

Soil organic matter content and its aliphatic character define the hydrophobicity of biocrusts in different successional stages

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Abstract

In humid areas, biocrusts cover topsoils of inland dunes and influence soil characteristics, which, in turn, may affect the hydrophobicity of soils. The hydrophobicity of topsoils typically increases with increasing organic matter content. In addition, the soil organic matter quality, for example, described by the ratio of its hydrophilic and hydrophobic functional groups, also influences hydrophobicity. Because biocrust development goes along with an increase in the organic matter content and a shift in microbial community composition, the chemical character of soil organic matter likely changes over time, which, in turn, affects the hydrophobicity of the crusts. We hypothesize that the hydrophobicity of biocrusts increases during succession because of increasing amounts and aliphatic character of organic matter. We compared organic matter contents and Fourier-transform infrared spectra of cyanobacterial biocrusts and moss-dominated biocrusts at two European inland dunes. The organic carbon content as well as the hydrophobicity increased during crust development at both sites. Older moss-dominated biocrusts showed the highest hydrophobicity and the highest organic carbon content. Moreover, at one study site, the hydrophobicity of the biocrusts did increase with decreasing ratio between hydrophilic and hydrophobic (i.e., aliphatic) moieties of soil organic matter. At the second study site, this effect was only visible for the moss-dominated biocrust. We conclude that biocrust development and organic matter accumulation go ahead with changes in the organic matter composition and induce increased hydrophobicity with a strong impact on water redistribution in inland dune ecosystems. This knowledge will help to improve nature protection strategies in rare ecosystems.

KEYWORDS

biological soil crusts, early ecosystems, inland dunes, organic matter composition, water repellency

1 | INTRODUCTION

In all ecosystems worldwide, biocrusts, a mixture of mineral soil particles and organic matter components enclosed in a biofilm matrix, cover young soil surfaces. Their matrix is build up by microorganisms with the ability to withstand extreme climate conditions (Belnap, 2006). In humid areas, biocrusts persist locally restricted to sandy soils, like inland dunes or military training grounds (Fischer, Veste, Wiehe, & Lange, 2010).

If environmental conditions allow it and depending on ecosystem type, successional development and local climate regime, biocrusts include cyanobacteria, algae, fungi, lichens and mosses. In general, initial biocrust development shows a first colonization of cyanobacteria, and with time, the community structure becomes more complex (Chamizo, Cantón, Miralles, & Domingo, 2012). The crust community composition changes during development including differences in the amount of photoautotroph and heterotroph bacteria, algae and lichens with mosses, pervaded with fungal hyphae, building up the crusts in wetter areas (Drahorad, Felix-Henningsen, Eckhardt, & Leinweber, 2013; Lan, Wu, Zhang, & Hu, 2013).

During development, biocrusts show changes in their biochemical composition with a large impact on biocrust characteristics and therefore soil properties (Chamizo et al., 2012). Dust trapping and active nutrient fixation (e.g., carbon and nitrogen) and the excretion of exopolysaccharides during growth cause these changes (Belnap, 2006; Garcia-Pichel & Pringault, 2001). Consequently, crust thickness, the amount of fine particles, water holding capacity, porosity and the amount of organic matter increase (Lan et al., 2013). However, not only the amount of organic carbon changes but also its composition. Studies on successional biocrust development showed an increase in carbohydrate and protein content (Dümig et al., 2014), as well as changes in amounts of N-containing compounds, lignin monomers and fatty acids (Drahorad et al., 2013) depending on biocrust types. Changes in the chemical composition of soil organic matter during biocrust succession may induce shifts in soil wettability and hydrophobicity, as different classes of chemical compounds, with their varying functional groups and structural building blocks, differ in their hydrophilic character.

