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SOIL MICROBIOLOGY

Biological Soil Crusts from Coastal Dunes at the Baltic Sea: Cyanobacterial and Algal Biodiversity and Related Soil Properties

Karoline Schulz[1] · **Tatiana Mikhailyuk**[2] · **Mirko Dreßler**[3] · **Peter Leinweber**[4] · **Ulf Karsten**[1]

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Abstract Biological soil crusts (BSCs) are known as "ecosystem-engineers" that have important, multifunctional ecological roles in primary production, in nutrient and hydrological cycles, and in stabilization of soils. These communities, however, are almost unstudied in coastal dunes of the temperate zone. Hence, for the first time, the biodiversity of cyanobacterial and algal dominated BSCs collected in five dunes from the southern Baltic Sea coast on the islands Rügen and Usedom (Germany) was investigated in connection with physicochemical soil parameters. The species composition of cyanobacteria and algae was identified with direct determination of crust subsamples, cultural methods, and diatom slides. To investigate the influence of soil properties on species composition, the texture, pH, electrical conductivity, carbonate content, total contents of carbon, nitrogen, phosphorus, and the bioavailable phosphorus-fraction (PO_4^{3-}) were analyzed in adjacent BSC-free surface soils at each study site. The data indicate that BSCs in coastal dunes of the southern Baltic Sea represent an ecologically important vegetation form with a surprisingly high site-specific diversity of 19 cyanobacteria, 51 non-diatom algae, and 55 diatoms. All dominant species of the genera *Coleofasciculus*, *Lyngbya*, *Microcoleus*, *Nostoc*, *Hydrocoryne*, *Leptolyngbya*, *Klebsormidium*, and *Lobochlamys* are typical aero-terrestrial cyanobacteria and algae, respectively. This first study of coastal sand dunes in the Baltic region provides compelling evidence that here the BSCs were dominated by cyanobacteria, algae, or a mixture of both. Among the physicochemical soil properties, the total phosphorus content of the BSC-free sand was the only factor that significantly influenced the cyanobacterial and algal community structure of BSCs in coastal dunes.

Keywords Cryptogamic crusts · Biocrusts · Sand dunes · Soil algae · Cyanobacteria · Diatoms · Phosphorus

Introduction

Coastal dunes are unique ecosystems in the transition zone between terrestrial and marine environments, where interactions between geology, climate, and vegetation create highly dynamic environments [1, 2]. These eolian and sand-driven landforms are formed by the interaction of wind and waves, and exhibit, related to their temporal and spatial dynamics, intrinsic values as important and unique habitats. Additionally, coastal dunes provide an essential source of natural sand replenishment and serve as protective barriers against coastal flooding and erosion [1, 3]. Coastal dune systems are harsh environments with a wide variety of environmental stresses such as strong wind and substrate mobility, scarcity of nutrients and soil water, occasionally extremely high temperatures near surface, intense radiation, flooding, and salt spray [1, 4].

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✉ Karoline Schulz
karoline.schulz@uni-rostock.de

[1] Institute of Biological Sciences, Applied Ecology and Phycology, University of Rostock, Albert-Einstein-Str. 3, 18059 Rostock, Germany

[2] M.H. Kholodny Institute of Botany, National Academy of Science of Ukraine, Tereschenkivska St. 2, Kyiv UA-01001, Ukraine

[3] Institute of Biological Sciences, Department of Botany and Botanical Garden, University of Rostock, Wismarsche Str. 8, 18051 Rostock, Germany

[4] Faculty of Agricultural and Environmental Science, Soil Science, University of Rostock, Justus-von-Liebig-Weg 6, 18051 Rostock, Germany

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Under these conditions, the growth and the development of a closed vascular plant cover are limited, and only specialized organism communities can be established, which include biological soil crusts (BSCs).

BSCs are soil particle-associated communities of cyanobacteria, algae, microfungi, lichens, liverworts, mosses, and bacteria in different proportions, living within or immediately on top of the uppermost millimeter of soil thereby forming coherent layers at the soil surface [5]. BSCs are distributed worldwide in all climatic zones [e.g., 6–8], and as multifunctional communities, they have important ecological roles. They stabilize the soil surface [9], increase the content of soil organic matter and the nitrogen concentration through photosynthesis and nitrogen fixation [10, 11], influence nutrient cycling [12], modulate hydrological processes [13], and consequently, influence the establishment and performance of vascular plants [14].

BSCs are highly diverse communities. There are hundreds of different species of cyanobacteria and algae which can be found in association with BSCs [15]. Especially, large filamentous cyanobacteria as well as filamentous algae are important for the development of BSCs, because their filaments and sticky mucilaginous sheaths glue soil particles together. In contrast, due to their limited biomass, unicellular cyanobacterial and algal species are usually of secondary importance in the formation of BSCs. Most of these unicellular species are green algae which can reach high species numbers in soil crusts [5]. Furthermore, Bacillariophyceae are also typical components to be found in BSCs [16, 17].

The distribution of all BSC-associated organisms and their further development result from complex interactions with the prevailing environmental factors. Microclimatic conditions (e.g., temperature and moisture), soil texture, pH, and carbonate content are only some of the abiotic factors that alter BSCs [18, 19]. However, these pedo-climatic and biogeochemical factors vary from site to site, sometimes over orders of magnitude, and thus, disclosing their effect on the BSC community structure still requires site-specific studies over a wide range of terrestrial habitats.

Most of the knowledge that exists about the distribution, adaptations, and functions of crust organisms is derived from studies on BSCs in semiarid and arid environments, where they can be a main component of the vegetation [20, 21]. Taking into account the crucial ecological functions of BSCs in terrestrial ecosystems, it is surprising that BSCs in habitats of temperate regions with more humid conditions are only fragmentarily investigated [see also 22]. One of these habitats is the coastal dune system. The limited literature about BSCs in coastal dunes worldwide indicates that they contribute to the stabilization, enrichment of nutrients, and the establishment of higher plants in these ecosystems [9, 23–25]. However, BSCs in coastal dunes of the temperate region are still almost unstudied.

Consequently, the aim of the present study was, for the first time, to comprehensively investigate BSCs in coastal dunes of the temperate zone on the German Baltic Sea islands Rügen and Usedom, with a special focus on the diversity of cyanobacteria and algae as well as on the influence of abiotic parameters.

The main questions of this study were the following:

1. Which species occur in these specific coastal dune BSCs and which are dominant?
2. Do certain soil properties influence the species composition of the BSCs in coastal dunes?

Material and Methods

Study Area

BSCs were investigated in coastal dunes on the two largest islands of Germany, Rügen, and Usedom (926 and 445 km^2, respectively). Rügen and Usedom are located at the southwestern shore of the Baltic Sea belonging to the German federal state of Mecklenburg-Western Pomerania (Fig. 1). Both islands are influenced by an oceanic continental transitional climate. The mean annual temperature is 8–8.5 °C with the lowest mean temperature of −3–1 °C in January and highest mean temperature of 19–20 °C in August. The mean annual precipitation varies between 500 and 600 mm, with February being the month with lowest mean precipitation and July that with the highest mean precipitation, 30–40 and 50–70 mm, respectively (measurement period of all climatic factors: 1961–1990; [26]).

