Structure and function of biological soil crusts along sand dune chronosequences

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Vorgelegt von

Sandra Kammann, M.Sc. Biodiversität

geboren in Mülheim an der Ruhr

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Thesis Reviewer

Prof. Dr. Ulf Karsten
Institute of Biological Sciences
Chair of Applied Ecology & Phycology
University of Rostock

Prof. Dr. Michael Bonkowski
Institute of Zoology
Department of Terrestrial Ecology
University of Cologne

Prof. Dr. Bettina Weber
Institute of Biological Sciences
Functional Diversity and Ecology
University of Graz

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Supervisor

Prof. Dr. Ulf Karsten

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BALTIC TRANSCOAST

'It is not the strongest species that survives, nor the most intelligent,
but the one that responds best to change.'

- Charles Robert Darwin

Table of Contents

List of figures for Chapters 1 & 2 ..... **I**

Abbreviations ..... **III**

Abstract ..... **V**

Zusammenfassung ..... **VII**

1 General Introduction **1**

1.1 Coastal formation at the Baltic Sea 1

1.1.1 Genesis of coastal areas in the Holocene 1

1.1.2 Genesis of coastal sand dunes 3

1.2 Living on a dune surface: Microbial pioneers in an extreme habitat 7

1.2.1 The successional development of the biocrust community 8

1.3 Phosphorus balance within ecosystems 12

1.3.1 Influences of biocrust microorganisms on the phosphorus cycle in sand dune ecosystems 12

1.3.2 Short insights into the sequential P fractionation 14

1.4 Goals of the Thesis and Hypotheses 15

1.5 Study sites 17

2 Synoptic discussion **20**

2.1 Synopsis of the species diversity and community composition of biocrusts in temperate sand dunes, and their succession 20

2.1.1 The dominating biocrust types along the dune successional gradients 20

2.1.2 Insights into the species diversity and community composition of microalgal and macrophytic cryptograms 24

2.1.3 Interim Conclusion on species diversity and community composition in biocrust from dunes 31

2.2 Synopsis of biocrustˈs functional traits and resulting ecosystem services 33

2.2.1 Early successional biocrusts 33

2.2.2 Mature successional biocrusts 35

2.3 Synopsis of soil formation on temperate sand dunes 36

2.4 Synopsis of P-cycling and transformation processes 39

2.5 General conclusions 42

2.6 Future perspectives and considerations 43

References for Chapters 1&2 ..... **44**

3 Publications **69**

3.1 Publication I 69

3.2 Publication II 101
3.3 Publication III 119
3.4 Publication IV 149
4 Appendices 187
4.1 Declaration of own contribution to the publications 187
4.2 Danksagung 189
4.3 Selbstständigkeitserklärung 191

List of figures for Chapters 1 & 2

Figure 1: (A) Erosive processes on an active cliff, sediment transport, and accumulation lead to the development of a sand hook on an equilibrium coast. (B) Image of a recent spit formed from a sand hook at Darsser Ort. 2

Figure 2: Scheme showing the trend of the successional development of the vascular vegetation along an ideal dune chronosequence. 4

Figure 3: Early successional biocrust types, dominated by microalgae and cyanobacteria on two sand dunes along the Baltic Sea coast. 7

Figure 4: Schematic diagram showing the successional development of biocrusts. 9

Figure 5: (A) Overview of the locations of the sampling sites. (B) A close-up of the peninsula Fischland-Darss-Zingst with the sampling sites Darsser Ort and Pramort, and the island of Rügen with the sampling site Schaabe. 17

Figure 6: Overview of all sampling plots investigated during field sampling campaigns. The white frame defines an area of 1 m^2. Light yellow labels indicate primary, bright yellow secondary, and brownish mature dune types. 18

Figure 7: Schematic representation of the workflow to attain an insight into the species diversity and community composition of biological soil crusts growing on the dune surfaces and subsequent sediment/soil core analyses. 19

Figure 8: Scheme showing the trend of the successional development of the biocrusts types along an ideal dune chronosequence. 21

Figure 9: Scanning electron microscopy pictures showing a diatom (*Pinnularia* spec.) attached to a sand gain. 26

Figure 10: Representatives of the genus *Nostoc*. A=*N*. cf. *linckia*, B=*N*. cf. *edaphicum*, C=*N*. cf. *commune* found in biocrusts of coastal and inland sand dunes. Red frame highlighting *N.* cf. *commune* cells. .. 28

Figure 11: P pools (as determined by sequential P fractionation) as a percentage of total P in early and mature biological soil crust types..... 40

Figure 12: Graphic illustrating the service provided by a biocrust to the dune ecosystem. 42

Abbreviations

ADP	Adenosindiphosphat
Al	Aluminum
Al^{3+}	Threefold positive charged Aluminum Ion
ASV	Amplicon Sequence Variant
ATP	Adenosintriphosphat
BNF	Biological Nitrogen Fixation
BP	Before Present
C	Carbon
CO_2	Carbon Dioxide
C_t	Total Carbon
Ca	Calcium
$CaCO_3$	Calcium Carbonate
Chl	Chlorophyll
DNA	Deoxyribonucleic Acid
DW	Dry Weight
EPM	Extracellular Polymeric Matrix
EPS	Extracellular Polysaccharides
Fe	Iron
Fe_t	Total Iron
Fe_{ox}	Oxalate Extracted Iron
Fe_{dit}	Dithionite-Citrate-Bicarbonate Extracted Iron
FW	Fresh Weight
H^+	Hydrogen Ion
H_2O	Water
H_2CO_3	Carbonic Acid
H_2SO_4	Sulfuric Acid
HPO_4^{2-}	Hydrogen Phosphate
$H_2PO_4^-$	Dihydrogen Phosphate
H_3PO_4	Orthophosphoric Acid
HTS	High-Throughput Sequencing
MAA	Mycosporine-like Amino Acids

N	Nitrogen
N_t	Total Nitrogen
$NaHCO_3$	Sodium Bicarbonate
NaOH	Sodium Hydroxide
NH_3	Ammonia
NH_4^+	Ammonium
NO_x	Nitrogen Oxides
NO_3^-	Nitrate
NGS	Next-Generation Sequencing
O	Oxygen
OH	Hydroxyl Group
P	Phosphorus
P_i	Inorganic Phosphorus
P_o	Organic Phosphorus
P_t	Total Phosphorus
PO_4^{3-}	Orthophosphate
rRNA	Ribosomal Ribonucleic Acid
SO_4^{2-}	Sulfate
UV	Ultraviolet

Abstract

Biological soil crusts (biocrusts) are cryptogamic communities forming complex biotic networks on the uppermost millimeters of the Earth's surface (12% coverage) where vascular vegetation is rare. 30% of these covered areas are dryland soils. Environmental factors and biotic interactions shape the community structure within the biocrust, which is characteristic of a particular type of biocrust. This community structure is constantly changing with its successive development. Biocrusts interact with their surrounding habitat, impacting ecosystem processes e.g., nutrient enrichment and soil stabilization. Thus, the diverse community has a broad influence on the functionality of its habitat. How these functions differ between the various biocrust types has been poorly studied, especially in temperate regions. Therefore, systematic studies are needed to understand how the biocrust community changes with succession in the first place. Aiming to close this knowledge gap and concluding possible applications of these results, the field studies of this thesis investigate the successional development of biocrust communities and the respective shifts in the phototrophic community structure along dune chronosequences of the German Baltic Sea coast and an inland dune area in Northern Germany. The changes in the biocrust community structure are closely related to the biotic and abiotic conditions in its environment. An in-depth pedological study should reveal the factors that shape community development. Additionally, the study investigates the interactions that the biocrusts have with the surrounding matrix and how they actively influence it (e.g., initial soil formation processes). The pedological investigation also includes a detailed soil-chemical study of phosphorus (P) within the differing successional biocrust types. It highlights how the organism community can potentially influence P pools, representing P forms of different bioavailability to the (micro)organisms.

The study results revealed that thin microalgae and cyanobacteria-dominated biocrusts were the dominating biocrust type on younger dunes, which are well adapted to this nutrient-poor and mobile habitat. On older and more stabilized dunes, macrophytic cryptogams i.e., mosses and lichens, formed the dominating biocrust types covering the majority of the dune surface. This development was linked to an increase in the organic biomass on the dune surfaces along the chronosequences (**Publication I** and **III**). The initial input of organic biomass into the dune environment allows for the further development of soil. Observed soil-forming processes along the dune chronosequences were decalcification, acidification, nutrient enrichment, and the accumulation of pedogenic iron oxides confirming parent material transformation through mineral weathering. As a result, the initial formation of soil horizons along the chronosequences was observed (**Publication III**). These transforming processes include shifts in the P pools. The overall total P content within the biocrusts increased along the chronosequences. Thereby, the relative proportion of the easily bioavailable P pool rose at the expense of more stable bound P, which was transformed into labile P.

This thesis provides an interdisciplinary approach between terrestrial ecology and soil science, and hence a fundamental baseline for a deeper understanding of the biodiversity and functions of the biocrust communities along with dune succession in a temperate environment. The findings offer new insights into the community structure of microalgae-dominated biocrusts and their shifts into a macrophytic cryptogamic community. In conclusion, temperate coastal sand dunes seem to be unique habitats for biocrust colonization forming productive microecosystems that hold the potential to actively influence the physicochemical and biotic conditions of their surrounding environment. On a larger scale, biocrusts' key functions offer opportunities for application-oriented use, for example in dune stabilization, restoration, and coastal protection.

Zusammenfassung

Biologische Bodenkrusten (Biokrusten) sind kryptogame Gemeinschaften, die komplexe biotische Netzwerke auf der Erdoberfläche bilden, wo Gefäßpflanzen selten sind. Umweltfaktoren und biotische Wechselwirkungen prägen die Gemeinschaftsstruktur, die für einen bestimmten Biokrustentyp charakteristisch ist. Diese Gemeinschaftsstruktur verändert sich mit ihrer sukzessiven Entwicklung. Biokrusten stehen in Wechselwirkung mit dem sie umgebenden Lebensraum und beeinflussen dadurch Ökosystemprozesse, wie z. B. die Anreicherung von Nährstoffen und die Stabilisierung des Bodens. Somit hat die vielfältige Gemeinschaft einen großen Einfluss auf die Funktionalität ihres Lebensraums. Wie sich diese Funktionen zwischen den verschiedenen Biokrustentypen unterscheiden, ist bisher wenig untersucht worden, insbesondere in gemäßigten Klimazonen. Daher sind Studien erforderlich, um zu verstehen, wie sich die Biokruste im Zuge ihrer Sukzession verändert. Mit dem Ziel, diese Wissenslücke zu schließen und mögliche Anwendungen dieser Ergebnisse abzuleiten, untersuchen die Feldstudien dieser Dissertation die Sukzessionsentwicklung von Biokrusten-Gemeinschaften und die entsprechenden Veränderungen in der phototrophen Gemeinschaftsstruktur entlang von Dünenchronosequenzen an der deutschen Ostseeküste und einem Binnendünengebiet in Norddeutschland. Eine eingehende bodenkundliche Untersuchung soll die Faktoren aufzeigen, die die Entwicklung der Gemeinschaft prägen und darüber hinaus die Wechselwirkungen beleuchten, welche die Biokruste mit der sie umgebenden Matrix hat und womit sie diese aktiv beeinflusst (z. B. anfängliche Bodenbildungsprozesse). Die bodenkundliche Untersuchung umfasst auch eine detaillierte bodenchemische Untersuchung von Phosphor (P) innerhalb der verschiedenen Biokrustentypen und zeigt auf, wie die Organismengemeinschaft potenziell P-Pools beeinflussen kann, in denen P-Formen mit unterschiedlicher Bioverfügbarkeit für die (Mikro-)Organismen zusammengefasst sind.