On the other hand, hydrophobicity could result from the attachment of amphiphilic organic substances to mineral surfaces: Amphiphilic organic substances like, for example, fatty acids, polysaccharides and phenolic compounds consist of hydrophobic and hydrophilic groups that attach to soil mineral surfaces resulting in hydrophobic or hydrophilic characteristics depending on organic matter content (Ellerbrock, Gerke, Bachmann, & Goebel, 2005). Besides this general process, most authors state the occurrence of long-chained organic molecules, like aliphatic carbon chains and amphiphilic substances like fatty acids and waxes, to be responsible for soil hydrophobic properties (Horne & McIntosh, 2000). Hydrophobic substances can result from degradation of residues from higher plants like pines or Ericaceae (Buczko, Bens, Fischer, & Hüttl, 2002), or they may be of microbial origin like exudates of algae and fungi found in biocrusts (Lichner et al., 2013; Rillig, 2005).

A study on biocrust development stages in southern Germany showed a correlation between an increase in water drop penetration time (WDPT), organic matter content and the potential wettability index of the soil organic matter, indicating the high importance of organic matter for soil hydrophobicity (Lichner et al., 2018). In addition, studies on sand dunes in eastern Germany showed a slight hydrophobicity for biocrusts that was correlated to the amount of carbohydrates (Fischer et al., 2010; Fischer, Yair, Veste, & Geppert, 2013), which are mainly exopolysaccharides of bacterial origin. Pereira et al. (2009) showed that exopolysaccharides could increase hydrophobicity depending on their chemical composition, which is determined by microorganism type and environmental conditions.

We investigated changes of wettability, soil organic matter content and soil organic matter quality of two successional types of biocrusts on two alternating sand dune areas in a humid climate to explore the following hypotheses:

1. Under humid climate, the organic matter content and hydrophobicity of biocrusts increase with crust succession.
2. Changes in organic matter composition during biocrust formation induce changes in hydrophobicity.

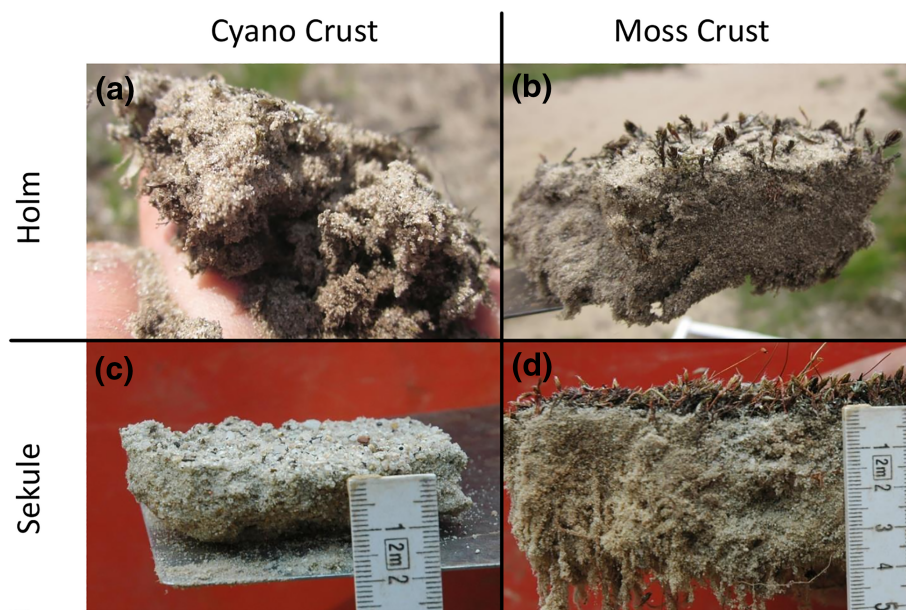
2 | MATERIALS AND METHODS

2.1 | Sampling sites description and sample preparation

The study site Holm is located at an artificial forest glade within a nature protection area 53 km south-eastwards of the Northern Sea in Northern Germany and characterized by a mean annual precipitation of 750 mm a⁻¹ and a mean annual temperature of 8.5°C a⁻¹. A 100-year-old plantation of pines (*Pinus sylvestris* L.) surrounds the glade. After partial clearing of the former planted pines in 2005, open sand dunes build up the soil surface on the glade. Biocrusts in different development stages cover the soil surface, including thin cyanobacterial crusts on lately disturbed spots and moss-dominated biocrusts in more protected areas (Figure 1a,b). In addition, several stages of recovery with heather (*Calluna vulgaris* L.) and grasses are found.