BSCs were investigated along a transect at the three study sites Glowe, Prora, and Baabe on Rügen and the two study sites Karlshagen and Zempin on Usedom, stretching from the northeast coast of Rügen in a southeastern direction to the northwest coast of Usedom (Fig. 1). The investigated coastal dune systems differed in their morphological characteristics, vegetation cover, and degree of degradation. The dunes in Glowe and Prora had a width between 4 and 8 m, while in Baabe, Karlshagen, and Zempin, the dunes reached widths between 15 and 20 m. Moreover, the two latter systems were with 4 m twice as high as the three other dunes. All dune systems were partly fenced except the one in Prora. Hence, this latter dune was highly degraded due to human trampling and showed only little vegetation with a dominance of *Festuca* sp. The other dune systems had undestroyed and dense vegetation mainly consisted of *Ammophila arenaria* (L.) Link. In addition, *Hippophae rhamnoides* L., *Artemisia campestris* L., *Artemisia*

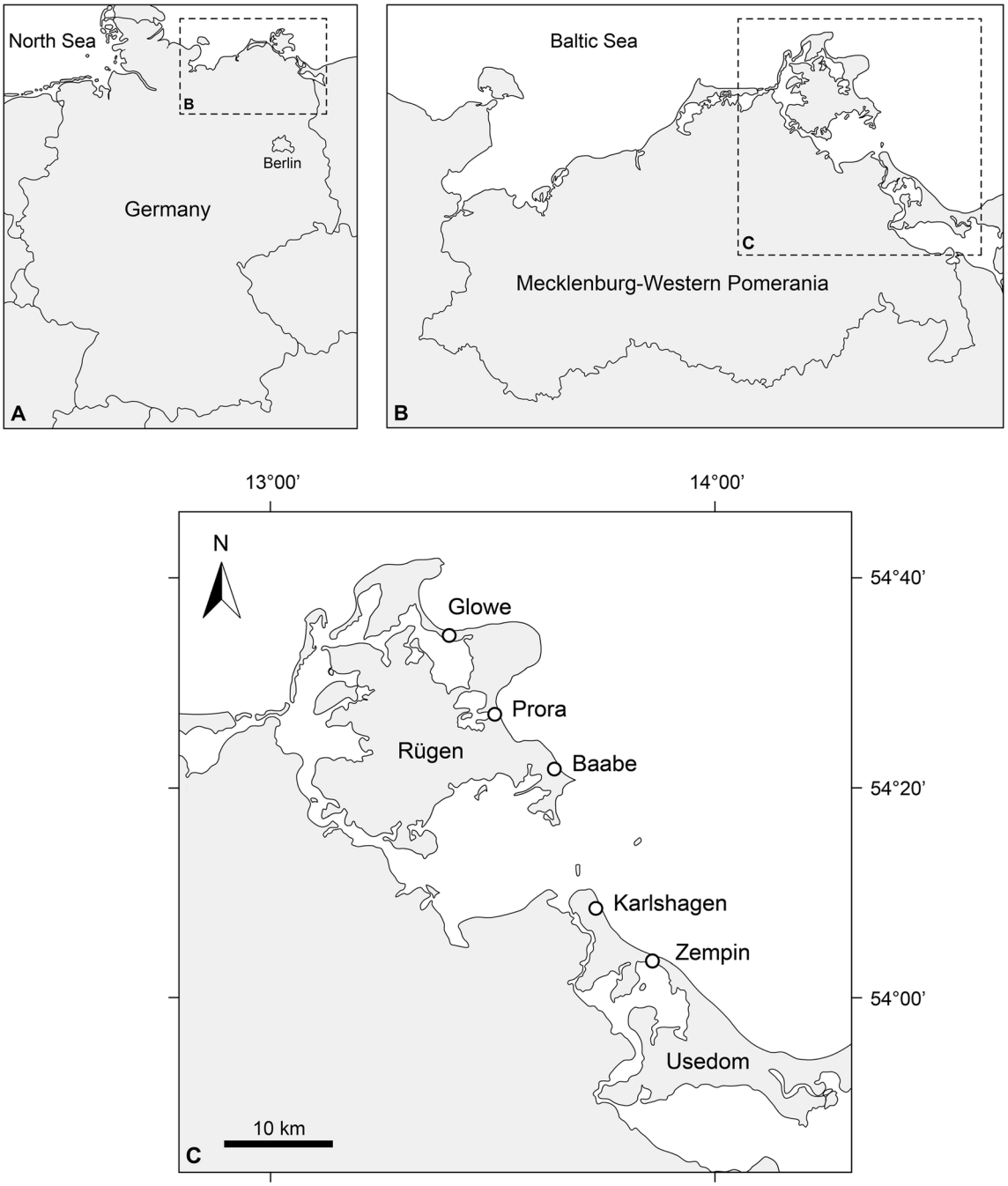


Fig. 1 The islands Rügen and Usedom, and the investigated dune study sites (**c**) belonging to the federal state of Mecklenburg-Western Pomerania (**b**) in the northeastern part of Germany (**a**)

maritima L., *Leymus arenarius* (L.) Hochstetter, *Rosa rugosa* Thunberg, *Tussilago farfara* L., *Dianthus* sp., *Carex* sp., *Pinus sylvestris* L., and single species of Fabaceae and Asteraceae were also present in different proportions at the dune systems. The bare sandy ground (ground without vegetation of higher plants) between the higher plants was covered by green cyanobacterial and algal crusts. At each dune, a plot with an area of 2×2 m was randomly chosen, and the coverage of BSCs in relation to the bare ground estimated. In Glowe, 40 % of the dune plot was bare ground of which 40 % was covered with BSCs. In Prora, 80 % of the dune plot was bare ground of which 10 % was covered with thin BSCs. In Baabe, 25 % of the dune plot was bare ground of which 30 % was covered with BSCs. In Karlshagen, 25 % of the dune plot was bare ground of which 95 % was covered with BSCs, and in Zempin, 40 % of the plot was bare ground of which 70 % was covered with BSCs.

Sampling

Two random cyanobacterial and algal BSC samples and two adjacent BSC-free soil samples were collected at each study site on 8 October 2013. Sampling of BSCs was carried out by pushing a spatula gently below the crust in order to take as sparse amounts of surrounding soil as possible. The spatula with the crust was then lifted, and the sample was carefully transferred in a small paper box for subsequent analysis of the diversity of cyanobacteria and algae. These samples of BSCs had a surface area of approximately 6×6 cm. With a shovel, a BSC-free soil sample next to the BSCs (max. 40 cm distance) of approximately 5×5×5 cm was taken and filled into a small freezing bag for nutrient analysis. An additional soil sample of approximately 10×10×10 cm was taken and filled into a big freezing bag for the determination of other soil properties. In total, ten BSCs and ten soil samples were collected. In the laboratory, the samples were air-dried and stored in the dark until further analysis.