Die Ergebnisse der Studie zeigen, dass dünne, von Mikroalgen und Cyanobakterien dominierte Biokrusten die vorherrschenden Biokrustentypen auf jüngeren Dünen sind, die an diesen nährstoffarmen und mobilen Lebensraum gut angepasst sind. Auf älteren und stabileren Dünen bilden makrophytische Kryptogamen, d. h. Moose und Flechten, die vorherrschenden Biokrustentypen. Diese Entwicklung ist mit einer Zunahme der organischen Biomasse auf den Dünenoberflächen entlang der Chronosequenzen verbunden (**Publikation I** und **III**). Der anfängliche Eintrag von organischer Biomasse in die Dünenumgebung ermöglicht die weitere Bodenentwicklung. Zu den beobachteten bodenbildenden Prozessen gehören Entkalkung, Versauerung, Nährstoffanreicherung und die Zunahme an pedogenen Eisenoxiden, die die Umwandlung des Ausgangsmaterials durch Mineralverwitterung bestätigen. Infolgedessen konnte die anfängliche Bildung von Bodenhorizonten beobachtet werden (**Publikation III**). Diese Umwandlungsprozesse beinhalten auch Verschiebungen in den P-Pools. Der Gesamt-P-Gehalt innerhalb der Biokrusten nimmt entlang der Chronosequenzen zu. Dabei steigt der relative Anteil des leicht bioverfügbaren P-Pools auf Kosten des stabileren gebundenen P, der in labilen P umgewandelt wird.

Diese interdisziplinäre Arbeit, zwischen terrestrischer Ökologie und Bodenkunde, liefert eine grundlegende Basis für ein tieferes Verständnis der Artenvielfalt und Funktionen der Biokrustengemeinschaften im Zusammenhang mit der Dünensukzession in gemäßigten Klimazonen. Die Ergebnisse bieten neue Einblicke in die Entwicklung von Mikroalgen dominierten Biokrusten und deren Übergang zu einer durch makrophytische Kryptogamen dominierten Gemeinschaft. Biokrusten sind produktive Mikroökosysteme und haben das Potenzial die physikalisch-chemischen und biotischen Bedingungen ihrer Umgebung aktiv zu beeinflussen. Die ökologischen Funktionen der Biokrusten bieten zudem die Möglichkeiten für eine anwendungsorientierte Nutzung, z. B. bei der Dünenstabilisierung und dem Küstenschutz.

1 General Introduction

1.1 Coastal formation at the Baltic Sea

From a geochronological viewpoint, the Baltic Sea is still fairly young. Decisive for the geomorphology of the coastline were the repeated advances of glacier ice from Scandinavia to the Central German Uplands during the Weichselian glaciation. These glacier movements led to a deep excavation of the Baltic Sea basin and transported clastic sediment material (Hoffmann, 2002). The Weichselian glaciation was the youngest glaciation period in the Pleistocene and ended approximately 11,590 years BP (Niedermeyer and Janke, 2011). With its end, the Pleistocene was taken over by the Holocene. The melting of the ice shields was the starting point of the Baltic Sea's changing history, with its fresh and saltwater phases. The Baltic Sea subsequently underwent strong fluctuations in the water level. Therefore, saltwater intrusions from the North Sea interrupted freshwater periods. The last time this happened on a large scale was about 8,000 years ago, during the Littorina transgression when marine waters entered the Baltic Sea via the Danish Straits. This event formed the brackish water-dominated Baltic Sea as we know it today (Janke and Lampe, 2000; Lampe, 2002a; Lemke, 1998).

1.1.1 Genesis of coastal areas in the Holocene

The glacial processes during the Pleistocene and the postglacial sea-level fluctuations critically impacted the erosion and accumulation processes of the Baltic Sea coastline (Lampe, 2005; Niedermeyer et al., 2011). These processes led to smoothing of the former irregular and hilly coastline into a more graded shape. This so-called coastal equilibration began thousands of years ago and continues to form graded shorelines until today (Coastal type: Equilibrium coast) (Lampe et al., 2011a). Various factors e.g., the relief and the sediment supply, influence the coastal equilibrium and determine its orientation and regime, both temporally and spatially (Müller et al., 2023). The redeposition of sediments is a key process here (Hoffmann, 2002). Erosion of the cliffs of the Pleistocene headland provides a constant supply of unconsolidated sediments. This gets transported by wind, currents parallel to the coast, and waves before it accumulates again in calmer areas along the coastline. Mostly sands get transported and sedimented along the nearshore areas (Lampe et al., 2011b; Tiepolt and Schumacher, 1999), resulting in a redeposition of sediments and a reworking of the coastal morphology. This creates elongated, partly curved sand hooks. Over time, these sand hooks grow in area and first beach ridges and dunes form on them. When several beach ridges joined, they built a system of almost parallel ridges (German = Reffe), resulting in a growing spit along with the sediment transport (Figure 1). Between the ridges, there are wet depressions (German = Riegen). These are former beach lakes. Growing spits can connect Pleistocene island cores. Thereby, smaller coastal water bodies are separated from the open Baltic Sea into smaller lagoon systems called 'Bodden' or 'Haff' in German, which are prominent, especially along the Mecklenburg-Western Pomeranian coast (Jurasinski and Buczko, 2023; Kliewe and Janke, 1991; Müller et al., 2023).

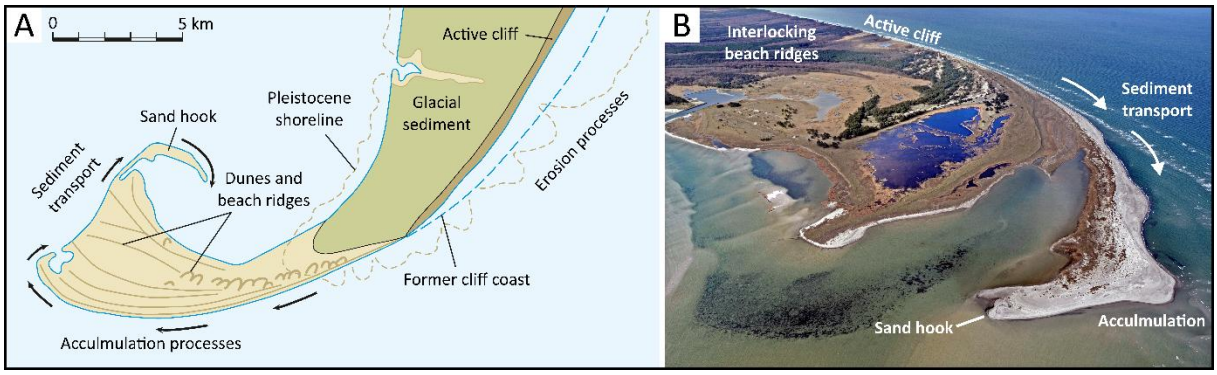


Figure 1: (A) Erosive processes on an active cliff, sediment transport, and accumulation lead to the development of a sand hook on an equilibrium coast (Graphic: Bird (2008), adapted after Dikau et al. (2019) © 2008 John Wiley & Sons Ltd). (B) Image of a recent spit formed from a sand hook at Darsser Ort (Aerial image from 2014: © Rolf Reinicke; www.kuestenbilder.de).

These transformation processes along the Baltic Sea coastline led to the formation of today's Bodden equilibrium coast which is the prevailing coastal form e.g., on the seaward side of the Fischland-Darss-Zingst peninsula and the island of Rügen, Mecklenburg-Western Pomerania (Niedermeyer and Schumacher, 2004). Sand hooks and spits are geomorphological characteristics and typical accumulation zones along an equilibrium coast (Lampe et al., 2011b). In the shallow water zones at the tip of the sand hooks, extensive sand accumulation areas can continue with sand transport parallel to the coast. Depending on the wind strength and its direction these areas get flooded or can fall dry (Eisma, 1998; Karsten et al., 2012). They are referred to as wind flats (German = Windwatt). In front of the eastern end of the Fischland-Darss-Zingst peninsula, a ~160 ha windflat is located, which is unique in Germany. The flooding situation of the area is highly variable over time and depends not only on the wind direction but also on the water level of the Baltic Sea (Niedermeyer et al., 2011).

Morphological coastal forms and dynamics along a Bodden equilibrium coast

Two coastal forms, the accumulation and abrasion coasts, alternate along an equilibrium coast. The material budged on an abrasion coast is negative. Active cliffs are characteristic for the abrasion coasts. The material eroded gets drifted and redeposited in shallower sections, the accumulation coasts. This is how initial beach ridges, sand hooks, and spit systems are formed over time and the coastline gets graded. It is a cyclic process, controlled by sea-level fluctuations and sediment supply (Ballantyne, 2002; Niedermeyer et al., 2011). A model of coastal formation by Kliewe and Janke (1991) describes this process for a Bodden equilibrium coast. In an initial phase, the sediments eroded during the Holocene get deposited next to Pleistocene island cores. In the following growth stage, the former submerged sediment accumulation zones rise above the water surface. With this, the coastline increases significantly until a mature stadium is reached. Sedimentation and erosion are in an equilibrium stage at this point. Storms and subsequent floodings cause renewed erosion and the beginning of the degradation phase.

1.1.2 Genesis of coastal sand dunes

As part of the coastal development, aeolian-driven sand accumulation leads to a further sand dune genesis on the initial beach ridges. This is particularly the case on flat coasts with a positive material budget (Niedermeyer et al., 2011). Dunes are located in the transitional zone between marine and terrestrial environments, which is a sand-sharing system of high material mobility. The size and shape of a sand dune depend greatly on sediment supply and the local wind regime. While on the beach the dunes constantly change, the dunes inland become increasingly stable (Martínez et al., 2004). Dunes along the Southern Baltic Sea coast belong to the 'temperate zone coastal dunes'. This implies a climate where they experience neither wide extremes of temperature nor low levels of precipitation (Wiedemann and Pickart, 2004). A prevailing onshore wind, a continuous sand supply, and obstacles that weaken the wind force in the lee of the obstacle are necessary to accumulate the mobile sand and form sand deposits (Maun, 2009a; Pott and Hüppe, 2007). These natural obstacles along the Baltic coast include, in particular, halophilic vegetation such as rush quackgrass (*Elymus farctus* (Viv.) Runemark ex Melderis) or lyme grass (*Leymus arenarius* (L.) Hochst.). With increasing sand accumulation small foredunes (primary dunes) form on the beach and mark the starting point of a potential further successional development of a dune system. Rain events cause the desalinization of the primary dunes. This reduces the salt content in the sediment and allows less salt-tolerant vegetation to colonize e.g., marram grass stands (*Ammophila arenaria* (L.) Link). The succession of vegetation indicates the development of secondary dunes (yellow dunes). At this point, the dunes are still within reach of the ocean water if strong storm flood events occur. Sand gets transported by wind between the individual dunes, filling the areas in between and thus creating a closed dune wall, where sand can accumulate on the lee side. With further sand deposition on the beach, the beach line moves towards the sea, while the secondary dunes move further inland. They are no longer exposed to salt spray or flooded by seawater, even during storm flood events. The dunes can be completely desalinized by rainwater and larger amounts of sand are no longer deposited here. The dune system has now reached the tertiary dune stage. The vascular plant community growing in this dune stage does not tolerate a larger covering with sand. Leaf litter and other dead plant material lead to an increasing formation of an initial humus layer and early soil formation. This humous soil gives the dunes their characteristic color, which is why they are called grey dunes. Without disturbance, a dry grassland interspersed with grey hair-grass (*Corynephorus canescens* (L.) P.Beauv.) can develop on the grey dunes in the course of succession. Birch and pine trees can form dune forests and mark the transition from the grey dune to the mature dune (synonym: brown dunes, Isermann, 2011). Grey and mature dunes with their shrubs and dune forests characterize the tertiary dune system (Pott and Hüppe, 2007).