The study site Sekule is located at south-western Slovakia with a mean annual precipitation of 550 mm a⁻¹ and a mean annual temperature of 9°C a⁻¹. The artificial glade at Sekule resulted out of the mining of sand for building purposes. A 30-year-old plantation of pines (*P. sylvestris* L.) surrounds the glade, and biocrusts cover the sandy surface. The Sekule biocrust is a thin, cyanobacterial dominated crust at freshly disturbed areas and a thick, moss-dominated crust at undisturbed areas (Figure 1c,d). For a detailed description of the forest glade side and the occurring biocrust species, see Lichner et al. (2013). In both areas, the main parent material is aeolian sand, deposited as inland dunes. The coarse-textured soils are Arenosol.

FIGURE 1 View of biocrusts dominated by cyanobacteria and mosses at the study sites Holm (Northern Germany, a,b) and Sekule (Slovakia, c,d)



At both study sites, the samples were taken at recently disturbed spots (cyanobacterial crust) and less disturbed areas (moss-dominated crust) along a disturbance transect. At each study site, four replicate samples were taken from the biologically active topcrust (TC; 0–2 mm) and the indurated subcrust (SC; 2–20 mm) for the soil characteristics of the biocrust types. All 16 samples were air dried at 40°C for 24 h, sieved (<2 mm), and an aliquot was finely ground (~0.05 mm) for the measurement of total organic carbon (TOC) and total nitrogen (N).

For the characterization of chemical hydrophobicity of the organic matter of biocrusts, we choose one sample from the start point of a disturbance transect (cyanobacterial crust) and one sample from the end point (moss-dominated crust) at each study site. These samples were prepared as described below. For each sample, 16 spectra were measured and averaged.

2.2 | Physical and chemical analysis of biocrusts

Particle sizes were determined using wet sieving, separating particle sizes from 2,000 to 63 μm . The pH value was measured in a water extract (1:5; weight:volume), the measurement of TOC and N by dry combustion (Vario EL analyser, Elementar, Hanau, Germany).

All samples were tested on their hydrophobicity using the WDPT test with four repetitions (Letey, 1969). According to Doerr (1998), the WDPT reflects not the exact intensity of hydrophobicity but rather its persistence. Therefore, we differentiated the following repellency classes after Doerr (1998): very hydrophilic (WDPT <5 s), hydrophilic (5 s < WDPT <60 s), slightly hydrophobic (60 s < WDPT <180 s), moderately hydrophobic (180 s < WDPT <600 s), strongly hydrophobic (600 s < WDPT <3,600 s), very strongly hydrophobic (WDPT >3,600 s). As WDPT measurements were stopped after 3,600 s, we use the WDPT classes provided by Doerr (1998) to avoid arbitrary cut-off points in the comparison of WDPT and TOC.

The abundance of hydrophilic and hydrophobic moieties in soil organic matter was characterized using Fourier-transform infrared spectroscopy (FTIR). For recording FTIR spectra, we used 1 mg of ground, desiccated soil (<0.5 mm) mixed with 80 mg of potassium bromide and dried over night over silicagel in an exsiccator. The mixture was then pressed into a pellet by applying a pressure of 6.8 t cm^{-2} . Infrared absorbance spectra of organic matter were collected in the wave number range of 4,000–400 cm^{-1} with 16 scans per spectrum. The spectra were smoothed (boxcar moving average algorithm, factor 45) and corrected for baseline shifts using WIN-IR Pro 3.4 software (Digilab, Massachusetts, USA). The spectra were smoothed using a boxcar moving average algorithm (factor 45) and corrected for baseline shifts using WIN-IR Pro 3.4 software (Digilab, Massachusetts, USA).