Cultivation and Determination of Cyanobacteria and Non-diatom Algae

For the determination of cyanobacteria and non-diatom algae enrichment cultures and unialgal cultures were used. To obtain enrichment cultures, small amounts of material (c. 2×2 mm) were taken randomly out of the crust and placed on the surface of solid 1 N Bold's Basal Medium (1 N BBM) made with 1.5 % agar in Petri dishes [27]. Afterward, the samples were exposed at room temperature under a photon fluence rate of approximately 30 μmol photons m^{-2} s^{-1} (light source: Osram Daylight Lumilux Cool White lamps (L36W/840); Osram) and a 16:8 h light-dark cycle. The identification of cyanobacterial and algal taxa started after a growth phase of 2 to 4 weeks. Because for the identification of cyanobacteria and algae knowledge of developmental stages of certain species and genera is necessary, enrichment cultures were purified into unialgal strains, using 1 N BBM for cyanobacteria and 3 N BBM (BBM modified by the addition of triple nitrate concentration; [28]) for algae. These cultures were kept under the same cultivation conditions as the enrichment cultures.

Cyanobacteria and non-diatom algae were determined morphologically under an inverted light microscope (Olympus IX70, oil immersion) at 1000-fold magnification. The identification was mainly based on Ettl and Gärtner [29] as well as on Komárek and Anagnostidis [30–32] for algae and cyanobacteria, respectively (further references about the identification of cyanobacteria and algae are given in Online Resource 1).

Determination of Diatoms

For the identification of diatoms, combusted slides were prepared. 0.5–0.6 g of crust material were filled in 5 mL glass vials with 4 mL of distilled water. These glass vials were strongly shaken. Immediately after shaking, 100 μL of overlaying water was gently dripped on glass cover slips, which were dried on air, combusted in a muffle oven (Elektra M26) at 550 °C for 35 min and after cooling mounted onto glass microscope slides using Naphrax®.

Diatom species were morphologically identified using a light microscope (Zeiss Axioplan, oil-immersion Plan-Apochromat objective, aperture 1.4) with 1000-fold magnification based on Krammer and Lange-Bertalot [33, 34], Krammer [35], Witkowski et al. [36], Lange-Bertalot [37], Lange-Bertalot et al. [38], and Hofmann et al. [39]. In the slides, the proportion of each single diatom taxa within the total Bacillariophyceae community was estimated independent from cyanobacteria and non-diatom algae of the crust samples with a scale ranging from 1 (very rare) over 2 (rare/occasionally), 3 (regular), 4 (subdominant), to 5 (dominant).

Direct Determination of Dominant Cyanobacterial and Non-diatom Algal Taxa

In addition to the culture approach and the diatom slides mentioned above, the dominant BSC phototrophic microorganisms were directly identified in freshly collected, undisturbed samples. For direct determination of cyanobacterial and non-diatom algal taxa in BSCs, three subsamples of crust material (c. 1×1 cm) were rewetted in tap water for 20 min. Cyanobacteria and non-diatom algae were morphologically identified under an inverted light microscope (Olympus IX70) with 400-fold and/or 1000-fold magnification, depending on size of soil particles within the crust samples. The portions of occurring cyanobacterial and non-diatom algal taxa were estimated using a scale ranging from 1 (very rare) over 2 (rare/occasionally), 3 (regular), 4 (subdominant), to 5 (dominant). In contrast to the numbers of species, which were identified in enrichment cultures, mostly only a small proportion of cyanobacteria and non-diatom algae were found directly in crust material. Thus, all cyanobacterial and non-diatom algal taxa, which were not found directly in crust material but were identified in the enrichment cultures, got 1 as dominance level, because they appeared to occur very rarely in the investigated BSCs.

Analyses of Soil Substrates

All soil analyses were done according to standard protocols [40]. Prior to the analyses, the air-dried soil samples were sieved <2 mm. For determination of the particle size

distribution, the soil was treated with hydrochloric acid (HCl), hydrogen peroxide (H_2O_2), and tetrasodium diphosphate ($Na_4P_2O_7$). For the determination of the sand subfractions (coarse 2–0.63 mm, medium 0.2–0.63 mm, fine 0.063–0.2 mm), 10 g of soil was transferred on a set of analytical sieves with decreasing mesh size which were rinsed with tap water. The sieves together with the remaining sand were dried at 105 °C and weighed before and after removal of the sand fractions. An automated sedimentation/decantation analysis (Sedimat 4–12, UGT GmbH, Müncheberg, Germany) was used to determine the percentage of silt (0.002–0.063 mm) and clay (<0.002 mm) fractions in an additional subsample of 10 g of soil. The pH was measured in a 1:2.5 soil/water solution by adding 10 g of soil to 25 mL of distilled water. This suspension was thoroughly mixed twice during 1 h, and the pH was measured with a glass electrode (pH Meter 540 GLP, WTW GmbH, Weilheim, Germany). The electrical conductivity was measured in a soil extract, prepared from a suspension of 10 g of soil and 100 mL of distilled water, which was mechanically shaken for 1 h and filtered through folded filters (Microprocessor Conductivity Meter LF196, WTW GmbH, Weilheim, Germany). For gas-volumetric determination of the carbonate content, the soil was finely ground to <1 mm using a Pulverisette 2 ball mill (Fritsch GmbH, Idar-Oberstein, Germany). The CO_2 released following the addition of HCl (37 %) was measured in a Scheibler apparatus and used for the calculation of the carbonate content.

Prior to elemental analyses, the air-dried soil samples were ground with a ball mill to <1 mm. Total carbon (TC) and total nitrogen (TN) were determined with a CHNS-Analyzer (VARIO EL, Elementar Analysensysteme, Hanau, Germany) using 30 mg of soil together with 30 mg of tungsten trioxide (WO_3) as catalyst, which were packed together in tin-foil and transferred into the analyzer for high-temperature combustion. Total phosphorus (TP) was determined by mixing 0.5 g of soil with 2 mL of nitric acid (HNO_3) and 6 mL of HCl for microwave-assisted digestion at 200 °C (Mars Xpress, CEM GmbH, Kamp-Lintfort, Germany). The digest was filled up with ultrapure water to 100 mL, and the P concentration in this solution was determined by atomic emission spectroscopy at 214.914 nm with inductively coupled plasma (ICP-AES, JobinYvon 238 Ultrace, Instruments S.A. GmbH, Grasbrunn, Germany). Bioavailable phosphorus (PO_4^{3-}) was determined photometrically using the malachite-green method by mixing 1.5 g of soil with 37.5 mL of ultrapure water. This suspension was incubated for 22 h at room temperature, mechanically shaken for 1 h and filtrated. The filtrate was mixed with 3 mL of sulfuric acid (H_2SO_4; 24 %), 5 mL of malachite-solution, and 5 mL of molybdate solution and filled up with ultrapure water to 50 mL. The PO_4^{3-} concentration was determined spectrophotometrically at 623 nm.

Statistics

All multivariate analyses of the data were performed using the statistic program Canoco for Windows 4.5. For the statistical analyses of species data (Table 1), the mean values of two BSCs for each study site were used. The frequency data of diatoms and the frequency data of cyanobacteria and non-diatom algae have two different reference systems, because of the different methods used for investigation and identification of diatoms and all other algae and cyanobacteria. For that reason, the diatom data were excluded from statistical analyses. However, the species data and the soil properties data of the dune study sites were analyzed with a direct gradient analysis. The direct gradient analysis was used to show similarities and differences in the crust communities at the five dune sites and to investigate the variations of species composition in relation to environmental factors. The longest gradient of the first unmodified detrended correspondence analysis (DCA) was 1.7; hence, a redundancy analysis (RDA) was performed. The RDA was run with focus scaling on inter-sample distance and centering and standardization by species. Species scores were post-transformed through divisions by standard deviation. The Monte Carlo permutation test with 499 performed permutations was used to test a significant influence of environmental factors on the obtained data distribution.