The above description is an idealized successional development of dune types and their characteristic vegetation (Figure 2). Such a successional sequence of dune types represents a chronological series. Those series allow studies at spatially distinct sites of varying ages that underwent identical abiotic factors and climatic conditions during succession (Salisbury, 1952; Stevens and Walker, 1970). A chronological series (chronosequence) of dunes provides the opportunity to reconstruct the long-term development of the ecosystem, the formation of soils, and the colonization by vegetation (Isermann, 2011; Pollmann et al., 2020; Ranwell, 1960; Walker et al., 2010). Along the Bodden equilibrium coasts of the Baltic Sea, the formation of such dune chronosequences can be observed. That makes this coastline a remarkable study area for the successional development of coastal sand dune habitats (Łabuz et al., 2018; Peyrat and Fichtner, 2011).

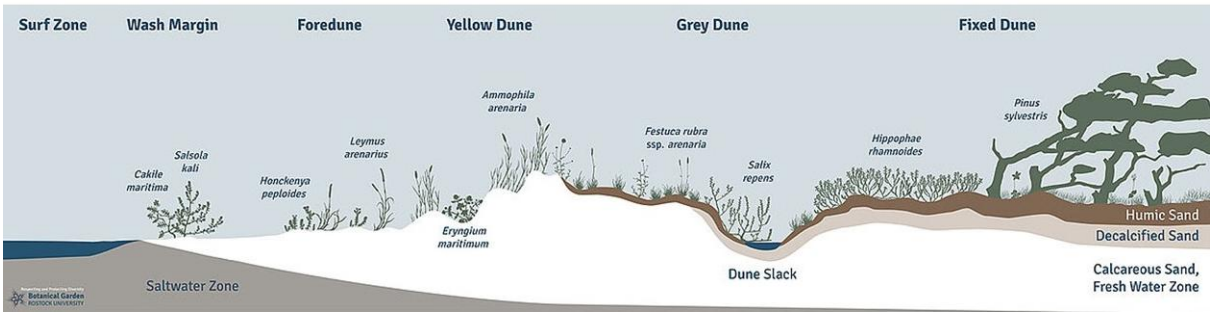


Figure 2: Scheme showing the trend of the successional development of the vascular vegetation along an ideal dune chronosequence.
Graphic: https://www.garten.uni-rostock.de/storages/uni-rostock/_processed_/4/9/csm_duene_2017_mod_engl_0b9532fc96.jpg; © Sarah Mamerow; 29.07.2024).

The sand dune environment

Depending on the individual environmental conditions, microhabitats can develop within each of these dune types. Factors such as moisture content, temperature, UV radiation, wind speed, and soil texture have a great impact on these microhabitats, and thus on the establishment of living communities on the dunes (Maun, 2009a). The soil moisture content is one of the most limiting factors for further colonization with vegetation. Sediments and sandy soils have a low water-holding capacity and therefore low water retention. Moreover, unvegetated and thus unshaded dune surfaces experience high evaporation (Lichter, 1998). The respective seasons and the associated rainfall intensity and frequency cause great variability in the soil moisture content (Oosting, 1954; Zunzunegui et al., 2022) and in the dune development, since wet sand grains are not easily transported by wind turbulences. Further, rain events have an impact on the dunes' salinity thus the water washes salt from the surface and leaches it out of the sediment (Maun, 2009a). The soil moisture content increases along a dune chronosequence, likely due to the accumulation of organic matter and humus formation in the upper soil horizon, as observed along a transect on sand dunes of Barbados (Gooding, 1947), at the Wilderness State Park, Lake Michigan, USA (Lichter, 1998), and on the island of Rügen, Baltic Sea (Hundt, 1985). Due to poor heat conduction of sand, the dune surface can reach up to 60°C during summer days. While the surface temperature increases, the temperature 5 cm below the surface declines quickly to about 30±4°C. The highest surface temperatures are expected at 2 p.m. and decrease overnight until the lowest value is expected at 6 a.m., referring to sand dunes in the Pinery Provincial Park, Ontario, Canada (Baldwin and Maun, 1983).
Macroelements such as nitrogen (N), phosphorus, and potassium occur only in very small quantities in the dune sediments. Atmospheric N gets transported into the sand dune ecosystem by N fixation and atmospheric deposition mainly caused by ammonia (NH_3) from agriculture and nitrogen oxides (NO_x) resulting from combustion processes (European Environment Agency, 2023). Wet N deposition (gaseous and particulate N compounds in the atmosphere transported to the Earth's surface by precipitation (rain or snow)) amounts to about 80% of the total deposition in Europe and can be determined with relatively high reliability. However, the additional dry N deposition is hard to quantify due to various N species in gases- and particle-phases and their input depending on wind exposure, precipitation, and vegetation form (Erisman et al., 2005; Remke et al., 2009; Zhang et al., 2021 and references therein). Once introduced into the ecosystem, N is fixed in plant material or dead organic matter, absorbed to soil particles, or dissolved in soil solution (Maun, 2009a). N can stay within a

closely linked ecosystem-internal cycle or get lost by leaching or denitrification (Ellenberg, 1977). For coastal dunes of the island Rügen (Southern Baltic Sea) Baumann et al. (2019) measured total N (N_t) values that varied around 0.2 g kg^{-1}. This is in range with data presented in **Publication III** where slightly higher N_t concentrations in mature dune areas (0.2-0.7 g kg^{-1}) in comparison to early dune successional stages (Ø 0.1 g kg^{-1}) were detected. If these values are compared with those of the topsoil of temperate forests, the N content in the forest is on average 10 times higher, regardless of the dominant tree species (Baumann et al., 2017). Further studies reported a general increase in the N_t content during dune development, e.g., at Lake Michigan, USA (Lichter, 1998) and on the island of Spiekeroog, Germany (Gerlach et al., 1994). The latter study dealing with dunes of temperate coastal regions reports a higher annual N turnover rate in the young dune sands (up to 18%) than in mature dunes (2%).

Besides N, phosphorus (P) (cf. Chapter 1.3) is an essential and at the same time a limiting nutrient in coastal dunes. In contrast to N, P is not available as an atmospheric gas. The inputs into the sand dune ecosystems come either from atmospheric wet or dry deposition (cf. Chapter 2.4 and Berthold et al., 2019), organic matter, or weathering of P-containing minerals such as apatite. P can be stored within the ecosystem-internal P cycle as it is absorbed by soil particles, immobilized within dead organic material or living biomass, or part of the soil solution (Filippelli, 2019). Baumann et al. (2019) determined total P (P_t) concentrations of dune top sediment layers ranging between 84-277 mg kg^{-1} for coastal dunes of the island of Rügen. These values are higher than those of the sediments measured in **Publication III** for early (27.4-62.2 mg kg^{-1}), and mature (48.7-61.5 mg kg^{-1}) dunes. The availability of P for plants depends strongly on the sandy dune sediment's pH (optimum pH is about 5.5 to 6.5) (Sims and Pierzynski, 2005). The calcium (Ca) phosphates are generally less soluble (= more stable) at high pH, while the aluminum (Al) and iron (Fe) phosphates are less soluble at low pH. Dissolved phosphates in the soil solution (e.g., dihydrogen phosphate $H_2PO_4^-$ and hydrogen phosphate HPO_4^{2-}) act as the source for further uptake of bioavailable P by plants and microorganisms (Kruse et al., 2015). The pH in the upper sediment layer of sand dunes decreases with dune development landwards (Averiss and Skene, 2001; Isermann, 1997). While primary dunes show a neutral to alkaline soil reaction, secondary dune sediments show an increasingly strong acidic soil reaction (Isermann, 2005; Pollmann et al., 2020). This development is caused by the respiration of soil microorganisms causing the formation of carbonic acid (H_2CO_3) and its dissociation to hydrogen carbonate and carbonate. Another mechanism is the production of organic acid anions by the vegetation, or processes within the nutrient cycles, such as the N cycle, where H^+ ions are released during nitrification (Pallant and Riha, 2009). Differences in pH can cause major changes in soil properties and the mobilization of elements. Further, the pH impacts chemical mineral weathering (for information on bioweathering cf. Chapter 1.2), thus influencing early soil horizon formation (Maun, 2009a; Schaaf et al., 2011).

Beach plains and early sand dunes are built by sand sediment and thus, do not contain much organic material. The first organic matter gets added and intermixed with the dune sediment by marine debris deposited at the beach. Those are mainly remains of marine vegetation (e.g., *Fucus vesiculosus* or *Zostera marina*) (Olsson-Seffer, 1909). After the establishment of plant communities on the dunes, organic material is also introduced into the dune sediment originating from plant debris, microbial biomass, and animal excrements and remains (Maun, 2009a). A study by Baldwin and Maun (1983) points to a decrease in the organic matter content with increasing sediment depth. Decomposition of the organic plant debris in the upper sediment layer over time leads to the formation of a humus accumulated top layer (Ampe and Langohr, 2003).

With the accumulation of organic matter, the soil-forming processes (transformation and translocation) and early pedogenesis in sand dunes start. The decomposition of plant debris/biomass causes the production of organic acid anions and a subsequent decrease in the dune sediment pH. Additionally, mineral transformation and rock weathering (physical, chemical, and biogenic) proceed. The release of carbonates, Fe and Al oxides, as well as the decalcification (calcite from e.g., marine mussel shells) of the sediment, is the result of these processes. The mobilization of Fe is of particular importance and is discussed in more detail in **Publication III** of this thesis. Fe is predominantly silicate-bound in primary minerals, for example, bound to quartz (SiO_2). As a result of initial weathering (in the presence of water), this silicate ligand is replaced by oxygen (-O) or a hydroxyl group (-OH), and Fe is then (hydro-)oxidically bound. This leads to the formation of hydrous Fe oxides and hydroxides. These oxides are initially amorphous and accumulate on surrounding soil particles such as sand grains, causing the 'brunification' of the soil (Amelung et al., 2018a; Gisi et al., 1997). Depending on their intensity and duration, the transformation and translocation lead to the formation of soil horizons according to the German classification system 'KA5' (Ad-hoc Arbeitsgruppe Boden, 2005). Those horizons can be litter-dominated in the topsoil (A(+h) horizon). Over the years weathered minerals and decomposed organic substances leach to lower sediment layers resulting in the formation of a subsoil horizon (B horizon) (Jansen et al., 2005; Maun, 2009a; Pollmann et al., 2018, 2020; Sauer et al., 2007).