The absorption bands that indicate the hydrophobic (CH groups) and the hydrophilic (C=O groups) functional groups are in the focus of the FTIR spectra analysis in this work. For hydrophobic methyl and methylene groups, the maxima of the CH bands occur at 2,920 cm^{-1} (asymmetric stretch) and at 2,860 cm^{-1} (symmetric stretch) (Capriel, Beck, Borchert, Gronholz, & Zachmann, 1995). Based on the work of Ellerbrock et al. (2005), the CH bands at the region between wavenumber (WN) 3,020 and 2,800 cm^{-1} were combined to a single one and marked as Band A. Here, we used the area between absorption band and local baseline for the region between WN 3,007 and 2,817 cm^{-1} as a measure for the amount of CH groups (Capriel et al., 1995). The hydrophilic C=O-groups occur at WN 1,640–1,615 cm^{-1} and 1,740–1,720 cm^{-1} (Celi, Schnitzer, & Nègre, 1997) and denoted both as absorption Band B (Ellerbrock et al., 2005). Here, we used the area at the maxima for a WN width of 1 cm^{-1} to exclude a possible overlap with C=C and amid bands as far as possible. The OH bands were not considered because they could possibly reflect differences in water contents. The areas at absorption Bands A relative to those of Bands B (A/B ratio) in the FTIR spectra were computed using BioRad WIN-IR Pro 3.4 software (Digilab,

Massachusetts, USA) to characterize the potential hydrophobicity of soil organic matter, with the hydrophobic character of SOM increasing with increasing A/B ratio (Ellerbrock et al., 2005).

Significant differences between the measured soil parameters are shown on a level of significance of 5% under use of a *t* test. A Mann-Whitney *U*-test shows the difference between hydrophobicity classes on a level of significance of 5%.

For the test of a linear relationship of WDPT and TOC, the measured data were unsuitable. Per definition, measurements stop if the penetration time exceeds 3,600 s for the highest WDPT class. This results in nominal scaled values with a cut-off point at 3,600 s. To avoid a statistical bias, we used a comparison of TOC and repellency classes. An analysis of variance (ANOVA) was used to detect significant differences between the TOC values for different repellency classes.

3 | RESULTS

3.1 | Soil characteristics and hydrophobicity patterns of biocrusts

As a general pattern, all examined biocrust types and depths (TC and SC) samples were acidic ($\text{pH} < 5$) and had very high percentage of sand (>95%) (Table 1).

For all biocrust samples, the N content was smaller than 0.5%, and the content of TOC was lower than 1% for cyanobacterial crust and the respective SCs. Only moss-dominated biocrusts showed TOC concentrations of up to 3%. Comparing the sampling depths at the separate study sites, the TOC and N contents were significantly higher

for the TCs compared with SCs ($p < .001$) for moss-dominated crusts at both study sites. For the cyanobacterial crusts, the TOC and N contents were only significantly different for the cyanobacterial crust of the Sekule site. Comparing the samples between the two study sites, the TOC and N contents were lower for the top- and subsoil biocrusts from Sekule ($p < .001$ and $p < .01$, respectively) as compared with those from Holm site. The TOC in the TC was lower at the Sekule as compared with the Holm site on a 10% probability level ($p = .06$ in both cases). At both study sites, the moss-dominated TCs showed, as expected, a significant higher TOC and N contents as compared with the cyanobacterial TCs (Holm $p < .05$, Sekule $p < .001$). The N content showed no significant difference for the cyanobacterial SC for both study sites. Remarkably, at the Sekule site, the moss-dominated SC had a significantly higher N content ($p < .05$) compared with the moss-dominated SC at the Holm site.