Results

Species Composition

In total, 125 cyanobacterial and algal taxa were found in association with BSCs in coastal dunes using a combination of direct determination, culture approach, and diatom slides (Tables 1 and 2). Nineteen species of cyanobacteria in 13 genera were determined (one species of Chroococcales, eight species of Nostocales, ten species of Oscillatoriales). Furthermore, 38 species of Chlorophyta in 27 genera (26 species of Chlorophyceae, 12 species of Trebouxiophyceae), seven species of Streptophyta in four genera (one species of Chlorokybophyceae, five species of Klebsormidiophyceae, one species of Zygnematophyceae), and 61 species of Heterokontophyta in 28 genera (four species of Xanthophyceae, two species of Eustigmatophyceae, 55 species of Bacillariophyceae) were identified.

Cyanobacteria and Non-diatom Algae

The total species number of cyanobacteria and non-diatom algae was smallest in the BSCs of Glowe (28 species) and largest in the BSCs of Karlshagen (40 species) (Fig. 2). All investigated BSCs had more non-diatom algal taxa than cyanobacterial species. Additionally, in terms of cyanobacteria,

Table 1 Complete list of cyanobacterial and non-diatom algal species found in ten BSCs from five coastal dune study sites on Rügen and Usedom and the estimated abundance of the single taxa in the investigated crusts

Species	Glowe		Prora		Baabe		Karlshagen		Zempin	
	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2
Cyanophyceae										
Calothrix cf. *elenkinii* Kossinskaja						1	1			
Chroococcus helveticus Nägeli										1
Coleofasciculus sp.	1			4						
Hassallia sp.							1		2	
Hydrocoryne sp.					4		1	5		
Leptolyngbya edaphica (Elenkin) Anagnostidis & Komárek	1		1	1		1	1		1	3
Leptolyngbya cf. *henningsii* (Lemmermann) Anagnostidis						3	1		1	1
Leptolyngbya cf. *notata* (Schmidle) Anagnostidis & Komárek					3		4	1	1	3
Lyngbya sp.	3	5	1	3						
Microcoleus vaginatus Gomont ex Gomont	2	1	5	4	1	1	2	3		1
Nodosilinea sp.	1		1	1	2	1	1	1	1	1
Nostoc cf. *commune* Vaucher ex Bornet & Flahault							3			3
Nostoc cf. *edaphicum* Kondrateva		1		1	2	2	4	2	1	4
Nostoc cf. *linckia* Bornet ex Bornet & Flahault	1					1		1		1
Nostoc sp.					1					1
Phormidium cf. *corium* Gomont ex Gomont					1					
Pseudophormidium hollerbachianum (Elenkin) Anagnostidis					1	1			1	1
Tolypothrix cf. *tenuis* Kützing ex Bornet & Flahault					2	2				
Trichocoleus sp.				2	1	1	1			1
Chlorophyceae										
Actinochloris sphaerica Korschikov			1							
Acutodesmus obliquus (Turpin) Hegewald & Hanagata	1	1	3		1		1	1		1
Bracteacoccus cf. *minor* (Chodat) Petrová		1	1							
Bracteacoccus sp.	1	1	1	1	1	1		1	1	
Carteria cf. *crucifera* Korshikov ex Pascher			1				1			
Chlamydomonas cf. *callunae* Ettl							1			
Chlamydomonas cf. *moewusii* Gerloff								2		
Chlamydomonas cf. *reisiglii* Ettl			1							
Chlorococcum cf. *oleofaciens* Trainor & Bold			1			1				
Chlorolobion lunulatum Hindák	1		1				1			1
Chloromonas cf. *augustae* (Skuja) Pröschold, Marin, Schlösser & Melkonian			1							
Chloromonas actinochloris Pröschold, Marin, Schlösser & Melkonian			1	1						1
Chloromonas cf. *reticulata* (Goroschankin) Wille emend. Pröschold, Marin, Schlösser & Melkonian		1	1							
Graesiella emersonii (Shihara & Krauss) Nozaki, Katagiri, Nakagawa, Aizawa & Watanabe						1				
Lobochlamys cf. *culleus* (Ettl) Pröschold, Marin, Schlösser & Melkonian						1				1
Lobochlamys spec	1	3	4		1					
Monoraphidium cf. *pusillum* (Printz) Komárková-Legnorová	1	1	1	1	1	1	1	1		1
Neochloris cf. *gelatinosa* Herndon		1								
Podohedra bicaudata Geitler								1		
Scenedesmus sp.						1	1			1
Spongiochloris cf. *incrassata* Chantanachat & Bold					1					1
Spongiochloris cf. *minor* Chantanachat & Bold			1					1		
Spongiochloris spongiosa (Vischer) Starr					1					

Table 1 (continued)

Species	Glowe		Prora		Baabe		Karlshagen		Zempin	
	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2
Tetracystis sarcinalis Schwarz				1	1	1	1	1		
Tetracystis sp.							1	1		
Trebouxiophyceae										
Chlorella chlorelloides (Naumann) Bock, Krienitz & Pröschold	1								1	1
Chlorella vulgaris Beyerinck	1	1	1		1		1	1		1
Chloroidium ellipsoideum (Gerneck) Darienko, Gustavs, Mudimu, Menendez, Schumann, Karsten, Friedl & Pröschold			1					1		
Dictyosphaerium sp.								1		
Diplosphaera chodatii Bialosukniá	1		1						1	
Elliptochloris subsphaerica (Reisigl) Ettl & Gärtner	1	1	1	1					1	
Geminella interrupta Turpin										1
Koliella sp.			1							
Leptosira cf. *erumpens* (Deason & Bold) Lukesová								1		
Myrmecia cf. *biatorellae* Petersen									1	
Pseudochlorella sp.								1		
Pseudococcomyxa cf. *simplex* (Mainx) Fott				1	1			1		
Stichococcus bacillaris Nägeli	1		1	1		1		1	1	
Chlorokybophyceae										
Chlorokybus atmophyticus Geitler							1			
Klebsormidiophyceae										
Interfilum paradoxum Chodat & Topali	1		1		1		1			1
Klebsormidium crenulatum (Kützing) Ettl & Gärtner	1								5	
Klebsormidium flaccidum (Kützing) Silva, Mattox & Blackwell	4	1	3		4	4		2	2	2
Klebsormidium cf. *nitens* (Meneghini) Lokhorst	1			1	1	1				
Klebsormidium cf. *subtile* (Kützing) Tracanna ex Tell		1		2			1			
Zygnematophyceae										
Cylindrocystis crassa De Bary	1			1						1
Xanthophyceae										
Pleurochloris meiringensis Vischer			1					1		
Bumilleriopsis cf. *peterseniana* Vischer & Pascher										1
Xanthonema cf. *bristolianum* (Pascher) Silva	1		1		1		1	1		1
Xanthonema exile (Klebs) Silva		1						1		
Eustigmatophyceae										
Eustigmatos magnus (Petersen) Hibberd					1		1	1	1	
Vischeria helvetica (Vischer & Pascher) Hibberd						1	1			

1 very rare, *2* rare/occasional, *3* regular, *4* subdominant, *5* dominant

the BSCs of Glowe and Prora (both seven species) had half as many species as the BSCs of Baabe, Karlshagen, and Zempin (12 to 14 species). For non-diatom algal species, the BSCs of Prora and Karlshagen (28 and 29 species) exhibited larger species numbers than those of Glowe, Baabe, and Zempin (20 to 22 species) (Fig. 2).

