

Successional shifts of phototrophic community composition in biological soil crusts on coastal and inland dunes

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Abstract

Aim

Biological soil crusts (biocrusts) are autonomous ecosystems consisting of prokaryotic and eukaryotic microorganisms growing on the topsoil. They colonize global climatic zones, including temperate dunes. This study examines changes in the community structure of biocrust phototrophic organisms along a dune chronosequence at the Baltic Sea compared to an inland dune in Northern Germany.

Methods

The community composition and their shift between different successional stages of dune development were related to physico-chemical sediment properties. A vegetation survey followed by species determination and sediment analyses were conducted.

Results

The findings highlighted a varying phototrophic community composition regarding the different dune successional stages. In both study sites, a shift from algae-dominated biocrusts in younger to lichen- and moss-dominated biocrusts in later successional dune types was observed. This underlined a zonation from young to mature biocrusts along a dune chronosequence. The algae community of the two study sites shared 50% of the identified species while the moss and lichen community shared less than 15%. This indicates a more generalized occurrence of the algal species along both dune chronosequences. The mosses and lichens showed a habitat-specific species community. Moreover, an increase in the organic matter and moisture content with advanced biocrust development was detected. The enrichment of phosphorus in the different biocrust types showed a similar relationship.

Conclusion

This relation is explainable by biomass growth and potential phosphorus mobilization from the underlying sediment by microorganisms. The observed biocrust development supported nutrient enrichment and biomass accumulation and potentially maintained in turn soil formation.

Introduction

Coastal dunes as transitional zone between the ocean shore and the terrestrial environment are shaped by harsh climatic and environmental conditions, like high temperatures near the sediment surface, UV radiation, drought and strong wind, the latter one causing constant sand movement (Martínez et al. 2004). Sandy dune soils are characterized by a low soil organic matter content along with low nutrient concentrations (Maun 2009). Moreover, flooding events and salt spray have a high impact on the

substrate mobility and thus on dune formations close to the shore (García Novo et al. 2004, Martínez et al. 2004). These environmental stressors and their interactions result in a highly dynamic ecosystem. Therefore, dune formations undergo a continual succession driven by wind, waves, and storm events, as well as acidification due to precipitation, shaping the dune geomorphology. These effects are especially important close to the sea, while more inland biomass typically accumulates creating a set of heterogeneous dune sites (Martínez et al. 2004). This so called dune chronosequence represents ideal geomorphological series of dune successions. In the ideal case, chronosequences differ only in time since the onset of their formation, but all other abiotic factors during pedogenesis remained relatively steady (Stevens and Walker 1970). Therefore, chronosequences are used for studying temporal habitat dynamics, reflecting vegetation and soil development (Walker et al. 2010). Starting with small foredune formations close to the shore followed by mobile yellow dunes, which are still highly influenced by flooding and storms. Grey dunes connect the yellow dunes with the mature dunes which are often forested (Hesp 2004). Both, the effects of the extrinsic stressors and intrinsic mechanism (e.g., succession) drive a dune ecosystem towards a particular assemblage of microbial and vascular plant communities, and lead to different dune types characterized by unique geomorphology and vegetation patterns (Miller et al. 2010). These environmental conditions make the establishment of a vascular plant cover challenging. This in turn facilitates the colonization by stress-tolerant microbial communities, like cryptogamic ground covers.

Cryptogamic ground covers are characteristic growth forms on top of various terrestrial soil or rock surfaces (Elbert et al. 2012). These living covers are of diverse appearance and include biological soil crusts (biocrusts). Biocrusts are particle-associated communities shaped by autotrophic and heterotrophic microorganisms, lichens, mosses, and their by-products, forming a coherent layer on the soil surfaces uppermost millimeters (Belnap and Eldridge 2001). Due to the wide range of ecosystem functions, biocrusts affect the inhabiting ecosystem processes and development (Veste et al. 2011). Several studies focused on different mechanisms through which biocrusts can increase soil stability (Felde et al. 2018; Rossi et al. 2018), an important function when considering soil erosion and blowouts (Van Ancker et al. 1985). The higher water holding capacity of biocrusts reduces water loss by reducing soil evaporation (Chamizo et al. 2016) This facilitates an increasing water input into the sediment underneath, leading to enhanced soil moisture (Fischer et al. 2012). Phototrophic biocrust organisms are important contributors to the global photosynthetic carbon assimilation within the community biomass (Lange 2001) and contribute with 15% to the global net terrestrial primary production (Rodríguez-Caballero et al. 2018). Moreover, nitrogen fixation accomplished by biocrust organisms (mainly cyanobacteria) represents 40% – 85% of the global terrestrial biologically fixed nitrogen (Fowler et al. 2015). Former studies could prove the importance of biocrusts in nutrient cycling (Wu et al. 2013), such as phosphorus (Baumann et al. 2017, 2019; Nevins et al. 2020; Richardson and Simpson 2011). Biocrusts can be found in every climate zone on earth (Belnap, Büdel et al. 2001) with a total estimated area of 17.9 million km², which equals 12.2% of the global terrestrial surface worldwide (Rodríguez-Caballero et al. 2018).

The performance of all these collectively mentioned ecosystem functions is strongly related to the development and successional stage of the respective biocrust cover. The successional development of biocrusts depends on many environmental factors, namely temperature (Garcia-Pichel et al. 2013), radiation, topography, soil texture (Lan et al. 2012; Zaady et al. 2000), microclimate (Veste and Littmann 2006), water availability (Fischer et al. 2012; Zaady et al. 2000), nutrient availability, as well as the season of the year (Bu et al. 2018). Disturbance by environmental factors such as fire and mechanical disturbance by human trampling can negatively affect biocrust covers, their species composition and functioning. How far-reaching the consequences of disturbance for biocrusts are depends on the severity, frequency, timing, and type of disturbance (Belnap and Eldridge 2001). Along with the changing environmental and abiotic variables, dominant organism components of biocrusts change and thereby, in turn, biocrust ecosystem functions, too. For arid regions, Zaady et al. (2000) described cyanobacteria as the pioneers in colonizing the soil surface, followed by green algae, mosses, and lichens. Likewise, Lange et al. (1992) described filamentous cyanobacteria as initializing microorganisms in sand dune colonization of the eastern Negev Desert. Older, and more established biocrust covers contain higher proportions of mosses and lichens, therefore representing well-developed successional biocrust stages characterized by slow growth rates (Büdel 2002; Eldridge and Greene 1994; Zaady et al. 2000). Biocrust successional development is therefore a process over time and in space influenced by multiple factors resulting in a heterogeneity of the community structures (Gypser, Herppich, et al. 2016).

The changes in the composition of the dominant organisms can be used to distinguish between the successional biocrust stages and allow the establishment of a categorization system for biocrusts. A study conducted by Büdel et al. (2009) distinguished between seven main types of biocrust types along a >2000 km long transect in Africa, that were further categorized into three successional biocrust stages: early, intermediate, and late successional stage. A similar classification system, even though in less small steps, was published by Williams et al. (2017). In this publication biocrust types were classified by the functional organismal groups dominating the biocrust cover and the respective ecosystem functions (N-fixation, primary production or soil stabilization).

Most studies focused on biocrust community development, functions and changes in arid or semi-arid regions (Büdel et al. 2009; Li and Hu 2021; Samolov et al. 2020). Much less is known for biocrusts in coastal sand dunes of temperate regions. Fernández-Alonso et al. (2021) provided insight into the effects of increasing aridity and biotic cover on soil attributes and functioning in coastal dune ecosystems of the Iberian Peninsula. This study was conducted along a natural climate gradient including humid, dry-subhumid, and arid environments. Likewise, Schulz et al. (2015) conducted a biodiversity survey of biocrusts in sand dunes from the Baltic Sea coast. This study highlighted the ecological importance of biocrusts in influencing soil properties and their high site-specific diversity of microorganism. Species composition of algae and cyanobacteria of these habitats was later additionally specified in Mikhailyuk et al. 2019, 2021 using combination of morphological and molecular methods (so-called integrative approach). However, the specific dune developmental stage was neglected here. In addition, Schaub et al. (2019) focused exclusively on early successional biocrust stages in yellow dunes at the Baltic Sea. Still, information on changes in successional stages along the natural dune development are still missing,

although they can be assumed to affect the ecosystem functionality and further vegetation colonization of coastal dunes significantly. Therefore, in the present study, shifts in species composition, coverage, and biomass accumulation were investigated. Further, the biocrust developmental patterns have to be linked with the dune successional stage along a dune chronosequence at the Baltic Sea compared to that of an inland dune in Northern Germany. The links between the crusts biodiversity and soil properties were tested. We hypothesized that I) biocrust successional stages, from a thin topsoil layer of algae to stable moss and lichen-dominated 'mature' communities, can be followed along a dune geomorphological gradient. II) The phototrophic biocrust community composition will be shaped by the developmental stage of the dunes along each chronosequence. III) The different geographic regions from which the biocrusts were collected will have resulted in regional differences in the community structure of the biocrusts.