Comparing the overall trend between TOC and the detected repellency classes of all examined biocrusts in the two study sites, a significant increase in biocrust repellency with increasing TOC content is visible (Figure 2). Interestingly, with increasing resistance of repellency, the variability in TOC content increases as well.

A more detailed view on biocrust types and sampling depths showed a very wide range of hydrophobicity persistence for all sampled biocrusts (Table 1). The WDPT ranged from very hydrophilic to very strongly hydrophobic for the TC and SC samples at the Sekule area. At Holm, the range of WDPT values was smaller, and the biocrusts were slightly hydrophobic up to very strongly hydrophobic. Nevertheless, comparing the median values of the occurring hydrophobicity classes, all crusts are slightly up to very strongly hydrophobic. Based on the median values, cyanobacterial TCs show a significantly lower hydrophobicity persistence than moss-dominated

TABLE 1 Biocrust pH, total carbon and nitrogen (TOC, N), texture characteristics, persistence of hydrophobicity (WDPT), median of occurring hydrophobicity classes and the ratio of hydrophobic to hydrophilic groups (ratio A/B) of the examined biocrusts (CC, cyanobacterial crust; MC, moss-dominated crust) in different depths (TC, topcrust; TC, subcrust) at the two study sites Holm and Sekule

Sample	pH value	TOC g kg ⁻¹	N total	Sand %	Coarse silt	Particles < 63 μm	WDPT s	Repellency class Mode	Ratio A/B (C-H/C=O)
Holm CC TC	4.9 ± 0.2	8.5 ± 5.5	0.6 ± 0.2	98.7 ± 0.6	0.3 ± 0.4	1.0 ± 0.2	58–210	3	0.111
Holm CC SC	5.0 ± 0.3	7.8 ± 4.9	0.5 ± 0.2	99.0 ± 0.3	0.3 ± 0.3	0.8 ± 0.1	27–1,444	3	0.033
Holm MC TC	4.6 ± 0.1	20.3 ± 6.8	1.0 ± 0.1	98.8 ± 0.4	0.4 ± 0.1	0.8 ± 0.3	992–2,322	5	0.091
Holm MC SC	4.8 ± 0.1	9.0 ± 0.7	0.6 ± 0.0	98.6 ± 0.2	0.5 ± 0.0	0.9 ± 0.2	254–840	4	0.036
Sekule CC TC	4.8 ± 0.1	5.0 ± 2.0	0.4 ± 0.1	97.0 ± 0.3	0.9 ± 0.3	3.1 ± 1.1	0–1,260	3	0.023
Sekule CC SC	4.9 ± 0.1	2.2 ± 1.0	0.2 ± 0.1	96.9 ± 0.9	1.0 ± 0.4	3.0 ± 1.2	0–3,600	3	0.024
Sekule MC TC	4.5 ± 0.1	14.2 ± 5.1	0.9 ± 0.2	95.5 ± 1.2	1.2 ± 0.4	4.6 ± 0.7	2,190 to >3,600	6	0.041
Sekule MC SC	4.5 ± 0.1	2.6 ± 0.7	0.3 ± 0.0	96.0 ± 0.3	1.4 ± 0.2	3.9 ± 1.6	3 to >3,600	5	0.037

Note: $n = 4$; ratio A/B $n = 1$; standard deviations in parentheses.

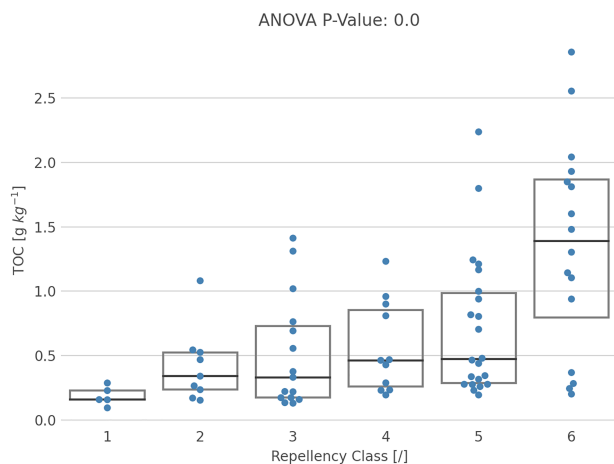


FIGURE 2 General relation between TOC content and hydrophobicity classes of biocrusts in the examined study sites

TCs for both study sites. This effect was not visible for the SC samples. Comparing the sampling depths, moss-dominated TCs tended to show higher hydrophobicity persistence than the underlain SCs. However, this trend was only significant for the moss-dominated crust at Sekule.