1.2 Living on a dune surface: Microbial pioneers in an extreme habitat

Coastal dunes are a challenging habitat for potential colonization by cryptogams and vascular vegetation. Strong seasonal fluctuations in surface temperature, water limitation, nutrient scarcity, and wind turbulences create a habitat difficult to persist in (Martínez et al., 2004; Maun, 2009a). Nevertheless, in the early stages of dune succession, microbial pioneer communities in particular manage to conquer this habitat (Maun, 2009b; Vázquez, 2004). These communities form cryptogamic ground (topsoil) covers shaped by photoautotrophic (e.g., cyanobacteria, algae, lichens, and bryophytes) and heterotrophic (e.g., bacteria, fungi, and archaea) organisms forming communities called biological soil crusts (biocrusts, Figure 3) (Belnap et al., 2001). Biocrusts, also known as the 'living skin of the Earth' (Büdel, 2011), have been studied worldwide and gained increasing interest during the last few decades (Weber et al., 2016). In 2018, Rodriguez-Caballero et al. calculated that globally biocrusts cover a total area of 17.9 million km^2, corresponding to ~12% of the global terrestrial surface. The phototrophic and heterotrophic microorganisms in the biocrusts excrete extracellular polysaccharides (EPS) which bind themselves and the soil particles together forming a cohesive living layer on the sediment/soil surface (addition to the definition from Belnap et al. (2001) by Weber et al. (2022)). Thereby, they contribute to soil aggregation at the soil surface leading to a hardened surface structure that is no more than 1 cm thick. At the same time soil aggregation is probably the key ecosystem service a biocrust provides for its surrounding habitat since it is essential for soil stability (Felde et al., 2018; Fischer et al., 2010). Especially in highly dynamic ecosystems, like coastal sand dunes, this trait can enhance sediment resistance against (aeolian) erosion and reduce blowouts (Belnap and Büdel, 2016; Belnap and Gillette, 1998; van Ancker et al., 1985; Zhang et al., 2006). Aeolian erosion promotes the formation of atmospheric dust (IPCC, 2014). This dust may blow away over long distances, transporting organic matter and nutrients, which will impact productivity and reshape the biogeochemical cycles of their deposition area (Field et al., 2010; Okin et al., 2004; Pabortsava et al., 2017; Prospero et al., 2020). Other potential negative effects are the alternation of the optical properties of the atmosphere (Kok et al., 2018) and the transport of harmful pathogens (Field et al., 2010). Rodriguez-Caballero et al. (2022) estimated that biocrusts reduce global atmospheric dust emissions by ~60%, preventing the release of ~0.7 Pg dust per year. This review highlights the important ecosystem service of aeolian dust control by biocrusts and its positive effects on the climate, human health, biogeochemical cycling, and the functioning of the ecosystems.

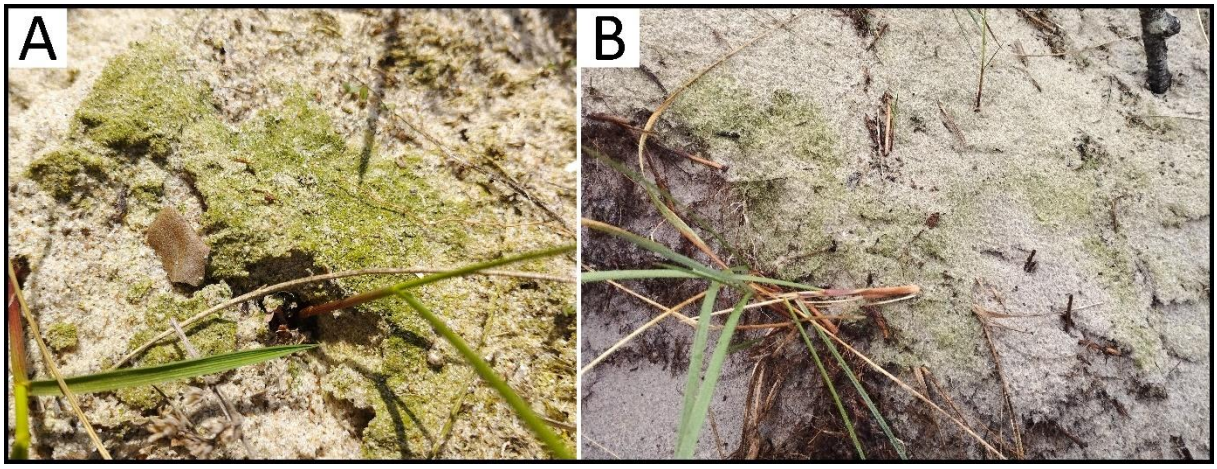


Figure 3: Early successional biocrust types, dominated by microalgae and cyanobacteria on two sand dunes along the Baltic Sea coast. Images: © S. Kammann.

Besides contributing to the stability of the soil, biocrusts actively mediate the biogeochemical cycle of the soil surface they grow on, due to processes of bioweathering performed by their cryptogamic community. These processes can either work mechanically or chemically. Lichens in the Atacama desert can penetrate the grit stones they grow beneath, via shrinking and swelling of the lichens' hyphae drilling them into the lithomatrix. Further processes such as alkalinolysis by the lichens' photobionts (like shown in endolithic cyanobacteria, Büdel et al., 2004), excretion and formation of acids, pH alternation, excretion of siderophores that chelate Fe-ions, and enzyme activities were observed supporting the bioweathering process. Wind can further cause the relocalization of the weathered rock material (Jung et al., 2020a; Weber et al., 2011). Additional ecosystem services provided by biocrusts are well-documented, like for example, their impact on local and regional water cycling (Chamizo et al., 2016; Eldridge et al., 2020; Kidron and Büdel, 2014). This topic is complex, as various factors e.g., biocrust type, soil texture, and climatic zone have an individual influence on soil hydrology (Chamizo et al., 2016; Fischer et al., 2012; Veste et al., 2011). Biocrusts significantly modify the water run-off infiltration balance since they provide a higher water-holding capacity than bare sand, thereby reducing water infiltration into the soil (Kidron and Büdel, 2014; Kidron and Yair, 2008). Moreover, biocrust organisms are involved in various essential element nutrient cycles, such as carbon (C) (Fischer and Veste, 2018; Sancho et al., 2016) and nitrogen (Barger et al., 2016; Castillo-Monroy et al., 2010). The impact of biocrust on the nitrogen cycle is well-studied in various ecosystems, while the metabolic processes within the phosphorus cycle (cf. Chapter 1.3.) are far less studied but have progressively received attention in recent years (Baumann et al., 2019; Kurth et al., 2020; Pushkareva et al., 2021; Xu et al., 2023).

The extent to which these services are pronounced in the respective ecosystem depends not least on the community attributes of the respective biocrusts, such as the number (richness), identity, and absolute abundance of species forming the community, which varies with climate, underlying soil, and disturbance (Belnap, 2006; Castillo-Monroy et al., 2011; Hooper et al., 2005). It is known that the composition of organisms forming biocrusts changes depending on (i) the developmental stage of biocrusts (Fischer et al., 2014; Fischer and Veste, 2018; Zaady et al., 2000), (ii) environmental factors like radiation, humidity, elevation, and temperature (prior references and: Eldridge and Greene, 1994; Fischer et al., 2012; Kidron and Büdel, 2014), and (iii) edaphic factors like soil pH, texture, and nutrient content (Belnap et al., 2001; Eldridge and Greene, 1994; Zaady et al., 2000). These factors taken together support the community formation of a specific biocrust type. Their external morphology and internal structures characterize these biocrust types, which are exposed to succession, due to environmental (biotic and abiotic) and edaphic factors.

1.2.1 The successional development of the biocrust community

Although the successional development of the biocrust community depends strongly on regional edaphic and climatic factors, cyanobacteria and microalgae were found to be the pioneers in colonizing the soil surface. Belnap and Eldridge (2001) expect these microorganisms to benefit from their high mobility in the soil matrix and their ability to easily drift in the air. They further withstand high surface temperatures and radiation (Singh, 2018), and hence typically form the early developmental stages of the biocrust (Lan et al., 2012; Langhans et al., 2009). A study by Zhang et al. (2009) in the Gurbantunggut Desert (China) described the cyanobacterium *Microcoleus vaginatus* as the dominant species in early successional biocrusts, which were superseded by *Palmellococcus miniatus* and *Scytonema ocellatum* in the course of biocrust succession. The dominance of *M. vaginatus* in early

biocrusts was also proven on the Colorado Plateau, USA (Gundlapally and Garcia-Pichel, 2006) and in the Negev Desert (Hagemann et al., 2015). In a study of South African biocrusts, Büdel et al. (2009) described the increase in species richness regarding cyanobacteria but also the establishment of eukaryotic algae, mostly green algae, as indicators for the shift to the intermediate successional stage of the respective biocrusts. Further colonization of the biocrusts by cyanobacterial lichens marks the following later successional stage in this dryland ecosystem. 'Biocrusts with bryophytes' were additionally assigned to the late successional stage. Büdel et al. (2009) concluded that the colonization of mosses and their richness depends on longer undisturbed periods with frequent rainfall and shorter drought periods (cf. Belnap et al., 2004). Further, bryophytes appear to be a greater component of mature temperate than of dryland biocrusts, which are more limited by water scarcity, and generally experience an annual moisture deficit and a large between-year variability in precipitation. Like Büdel et al. (2009), Maier et al. (2018) described a similar successional development for biocrusts also of South Africa (Figure 4). This study highlights an increase in the alpha diversity of the bacterial and fungal community in the biocrust with ongoing succession. Overall, a general increase in the thickness of the biocrust, accompanied by an increase in biomass values and chlorophyll *a* content, provides indications of succession in biocrusts (Büdel et al., 2009; Lan et al., 2012).

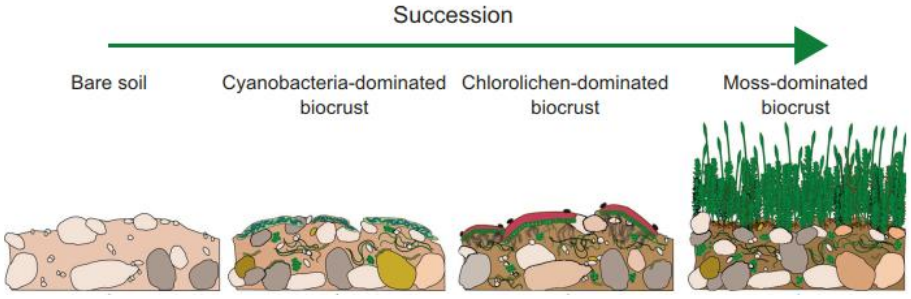


Figure 4: Schematic diagram showing the successional development of biocrusts (Maier et al., 2018).

Bacteria are among the smallest and at the same time probably the least studied biocrust organisms. However, since high-throughput-sequencing analyses are increasingly applied in biodiversity analyses more and more details become known about this kingdom (Miralles et al., 2020; Moreira-Grez et al., 2019; Wasserstrom et al., 2017). In drylands, these studies highlight Acido-, Actiono-, and Proteobacteria as the main biocrust-inhabiting bacteria (Abed et al., 2019; Moreira-Grez et al., 2019). With succession, these communities are expected to shift from more generalized to specialized microorganism communities (Maier et al., 2018). Further, Miralles et al. (2020) showed that the bacterial alpha diversity was higher in soils colonized by late-successional biocrusts. Comparable to the studies on dryland biocrusts, a dominance of Proteobacteria, followed by Actino- and Acidobacteria could be demonstrated from biocrusts of temperate forests and sand dunes (Glaser et al., 2022a, 2022b). These investigations describe a recruitment pattern after which bacteria in biocrusts are a specialized subset of the overall neighboring soil bacteria.

Further important heterotrophic biocrust organisms are fungi. While lichenized fungi are well documented, free-living fungi within biocrusts are less studied. Research on them has been conducted in desert regions e.g., the Colorado Plateau (Bates and Garcia-Pichel, 2008), the Negev Desert (Grishkan et al., 2006), and the Sultanate of Oman (Abed et al., 2013). Bates et al. (2011) used molecular methods to study the fungal biocrust community in desert biocrusts. These researchers showed a high variation in fungal diversity with biocrust age and type. They detected a higher fungal diversity in later successional biocrust stages than in early ones. Further, they found the majority of

biocrust fungi belonging to the Ascomycota. Another recent study on the fungi in desert biocrusts identified that changes in the bacterial community are associated with changes in the fungal community (Elliott et al., 2024). Again, these researchers highlighted the dominance of Ascomycota within the studied biocrusts.

Heterotrophic protists are another essential organismic group within biocrusts. This group was studied in biocrusts along the Baltic Sea coast by Khanipour Roshan et al. (2020). These researchers concluded that members of Stramenopiles and Cercozoa dominate the heterotrophic protist community in coastal sand dunes. Concerning the driving factors shaping the protist community within biocrusts edaphic factors could be excluded and further, no co-occurrence pattern could be observed. In a following study of Khanipour Roshan et al. (2021) the researchers detected that other factors like the prey communities potentially shape the protist community. For example, algae in dune biocrusts create an opportunity for a more algivores-dominated protist community.