The most common species, which occurred in almost all investigated BSCs, were the cyanobacteria *Nodosilinea* sp., *Leptolyngbya edaphica* (Elenkin) Anagnostidis and Komárek, *Microcoleus vaginatus* Gomont ex Gomont and *Nostoc* cf. *edaphicum* Kondrateva and the algae *Bracteacoccus* sp., *Monoraphidium* cf. *pusillum* (Printz) Komárková-Legnorová, *Acutodesmus obliquus* (Turpin) Hegewald and Hanagata, *Chlorella vulgaris* Beyerinck, and *Klebsormidium flaccidum* (Kützing) Silva, Mattox and Blackwell (Table 1). In contrast, some cyanobacteria and non-diatom algae were only found in BSCs from one of the five study sites (Table 1).

Table 2 Complete list of diatom species found in ten BSCs from five coastal dune study sites on Rügen and Usedom and the estimated abundance of the single species of all diatom taxa in the investigated crusts

	Glowe		Prora		Baabe		Karlshagen		Zempin	
Species	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2
Achnanthes coarctata (Brébisson) Grunow	5	5	5	3	2	3		1		1
Actinocyclus sp.						1				1
Amphora cf. *indistinct* Levkov				1						
Amphora indistinct Levkov		1			1					
Caloneis amphisbaena (Bory de Saint Vincent) Cleve						1				
Catenula adhaerens (Mereschkowsky) Mereschkowsky					1		1			
Cocconeis cf. *neothumensis* Krammer					1		1			
Cocconeis neothumensis Krammer					1		1			
Cocconeis placentula Ehrenberg			1							
Cocconeis placentula var. *euglypta* (Ehrenberg) Grunow		1								
Cocconeis scutellum var. *scutellum* Ehrenberg	1	1								
Cocconeis sp. A			1				1	1		
Cocconeis sp. B					1			1		1
Cocconeis sp. C				1						
Cocconeis sp. D	1									
Epithemia cf. *turgida* (Ehrenberg) Kützing				1						
Fallacia cf. *florinae* (Møller) Witkowski	1									
Fallacia cf. *tenera* (Hustedt) Mann	1									
Fallacia clepsidroides Witkowski	1	1			1	1				1
Fallacia tenera (Hustedt) Mann	1	1								
Fistulifera cf. *pellicolosa* (Brébisson) Lange-Bertalot				1						
Fragilaria martyi (Héribaud-Joseph) Lange-Bertalot				1			1			
Fragilaria s.l. A	1									
Fragilaria s.l. B							1			
Fragilaria s.l. C								1		
Fragilaria s.l. D								1		
Fragilaria s.l. E								1		
Fragilaria schulzii Brockmann				1						
Hantzschia abundans Lange-Bertalot		4				4				
Hantzschia amphioxys (Ehrenberg) Grunow	4	2		5	2	5	3	3		1
Hantzschia sp.						2				
Luticola cf. *cohnii* (Hilse) Mann			1				2	2		1
Luticola cohnii (Hilse) Mann group	1	3	3	1	1		4	5		1
Luticola sp.						1				
Mayamaea atomus var. *atomus* (Kützing) Lange-Bertalot								1		
Muelleria sp.	2	1								
Navicula cf. *paul-schulzii* Witkowski & Lange-Bertalot				1						
Navicula cf. s*yvertsenii* Witkowski, Metzeltin& Lange-Bertalot		1								
Navicula vimineoides Giffen			1	1			1	1		
Opephora burchardtiae Witkowski							1	1		
Opephora cf. *minuta* (Cleve-Euler) Witkowski							1			
Opephora sp.							1			
Pennate A						1				
Pennate B	1									
Pennate C							1			
Pinnularia aff. *intermedia* (Lagerstedt) Cleve	3	3	1		2			1		1

Table 2 (continued)

Species	Glowe		Prora		Baabe		Karlshagen		Zempin	
	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2	BSC 1	BSC 2
Pinnularia borealis var. *borealis* Ehrenberg					1	2				
Pinnularia cf. *intermedia* (Lagerstedt) Cleve					2	1		1		1
Pinnularia intermedia (Lagerstedt) Cleve	5	5	3	2	5	4	5	4		5
Placoneis clementis (Grunow) Cox					1					
Planothidium cf. *lemmermannii* (Hustedt) Morales						1				
Planothidium delicatulum (Kützing) Round & Bukhtiyarova		1	2	1	1	2	1	1	1	
Planothidium lemmermannii (Hustedt) Morales		1	1	1	1		1			1
Planothidium sp.	1	2	1	1	1	2	1	1		1
Staurophora sp.			2		3	4				1

1 very rare, *2* rare/occasional, *3* regular, *4* subdominant, *5* dominant

Diatoms

The total number of diatom species at a single study site ranged from 14 species in the BSCs of Zempin to 26 species in the BSCs of Karlshagen (Fig. 2). Diatom species, which were present in nearly all dune BSCs were *Achnanthes coarctata* (Brébisson) Grunow, *Hantzschia amphioxys* (Ehrenberg) Grunow, *Pinnularia intermedia* (Lagerstedt) Cleve, *Planothidium* sp., and species of the *Luticola cohnii* (Hilse) Mann group (Table 2). Additionally, there were also several diatom species, which occurred only in the BSCs from one study site (Table 2).

In comparison with cyanobacteria and non-diatom algae, the diatoms were not dominant in BSCs, but several species showed a higher abundance than others. Six highly abundant diatom species could be identified, which represent typical aero-terrestrial species and showed differences between BSCs of the study sites (Fig. 3 and Table 2). The most abundant diatom species was *Pinnularia intermedia*, followed by *Hantzschia amphioxys*. The two diatom species *Achnanthes coarctata* and *Hantzschia abundans* were only abundant in BSCs from the Rügen sites. In addition, *Staurophora* sp. was abundant only in BSCs of Baabe. In the BSCs from Zempin, *Pinnularia intermedia* was identified as the only abundant species (Table 2).