3.2 | Chemical hydrophobicity of the organic matter of biocrusts

The FTIR spectra of biocrust samples show relative similar transmissions even though the samples included different crust types, depths and distinct locations. The C=O band intensities (WN 1,720–1,600 cm^{-1}) were generally much higher than the C–H band intensities (WN 2,944–2,849 cm^{-1}). The intensities of the C–H bands differed between the two sampling depths (TC vs. SC) at the Holm site, whereas at the Sekule site, only the TC of the moss-dominated biocrust shows a slightly higher band intensity for the C–H band. At Sekule site, the relative intensities of absorption Band B in FTIR spectra were lowest for moss-dominated SCs and highest for moss-dominated TCs. The cyanobacterial TC and SC lay intermediate and show the same relative intensity (Figure 3b). The FTIR spectra of biocrusts at Holm show the lowest relative intensities of absorption Band B for the moss-dominated TC. All other samples of this study site show the same relative intensities of absorption Band B (Figure 3a). All samples show a very intense, comparable absorption band around 1,080 cm^{-1} , and in addition, the TC samples of the moss-dominated biocrusts show higher intensities at the absorption band 3,400 cm^{-1} .

The ratio of hydrophobic to hydrophilic groups (A/B ratio) are in the same range (0.02 for cyanobacterial crust, 0.04 for moss-dominated crusts) for both sampling depths at the different crust types for Sekule samples. This indicates no changes in the chemical hydrophobicity of the organic matter for the TC and SC of cyanobacterial crust and moss-dominated crusts. Contradictory to