Regarding the phototrophic community components, Gypser et al. (2016a) investigated the spatial variance of biocrusts covering initial soils of post-mining sites in Northeast Germany. These researchers described early biocrust covers dominated by green algae of the genus *Zygogonium* (Zygnemataceae) and *Ulothrix* (Ulotrichaceae). They found the green algae layer to grow to smooth and later rougher, dense green algae biocrusts with succession. In congruence with Gypser et al. (2016a), Hoppert et al. (2010) identified biocrusts mainly composed of *Zygogonium ericetorum*, accompanied by *Ulothrix* spec. filaments on a sandy terminal moraine located in Brandenburg, Germany. Glaser et al. (2018) identified Chlorophyta as the algal phylum with the highest species richness in biocrusts of temperate forests in Northern Germany. Key microalgae forming early successional stages of biocrusts in temperate coastal sand dunes likely belong to the genera *Klebsormidium* and *Lobochlamys* (Mikhailyuk et al., 2019; Schaub et al., 2019; Schulz et al., 2015). Further, Schulz et al. (2015) identified *Coleofasciculus*, *Lyngbya*, *Microcoleus*, *Nostoc*, *Hydrocoryne*, and *Leptolyngbya* to be the most important cyanobacterial genera in biocrusts from dunes along the Baltic Sea coast and microscopically identified 55 diatom taxa. Diatom species detected in nearly all dune biocrusts in the investigation of Schulz et al. (2015) were *Achnanthes coarctata*, *Hantzschia amphioxys*, *Planothidium* spec., and *Pinnularia intermedia*. Later successional biocrust stages are likely dominated by mosses, predominantly *Ceratodon purpureus,* and *Polytrichum piliferum* (Gypser et al., 2015; Thiet et al., 2014). The latter researchers concluded that green algae and moss-dominated biocrusts initially stabilize the soil surface and shape the soil conditions supporting the development of characteristic moss-lichen biocrusts. Looking at further moss species, Langhans et al. (2009) documented the occurrence of *Brachythecium albicans*, *Bryum argenteum*, *Hypnum lacunosum*, *Tortula ruraliformis*, and *Tortella inclinata* in stable biocrusts in a sandy temperate region in Southwest Germany. In a following 3-year field experiment at the same study site, Langhans et al. (2010) identified *T. ruraliformis* to be a fast recolonizer after mechanical disturbance of biocrusts. *Tortula ruralis* was described as a typical moss for pioneer macrophytic colonization by Isermann (2011) on young grey dunes on the island of Spiekeroog (Germany, North Sea). With dune succession, bryophytes of later succession stages such as *Dicranum scoparium* and *Hypnum lacunosum* increased in the former mentioned study area.

Biocrust lichens are still poorly studied in temperate regions, whereas in dryland regions there are already several studies on their occurrence and the formation of biocrusts (Baumann et al., 2018; Büdel et al., 2013; de los Ríos et al., 2022; Jung et al., 2020a; Lalley and Viles, 2005). But still, there are knowledge gaps that limit a profound understanding of lichens' function within biocrusts in temperate regions. Lichens are symbiotic associations between a fungus (mycobiont) and one or several photosynthetic partners that can be either green algae or cyanobacteria (photobiont) (Jung et al., 2024). As poikilohydric strategists, lichens are well adapted to a life within biocrusts, characterized by

harsh seasonal and diurnal climatic fluctuations, since their water content can adapt to the surrounding environment (Rosentreter et al., 2016). Biocrust lichens can be found worldwide. Some taxa are only found locally, while others can be globally found. *Buellia* spp., *Diploschistes* spp., *Fulgensia* spp., *Psora* spp., and *Toninia* spp. are described as dominant biocrust-forming lichens with diverse morphology and chemical traits in drylands (Concostrina-Zubiri et al., 2021; Rosentreter et al., 2016). A special form of lichen-dominated biocrusts was discovered by Jung et al. (2020b) in the Atacama desert. This newly discovered biocrust type (full approval still under discussion) is called grit crust. These biocrusts are formed by green-algal lichens (chlorolichens), free-living green algae, and cyanobacteria. It is a unique community between lithobiontic and biocrust biocenoses. This biocrust type grows beneath (hypolithic) and into granitoid grit stones (bioweathering, Jung et al. (2020a). However, these results do not relate to lichens in temperate zones. Concerning lichen communities in temperate sand dunes, Isermann (2011) identified species of the genus *Cladonia* to be dominant in older grey dunes on the island of Spiekeroog. Thiet et al. (2014) also reported *Cladonia* as the most common genus in a system of migrating parabolic dunes northernmost tip of Cape Cod, USA. Given the limited lichen data availability, the existing gaps in knowledge within temperate biocrusts are particularly evident in this macrophytic cryptogamic group.

1.3 Phosphorus balance within ecosystems

Henning Brand 1669 „mein Δ“

Phosphorus (P) is essential to all living organisms and a productivity-limiting key factor in various ecosystems due to its central role in energy transfer, cell structure, metabolism, and signaling (Bünemann et al., 2011). In contrast to N, P largely lacks a supply via the atmosphere, and P replenishment in natural ecosystems occurs mainly through weathering processes, which can be physically, chemically, or biologically driven. Released phosphates thus enter the soil solution and can be taken up by plants and microorganisms. By mineralization of their residues, P returns to the soil. Therefore, the P cycle of an ecosystem is relatively closed (Amelung et al., 2018a). The largest global reservoir of P and at the same time the initial source are primary P-containing minerals within rocks are apatites. These minerals contain orthophosphates (PO_4^{3-}; deprotonated salt of the orthophosphoric acid (H_3PO_4) bound by Ca). Weathering of P-containing minerals during soil development leads to P release into the surrounding soil solution (Filippelli, 2019; Jones and Oburger, 2011; Sims and Pierzynski, 2005; Walker and Syers, 1976). The P content in the soil solution together (inorganic and organic, dissolved or colloidal) accounts for <0.1 % of the P_t content in the soil and is mostly available as phosphate anions (dihydrogen phosphate $H_2PO_4^-$ and hydrogen phosphate HPO_4^{2-}). These are essential for the growth of soil microorganisms and vegetation which can only take up dissolved inorganic phosphate from the soil solution (Amelung et al., 2018a; Jones and Oburger, 2011). P in the soil biomass is bound as phosphate esters in phospholipids, nucleic acids, and phytin. It is used for energy transfer (ATP, ADP), for the synthesis of cell structures (phospholipids), and metabolic and signaling pathways and thus is immobilized (Amelung et al., 2018a; Bünemann et al., 2011; Oberson and Joner, 2005). Organic P bound within dead plant material can return to the soil solution via mineralization. Therefore, the soil microbial biomass, as well as the non-living soil organic matter, can be seen as a P sink and source at the same time. If the P content in the soil solution is greater than the current requirement by the microorganisms and the vegetation, sorption and precipitation of P predominate maintaining an equilibrium state. In acidic soil conditions, P gets adsorbed to the mineral matrix (Fe and Al oxides) and is further potentially physically occluded by slow diffusion of phosphate into microaggregates. Precipitated phosphates (e.g., Ca-, Fe-, Al-phosphates) are stable and hardly soluble inorganic compounds. The soil pH influences the availability of P generally due to its direct impact on the weathering of minerals (Kruse et al., 2015).

1.3.1 Influences of biocrust microorganisms on the phosphorus cycle in sand dune ecosystems

Microorganisms and macrophytic cryptogams of biocrusts represent a source and sink of P to the ecosystem by incorporating P in their organic material. Biocrusts in temperate forests are involved in the accumulation of P_t with high shares of organic P (P_o) and the transformation of inorganic P (P_i) to P_o fractions (Baumann et al., 2017). P bound in the microbial biomass serves as a mobile and quickly available source of soil-P. Due to the high proportion of nucleic acids, the microorganisms are quickly mineralized after their death (Kruse et al., 2015; Negassa and Leinweber, 2009).

The availability of microbial P is strongly linked to the environmental conditions to which the microorganisms are exposed. In temperate regions, it is assumed that microbial activity is high, particularly in the summer months (Bol et al., 2016), as cool conditions can slow down metabolic processes (Nash et al., 2014). Further, microbial metabolism strongly depends on water availability in their environment (Fischer and Subbotina, 2014; Pushkareva et al., 2015; Williams and Rice, 2007).

Fast changes between dry and wet extreme conditions can cause osmotic stress to the microorganisms finally leading to cell damage and the release of organically bound P which can get mineralized quickly (Achat et al., 2012; Dinh et al., 2016). In addition to the build-up of organic P-containing biomass by the microorganisms themselves, they can also actively influence the release of adsorped or precipitated P from the soil matrix (Oberson and Joner, 2005). The excretion of protons during the respiration of vegetation and microorganisms or their secretion of organic acid anions causes a decrease in the soil pH and remobilizes precipitated Ca phosphate (formed under alkaline pH). With decreasing soil pH, the P availability increases until it reaches its maximum between pH 5.5-6.5. Below this pH, the P availability declines again due to the formation of stable Al and Fe phosphates (Belnap, 2011; Fox, 1995; Kruse et al., 2015; Sims and Pierzynski, 2005; Tiessen et al., 1984). Moreover, biocrust microorganisms secret metal chelators, e.g., siderophores, that maintain metals in solution thereby increasing the P availability in the soil (Jones and Oburger, 2011 and references therein; McLean and Beveridge, 1990). Enzyme-mediated P release by P-mobilizing microorganisms represents an additional mechanism of P acquisition. Cell-wall-bound or free phosphatase enzymes (acid and alkaline phosphatase) whose release is mainly driven by P demand, mineralize organic P compounds and thereby liberate inorganic P (reviewed by Nannipieri et al., 2011). Additionally, soil water availability is crucial for maintaining the soil enzymes' catalytical activity (Jiang and Zhang, 2002), also proven by Baldrian et al. (2010) in forest soils. The findings of Pushkareva et al. (2020) confirm a positive correlation between the soil water content and alkaline phosphatase activities in biocrusts on a coastal plain along a moisture gradient in the High Arctic. However, an investigation of the phosphatase activities from biocrusts on the Baltic Sea dunes revealed low phosphatase activity levels indicating a lack of P deficiency in biocrust microorganisms or the preferable use of inorganic P sources (Schaub et al., 2019).

All these microbial-mediated turnover processes in the soil lead to changes in the P availability and proportions of P in different P pools (see next Chapter for more details). Baumann et al. (2019) identified an increase in the proportions of labile and moderately labile P pools accompanied by a decrease in the stable and residual P fractions in biocrusts from temperate coastal sand dunes. The impact of the bacterial community on the P cycle in biocrusts of temperate forests was intensively studied by Kurth et al. (2020). These researchers discovered that the absolute and relative bacterial abundance involved in P turnover increased in biocrusts compared to bare soil. In studies on possible P uptake strategies by bacteria, solubilization was identified as a key mechanism in P-rich forest soils (Bergkemper et al., 2016; Kurth et al., 2020). Further, Kurth et al. (2020) found that the combination of a low pH and the sandy texture of the parent material reduced the sorption capacity of soil minerals for phosphate (cf. Baumann et al., 2017). Under these conditions, dissolved phosphate can be taken up directly by the bacteria (and other microorganisms) of the biocrusts and thus becomes immobilized.