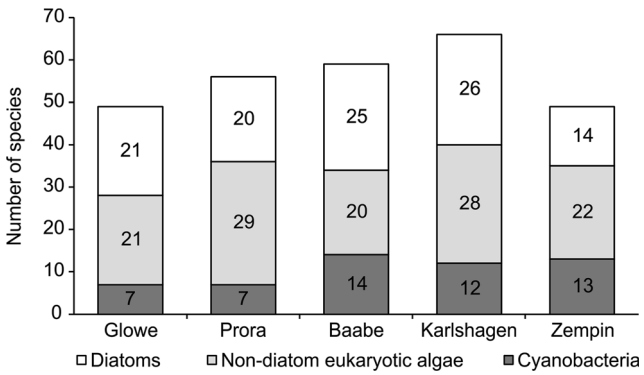


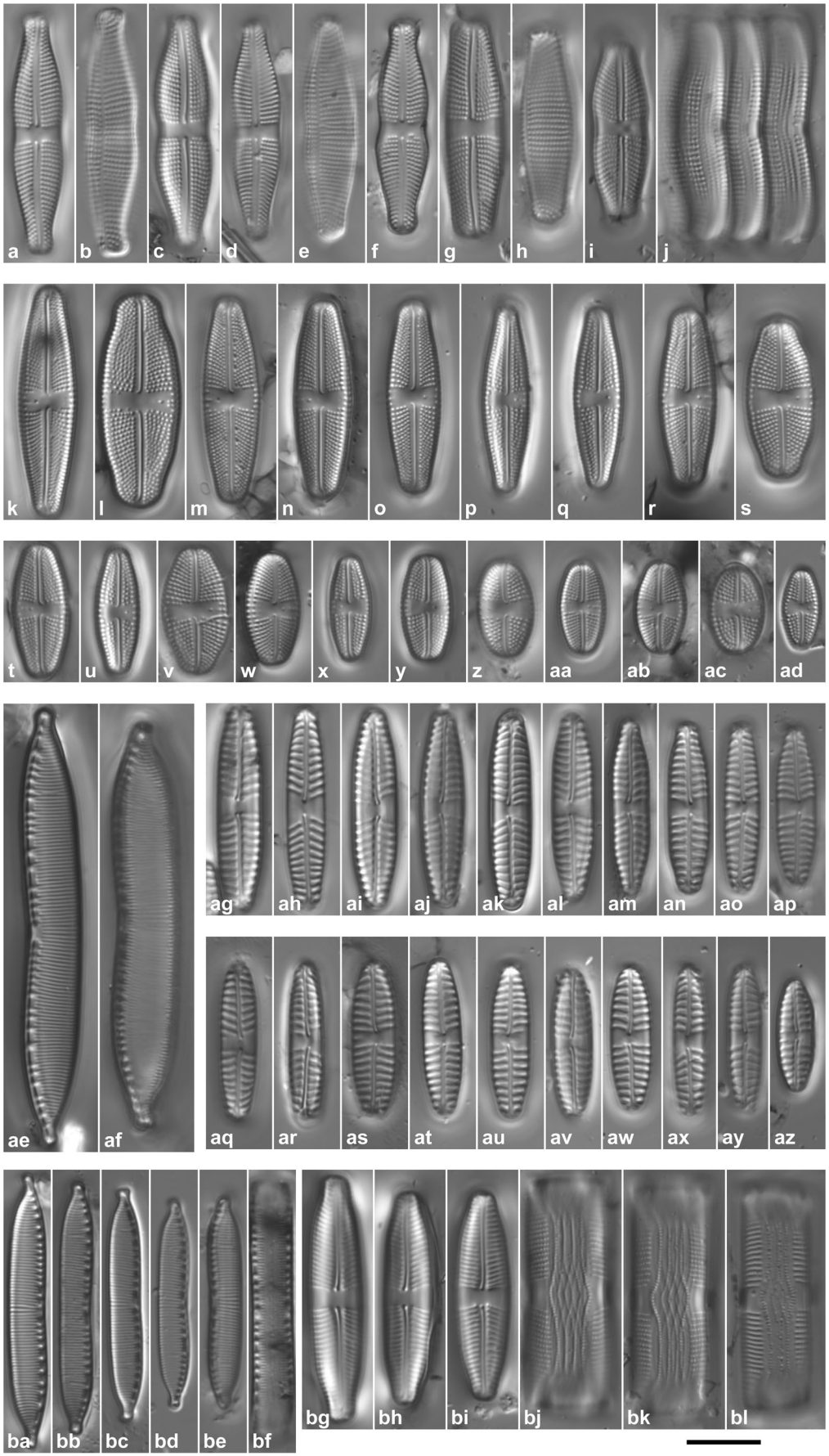
Fig. 2 Total species number of cyanobacteria, non-diatom algae, and diatoms in two BSCs for each of the five coastal dune study sites on Rügen and Usedom. *Numbers in bars* indicate the species numbers

Dominant Species

In total, nine dominant cyanobacteria and algae were identified in the investigated BSCs with six species of cyanobacteria (*Microcoleus vaginatus*, *Hydrocoryne* sp., *Nostoc* cf. *edaphicum*, *Coleofasciculus* sp., *Leptolyngbya* cf. *notata*, and *Lyngbya* sp.) and three species of algae (*Klebsormidium flaccidum*, *Klebsormidium crenulatum*, and *Lobochlamys* sp.) (Fig. 4). There were five BSCs dominated by cyanobacteria and three BSCs dominated by algae, and two BSCs showed a mixed dominance of cyanobacteria and algae (Table 1). Each crust was different in terms of the dominant species even at the same study site. However, the two soil crusts of Karlshagen were only dominated by cyanobacteria. The algal species *Klebsormidium flaccidum* and *Lobochlamys* sp. were only dominant in BSCs of Rügen. Except the one *Klebsormidium crenulatum* dominated crust of Zempin, all investigated BSCs of Usedom were dominated by cyanobacteria (Table 1).

Physicochemical Soil Properties

The soil texture classification according to the German texture classification system [41] revealed for all sites the texture class “Sandy sand” (Ss). The further differentiation revealed the subclasses “medium sand” for the samples from Glowe and Prora, “fine sandy medium sand” for the sample from Baabe and Zempin, and “fine sand” for the sample from Karlshagen (Table 3). However, in the samples of Baabe and Zempin, the subfractions medium sand and fine sand were visually very similar, and thus, the soil texture was close to the border of the respective adjacent texture subclass. Generally, it appeared that the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◀ **Fig. 3** Abundant diatom species of BSCs from five dune study sites on Rügen and Usedom. *Achnanthes coarctata* (**a**–**j**), *Luticola cohnii*-group (**k**–**ad**), *Hantzschia abundans* (**ae**–**af**), *Pinnularia intermedia* (**ag**–**az**), *Hantzschia amphioxys* (**ba**–**bf**) and *Staurophora* sp. (**bg**–**bl**). *Scale bar* at 10 μm

texture became finer and the specific surface of the mineral part of the BSCs larger in a northwestern to southeastern direction, except for the site Zempin. The pH was neutral at all investigated sites, ranging from 7.1 (Zempin) to 7.5 (Karlshagen). The electrical conductivity and the carbonate content decreased from Glowe (41.5 μS cm^{-1}; 11.1 %) to Zempin (15.5 μS cm^{-1}; 0.7 %), but there were only slight differences between Baabe, Karlshagen, and Zempin (Table 3).