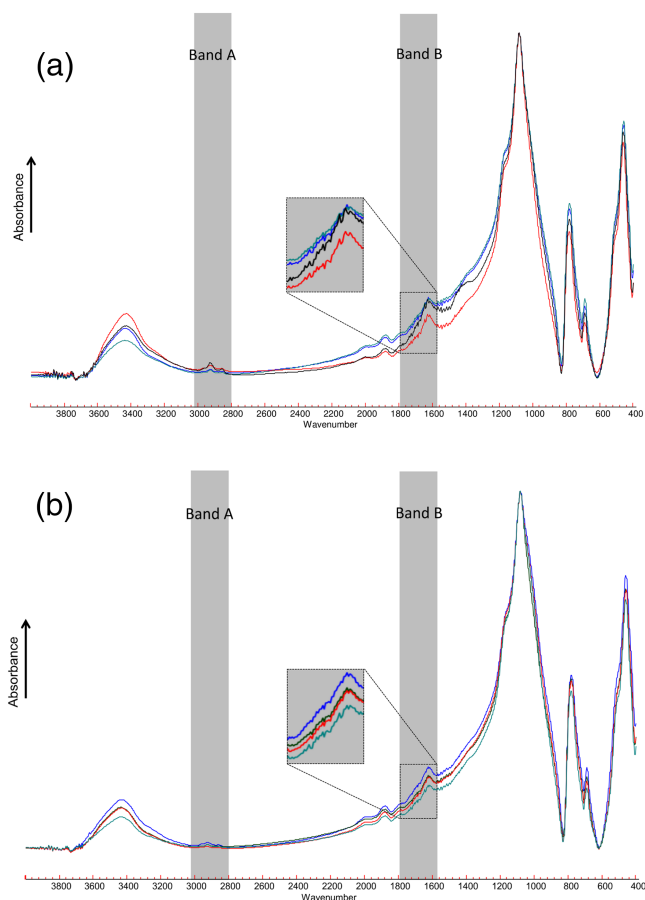


FIGURE 3 (a,b) FTIR spectra of biocrusts at Holm (Figure 3a) of cyanobacterial (CC) and moss-dominated (MC) biocrusts in two sampling depths (topcrust = TC; subcrust = SC) (black = CC_TC; blue = CC_SC; red = MC_TC; green = MC_SC). Band A and Band B intervals associate with the absorbance of aliphatic CH groups and hydrophilic components (C=O groups), respectively. FTIR spectra of biocrusts at Sekule (Figure 3b) of cyanobacterial (CC) and moss-dominated (MC) biocrusts in two sampling depths (topcrust = TC; subcrust = SC) (black = CC_TC; red = CC_SC; blue = MC_TC; green = MC_SC). Band A and Band B intervals associate with the absorbance of aliphatic CH groups and hydrophilic components (C=O groups), respectively

this, at the Holm site, the A/B ratios are in the same range for the same sampling depths (0.1 for TC, 0.035 for SC) of the biocrusts, regardless of the crust type. Data show a connection between WDPT, TOC content and the changes in organic matter quality for the moss-dominated crusts but not for the cyanobacterial crust.

4 | DISCUSSION

4.1 | Accumulation of TOC and N

At both study sites, the biocrusts show an accumulation of TOC and N compared with the bare sand. This is typical for initial biocrust development and ongoing growth in extreme ecosystem (Chamizo

et al., 2012). The stronger accumulation of TOC and N in TCs and moss crusts are related to higher biomass build-up (Lan et al., 2013). Comparing the Sekule site and the Holm site, all biocrusts show higher TOC concentrations at Holm than at Sekule. Although Holm shows the higher annual precipitation, at Sekule, the continental climate includes a long dry season in the summer month. This dry season reduces the buildup and turnover of organic matter in the Sekule biocrusts, whereas in Holm, a higher biomass build up occurs due to more available moisture (Fischer et al., 2010).

The FTIR spectra show absorption bands that correspond to the typical organic and inorganic soil components. The composition of the organic matter is nearly identical for the examined biocrust types and study sites, as the FTIR spectra show the same progression. This relates to the microbial composition of the biocrusts with a high amount of bacteria. Filip and Hermann (2001) found almost identical spectra with only minimum differences in the intensity of the individual absorption bands for different soil bacteria. A strong peak around $3,400\text{ cm}^{-1}$ occurs for moss-dominated TCs at both sites; this peak relates to the plant material of mosses in organic matter (Heller, Ellerbrock, Roßkopf, Klingenfuß, & Zeitz, 2015). The intense absorption band around $1,080\text{ cm}^{-1}$ generally fits with the Si-O-Si groups in quartz and C-O-C groups of polysaccharides. The parent material and the typically high amount of exopolysaccharides in biocrusts explain this peak (Fischer et al., 2013)

4.2 | Persistence of hydrophobicity

The overall persistence of hydrophobicity showed a wide range of values for the examined biocrust types and study sites. In Holm, the biocrusts were hydrophilic to slightly hydrophobic, whereas in Sekule, the biocrusts were slightly hydrophobic to very strongly hydrophobic. These values are much higher compared with earlier studies on sand dunes in Germany (Fischer et al., 2010). This study showed no to very low water repellency for biocrusts.