1.3.2 Short insights into the sequential P fractionation

Phosphates differ in terms of their chemical species, reactivity, solubility, and bioavailability. Based on these criteria, phosphates with similar characteristics can be grouped into so-called P pools. These pools are connected via the highly dynamic chemical and biological processes described above. Tiessen et al. (1984) developed a conceptual model of the P-pathways based on the sequentially extractable P-fractions according to Hedley et al. (1982). This sequential P extraction procedure was further modified by Tiessen and Moir (1993) and is one of the most widely used wet chemical methods to characterize the different pools of P today (Do Nascimento et al., 2015; Negassa and Leinweber, 2009; Prüter et al., 2022).

The method of sequential P fractionation by Hedley et al. (1982) and modified by Tiessen and Moir (1993) is an approved P research method in soil science to characterize the P pools, reveal the transfer pathways of P compounds, and better understand the complexity of interactions between inorganic, organic, and microbial P (Condron and Newman, 2009; Kruse et al., 2015). A series of reagents with increasing extraction strengths are applied to a sample (e.g., soil or biocrusts) to successively extract various forms of P. Depending on their solubility, the extracted P compounds are classified into the defined P pools of identical P forms (P-fractions). Within these pools, P forms with similar stability and therefore similar bioavailability are grouped (Cross and Schlesinger, 1995; Tiessen et al., 1984).

These fractions/pools are assumed as follows.

- Labile fraction:
  - Resin extractable P: representing soil solution P, easily bioavailable
  - Bicarbonate ($NaHCO_3$) extractable P: representing labile P_i and P_o, weakly adsorbed on surfaces of more crystalline P compounds, sesquioxides, and very labile pools of Ca phosphates, microbial P, and an unknown portion of the soil P_o
- Moderately labile fraction:
  - Hydroxide (NaOH) extractable P: P_i which is assumed to be chemically adsorbed on surfaces of amorphous and crystalline Al and Fe oxides as well as Al and Fe carbonates, P_o associated with the soil organic matter
- Stable fraction:
  - Acid (H_2SO_4) extractable P: largely Ca-bound P_i (e.g., apatite)
- Residual fraction:
  - Non-extractable P. Calculated as the difference between the sum of the P fractions and the P_t concentration determined after digestion with aqua regia.

The stability of the pools is assessed according to their availability for plants and soil organisms. The labile P is characterized by its rapid turnover within plants and their residues, microorganisms, the soil solution and belongs to the P pools of weakly fixed and easily mobilizable inorganic and organic compounds. On the other hand, there is the stable P pool, which is relatively insoluble from a bioavailable point of view. A detailed description of the laboratory workflow, downstream application, and measurement techniques can be found in the supplemental material of **Publication III**.

1.4 Goals of the Thesis and Hypotheses

Community composition and succession

Given the information provided in the general introduction, it becomes clear that there are still major gaps in our knowledge regarding biocrust succession and the respective shifts in their phototrophic community structure on sand dunes in temperate regions. Dune chronosequences are suitable for filling these gaps and understanding the successive biocrusts' community changes.
Therefore, this thesis aims to generate fundamental knowledge of the dominant biocrust successional stages along dune chronosequences and to track their changes in the biodiversity of phototrophic organisms (**Publication I** and **III**).
Publications II and **IV** take a detailed look at individual organism groups in the biocrusts. Since only a few is known about the bacterial community in the study regions (Baltic Sea coast and an inland dune in Northern Germany), **Publication IV** focuses on this organism group, their community structure, and development along the dune chronosequences. In addition to the insight into the bacterial community, **Publication II** deals with the phototrophic group of terrestrial diatoms and highlights their so far unstudied ecophysiological performance and stress tolerance under desiccation and temperature extremes, mimicking the dune environment in the laboratory.
In addition to characterizing the biocrusts' community structure with succession, this thesis investigates the soil-chemical conditions impacting community formation. Moreover, these pedological investigations intend to identify initial soil formation processes and find potential links to the biocrust development (**Publication I** and **III**).

Implications in the phosphorus cycle

Publications about the alteration and composition of P compounds along a successional gradient of biocrust development are rare. Therefore, the phosphorus cycle was of particular interest in this thesis as part of the investigation of the soil-chemical conditions. Detailed information is collected to characterize the impact of biocrust organisms on the turnover and accumulation of this essential nutrient in the dune ecosystem. **Publications I, II, III,** and **IV** evaluate changes in the total P content and various P pools of different bioavailability to microorganisms and macrophytic cryptogams along with successional biocrust development.

Following these goals, **three hypotheses** were developed and discussed in the synoptic discussion.

Hypotheses 1:

The biocrust species composition changes from thin microalgae to moss and lichen-dominated types along the studied coastal dune chronosequences. Further, an increase in biocrust coverage and biomass is expected.

Vegetation surveys in coastal sand dunes and one inland dune area in Northern Germany were conducted between April 2020 and January 2021 to reveal changes in the biocrust community composition between different stages of dune succession. At each sampling site, a transect starting from the first foredune ridges, passing through the dune area, and ending in the mature dunes was considered as dune chronosequence. The coverage of different biocrust types and further, their phototrophic (algae, cyanobacteria, mosses, and lichens) and heterotrophic (bacteria) communities were determined using morphological and molecular methods, respectively. The chlorophyll *a* content was used as a proxy for the photosynthetic biomass of the biocrusts.

Hypotheses 2:

With ongoing biocrust succession on the sand dunes along the chronosequences, early soil genesis can be observed in the top sediment layer. These processes are strengthened by the colonization of the uppermost sediment layer by the biocrusts.

As part of the pedological investigations sediment/soil cores of the different dune types were analyzed to uncover the potential impacts of the biocrust community on initial soil formation processes. These investigations included analyses of the physicochemical*[1] and biotic characteristics*[2] in different sediment/soil core sections. That allowed for a subsequent interpretation of soil horizons according to the German classification system KA5 and conclusions about the ongoing processes of soil genesis. Potential links between the soil parameters and the respective biocrust community composition were derived from this information.

*1 water content, pH, calcium carbonate content, total carbon, nitrogen, phosphorus, and aluminum, iron, and manganese contents from poorly and well-crystalline pedogenic oxides

*2 organic matter content and chlorophyll *a*

Hypotheses 3:

Biocrust succession is positively linked to an overall increase in the total phosphorus content within the biocrusts. The proportion of bioavailable phosphorus increases with ongoing succession due to the biocrusts' impact on the P cycle. This leads to a reduction in the proportion of phosphorus in the more stable P pools.

For all study sites in-depth analyses of the total phosphorus content and the different P pools were conducted applying the well-established method of P fractionation, a wet chemical method to characterize pools of P, established by Hedley et al. (1982), modified by Tiessen and Moir (1993). The sequentially extracted P pools reflect the different availability of P to microorganisms and allow for a connection between the P pools and the successional stages of the biocrusts.

1.5 Study sites

The main study sites of this thesis are located in Northern Germany, primarily along the Southern Baltic Sea coast, in Mecklenburg-Western Pomerania where the flat coasts are the dominating coastal type. With a length of 1,594 km, flat coasts account for around 82% of the total coastline of Mecklenburg-Western Pomerania. Two of the three coastal study sites are located on a flat accumulation coast. Both are spits with a positive sediment budget. One at the Pramort, the eastern end of the peninsula Fischland-Darss-Zingst, and the other on the Schaabe spit on the island of Rügen. The study site Darsser Ort itself represents an abrasion coast with an active cliff. It is located on the Neudarss, a foreland in the West of the peninsula Fischland-Darss-Zingst (Figure 5). This almost triangular foreland started forming approximately 3,000 years BP (Fukarek, 1961). The marine and aeolian sediments that led to the formation of the Neudarss originate from a region southwest of the former Pleistocene island cores: the Fischland cliff (Ahrenshoop) and the Rostocker Heide. The Neudarss consists of two large interlocked beach ridge systems (cf. Figure 1) that make a total of about 120-140 beach ridges (Lampe, 2002b; Lampe and Lampe, 2018; Naumann et al., 2010). The western coastline of the Neudarss is subject to an annual coastal retreat of approx. 1 m yr^{-1}. The eroded material from the Neudarss, as well as from the two erosion zones mentioned in the Southwest, gets transported further north and forms a new recurved spit (approx. 2m yr^{-1} length growth) (Lampe, 2002b; Naumann et al., 2010; Reimann et al., 2010; Tiepolt and Schumacher, 1999). The two sampling sites Pramort and Darsser Ort on the peninsula Fischland-Darss-Zingst are protected by the national park 'Vorpommersche Boddenlandschaft'. The three coastal study sites investigated show individual successive dune types, which form their respective chronosequences. Depending on the coastal types, the accumulation coast (spit) and the abrasion coast (active cliff), different dune types can be found along the chronosequences. These can be classified into the dune successional stages (primary, secondary, tertiary, and mature) described in Chapter 1.1.2. For a detailed list of these respective dune types along the individual coastal chronosequences, see the section 'sampling plots' below.

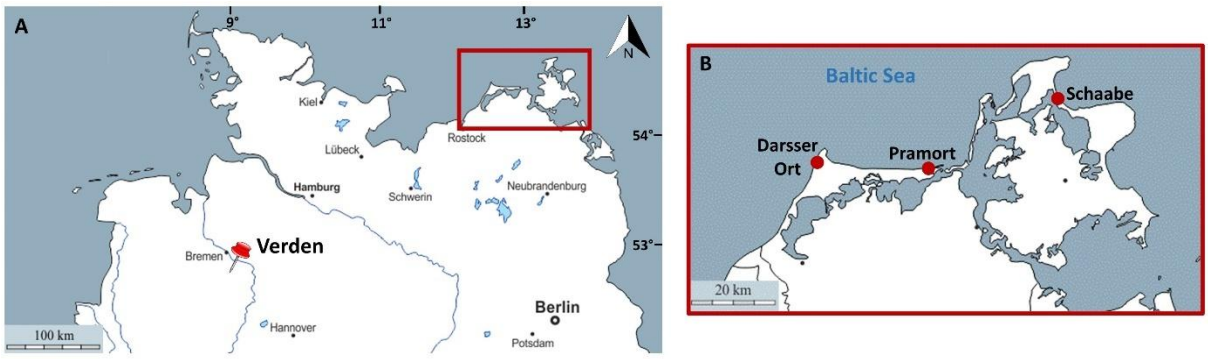


Figure 5: (A) Overview of the locations of the sampling sites. (B) A close-up of the peninsula Fischland-Darss-Zingst with the sampling sites Darsser Ort and Pramort, and the island of Rügen with the sampling site Schaabe. © d-maps.com.

The contrasting inland dune area, 100 km away from the North Sea coast in Lower Saxony, is located in the nature reserve 'Dünengebiet und Halsetal bei Verden-Neumühlen', Verden (Figure 5). The chronosequence at this sampling site started in the dune center, where the sand mobility is expected to be high due to wind exposure. The sediment material gets continuously blown to the edge region of the inland dune area. Therefore, the chronosequence continued up to a dune slope and further to the dune crest. At this point, the dune area passes into a mixed dune forest dominated by pine trees. All four sites have their geomorphologic origin in the past ice ages of the Pleistocene period (Niedermeyer and Janke, 2011). Repeated glacier advances and their retreat caused material erosion and its transport, thereby forming the parent material of these regions today (cf. Chapter 1.1.1)

Sampling plots

At each site, a transect following the natural dune geomorphological succession (chronosequence) was investigated. A 1 m^2 sampling plot was established in each dune type along the gradients. Depending on the respective site, the dune types differed in their developmental stages. Thus, there are some unique characteristics (i.e., windwatt at Pramort and the foredune at the Schaabe spit) and dunes in transitional phases (i.e., intermediate dune at the Schaabe spit and subdivision of the grey dune area at Darsser Ort) that cannot be clearly assigned to an ideal dune type within a dune chronosequence. In principle, however, it was possible to classify the dune types into early (primary and secondary dune types, no soil horizon formation, mobile sediment) and mature (starting soil genesis, immobile sediment) successional stages. This classification is based on the visual assessment of the sediment and the prevailing dune-typical vegetation (Figure 6).

