocrust, particularly as the biomass becomes thicker and more developed (Li et al. 2021; Wang et al. 2017). Our results suggest that the structural complexity of the moss- and lichen-dominated biocrusts plays an important role in regulating moisture dynamics. Nevertheless, the algae-dominated biocrusts have dark pigmentation (Fig. 1), which could increase evaporation in the natural environment due to its effect on surface energy balance and temperature. Dark surfaces absorb more incoming solar radiation and retain more heat. This causes accelerated surface warming which could increase the vapor pressure gradient between the wet biocrust and the drier air above that leads to faster evaporation (Kidron and Tal 2012; Chamizo et al. 2013a). However, to support this proposed mechanism, field-based studies are necessary to evaluate whether it influences evaporation and moisture dynamics under natural environmental conditions.

So far, many studies regarding evaporation in biocrust have been conducted in arid and semi-arid climates and most of them concerned moss- and cyanobacteria-dominated biocrust (e.g., Li and Xiao 2022). On the other hand, scientists rarely studied lichen- or algae-dominated biocrust, while they commonly occur in temperate climates, which was confirmed by our previous studies (e.g., Chowaniec et al. 2024, 2025). The role played by biocrusts in controlling evaporation is ambiguous. Kakeh et al. (2021) found that biocrust led to decrease in evaporation, because they create mats on the soil surface, and swelling of mats blocks the soil pores in wet condition, and the large pores of biocrusts may disrupt the hydraulic connectivity between topsoil and subsoil, which minimizes the capillary rise. On the contrary, some authors reported the positive effect of biocrust on evaporation, which may be attributed to the biocrust biomass, organic matter content and EPS accumulation (e.g., Durrell and Shields 1961; Karnieli et al. 1999). It was confirmed by several studies that moss-dominated biocrust had higher evaporation rate and cumulative evaporation amount than cyanobacteria-dominated biocrust, which could result from their larger biomass and thickness (e.g., Sun et al. 2024; Li and Xiao 2022). On the other hand, the moss-dominated biocrusts showed higher vapor adsorption than cyanobacteria-dominated biocrusts, mainly due to their greater cation exchange capacity and specific surface area (Sun et al. 2024). It may result from the fact that moss-dominated biocrusts induce important changes in soil properties as they develop. Increased surface roughness, biomass, and thickness in moss-dominated crusts enhance carbon fixation and the accumulation of fine particles within the biocrust (Karnieli et al. 1999) more than in cyanobacteria-dominated biocrusts. In temperate climates, prolonged summer droughts can substantially limit liquid water availability, making early-morning water vapor an important supplementary moisture source, where vapor adsorption may help sustain biocrust metabolic activity and surface functioning during these periods. In the present study, comparable mechanisms are likely influencing the observed patterns, despite the focus on algae-dominated biocrusts, which share some morphological similarities (e.g. low thickness) with cyanobacteria-dominated biocrusts. Notably, our results indicate that the lichen-dominated biocrusts exhibited even greater thickness and microbial biomass than the moss-dominated biocrusts, potentially leading to enhanced vapor adsorption, evaporation, and greater water holding capacity. Nevertheless, it should be remembered that the evaporation behavior of similar biocrust types can vary significantly even between biocrusts developing in semiarid and hyperarid climate. For example, Kidron and Tal (2012) observed that the biocrust increased the evaporation rate by 1.38-fold compared to bare sand, while Eldridge and Greene (1994) found that biocrust could reduce evaporation due to its higher retention of moisture than sandy soil.

Climate change is expected to alter biocrust species composition, favoring early-successional biocrusts with cyanobacteria and algae (Ferrenberg et al. 2015). Many studies from various climate zones indicated that lichens are especially vulnerable to increasing temperatures and prolonged droughts (Finger-Higgens et al. 2022; Phillips et al. 2022). Given the increasing frequency of summer droughts and heatwaves in Central Europe (Beobide-Arsuaga et al. 2025), climatic changes are likely to adversely affect lichen performance even in temperate regions. This has been confirmed by numerous experiments demonstrating that water availability is a key factor controlling lichen physiology (Paoli et al. 2017; Munzi et al. 2019). It will likely have several important consequences for water relations in temperate sandy ecosystems. Lichens possess the highest water-holding capacity among the biocrust types and are also the most effective at adsorbing atmospheric vapor and releasing moisture through evaporation. These findings suggest that although the lichen-dominated biocrusts enhance early soil function, they may also intensify short-term water fluctuations in sandy soils. Consequently, the decline in the lichen-dominated biocrusts could diminish the ecosystem capacity to capture non-rainfall water inputs and might reduce the water retention capacity of the topsoil. In turn, with less water retained in the biocrust layer, surface runoff may increase during rain events, increasing the risk of soil erosion and further land degradation. The algae-dominated biocrusts, though limited in water uptake, may gain importance due to their very low evaporation rates, helping retain surface moisture over time. The moss-dominated biocrusts, which combine relatively high vapor absorption