The elemental contents of the soils showed the lowest TC (0.67 g kg^{-1}) in Karlshagen and the highest TC (10.79 g kg^{-1}) in Glowe (Table 3). TN was more uniform among the study sites, ranging from 0.09 g kg^{-1} in Zempin to 0.21 g kg^{-1} in Baabe with the values for Glowe (0.13 g kg^{-1}), Karlshagen (0.13 g kg^{-1}), and Prora (0.14 g kg^{-1}) in between and very similar. The soil sample from Karlshagen had the lowest TP

Fig. 4 Dominant cyanobacterial and non-diatom algal species of BSCs from coastal dune study sites on Rügen and Usedom. Cyanobacteria and algae in culture (**a**, **b**, **d**, **f**–**k**, **o**, **p**, **r**, **s**) and direct in crust material (**c**, **e**, **l**–**n**, **q**): *Microcoleus vaginatus* (**a**–**c**), *Hydrocoryne* sp. (**d**, **e**), *Nostoc* cf. *edaphicum* (**f**, **g**), *Coleofasciculus* sp. (**h**, **i**), *Leptolyngbya* cf. *notata* (**j**, **k**), *Lyngbya* sp. (**l**–**n**), *Klebsormidium flaccidum* (**o**), *Klebsormidium crenulatum* (**p**, **q**), and *Lobochlamys* sp. (**r**, **s**). *Scale bars* at 10 μm

Table 3 Physical and chemical properties of BSC-free surface soils of the coastal dune study sites on Rügen and Usedom used in this study

Coordinates	Glowe 54° 34.196′ N 13° 27.486′ O	Prora 54° 28.525′ N 13° 34.360′ O	Baabe 54° 21.759′ N 13° 42.954′ O	Karlshagen 54° 08.256′ N 13° 49.683′ O	Zempin 54° 04.172′ N 13° 58.035′ O
Clay (%)	0.9	0.7	0.7	0.1	0.6
Silt (%)	2.6	2.7	1.3	2.9	3.0
Fine sand (%)	12.8	2.5	22.6	89.2	16.7
Medium sand (%)	83.2[a]	89.0[a]	75.0[b]	7.8[c]	79.7[b]
Coarse sand (%)	0.5	5.2	0.3	0	0
pH (H_2O)	7.17	7.22	7.29	7.53	7.05
Electrical conductivity (μS cm^{-1})	41.5	32.5	21.0	17.0	15.5
$CaCO_3$ (%)	11.1	5.6	1.5	0.8	0.7
TC (g kg^{-1})	10.79	5.42	2.25	0.67	0.79
TN (g kg^{-1})	0.13	0.14	0.21	0.13	0.09
TP (g kg^{-1})	0.31	0.23	0.11	0.09	0.16
PO_4^{3-} (mg kg^{-1})	0.64	3.04	2.76	5.18	4.32
PO_4^{3-}-P (% TP)	0.067	0.432	0.820	1.881	0.882

TC total carbon, *TN* total nitrogen, *TP* total phosphorus, PO_4^{3-} bioavailable phosphorus, PO_4^{3-} *-P* calculated solubility of TP

[a] Soil texture class: medium sand

[b] Soil texture class: fine sandy medium sand

[c] Soil texture class: fine sand

(0.09 g kg^{-1}), and that from Glowe had the highest TP content (0.31 g kg^{-1}). In contrast, the PO_4^{3-} concentration and the calculated solubility of TP (PO_4^{3-}-P as percentage of TP) were largest in Karlshagen (5.18 mg $PO_4^{3-}kg^{-1}$=1.881 % of TP) and smallest in Glowe (0.64 mg $PO_4^{3-}kg^{-1}$=0.067 % of TP). The TP content and its solubility were similar in Baabe and Zempin, and the soil sample from Prora showed more TP than the latter two samples; however, a smaller portion of this was soluble as PO_4^{3-} (Table 3).

Species Composition and Soil Properties

The species compositions of cyanobacteria and non-diatom algae in ten dune BSCs as well as the relationship of these species compositions with the soil properties from the five dune study sites were analyzed with an RDA. The RDA separated all dune study sites from each other and indicated a significant correlation between the species composition of the BSCs and the TP in the soil ($p<0.026$) in our data set (Fig. 5). On the first axis, which explains approximately 51 % of the variance within the species composition of the sites, Karlshagen, Zempin, and Baabe are on the left side of the RDA plot closer to each other compared to Prora and Glowe on the right side of the plot (Fig. 5). This arrangement of Baabe, Karlshagen, and Zempin as one group and Glowe and Prora as a second group was found to be statistically significant ($p<0.018$). The direction of the arrows in the plot indicates at which study site the parameter has a greater influence. Except TP, all other analyzed factors showed no significant correlation with the species composition of BSCs from the dune study sites ($p>0.346$) in our data set (Fig. 5). However, the soil parameters electrical conductivity, carbonate content, and particle size distribution are also arranged along the first axis, indicating that they might have an influence on the species composition of the BSCs as well, but exhibited no statistical significance in the presented data set. Total carbon (TC) is also arranged along the first axis in the RDA plot but was not considered for the interpretation, because it is strongly co-correlated with the carbonate content at the study sites (R^2=0.993).

Discussion

Species Composition and Dominant Species

BSCs can host a variety of many different species. Several studies on cyanobacterial and algal composition of BSCs in different ecosystems revealed a diversity of cyanobacteria and algae ranging from just a few up to over one hundred species [42–44]. Overall, in the present study, 125 cyanobacteria and algae were identified in association with BSCs of dunes from the Baltic Sea coast. Compared to former studies on BSCs in coastal dunes, which described 1 to 11 cyanobacterial and algal species, our study showed a remarkable high diversity of cyanobacteria and algae [23, 25]. Studies on BSCs in drier

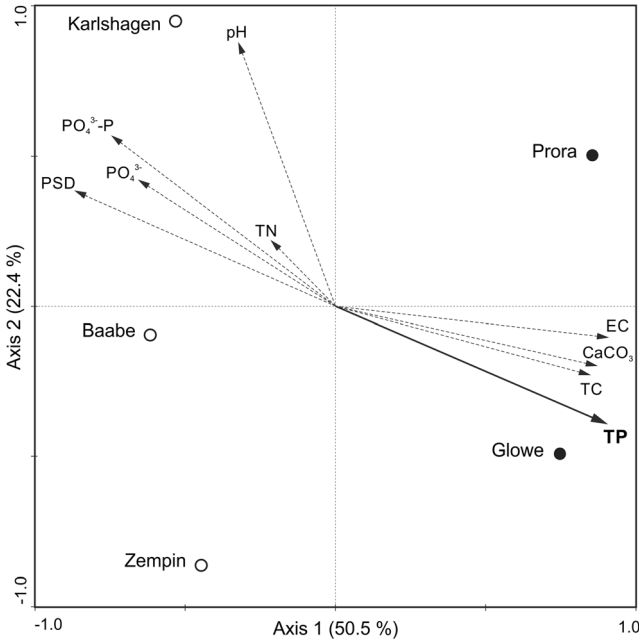

Fig. 5 RDA based on the cyanobacterial and non-diatom algal species composition of ten BSCs (mean of two BSCs for each study site) and the soil properties from five coastal dune study sites on Rügen and Usedom. Study sites with *open circles* represent one group which is statistically significant different from another group build of study sites with *filled circles* ($p<0.018$). Soil properties without statistical significance are shown with *dotted arrows* ($p>0.346$), and those with statistical significance with *bold arrows* ($p<0.026$). Percentage at the axis indicates the variance within the species data explained by each axis for the distribution of the study sites in the plot. *TP* total phosphorus, PO_4^{3-} bioavailable phosphorus, PO_4^{3-}-*P* calculated solubility of TP, *TN* total nitrogen, *TC* total carbon, $CaCO_3$ calcium carbonate, *PSD* particle size distribution, *EC* electrical conductivity

regions, for instance, of Mexico [17], South Africa [21], and Central Europe [45] indicated 66, 88, and 45 cyanobacterial and algal species, respectively. Hence, our recorded species number is more comparable with investigations made in other environments than coastal dunes.