Material And Methods

Study sites

Biological soil crust samples were collected in April and May 2020, along two dune succession sequences in northern Germany (Fig. 1). Samples from coastal dunes were taken on the Schaabe (54.60318, 13.38872), a spit on the Baltic Sea island of Rügen (Mecklenburg-Western Pomerania, Fig. 1A). This spit connects the peninsulas of Jasmund and Wittow. The dune chronosequence under investigation belongs to the landscape conservation area 'Ostrügen'. The second contrasting sampling site was located in Verden (Aller, Lower Saxony, Fig. 1B) and represented an inland dune area (52.93865, 9.24917). This area is located within the nature reserve 'Dünengebiet und Halsetal bei Verden-Neumühlen' and includes a fauna-flora-habitat area (nature protection area network Natura 2000).

Both dune complexes are disturbed by anthropogenic impacts through tourism in the past. Trampling in the dunes is prohibited but cannot be excluded. Moreover, even environmental protection measures like an adjacent reforestation area to curb further dune movement might impact the dune development.

Sampling

Transects

Biocrust samples were taken along one transect per study site. Each transect followed a natural succession gradient in the dune area. The **transect at the Schaabe** spit started from the shoreline to the first dune formation identified as a small foredune (FD) and passed through a former grey dune which gets continuously covered with a large amount of sand due to wind transport during storm events. Hence the surface area of this dune is covered with several centimeters of mobile sediment. In this study, it will be seen as an interface between a fixed grey dune getting frequently repulsed to a more mobile yellow dune phase. This hereinafter called intermediate dune (ID) stage was followed by a grey dune area (GD) and ended in the mature dune area (MD), which was already overgrown with pine trees. The transect in the **inland dune in Verden** started in the center of the dune area (DC) characterized by mobile bare sand

representing a typical deflation hole. It crossed a dune slope (DS) where changes in vegetation cover were obvious, finally reaching to the crestline of the parabolic dune. Close to the dune crest the transect ended in a mixed dune forest area (DF) dominated by pine trees. Along each transect, these described different successional dune stages were selected and further named as dune subsites. At each subsite, a plot of 1 m² was established and used for further vegetation analyses, biocrust and sediment sampling. In total, seven sampling plots at two study sites were under investigation in this study. Along the Schaabe spit transect four subsites with one sampling plot each were established (Fig. 2).

Three subsites were established in the inland dune in Verden (Fig. 3). Five out of these seven plots showed biocrust growth in different successional stages (Online Resource 1). Those plots were called biocrust-holding plots.

Vegetation

In preparation for the vegetation survey, seven different functional groups were defined describing the overall surface coverage (Online Resource 2). These included four biocrust functional groups based on the established categorization systems by Büdel et al. (2009), Lan et al. (2012) and Williams et al. (2017) but were slightly modified. Thin (1-3 mm) green algae-dominated biocrusts (GA) were defined as early successional stages. Later successional stages, in which the green algae biocrusts became slightly thicker (3-8 mm) and moss-covered, were defined as the intermediate successional biocrust stage (GA/M). Moss-dominated biocrusts (MD) and those who additionally lichenized (MD/L) characterized the mature successional stages of biocrusts. Vascular plants, and litter (dead material, i.e., pine needles, leaves, and branches) were two of the non-cryptogamic but still biotic functional groups. Bare sediment was the only abiotic functional group.

The predefined functional groups were recorded within each plot according to the point intercept method by Levy and Madden (1933). Each of the seven sampling plots was divided into 16 equal subplots (0.0625 m²). A 25 cm x 25 cm (0.0625 m²) grid of 25 intersections (Online Resource 3) was placed randomly into 4 of these subplots. Within each sub-plot, the functional groups were recorded by 25 point measurements according to the approach of Williams et al. (2017). Therefore, a metal pin was dropped next to each intersection, and the ground covering functional group, including bare sediment, was recorded. That allowed 100 point measurements per sampling plot (1 m²).

Sample collection

Petri dishes (92 mm in diameter) were used for biocrust sampling. Each Petri dish was dropped and pushed gently into the respective biocrust. A spatula was then used to lift and separate the biocrust from the underlying sediment. The biocrust distribution in each sampling plot (1 m²) showed a high heterogeneity concerning the respective functional groups. The established 16 subplot-grid known for the vegetation survey was used again to collect the samples randomly. The grids were organized in rows labeled with letters (A-D) and columns labeled with numbers (1-4). A random generator was used to decide in which of the 16 subplots biocrusts should be taken from. One Petri dish was collected per

subplot. Thus, all biocrust samples per plot were randomly collected and taken as independent biological replicates. In the central plot (DC) in the inland dune and at the foredune (FD) on the Schaabe spit, no biocrusts were found. For keeping the sampling design at each plot uniform, samples were also taken from these two plots using Petri dishes even when containing no visible biocrusts. Within each plot, three biocrust samples using Petri dishes were collected for chlorophyll *a* analyses, as well as for algae community cultivation, direct microscopy and identification. Additional three biocrust samples were taken for analyses of sediment properties (moisture and organic matter content, and phosphorus concentration). That resulted in a total of six Petri dishes per plot. The three biocrust samples for chlorophyll *a* analysis and isolation of cultivable algae were wrapped with aluminum foil and stored in a cooling box for transportation. If detectable, one additional sediment sample was collected in unvegetated areas within each of the seven sampling plots and stored in zip lock bags. These samples represented the crust-free area of each plot and were used for sediment pH measurements. All mosses and lichens detected in the sampling plots were collected by hand and stored in paper bags.

Sample preparation and sediment analyses

For chlorophyll analyses, three subsamples were punched out of each Petri dish using a cork drill (\varnothing 1.5 cm) to ensure they represented the same area for all samples. Those subsamples were treated as technical replicates per Petri dish and stored separately in a 15 ml falcon tube and frozen at -20 °C until chlorophyll *a* extraction. The remaining biocrust or sediment in the Petri dish was air-dried for further algae isolation and identification, and stored in the dark.

Biocrust and sediment samples used for environmental analyses were removed from the Petri dish in the lab and a razor blade was used to separate the visible biocrust from the underlying sediment. The samples were further sieved (2 mm mesh size) and weighed for fresh mass (FM g) determination. Afterward, the samples were dried at 105 °C for 24 h and weighed again to determine the dry mass (DW g) and calculate the water content. The organic matter (OM) content was calculated based on the weight loss after combustion at 450 °C for 5 h. The moisture content was expressed as a percentage of total fresh mass (% FM) and the organic matter content as a percentage of total dry mass (% DW). The pH of the each crust-free sediment sample was measured in a calcium chloride (0.01 M) solution after one hour (w/v ratio 1:4) with a pH meter (METTLER TOLEDO SevenMulti).