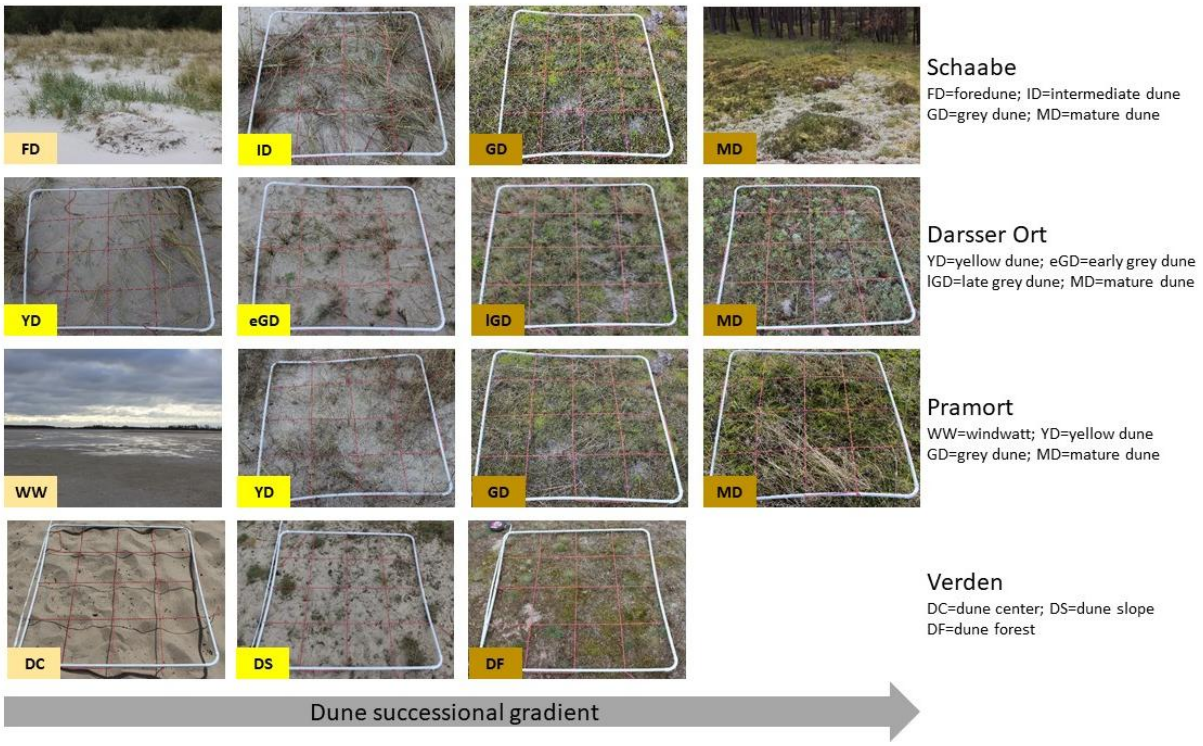


Figure 6: Overview of all sampling plots investigated during field sampling campaigns. The white frame defines an area of 1 m^2. Light yellow labels indicate primary, bright yellow secondary, and brownish mature dune types. Images: © S. Kammann.

Methodological overview

The field studies in this thesis were conducted according to the schematic workflow illustrated in Figure 7. Details of the laboratory experiments testing the ecophysiological responses of terrestrial diatoms to temperature, irradiance, and desiccation can be found in **Publication II**.

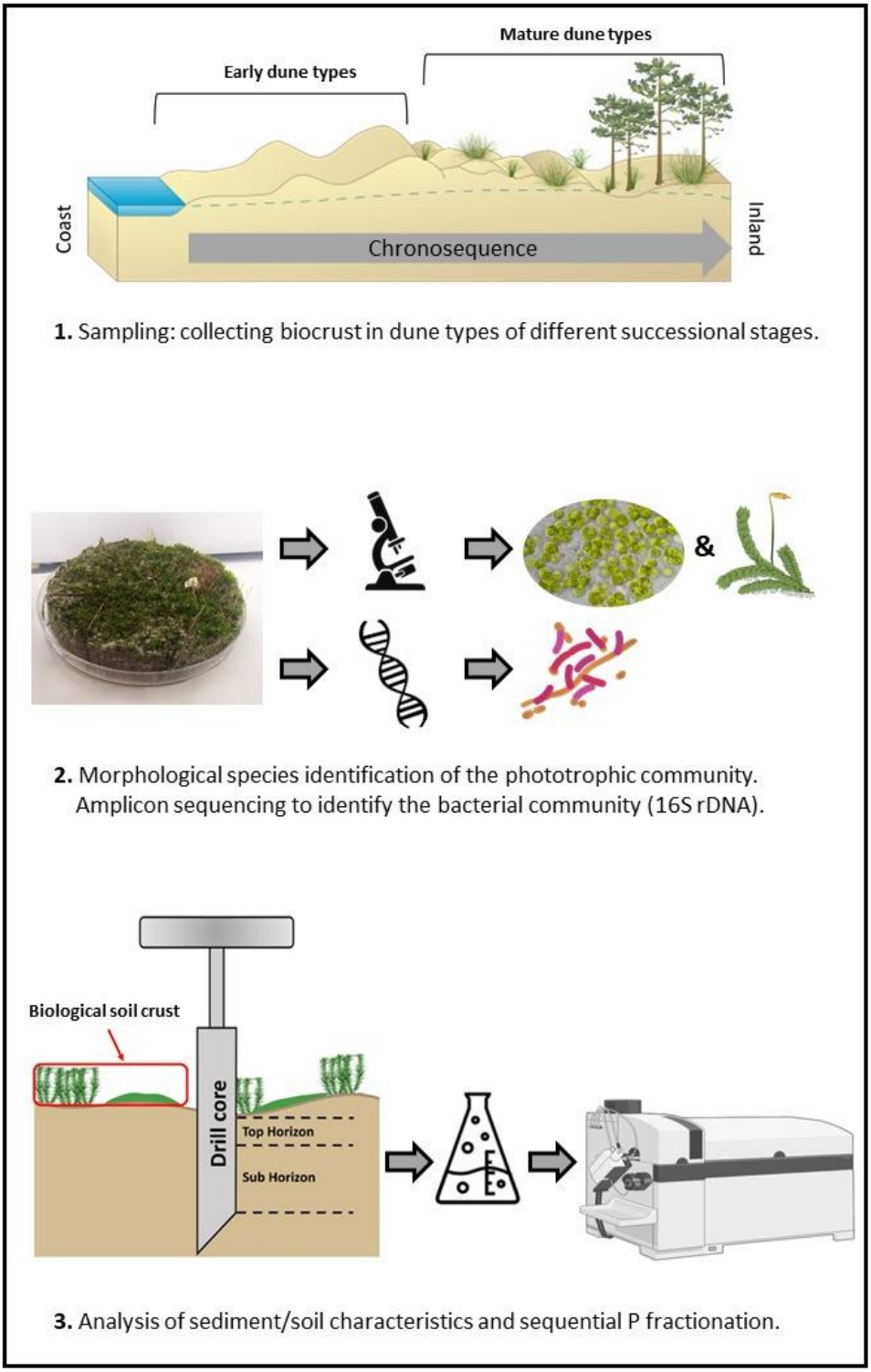


Figure 7: Schematic representation of the workflow to attain an insight into the species diversity and community composition of biological soil crusts growing on the dune surfaces and subsequent sediment/soil core analyses. The figure was created using Microsoft Office PowerPoint (2016) and the scientific image and illustration software Biorender.com.

2 Synoptic discussion

2.1 Synopsis of the species diversity and community composition of biocrusts in temperate sand dunes, and their succession

The biodiversity of microorganisms and macrophytic cryptogams of biocrusts on sand dunes in temperate regions and their community shifts along with succession were addressed in **Publications I, II, III,** and **IV**. The following chapter discusses the data on the vegetation surveys and species determinations of the biocrust organisms. The aim was to identify the dominating biocrust types along dune chronosequences and to describe their community composition and potential traits favoring their development within the different stages of biocrust succession.

Therefore, this chapter deals with the **first overarching hypothesis** developed in this thesis.

> **Hypothesis 1:** *The biocrust species composition changes from thin microalgae to moss and lichen-dominated types along the studied coastal dune chronosequences. Further, an increase in biocrust coverage and biomass is expected.*

2.1.1 The dominating biocrust types along the dune successional gradients

An extensive literature review preceded the classification of the biocrusts into the different types used in the vegetation surveys (**Publication I** and **III**). This resulted in a grouping of the biocrusts into the early and late types, depending on the dominant organism group (adapted after Büdel et al., 2009; Lan et al., 2012; Williams et al., 2017). The detailed table containing the biocrust type descriptions and visual examples for each type can be found in Figure 8 and the supplementary material of **Publication I** and **III**. In brief, biocrusts dominated by microalgae (greenish shimmering top sediment layer) and those in which a sparse occurrence of mosses was detected were defined as early successional stage biocrusts. These biocrusts were slightly brittle and no more than 3 mm thick. Moss-dominated biocrusts and those occasionally interspersed with lichens were considered as mature successional biocrust stages. The physical structure of these mature biocrusts showed a hardened upper surface structure and was less than 1 cm thick. Studies on the successional development of biocrusts from other than temperate regions assumed the pre-presence of early microalgal biocrust before the later establishment of mature moss and lichen-dominated biocrusts (Lan et al., 2012). In addition to the biocrust types, other structural components were also recorded on the dune sediment. These included 'vascular plants' and their dead remains ('organic litter'). Areas of the dune that were not covered by one of the biotic groups were recorded as 'bare soil'. The point intercept method according to Levy and Madden (1933) was applied to record the proportion of coverage of the seven groundcover groups.

The chlorophyll *a* (Chl *a*) content was taken into account as an indicator of both the presence of photoautotrophs and the degree of biocrust development (living phototrophic biomass accumulation), as shown by Chowaniec et al. (2024) for temperate inland sandy grasslands. Further, these scientists draw a link between the photosynthetic biomass and the microbial activity of the biocrust concluding photoautotrophs constitute a major biocrust component.

The three coastal chronosequences studied in this thesis differ in particular at their starting points, which are closest to the sea and therefore still strongly exposed to the wind and waves. These are the two most important forces in coastal geomorphology, causing sediment erosion, material drift, and redeposition (cf. Chapter 1.1.2). At the inland dune center, on the dunes closest to shore, and the windwatt, none of the dune chronosequences showed the establishment of biocrusts, but the first settlement of early microalgal pioneers could be proven at the windwatt.