BSCs of dunes of the Baltic Sea in the present study contained a common suite of species, with abundant non-diatom algae and cyanobacteria, as well as diverse diatom floras. Although cyanobacteria are often most abundant in BSCs [16, 21], the investigated dune BSCs showed higher numbers of non-diatom algae compared to cyanobacteria. However, former studies on BSCs also identified more algae than cyanobacteria [17, 42, 44]. Hence, the high non-diatom algal diversity found in the present study is in agreement with other investigations.

Nevertheless, it could be possible that the number of cyanobacterial and algal species was still underestimated. Previous studies showed that a combination of several independent techniques is necessary for a comprehensive evaluation of the species diversity in BSCs, because algae are often underestimated with direct determination, while cyanobacteria are difficult to detect with a culture approach [e.g., 45, 46]. In the present study, three dominant cyanobacteria (*Coleofasciculus* sp., *Lyngbya* sp. and *Hydrocoryne* sp.), as detected by direct microscopy, were only rarely found in the enrichment cultures and could not be cultivated. To overcome these problems, many researchers started to combine the morphological identification of species with molecular analyses [21, 25]. But, even the molecular techniques still sometimes fail to detect some cyanobacteria and algae [47, 48].

In contrast to cyanobacteria and non-diatom algae, diatom species are typically identified with the help of specific diatom slides [49]. With 55 species, the diatom flora of the investigated BSCs was surprisingly high, compared to most other biodiversity studies on BSCs, where the number of diatom species often varied between no and up to ten species [17, 23, 50]. Nevertheless, studies on BSCs in the 1980s in xeric habitats of North America also revealed with 20 and 24 taxa considerable diatom richness and a widespread distribution of diatoms in soils [16, 51]. In these studies, specific diatom slides were prepared for their identification, a quality approach which seems to be neglected in current investigations. Whether all the recorded diatom species in the present study represent, indeed, components of BSCs remains an open question. Diatoms and other microalgae are known to be air-transported over hundreds of kilometers [52]. Especially near beaches, marine and brackish water diatoms can be wind-blown during stormy conditions [53]. Hence, it could not be excluded that some of the diatom species found were wind (sea-spray) or wave transported and hence only temporary guests in the coastal dune BSCs.

The community structure of BSCs at the sampling date is normally characterized by the organisms, which are identified directly in soil crust material [45]. In most cases, filamentous soil cyanobacteria and algae dominate BSCs, because they play a major role in the development of these micro-systems [49]. Consequently, it is not surprising that most of the investigated dune BSCs were dominated by filamentous cyanobacterial and algal species. The most important cyanobacterial genera for the soil crust formation in the Baltic Sea dunes were *Coleofasciculus*, *Lyngbya*, *Microcoleus*, *Nostoc*, *Hydrocoryne*, and *Leptolyngbya*. Filamentous algae of the genus *Klebsormidium* were essential as well. In addition, one unicellular algal species of the genus *Lobochlamys* showed dominance in one of these dune BSCs. All the dominant filamentous cyanobacterial and algal genera present in the investigated BSCs of coastal dunes are most common and widespread genera with a broad ecological amplitude, which frequently occur in terrestrial habitats of dry regions (for comparison, see [15]).

Influence of Abiotic Parameters on Species Composition

BSCs develop through the interaction of cyanobacterial and algal filaments and sheaths with soil particles. The considerable physiochemical heterogeneity of soils results in a number of specific microenvironments, which might have effects on the species composition of newly developing soil crusts. In this first investigation of BSCs of coastal dunes, a statistically significant influence of the total phosphorus (TP) concentration in the sand on the species composition of cyanobacteria and algae at the study sites ($p<0.026$) was found (Fig. 5).

Phosphorus (P) is one of the essential elements for growth of phototropic organisms but in most cases not easily bioavailable for organisms because it is bound in unweathered minerals [54]. The addition of easily soluble P (NaH_2PO_4 + Na_2HPO_4) to developing BSCs in virgin soils at newly deglaciated areas of the high Andes, Peru, allowed the phototrophs to grow sooner and faster, and to reach a higher percentage areal cover than treatments just receiving nitrogen (N) or the control [55]. Thus, there is strong evidence that P limitation may be an important factor controlling initiation and development of BSCs in such areas [55]. These and our finding could be a hint to consider P as a factor that influences the establishment and species composition of cyanobacteria and algae of BSCs in coastal dunes. However, future studies are necessary to test this hypothesis, because it cannot be proven with the available data only.

Furthermore, it seems unlikely that a single environmental factor is responsible for the differences in BSC community structures. Except the amount of TP in the sand, no other tested factor showed a statistically significant correlation with the species composition in the present study ($p>0.392$). This might be due to the small number of samples and analyzed environmental factors as well as to the lack of replicates. However, electrical conductivity, carbonate content, and particle size distribution were also arranged along the first axis in the RDA plot (Fig. 5) indicating that these factors might have an influence on the composition of cyanobacteria and algae of BSCs as well. Electrical conductivity and carbonate content have been shown previously to influence the species composition of BSCs [56]. In addition, an influence of soil texture on the development and composition of BSCs has also been reported, and some authors even hypothesize that soils with higher silt and clay content promote the succession and species richness of BSCs [21, 56]. This can of course not been tested in coastal dunes, as they are wind- and wave-driven deposits of sand with only minimal proportion of silt and clay. However, the investigated dunes differed in their sand subfractions as well as in the presence of cyanobacteria. BSCs of dunes consisting of finer sand material showed a higher diversity of cyanobacteria with many Nostocales species. In contrast, BSCs developed on coarser sand were dominated by large and highly mobile cyanobacteria (*Coleofasciculus* sp. and *Microcoleus vaginatus*). Belnap and coauthors [5, 13] noted that less stable sediments and very sandy soils (>90 %) are generally dominated by cyanobacteria. In contrast to this general statement, in the present study, BSCs were also dominated by algae or a combination of both. Other studies also identified filamentous algae as dominant species in BSCs on sandy substrates, including coastal dunes [9, 25, 57].

Almost all studies on BSCs where a dominance of algae was recorded were conducted in the temperate zone [9, 18, 23, 45]. As Büdel [15] summarized, BSCs with a dominance of algae appear to be limited to soils in temperate regions. Nevertheless, this statement is only valid concerning the dominance of algae. Although algae are not dominant in dry regions, they are successful colonizers of BSCs as they are present in high species numbers [21, 42].

In conclusion, BSCs of dunes of the Baltic Sea coast represent an ecologically important and abundant, but so far unstudied, vegetation form. The high biodiversity of cyanobacteria and algae, particularly diatoms, as BSC components was surprising. The diverse diatom flora found in dune BSCs emphasizes the use of specific diatom slides, an easy method for a comprehensive recording of the diatom richness in future studies. From all the tested physicochemical parameters, only TP could be identified as factor shaping site-specific species composition of cyanobacteria and algae. But, there is additional evidence that electrical conductivity, carbonate content, and soil texture might influence the coastal dune BSCs as well. More in-depth investigations are needed for a better understanding of crust composition and development in coastal dunes and the role of TP in these processes. Therefore, a wide set of BSC samples as well as environmental factors should be analyzed especially to prove the influence of the TP and other soil parameters.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

Ethical Approval This article does not contain any studies with human participants or animals performed by any of the authors.

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