Analyzed parameters

Chlorophyll a

Chlorophyll *a* (Chl *a*) content was taken as a measure for the photosynthetic biomass (chlorophyll *a* m⁻²) in biocrust (biocrust-holding plots) and sediment samples (plot DC=Verden, FD=Schaabe). Further, the samples were each extracted in a 15 ml falcon tube. 0.1 g of MgCO₃ was added to each sample to avoid acidification. Chlorophyll *a* was extracted in 3 ml of 96% ethanol (v/v) for 30 min at 78°C. Samples were shaken afterward and cooled on ice for 10 min followed by centrifugation at 5088 *g* for 5 min at 5°C to decrease turbidity. The supernatant was carefully pipetted into a 1 cm quartz cuvette. A

spectrophotometer (Shimadzu UV-2401 PC, Kyoto, Japan) was used for measuring the Chl *a* absorbance at wavelengths of 632, 649, 665, and 696 nm. The chlorophyll *a* content was calculated according to (Ritchie 2008) and normalized to a square meter (m²).

$$\text{Chl } a \text{ (g m}^{-3}\text{)} = 0.0604 \cdot (A_{632\text{nm}} - A_{750\text{nm}}) - 4.5224 \cdot (A_{649\text{nm}} - A_{750\text{nm}}) + 13.2969 \cdot (A_{665\text{nm}} - A_{750\text{nm}}) - 1.7453 \cdot (A_{696\text{nm}} - A_{750\text{nm}})$$

Algae isolation, community cultivation and identification

Further processing of samples and identification of the most frequent and dominant species were conducted in the laboratory. To obtain enrichment cultures, fragments of biocrusts were placed in Petri dishes with Bold Basal (1N BBM) agarized medium (Bischoff and Bold 1963). Cultures were grown under standard laboratory conditions: with a 12-hour alteration of light and dark phases and irradiation of 25 μmol photons m⁻² s⁻¹ at a temperature 20 ± 5 °C. Microscopic study of these raw cultures began in the third week of cultivation. Morphological examinations were performed using Olympus BX53 light microscope with Nomarski DIC optics (Olympus Ltd, Hamburg, Germany). Micrographs were taken with a digital camera (Olympus LC30) attached to the microscope, and processed by the Olympus software cellSens Entry. Direct microscopy of rewetted samples was performed in parallel with cultivation for evaluation of dominating species of algae and cyanobacteria in the original samples. Morphological identification of the biocrust organisms was based mainly on Ettl and Gärtner (2014) for green microalgae, and on Komárek (2013) for cyanobacteria, as well as on some monographs and papers devoted to taxonomic revisions of the taxa of interest (Dariencko and Pröschold 2019).

Moss and lichen determination

Moss and lichens samples were air-dried after collection. For determination, a microscope with a maximum magnification of 400x was used. Morphological identification of mosses followed Frahm and Frey (2004) with taxonomical reference to (Hodgetts et al. 2020). Lichens were determined according to Wirth et al. (2013). Morphologically critical species of the genus *Cladonia* were additionally analyzed by thin-layer chromatography according to (Culberson and Ammann 1979) in solvent system A.

Statistical analyses

Differences in the overall community composition of biocrusts from the two sampling sites Verden and Schaabe and along the transects following the dunes succession stage were visualized by non-metric multidimensional scaling (nMDS) using the vegan package and Bray–Curtis dissimilarity index implemented in R (version 4.1.1). Following, the data on community composition were statistically analyzed via permutational multivariate analysis of variance (PerMANOVA) using Bray-Curtis distance matrix implemented using the R Package Vegan (Oksanen et al. 2018). The presence/absence data of the biocrust inhabiting species were visualized with a Venn diagram using the software Microsoft Excel 2013.

Results

Sediment and biocrust properties

The pH of the sediment at the Schaabe spit conspicuously decreased starting from the foredune (6.39) to the mature dune (3.98). The intermediate and grey dunes within this transect exhibited pH values of 6.13 and 5.58, respectively (Tab. 1). Hence, the pH value continuously declined along the natural dune succession sequence, but all values were slightly to moderate acidic. A similar trend was observed at the inland dune. The pH value of 4.49 was measured in the sediment of the dune center and decreased following the transect to the sampling plot closest to the dune surrounding forest (3.35). Similar to the Schaabe spit the pH value of the inland dune was always acidic (Tab. 1). The organic matter content (OM) of the biocrusts at the Schaabe spit increased along the transect when starting at the foredune with very low contents (0.11 ± 0.01 % DW). OM accumulated towards the mature dune up to a value of 25.19 ± 7.7 % DW in the biocrust. The intermediate and grey dune exhibited OM concentrations of 1.38 ± 0.3 and 7.14 ± 0.89 % DW, respectively (Tab. 1). For the inland dune, the OM content showed a similar pattern. It started in the biocrust-free sediment of the dune centre with a OM value < 1 % DW and increased from 3.0 ± 0.72 % DW at the dune slope to 24.03 ± 2.66 % DW at the plot close to the dune forest. The gravimetric water content in biocrusts at the Schaabe spit ranged between 0.52 % DW (FD) and 3.11 % DW (MD). As for the pH and OM content, the water content increased along the dune succession gradient towards the mature dune. The same applies to the biocrust samples of the inland dune. The water content of the dune center sediment was 0.02 % of the dry weight and reached 1.73 % DW in the biocrusts close to the forest. The total phosphorus (P_t) concentration in the biocrusts along both transects increased towards older dune successional stages. P_t concentration in the dune center (29.89 mg kg^{-1}) and the dune slope (71.85 mg kg^{-1}) of the inland dune were lower than all measured P_t concentrations along the transect on the Schaabe spit. On the spit the lowest P_t concentration was measured in the small foredune (113.9 mg kg^{-1}). Like in the inland dune P_t concentrations increased toward the mature dune area. No significant differences in the P_t concentrations between the grey dune ($173.16 \text{ mg kg}^{-1}$) and the mature dune ($172.23 \text{ mg kg}^{-1}$) were revealed. The highest P_t concentration at the two sites was measured close to forest ($291.25 \text{ mg kg}^{-1}$) in the biocrust of the inland dune (Tab. 1)

Vegetation

Biocrust cover changed along the dune succession gradient at both study sites. On the one hand, the percentage of coverage of each defined biocrust functional group reflected the vegetation dynamics along with the dune succession (Fig. 4). On the other hand, these changes became visible based on the described changes of biocrust species composition in the following section.

At the Schaabe spit, the first dune type under investigation was a small foredune. No cryptogamic cover was found within this dune type (Fig. 4). The surface was mainly bare sediment (48 %) or covered by organic litter (44 %). Occasionally occurring vascular plants (8 %) were *Ammophila arenaria* (L.), which

was planted for coastal protection management of dunes. Following the transect inland into the intermediate dune earliest biocrust covers were detected. These covers were dominated by green algae, defined as initial biocrusts, smaller mosses, and occasionally lichens growing only on litter and debris. Here, biocrusts were the dominant surface cover with 44 %, followed by the surface cover of a litter layer (36 %) (Fig. 4). The grey dune exhibited the highest biocrust coverage of all dune types (80 %) and showed a change in dominant biocrust functional groups. Moss-dominated biocrusts (52 %) replaced the green algae biocrusts. Additionally, 28 % of moss-dominated biocrusts associated with lichens covered the grey dune (Fig. 4). Contrasting to the intermediate dune where lichens occurred only occasionally on plant debris, they became more dominated and area-covering in the grey dune. In the mature dune, a thick moss and lichen carpet, characteristic for more developed successional biocrust stages, dominated the dune surface. The functional groups of moss-dominated and moss-dominated biocrusts associated with lichens overgrew the dune in equal parts (both 36 % areal coverage) (Fig.4). In addition, the litter layer was formed mainly by pine (*Pinus sylvestris* L.) needles and covered 24 % of the surveyed dune surface. Bare sand was rare in the grey and the mature dune. Most likely human trampling, animals, or abiotic factors like wind and rain caused such small bare sediment spots in these dune types.