As hypothesized, the persistence in hydrophobicity increased with an increase in TOC and therefore organic matter. The increase in hydrophobicity with ongoing crust development towards moss-dominated crusts was already proofed for the Sekule site (Lichner et al., 2013). In contrast to this, for moss-dominated crusts Fischer et al. (2013) found a decrease in hydrophobicity for a site in north-eastern Germany. They concluded that the occurrence of mosses changes the surface polarity. Our results support the idea that the succession to mosses can generally increase hydrophobicity. The succession to mosses is linked to a reduction in cyanobacteria biomass, an increase in biomass of heterotrophic bacteria and a shift of the organic matter composition towards more bioavailable compounds like carbohydrates and peptides (Drahorad et al., 2013). With ongoing development, moss-dominated crusts with a higher amount in chlorophyll, proteins and carbohydrates and a much higher isolate density of microfungus communities occur (Grishkan & Kidron, 2013). Filamentous fungi are a large fraction of soil

microbial biomass, and they produce hydrophobins that are able to build hydrophobic coatings (Rillig, 2005).

Our second hypothesis was that hydrophobicity changes in relation to organic matter composition. As the FTIR spectra show a similar pattern for all crust types, depths and study sites, the influence of the surrounding vegetation is very low. Nevertheless, the input of organic layer material of the nearby pine forests may influence the biocrusts at both study sites to an unknown extend, as this material can induce very strong, long-lasting hydrophobicity (Butzen et al., 2015). Using the C-H/C=O ratio as an indicator of the wettability of organic matter in biocrusts, the Holm biocrusts show ratios in the typical range of soils, comparable with ratios of lichen-dominated biocrusts in Germany (Lichner et al., 2018). At the Sekule study site, the A/B ratios are rather narrow and only for the cyanobacterial crust comparable with an earlier study at this site (Lichner et al., 2018). Comparing the A/B ratios, WDPT and TOC values, all SCs and the TCs at Sekule show an increase in the WDPT, TOC and A/B ratio with crust development as expected. Interestingly, the cyanocrust at Holm does not follow this pattern. Here, the A/B ratio is rather high, but the WDPT is moderate. Further studies are needed to check, if this effect is related to the structure and orientation of hydrophobic and hydrophilic groups (Ellerbrock et al., 2005).

Based on the results in each study area, a first rough estimate of the temporal dynamics of the changes in hydrophobicity shows that the development of biocrusts from a first initial stage (cyanobacterial biocrusts) to older, more developed biocrusts with mosses results in an accumulation of organic matter and an increase in hydrophobicity (Figure 2). With crust development, the A/B ratio rises together with the WDPT. This proves a connection between the increase in TOC content, changes in organic matter quality and an increase in hydrophobicity. In general, initial soil development goes ahead with changes in the properties of the site and changes in biocrust communities inducing higher hydrophobicity and changes in organic matter composition (Drahorad et al., 2013; Lichner et al., 2018). The destruction of more hydrophobic biocrusts, for example, by grazing, can be an effective way to keep hydrophobicity and the related hydrological implications on a reasonable level.

The hydrological implications of the obtained results are of high interest for areas with permanent biocrust cover in humid and in semi-arid and arid areas. The results prove an increased hydrophobicity of biocrust-covered soils that can reduce or prevent infiltration and induce surface run-off. The resulting redistribution of water at the surface towards cracks or local depressions can reduce plant growth or induce local structures like vegetation islands (Belnap, 2006). Within the soil, preferential flow can induce zones of higher organic matter and aggregate stability protected against degradation by dryness as hydrophobicity is an important organic matter stabilization mechanism (reviewed by Goebel, Bachmann, Reichstein, Janssens, & Guggenberger, 2011). Comprehensive studies with large sample sizes including the relation between organic matter composition and stability, hydrophobicity and water redistribution for soils with biocrust cover are still missing.

We conclude that biocrust development induces an accumulation of organic matter, a change in organic matter quality and an increase in hydrophobicity in humid inland dune ecosystems. Compared with other biocrust studies, the very high hydrophobicity of the moss-dominated crusts sites is remarkable and should be examined more in detail in relation to land use and vegetation history. Furthermore, the correlations between organic matter quality, organic matter and aggregate stability and hydrophobicity need to be evaluated systematically to understand the mechanisms behind biocrust hydrophobicity and the influence on landscape scale.

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CONFLICT OF INTEREST

No conflict of interest was declared.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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