with moderate evaporative loss, may offer a more balanced contribution to water retention under changing climatic conditions. Together, these patterns suggest that shifts in biocrust composition may reshape ecohydrological processes. Consequently, promoting or preserving functionally diverse biocrust communities could buffer climate-driven impacts on water availability and improve ecosystem stability in sandy soils. However, it should be noted that this study was conducted under controlled laboratory conditions to isolate the specific functional influence of different biocrust types. While this approach ensures high reproducibility, it does not fully account for the complex dynamics of field conditions, where evaporation and vapor adsorption rates are likely to be modified by temporal variation in vapor pressure deficit, diurnal temperature range, wind speed, and solar radiation. Compared with the fixed RH levels used in our experiment, 50% during evaporation and 90% during vapor adsorption, natural conditions may generate stronger evaporative demand during warm, dry, and windy periods, while cool and humid nights may enhance vapor adsorption. Future research incorporating field-based lysimetric measurements would be beneficial to validate these findings under natural environmental cycles.

The hydrological effects of biocrusts, together with their development under different climatic conditions, are key to understanding the role of biocrusts in ecosystem development (Schaaf et al. 2011). The desert soil surface represents one of the most extreme environments on Earth, due to intense solar radiation and high surface albedo, resulting in high irradiance at the soil–atmosphere interface. Comprehensive studies that were carried out in the arid dune systems of the Northern Negev demonstrated that the species composition had drastic effects on infiltration, run-off processes and on the soil moisture content below the biocrusts (Kidron and Yair 1997; Kidron et al. 2003). However, it is widely recognized that biocrusts have varying impacts on soil water conditions (Chamizo et al. 2013b; Kidron and Tal 2012). The study on the Chinese Loess Plateau showed that moss-dominated biocrusts increase the input of non-rainfall water to the soil surface, but they also enhance evaporation, particularly after rainfall events. This suggests that their effect on soil water balance is mixed, and in some areas may be negative for the overall soil water budget (Li et al. 2022). In contrast to the extensively studied biocrusts of arid and semi-arid regions, those occurring in temperate climates have received much less attention, despite functioning under markedly different hydrological conditions. In temperate ecosystems, biocrust hydration depends not only on rainfall and liquid water input, but also on frequent access to fog, dew, and high atmospheric humidity (Ritter et al. 2019), which means that these communities may become wet and metabolically active more often and for longer periods. Fisher et al. (2023) found that the moss and lichen biocrusts in temperate climate shape soil water management differently: mosses have higher water-holding capacity and contribute to higher accumulation of organic matter in the upper mineral soil under mosses, which results in higher amounts of water stored near the surface, while lichens promote deeper infiltration of rainwater. Gypser et al. (2016) found that based on the decreased repellency index and higher water holding capacities, mature biocrusts dominated by mosses and lichens might have reduced small-scale run-off on the crust under low rainfall intensities. In the present study concerning temperate post-mining areas, biocrusts appear to function as a dynamic hydrological buffer. Specifically, the high vapor adsorption and water-holding capacity observed in the lichen-dominated crusts suggest an adaptive mechanism for rapid moisture cycling, utilizing non-rainfall water such as dew or high humidity a trait that facilitates metabolic activity even in the absence of significant precipitation. Furthermore, the functional heterogeneity observed in our study, where the algae-dominated crusts prolong moisture retention through low evaporation rate, while mosses and lichens manage rapid water turnover expands the existing paradigm. It suggests that in temperate climates, biocrusts create a hydrological mosaic that mitigates extreme moisture fluctuations. This diversity is likely key to enhancing ecosystem resilience in anthropogenic sandy substrates, offering a more nuanced understanding of biocrust-water interactions that moves beyond the arid-centric model.

5 Conclusions

Our findings highlight the functional importance of biocrust heterogeneity in regulating soil water dynamics during early succession in temperate sandy post-mining ecosystems. By influencing water uptake, retention, and release, different biocrust types may create distinct microsite conditions relevant for vegetation establishment in post-mining landscapes. For example, the lichen-dominated biocrusts, despite their high water uptake capacity, may also promote rapid water loss after rainfall, potentially reducing short-term water availability for seedlings. In contrast, less structurally developed the algae-dominated biocrusts may retain moisture for longer periods, although their overall hydrological and functional capacity appears lower. Thus, a mosaic of biocrust types may support more stable microsite conditions and contribute to restoration processes in temperate disturbed ecosystems. Future field-based lysimetric studies are needed to validate these patterns under natural environmental cycles.

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Author contribution Karolina Chowaniec: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Funding acquisition, Data curation, Resources, Project administration, Writing – original draft. Kinga Szafrańska: Conceptualization, Investigation, Writing – review & editing. Kaja Skubała: Conceptualization, Investigation, Methodology, Supervision, Writing – original draft.

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Data availability The data presented in this article were deposited in public repository RODBUK Cracow Open Research Data Repository and are available at the following link: https://doi.org/10.57903/UJ/2NRWMJ.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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