The abiotic ground cover decreased along the transect at the inland dune in Verden and was replaced by biocrusts in the oldest dune area close to the forest. Bare sediment (80 % areal coverage) and organic litter (20 %) characterized the center of the inland dune (Fig. 4). The first biocrusts along the transect were recognized on the dune slope. This sampling plot was dominated by early green algae biocrusts associated with the occasional occurrence of small mosses (36 %) (Fig. 4). Moreover, a few moss-dominated biocrusts could be observed (4 %). The dune area close to the forest had the highest biocrust coverage of all three investigated subsites (68 %) (Fig. 4). Besides, the first lichen development was found in the area close to the forest (12 %). But still, mature moss-dominated biocrusts were the characteristic functional group within this dune area (32 %) (Fig. 4). Comparing the study sites, a general transition from bare sediment via green algae-dominated biocrusts to moss and lichen-dominated biocrust carpets was observed. No biocrusts were detected at the beginning of each transect (dune center of the inland dune, foredune on the spit). Along each succession gradient, older and more stabilized dune areas followed these mobile primary dunes. On the dune slope (Verden) and the intermediate dune (Schaabe), respectively, the biocrust development started. These dune areas were mostly dominated by biocrusts formed by green algae, whereas mosses and lichens were sparse. An increase in the proportion of the ground cover by biocrusts was detected along each transect. The oldest and most established dune types of each transect (DF = Verden; MD = Schaabe) showed the highest proportion of moss-dominated biocrusts compared with the other plots.

The chlorophyll *a* content of the biocrusts along the transects at both study sites was associated with the transition in species composition and resultant changes in dominant functional groups. In the inland dune, the chlorophyll *a* concentration was lowest in the dune centre (DC = 5.86 mg m⁻²) and rose to 112.07 mg m⁻² ± 20 on the dune slope where the green algae-dominated crusts and some mosses were most present. In the area close to the forest chlorophyll *a* content was highest (210.8 ± 109.01 mg m⁻²). A

similar pattern could be observed along the transect on the Schaabe spit. At the beginning of the transect in the foredune, no chlorophyll was measurable in the bare sediment. In the following intermediate and grey dunes, the chlorophyll *a* concentration was similar (ID = $161.34 \pm 56.51 \text{ mg m}^{-2}$, GD = $150.92 \pm 26.49 \text{ mg m}^{-2}$). The moss-dominated biocrusts in the mature dune showed the highest values ($287.63 \pm 49.07 \text{ mg m}^{-2}$).

Species composition

The community composition of moss, lichen and algae in the biocrusts differed between the sampling sites and along the transects (Fig. 5). Community composition in intermediate and grey dunes from Schaabe were similar to each other. The mature dune was quite dissimilar from the other two Schaabe plots and more similar to the latest stage in the transect of Verden. Both Verden plots differed from each other and from the Schaabe sites. The earliest stage in the transect of Verden had to be excluded from the analyses, as only two algal species and no moss or lichen species were detected. This observation was verified using PerMANOVA: the community composition was significantly shaped by the sampling site (explained variance 42%, p -value < 0.02 , PerMANOVA) and developmental stage of the dunes (explained variance 36%, p -value < 0.02 , PerMANOVA).

Algae and cyanobacteria

Within five biocrust samples and one sediment sample, 13 algae species (nine in the inland dune, twelve at the Schaabe spit), and one cyanobacterium species (plot DC in the inland dune) were detected using culture-dependent methods followed by morphological identification (Tab. 2). The richness of species was expressed as the total species number identified per plot. Along both transects algae were detected with species numbers ranging between one and eight per sampling plot. Along the inland dune transect, the dune slope showed the highest algal species richness (8 out of 14 species). At the Schaabe spit, the interdune dune plot was most rich in species (8 out of 14 species).

Twelve species of Chlorophyta belonging to two classes were determined (three members of Chlorophyceae, nine members of Trebouxiophyceae). One species of Charophyta was detected and assigned to the Klebsormidiophyceae. One species (*Nostoc cf. edaphicum*) of Cyanobacteria was found. The most frequently detected taxa were *Myrmecia cf. irregularis* (Fig. 6 h) and *Stichococcus cf. bacillaris* (Fig. 6 c). Individuals of both genera were found at two sampling plots (*Myrmecia cf. irregularis*: DC, DS; *Stichococcus cf. bacillaris*: DS, DF) in Verden and at three plots (ID, GD, MD) on the Schaabe spit. Both species were followed by *Watanabea cf. acidophila* (Fig. 6 e) in four out of six samples. The other species occurred in half or less biocrust samples. *Nostoc cf. edaphicum* was detected once in the intermediate dune on the Schaabe spit. 38.5 % of all detected species were detected uniquely. Both study sites had 50 % of the identified species in common. Six of these shared species belonged to the Chlorophyta and one to the Charophyta (Online Resource 4A).

Mosses

16 moss species were identified at five of seven sampling plots in this study. Across all five moss-holding plots the species richness ranged between three and nine species. The grey dune plot at the Schaabe spit showed the highest species number of all investigated plots (9 out of 16 species). The species richest plot along the inland dune transect was the one close to the forest (Tab. 3).

14 species of Bryophyta were determined, all belong to the class of Bryopsida. The remaining two species were assigned to the Jungermanniopsida in the phylum Marchantiophyta. The almost omnipresent species *Ceratodon purpureus* could be found at the inland dune sampling plots DS and DF and ID, GD, MD at the Schaabe spit. All other species occurred in two or less of the five moss-holding sampling plots. 50 % of all detected species were detected uniquely. The study sites showed only two out of 16 identified species in common (12.5 %), namely *Ceratodon purpureus* and *Dicranum scoparium* (Online Resource 4B).

Lichens

26 lichen species were found at four of seven sampling plots in this study. (Tab. 4) Across all four lichen-holding plots the species richness ranged between four and 15 taxa. The intermediate dune plot at the Schaabe spit had the highest species number of all investigated plots (15 out of 26 species). Along the inland dune transect the sampling plot close to the forest was the only one on which lichens could be found. At this plot four out of 26 overall detected lichen species were observed (Tab. 4).

All determined fungal species belong to families of lichen-forming ascomycetes (class: Lecanoromycetes), and 21 out of 26 species belong to the order Lecanorales. Four different orders were determined in total. *Cladonia furcata* was the only lichen species found at all lichen-holding plots of this study. *Cladonia scabriuscula* and *Hypogymnia physodes* were the second most present species. Both could be found at all lichen-holding plots on the Schaabe spit (ID, GD, MD) but not in Verden. The remaining 23 species were present in less than three plots. 15 species were detected at one plot only. *Cladonia furcata* and *Cladonia portentosa* were the only lichen species both study sites had in common (Online Resource 4 C).

Discussion

The study results pointed out to a connection between the different dune successional stages and the phototrophic community living on it. The enrichment of organic matter, moisture, and phosphorus content with advanced biocrust development was detected.

Vegetation

The vegetation survey revealed a successional development of biocrust stages from a thin topsoil layer of algae to stable moss and lichen-dominated 'mature' communities, along the two investigated dune chronosequences. This confirmed our first hypothesis. In addition, the overall areal cover of biocrusts across the sampling plots increased along the succession gradient. These results are in line with a strong

zonation from grey dunes to mature dunes regarding the vascular plant communities at the German Wadden Sea coast described with (Isermann 2011). Along the dune chronosequences and the succession series, respectively, the organic matter and moisture content increased at both our study sites, thus reflecting a shift in the biocrust communities.

Foredunes or equivalent the center of the inland dune are characterized by the influence of strong wind resulting in a highly mobile substrate. Additionally, nearshore higher sediment salinity and air-borne salt spray cause harsh conditions at coastal dunes. Along with a scarcity of nutrients, neither a stable plant nor a biocrust cover could establish at both study sites (García Novo et al. 2004; Hesp 1991; Lane et al. 2008; Martínez et al. 2004). Consequently, the organic matter and chlorophyll *a* content were lowest in these mobile dune types. In addition, microorganisms such as filamentous green algae or cyanobacteria, which might glue sand particles together by excreted exopolysaccharides (van Ancker et al. 1985; Belnap 2006; Zhang 2005), were missing. Hence, no coherent top-soil layer can be formed. Consequently, precipitation will easily seep away in loose sandy sediment (Gypser, Veste, et al. 2016). The earliest successional stages of biocrusts were found in the chronologically following intermediate dune at the Schaabe spit and on the dune slope in the inland dune (Verden). They were mainly formed by green algae, covering approximately half of the dune's surface, forming patchy and thin microbial layers. The occasionally growth of mosses and lichens could be observed as well. However, the establishment of mature biocrust types could hardly be observed in intermediate dunes due to the frequent disturbance by erosive wind forces leading to sand mobility (Martínez et al. 2001) or due to water limitation caused by the low-holding capacity of sand (Chamizo et al. 2016; Gypser, Veste, et al. 2016). Soil moisture can positively affect carbon and nitrogen fixation by microorganisms, as it was observed for biocrusts in arid regions (Belnap and Eldridge 2001). Especially the accumulation of organic carbon by microbial biomass formation plays an essential role in the early pedogenesis (Kaviya et al. 2019). Organic carbon accumulation is controlled by the turnover rates of soil organic matter (Šourková et al. 2005). The present organic matter accumulation was assumed to be based on faster biomass formation and litter input than decomposition within the studied two dune areas. It is assumed that the increase in organic matter within the biocrust has the potential of increasing the plant-available P concentration in the sediment. Inorganic bound P can be solubilized from parent material either by the secretion of organic acids by the microorganisms (Fox 1995) or by an increase in the pH (Blume et al. 2010). Phosphatases, produced by the biocrust organisms are known to hydrolyze organic phosphates releasing P (Nannipieri et al. 2011). The increase in total P in the biocrusts along both chronosequences can be explained by sedimentation, but mainly by the general increased biomass formation. Increased phototrophic biomass is revealed by the chlorophyll *a* content. Depending on sampling site, season, biocrust communities, and successional type the Chl *a* content varies clearly. Lange (2001) reported a Chl *a* content up to 100 mg m⁻² in biocrusts formed by cyanobacteria and eukaryotic algae, whereas lichen- or bryophyte-dominated biocrusts reached values above 900 mg m⁻². Just as it is proposed by Büdel et al. (2009) the presented study could prove a significant increase in the chlorophyll content from biocrusts of the early successional stage to later ones. In a semi-arid desert, Büdel et al. (2009) measured a mean Chl *a* value of 118.9 ± 35.8 mg m⁻² in an area with strong coverage of biocrusts with bryophytes, dominated by mosses. These findings fit in

with the Chl *a* value of the dune slope of the inland dune, which was also dominated by green algae biocrusts associated with mosses ($112.07 \pm 20 \text{ mg m}^{-2}$). The Chl *a* value of the intermediate dune ($161.34 \pm 56.51 \text{ mg m}^{-2}$) and grey dune ($150.92 \pm 26.49 \text{ mg m}^{-2}$) on the Schaabe spit exceeded this value slightly but lay close together. This finding highlighted these two dune types as an interface of succession concerning their phototrophic biomass accumulation. One reason could be their largely shared moss and lichen community composition. Along the dune chronosequences, the successional stages of biocrusts gain more biomass due to thicker green algae layers and their by-products. Moreover, the gain in biomass (Chl *a*) and sediment organic matter might be caused by the increased establishment of mosses. The values of moss-dominated biocrusts in the presented study (DF inland dune = 210.80 mg m^{-2} ; MD coastal spit = 287.63 mg m^{-2}) were significantly higher than those measured by (Gypser, Herppich, et al. 2016). Gypser, Herppich, et al. (2016) described the mean Chl *a* content of moss- and lichen-dominated biocrusts in an artificial temperate sand dune are of 68.9 mg m^{-2} .

Moss-dominated biocrusts took over and covered about half of the investigated plot within the grey dune at the Schaabe spit. These biocrust types formed a denser and coherent layer on the sediment surface. The growth of lichens increased significantly. No bare sediment was detected in this dune area. The increase in moss and lichen biomass along the chronosequence characterized the transition from the intermediate dune to the established grey dune area (Vázquez 2004). However, the percentage coverage by vascular plant was highest in this dune type, mostly dominated by Poaceae. The development of grey dunes was characterized by increased sand stabilization due to less sand accumulation (Martin 1959). Therefore, vegetation cover could expand and support the formation of an organic matter layer on the sediment surface (Isermann 2011). Such a layer was composed of dead plant material along with living phototrophic and heterotrophic biomass, originating from the biocrust. A similar trend was reported by (Gypser, Herppich, et al. 2016), who showed a progressively increase of biomass and the total chlorophyll content from initial to moss-lichen dominated biocrusts at post-mining sites in Lower Lusatia, north-east Germany. The mature dune area landwards at the Schaabe spit and respectively the area close to forest in the inland dune represented the oldest successional stages of dunes along the investigated dune chronosequences. They differed from (younger) dune types by a closed biocrust cover dominated by mosses with the highest occurrence of lichens. These covers grew under a light canopy of a coastal pine forest. Mature dunes, as the latest phase of dune succession, represented a high organic matter content as an indicator of soil formation (Dümig et al. 2014). This assumption is consistent with the observations made in the present study and in line with Isermann (2011). Here, the organic matter accumulation originated from annual vascular plants, scrubs, and smaller trees. The observed increase in the sediment moisture content could be ascribed to the thick biocrust, by absorbing water into the cellular mucilage and reducing evaporation, thereby stimulating infiltration (Belnap et al. 2013; Chamizo et al. 2012) and soil water content (Berdugo et al. 2014). Chamizo et al. (2016) highlighted the later stages of biocrust succession as dominated by lichens and mosses by their higher infiltration capability and water retention finally leading to higher soil moisture. The presented results showed similar patterns and are in line with a study of Gypser, Veste, et al. (2016) in which green algae tend to inhibit water infiltration due to pore-clogging by algal filaments, thereby increasing water runoff. In contrast, later successional stages of

biocrusts, dominated by mosses and lichens, can absorb more water and reduce runoff compared to the algae-dominated biocrusts. Particularly moss rhizoids can facilitate water infiltration into deeper soil layers (Dümig et al. 2014).

Species composition

As proposed in the second hypothesis, the phototrophic biocrust community composition was shaped by the developmental stage of the dunes along each chronosequence. While algae were found in all biocrust-holding plots, their individual species compositions and most frequently detected taxa shifted between the developmental dune stages. The same trend applied for the moss and lichen species. Only a few species were omnipresent along each chronosequence. Comparing both study sites, regional differences concerning the community structures became visible. While the algae community showed many similarities, the moss and lichens community differed significantly more between the two study sites. Based on these findings, the third hypothesis could be partly confirmed. The differing geographical regions had a noticeable impact on the specific biocrust community.

Algae and cyanobacteria in biocrusts

Comparing the overall green algae and cyanobacteria species richness at the Schaabe spit with the latest studies on biocrust microbial community diversity in this area conducted by Schulz et al. (2015) similarities but also conspicuous differences were obvious. Even though biocrusts are consistently formed by algae rather than cyanobacteria species richness can differ. While Schulz et al. (2015) detected 70 cyanobacterial and non-diatom algal taxa in association with biocrusts in coastal dunes at the Baltic Sea the recent study could reveal only twelve. Since species composition in biocrusts very likely varies with season (Bu et al. 2018) this might be one reason for dominance of green algae in spring biocrusts and cyanobacteria in autumn biocrusts (October Schulz et al. 2015, April/May in this study). Much less species number was detected in biocrusts of the present study mostly concerned with identification of the most frequent and dominating species. While complete species composition of algae and cyanobacteria of biocrusts was showed in Schulz et al. 2015 and related papers (Mikhailyuk et al. 2019, 2021). It was determined using different methods and so-called integrative approach: direct microscopy, enrichment and pure cultures, molecular identification of some species etc.). Biocrusts consisted mainly of few green algae and cyanobacteria in the early successional stages of dune development at both temperate study sites. This is contrasting to studies carried out in arid or semiarid deserts where cyanobacteria were always dominant in early successional biocrusts (Ashley et al. 1985; Büdel et al. 2009; Lange et al. 1992; Veste et al. 2011; Zaady et al. 2000). However, the presented findings are comparable to other studies conducted in temperate areas. In temperate forests Glaser et al. (2017) recorded 52 algal species and only very few cyanobacteria in biocrusts. Additionally, 17 eukaryotic algae and 15 cyanobacteria species were found in initial biocrusts in a sand ecosystem in the northern upper Rhine valley (Germany) (Langhans et al. 2009).

In the center of the inland dune only a few algae taxa could be observed in the bare sand, even if they did not form a thin biocrust layer. Contrary to the foredune close to the Baltic Sea microorganisms at inland

dunes do not have to cope with salt and wind stress. This might facilitate their survival in the mobile sediment of the inland dune center. But it can not be excluded that the detected algal species were dormant stages. These algae can act as pioneer colonizers of the mobile sand facilitating further stabilization and colonization. Light green algae dominated biocrusts were the only one containing cyanobacteria along the whole dune chronosequence. One reason for the rare occurrence of cyanobacteria could be the sediment conditions, in particular the pH. For optimum growth of cyanobacteria-containing biocrusts sediment pH should be neutral to slightly alkaline (Singh et al. 2014). Under acidic sediment conditions (pH less than 4 or 5) Brock (1973) could confirm that cyanobacteria were completely absent. The sediment pH along the two dune chronosequences showed a landward strong decrease from 6.4 to 4.0 (coastal spit, Schaabe) and from 4.5 to 3.4 (inland dune, Verden). These acidic conditions in the inland dune might limit the growth of cyanobacteria. The biocrusts in the intermediate dune at the Schaabe spit showed only slightly acidic conditions (6.1) and thus few cyanobacteria could grow. Besides the geological impact on pH dynamics the coniferous vegetation (e.g., *Pinus sylvestris* L.) typically leads to a decrease in the soil pH due to the microbial decomposition of pine tree litter (Maun 2009). Considering the shifts in vegetation cover along both dune chronosequences, the oldest successional dune areas were located under or close by the dune forest. These areas, dominated at both study sites by pine trees, could be one potential reason for the decrease in sediment pH and causing unfavorable growth conditions for cyanobacteria in the mature dune area. Nevertheless, it could be possible that not all cyanobacteria were detected due to chosen cultural approach. Previous studies showed the necessity to use different determination approaches e.g., morphological and molecular-based revealing a more complete community structure of biocrusts (Mikhailyuk et al. 2019; Rippin et al. 2018).

The biocrusts on the dune slope of the inland dune mostly consisted of Chlorophyta and representatives of the Charophyta, class Klebsormidiophyceae. Moreover, this dune successional stage was the species richest along the whole chronosequence. These findings were identical to those of the intermediate dune on the Schaabe spit. Here, most algal species could be detected. Representatives of the genus *Klebsormidium* were only found in this dune successional stage. Many studies point to *Klebsormidium* as a genus, holding species with a wide tolerance range in temperature, water availability, or sun radiation (Holzinger and Karsten 2013; Karsten and Rindi 2010; Kitzing et al. 2014). To cope with such extreme changing environmental conditions Donner et al. (2017) assume certain plasticity of the genus morphology as a benefit to adapting to these varying abiotic stress. These filamentous algae are known as major biocrust forming taxa (Holzinger and Karsten 2013). Glaser et al. (2017) could prove *Klebsormidium* was the most important biocrust-initiating algae in a temperate forest ecosystem. In an inland dune area in the Netherlands Pluis (1994) found *Klebsormidium* to be the initial green algae genus in the successional development of the biocrust community. Likewise, representatives of the genus *Klebsormidium* were found in dynamic dune successional stages along both transects, highlighting the initialization of biocrust development.

With further dune succession, the algal species richness declined. Four species of the family Trebouxiophyceae were found in the area close to forest in the inland dune and the mature dune on the Schaabe spit, having two of those species in common. Such clear differences between the algal

community structure of initial and later successional biocrust stages were also shown in a sand ecosystem in the northern Rhine valley (Germany). Here, Langhans et al. (2009) could show a decrease from 17 eukaryotic algae in early successional biocrust stages to 13 species in later successional biocrust stages, which is in common with this study.

Mosses and lichens

Moss- and lichen-dominated biocrusts were distinctive of older stages of development. In phytosociology (Ellenberg 1996), the development of a cryptogam layer marks the beginning of grey dune development, as drifting sand will not cover the small cryptogams. On the other hand, the cryptogam layer helps to fix small amount of still drifting sand and bring organic litter into the sediment.

An incipient moss and lichen growth could be described on the dune slope of the inland dune and the intermediate dune on the Schaabe spit, respectively. *Ceratodon purpureus* was found in both transitional stages of dune succession. This moss species is typical for mobile dune types due to its high tolerance to sand deposition. A study on response of mosses to experimental burial by Martínez and Maun (1999) could show a high tolerance of *C. purpureus* of up to 7 cm. This species is the only one the dune slope in the inland dune and the intermediate dune on the Schaabe spit had in common. Along both chronosequences, *C. purpureus* was observed in transitional dune types as well as in later dune stages, like the area close to forest in the inland dune and on the fixed grey dune on the Schaabe spit. These findings are in line with Gypser, Herppich, et al. (2016) who described the growth of *C. purpureus* as an initial moss as well as dominant in mature moss-lichen biocrusts. Another species only found on the dune slope of the inland dune is *Syntrichia ruraliformis*. This species is highly desiccation-tolerant (Mishler and Oliver 1991). This trait is favourable for a moss growing on dune types which are under constant abiotic stress, like higher irradiation and low water holding capacity. Surprisingly, by chance this species was not found along the Baltic Sea chronosequence. Nevertheless, it is quite common in other sand dunes along the Baltic Coast (Meinunger and Schröder 2007). The following later stages of dune succession revealed a shift in community composition along each chronosequence. Pioneer moss species, like *C. purpureus*, decreased and were supplemented by mosses of later successional stages like *Dicranum scoparium* and *Hypnum cupressiforme* var. *lacunosum*. Gypser, Herppich, et al. (2016) described *Polytrichum piliferum* as dominant species of mature biocrusts which is in line with this study where *P. piliferum* was only found in the later successional stage close to forest of the inland dune chronosequence. The mature dune on the Schaabe spit chronosequence was low in moss species richness and was dominated by mosses of the genus *Hypnum*. The dune area close to forest on the inland dune showed the first growth of lichens along this chronosequence. Exclusively lichens of the genus *Cladonia* were found. Along the dune chronosequence on the Schaabe spit the intermediate and grey dune were the lichen species richest dune types. Whereas, in the intermediate dune lichen species primarily growing on litter and debris were found. Which includes *Bacidina etayana*, *Lecanora persimilis*, and *Caloplaca cerinella*. Moreover, *Placynthiella uliginosa* is a species also growing on bare sandy soil and was described to inhabit a sandy inland dune area of Sorgwohld (Schleswig-Holstein, Germany) (Dolnik and Neumann 2020). Later successional dune stages along both

investigated chronosequences were dominated by representatives of the genus *Cladonia*. *Cladonia* primarily inhabits nutrient-poor soils and forests. This corresponds to the environmental conditions under which they were found.

Declarations

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Conflicts of Interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Author Contribution

S. Kammann designed the field work campaign. Fieldwork was conducted by S. Kammann and U. Schiefelbein. Following lab work on sediment analysis was carried out by S. Kammann. Algae cultivation and determination were performed by T. Mikhailyuk and E. Demchenko. U. Schiefelbein was in charge of the determination of lichen species. C. Dolnik was responsible for the determination of moss species. The data were statistically analysed by K. Glaser. The first draft of the manuscript was written by S. Kammann with substantial contributions from all co-authors. All authors read and approved the final manuscript.

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Tables

Tables 1 to 4 are available in the Supplementary Files section.

Figures

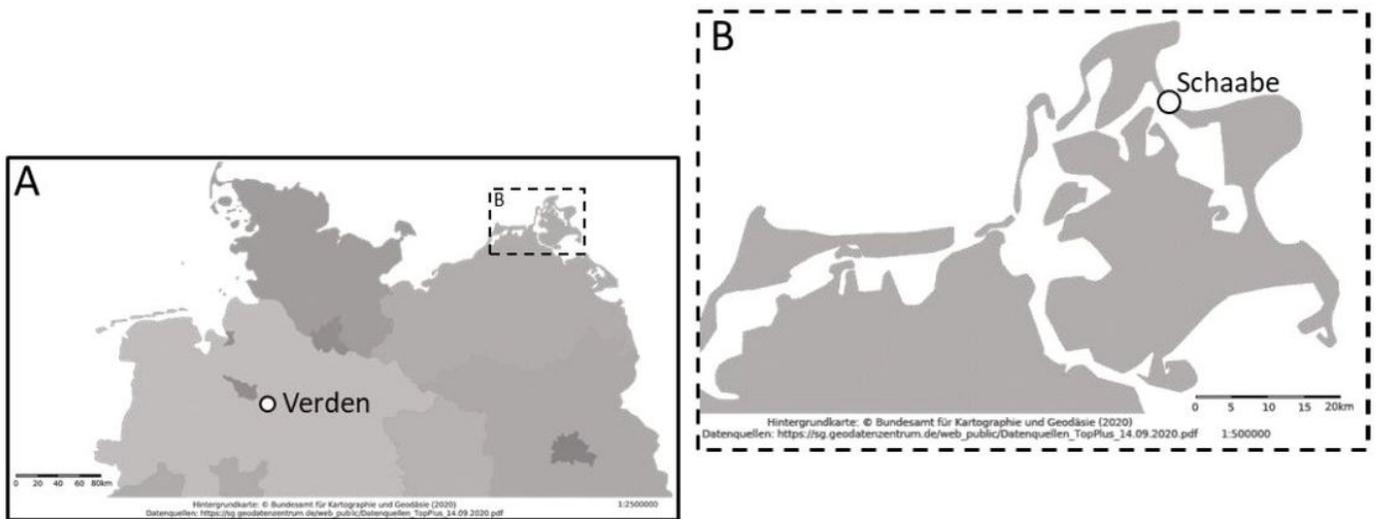


Figure 1

The inland dune in Verden and the island of Rügen in the northern part of Germany (A). A close up of the island Rügen (B) and the investigated dune sampling site on the Schaabe spit (circle)

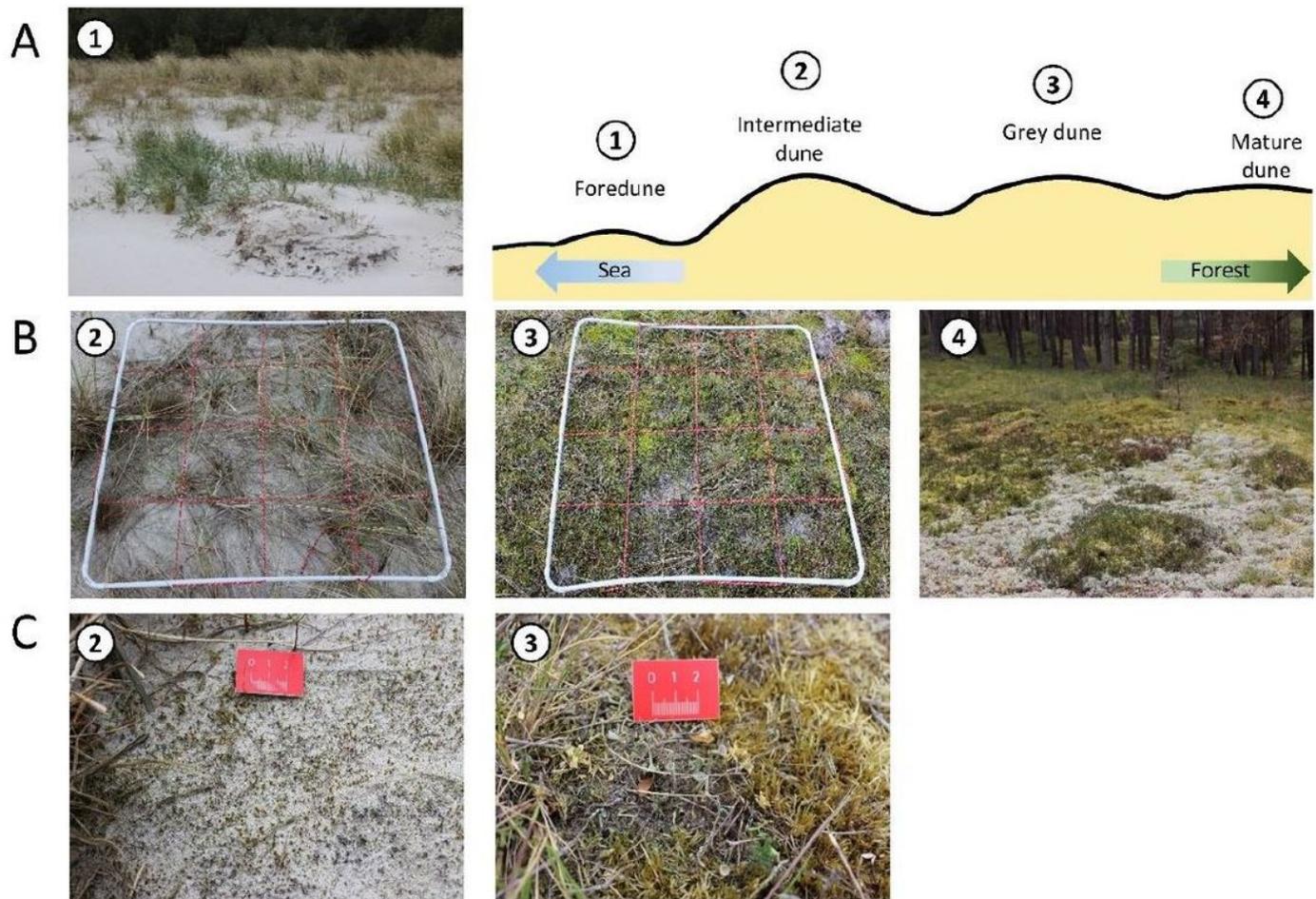


Figure 2

Overview of the transect on the Schaabe spit (Rügen), numbers indicate the sampling plots: foredune (FD) = 1, intermediate dune (ID) = 2, grey dune (GD) = 3, mature dune (MD) = 4 (A). Close ups of the biocrust-holding sampling plots (B) and detail pictures of the dominant biocrust types in the respective plot (C)

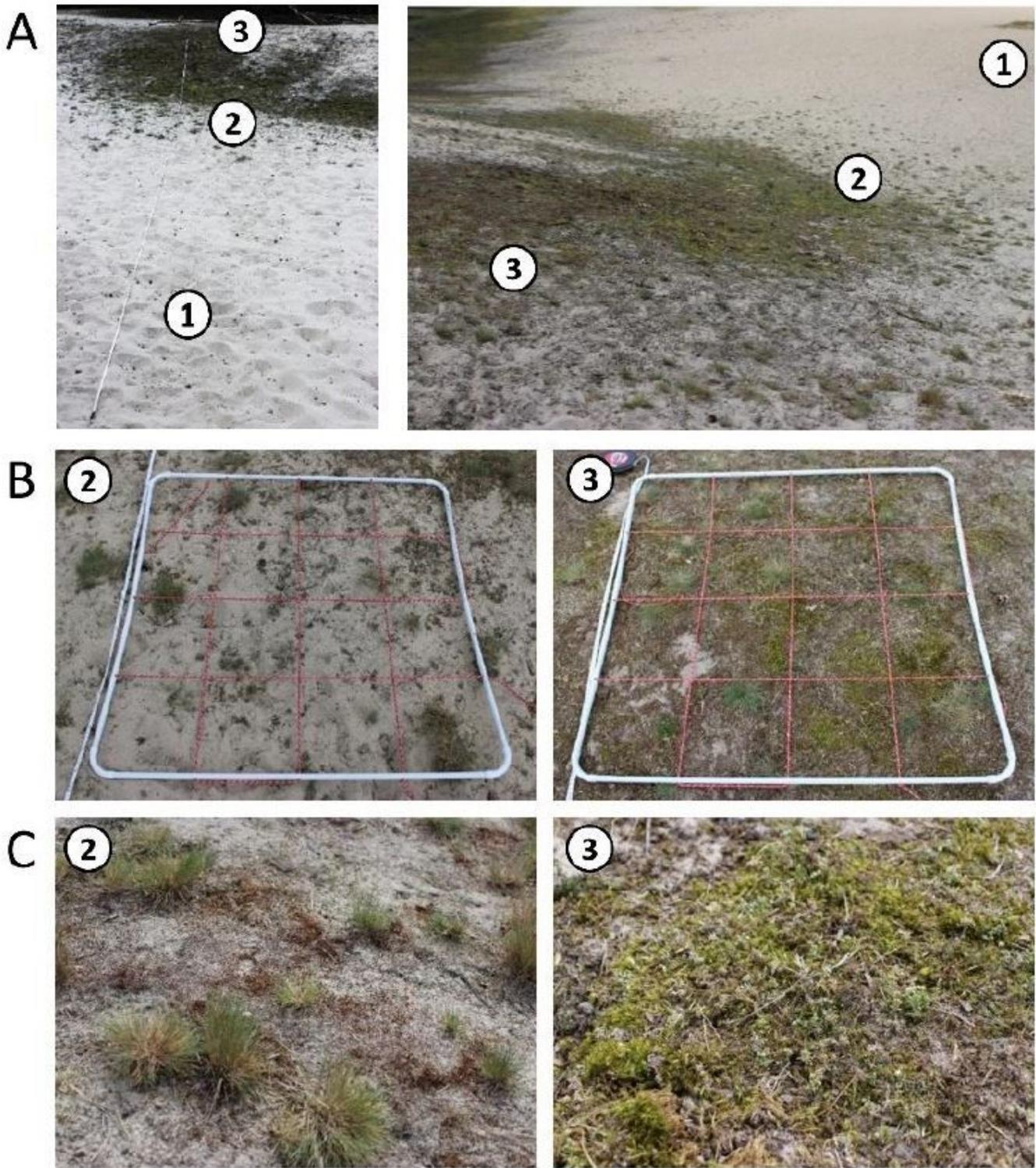


Figure 3

Overview of the transect in the inland dune in Verden (Aller), numbers indicate the sampling plots: dune center (DC) = 1, dune slope (DS) = 2, dune forest (DF) = 3 (A). Close ups of the biocrust-holding sampling plots (B) and detail pictures of the dominant biocrust types in the respective plot (C)

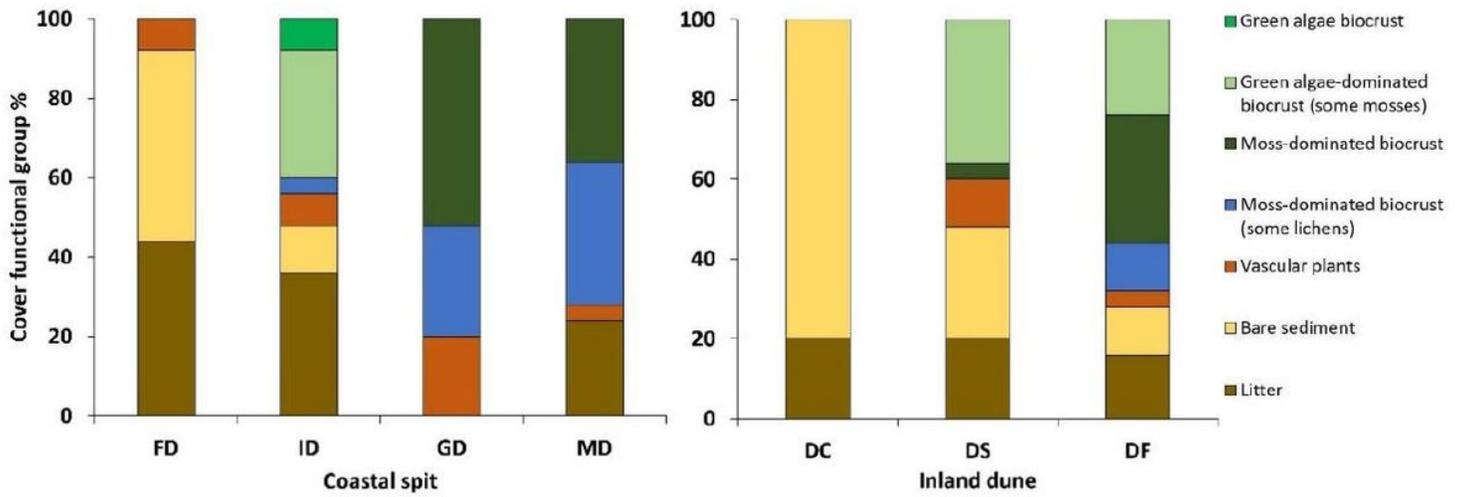


Figure 4

Summary of the vegetation survey. Percentage of area covered by the different functional groups as determined with the point intercept method on the whole two transect. . Sites: Coastal spit (Schaabe); Dune types: FD = foredune, ID = intermediate dune, GD = grey dune, MD = mature dune. Site: Inland dune (Verden); Sampling plots: DC = dune center, DS = dune slope, DF = dune forest)

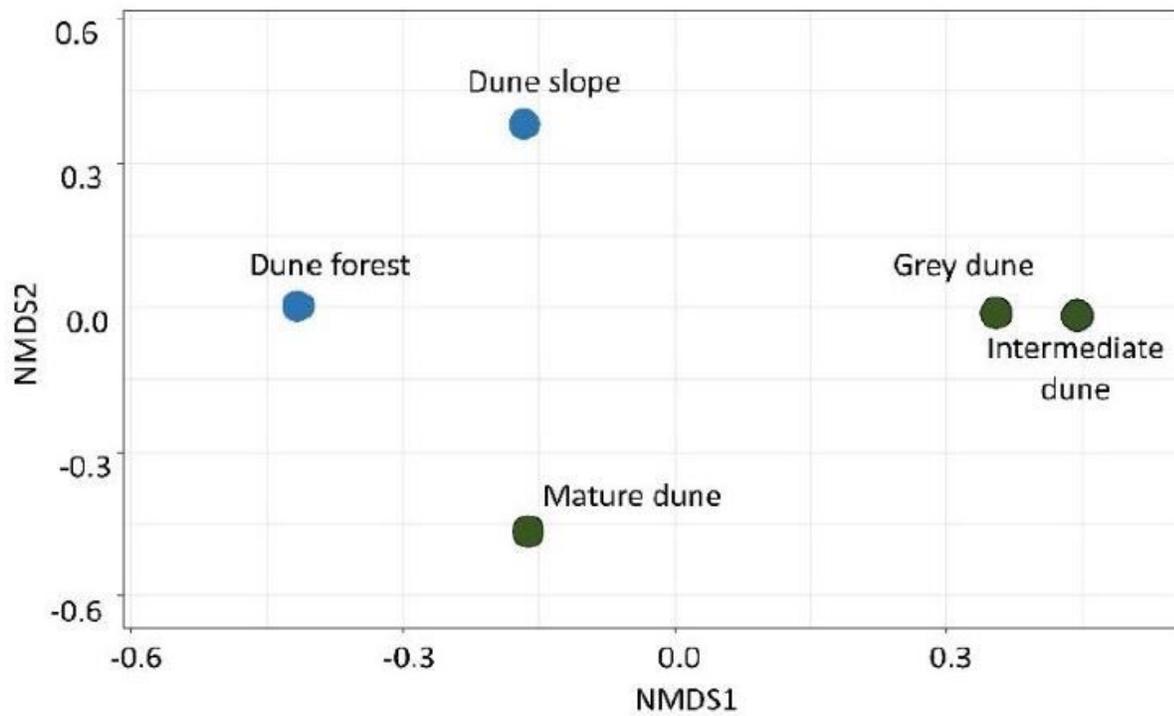


Figure 5

nMDS plot visualizes the differences in the community composition of lichen, mosses and algae between 5 sampling sites. Blue: inland dune, Verden; Green: coastal spit, Schaabe



Figure 6

Algae and cyanobacteria from different dune succession stages along the two transects. a *Klebsormidium* cf. *subtile*, b *Stichococcus* *allas*, c *Stichococcus* cf. *bacillaris*, d *Chloridium* sp., e *Watanabea* cf. *acidophila*, f *Diplosphaera* *chodatii*, g *Parietochloris* *alveolaris*, h *Myrmecia* cf. *irregularis*, i *Bracteacoccus* sp., j *Elliptochloris* *subsphaerica*, k *Coelastrella* sp., l *Chlorolobion* sp., m *Nostoc* cf. *edaphicum*. Scale bars 10 μ m

Supplementary Files

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