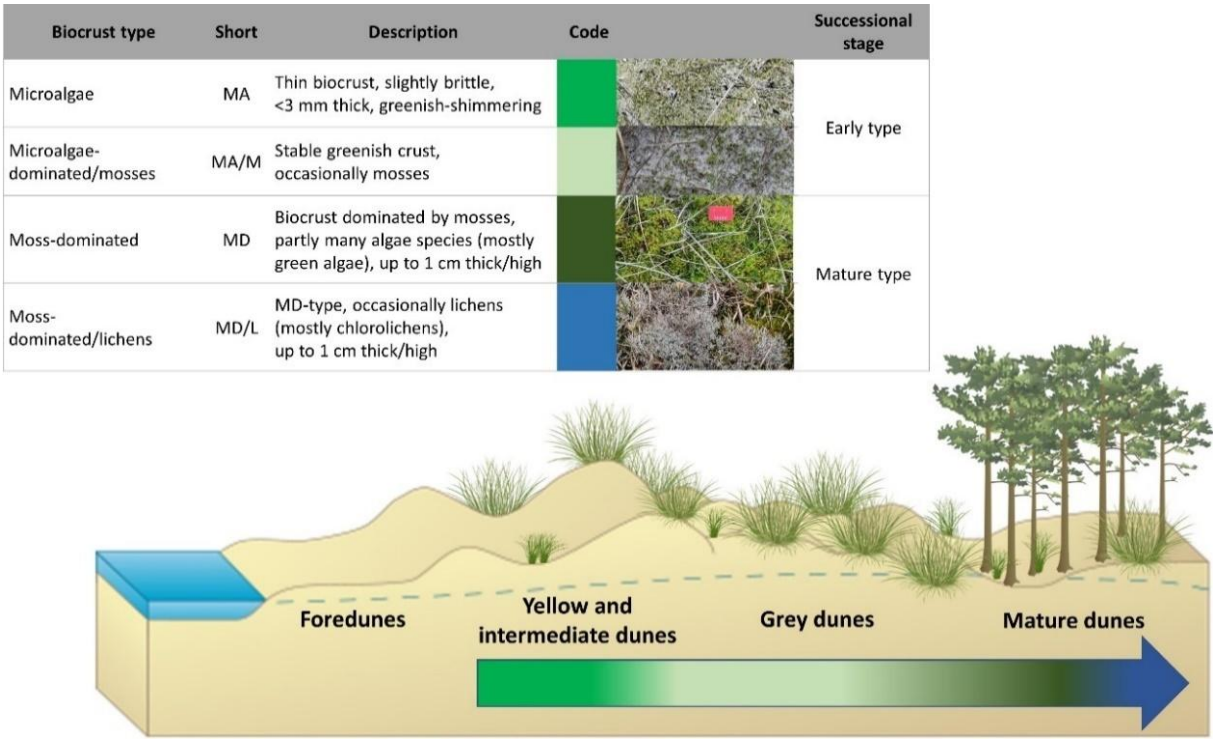


Figure 8: Scheme showing the trend of the successional development of the biocrusts types along an ideal dune chronosequence. Adapted and modified from Kammann et al. (2024).

Challenging habitats for biocrust pioneers

The center of the inland dune area represents a highly mobile sand habitat. Therefore, the dominating groundcover group was organic litter (**Publication I**). No biocrust formation was visible. At the Schaabe spit (**Publication I**) the accumulation of marine sand along the coastline leads to a widening of the beach and extends to the first foredunes. This primary dune type is dynamic in its formation due to wind-driven erosional and accretional processes of the adjacent beach. The inland shift of sediment from the foredunes potentially supports the formation of transgressive coastal dune forms over time. This causes a subsequential enlargement of the dune area and variation in dune morphology which emphasizes the initial importance of foredunes for the successive development of the entire dune area (Hesp, 2002; Psuty, 2004). The establishment of vegetation on the primary dunes plays a key role as the wind force is slowed down when it meets against an annual plant or shrub formation and sand is deposited on the lee side of the obstacle. In temperate coastal zones, a group of pioneer plant species is responsible for forming foredunes: rush quackgrass (*Elymus farctus*) and lyme grass (*Leymus arenarius*) (Hesp, 2004; Jun et al., 2004; Pott and Hüppe, 2007).
Both species are tolerant to salt spray, strong winds, and sand burial (Wiedemann and Pickart, 2004). The dune chronosequence on the Schaabe spit (Rügen) was the only studied successional sequence in

which a foredune adjoins the beach plain. This primary dune was exclusively dominated by the named lyme grass (*Leymus arenarius*). Microscopical analyses of the uppermost dune sediment layer revealed no occurrence of algae in this dune type and no biocrust formation was observed. Also, mosses and lichens were absent here. Strong winds causing frequent sand redeposition form a habitat challenging for biocrust formation. Additionally, the sea-born salt spray creates a high sediment salinity, especially in the uppermost sediment layer, in which only the colonization of halophilic species is to be expected (García Novo et al., 2004; Lane et al., 2008; Martínez et al., 2004).

A comparable situation was also observed at Darsser Ort. The chronosequence on the abrasion coast started at the edge of the dune cliff identified as a former grey dune due to slight accumulations of iron oxides and humus in the underlying soil horizon. Secondary dune development has taken place here. The dune cliff gets continuously covered with a large amount of sand due to aeolian transport during storm events creating a loose sand layer down to a depth of approximately 30 cm on the former grey dune. This geomorphic trait is typical for the yellow dune type, which is also supported by the growth of marram grass (*Ammophila arenaria*) (Pott and Hüppe, 2007). Consequently, this area along the chronosequence at the Darsser Ort is referred to as a (secondary-formed) yellow dune. However, such a highly dynamic habitat does not come without consequences. In this dune type, neither biocrust formation nor the colonization of microalgae could be detected (**Publication III**). Erosive wind forces are the most likely reason for the lack of biocrust formation in this type of dune, comparable to the foredune at the Schaabe spit (Martínez et al., 2001). Other factors causing stress to microalgae at this point along the chronosequence can be a high light intensity and/or nutrient deficiency (Hesp, 1991; Martínez et al., 2004; Maun, 2009a).

Contrary to the Darsser Ort the studied dune chronosequence at the Pramort is located on an accumulation coast. This dune successional sequence starts with a geomorphological peculiarity, a unique tidal wind flat, the windwatt. The windwatt is a shallow water area and part of the foreshore, which sometimes is flooded due to wind-generated water-level fluctuations. By definition, a windwatt is free of higher vegetation and is only colonized by smaller benthic species e.g., microalgae, cyanobacteria, and bacteria (Eisma, 1998; Obst et al., 2022). These organisms and the sedimentary matrix form organo-sedimentary structures defined as microbial mats. They serve as an important food source for the meiofauna and support the input of biomass and nutrients into the ecosystem (Karsten and Kühl, 1996; Wölfel and Karsten, 2004). The microphytobenthic organisms (e.g., *Microcoleus chthonoplastes* and *Lyngbya aestuarii* cf. van Gemerden, 1993; Witte et al., 2004) in these mats are exposed to extreme abiotic conditions, such as strong erosion processes, desiccation as well as strong salinity and temperature fluctuations (Karsten et al., 2012; Wölfel and Karsten, 2004). Consequently, it is a habitat especially challenging when it comes to the establishment of biocrusts, the terrestrial equivalent of the marine microbial mats. Thus no biocrusts have been found in the windwatt. However, the occurrence of microalgae and one cyanobacteria species was proven (**Publication III**, cf. Chapter 2.1.2). They may represent the pioneer community for primary biocrust formation in the further course of the successive development of this area. Today the accumulation processes in this area are heavily accelerated due to voluminous beach nourishment off Zingst. Janke and Lampe (1998) determined an accumulation of about 6200 m^3 km^{-1} in the area east of Pramort annually since 1835. Therefore it can be assumed, that the current partially submerged area will become permanently dry in the future and enter the process of successional dune formation allowing for biocrust development. In conclusion, it can be observed that early dune stages at the beginning of each of the chronosequences investigated show little or no formation of biocrusts. These dunes represent a habitat that is still too mobile, which prevents the formation of a coherent microbial layer.

Primary succession: The formation of early successional biocrusts

A visible early biocrust formation was observed on the slope of the inland dune area. Early microalgae biocrusts dominated here. Moreover, a few moss-dominated biocrusts could be observed. Following each of the three coastal dune chronosequences further inland revealed the first visible formation of early successional biocrust covers along the dune gradients (Figure 8). On the Schaabe spit, this was the case in the intermediate dune. Due to the occurrence of moss-dominated biocrusts and also lichens (later successional biocrust stages, 4% coverage), this type of dune is to be understood as a transitional form between yellow dune and grey dune. Its habitus is most comparable with the early grey dune at Darsser Ort. Nevertheless, this dune successional stage was dominated by microalgal biocrusts interspersed with some mosses (32% coverage) which are assigned to the early biocrust types (**Publication I**). Microalgal biocrusts (44% coverage) also dominated the early grey dune along the chronosequence at Darsser Ort. Low coverage with moss-dominated biocrusts, which are no longer classified as the early successional biocrust stage was found (4% coverage). At this sampling plot, the formation of an initial and humic A-horizon (Aih) and silicon-rich, loose soil parent material C-horizon (ilC) (**Publication III**) was detected which speaks for a classification of this plot as grey (secondary) dune. The yellow dune at the Pramort, which adjoins the windwatt landwards, showed the occurrence of microalgae-dominated biocrusts (44% coverage). Only a few occurrences of mosses within microalgae-dominated biocrusts were observed. However, their coverage did not exceed 12%. This finding is comparable to the Darsser Ort early grey dune. But moss-dominated biocrusts did not occur here at all (**Publication III**). It could be observed that with increasing immobilization of the dune sediment, the formation of early still thin biocrusts, which are dominated by microalgae, starts.

Coming of age: The development of mature successional biocrusts

The grey and mature dunes of all three coastal dune chronosequences as well as the area close to the forest of the inland dune showed the dominance of moss and moss-lichen biocrusts (**Publication I** and **III**) (Figure 8). These biocrust types, summarized as the mature successional biocrust stage, formed denser and more coherent layers on the sediment surface of the dunes. There were barely any uncovered sediment patches. Biocrusts growing in these dune types experience less wind and sand mobility than the younger and more mobile dunes closer to shore (Maun, 2009c). The dominance of mosses and lichens and their biomass accumulation was reflected in the rising Chl *a* content in the biocrusts compared to the early successional biocrust stages in younger and more mobile dune types. This is in line with former studies of Büdel et al. (2009) and Chowaniec et al. (2024). Gypser et al. (2016a) also identified the final developmental stages of moss-lichen biocrusts to be associated with a higher Chl *a* content in biocrusts compared to less developed ones. Bryophytes and lichens are good indicators of succession of sand dunes (Jun et al., 2004), and they are also well-established bioindicators of air pollution, soil and water acidification, or indicator plants for climate change (Stapper and Kricke, 2004 and references therein). Jun et al. (2004) reported bryophyte and lichen establishment in semi-mobile and later dune stages. Further, the input of dead organic material and its decomposition by microorganisms leads to the accumulation of humus on the top sediment layer, an indication of early soil development (Kaviya et al., 2019 and cf. Chapter 2.3). In conclusion, in the late stages of dune development along the dune chronosequences mature biocrust successional types, dominated by mosses and lichens were most common. Dune-specific traits e.g., less wind and sand mobility likely favor their dominance here.

2.1.2 Insights into the species diversity and community composition of microalgal and macrophytic cryptograms

Following the vegetation surveys in the dunes, the microalgae community within the various types of biocrust was investigated morphologically under a light microscope (**Publication I** and **III**). The advantage of the direct microscopy method is that it can be applied to fresh and rewetted dune biocrusts without having to isolate, purify, and cultivate them in advance. This approach was used to evaluate the dominating species of algae and cyanobacteria in the original samples. Nevertheless, enrichment cultures of the biocrust samples were established to identify the species community in more detail. This is often not possible in field material, as the morphological characteristics required for identification can be hidden in filament or cell packets, soil particles, and dead organic material or occur only in dormant resting stages (Büdel et al., 2016). The culture approach allows the detection of microorganisms that were only present in low cell numbers or dormant in the original sample. The unialgal cultures resulting from the subsequent isolation steps were not only used for morphological determination (**Publication I** and **III**) but also for ecophysiological experiments (**Publication II**). Permanent slides were used to determine the terrestrial diatom community in biocrusts via light microscopic analyses of the diatom valves from the field material (**Publication II**).
When it comes to the identification of the bacterial communities (**Publication IV**) within the biocrusts direct microscopy and morphological determination reach their limit. Culture-independent high-throughput sequencing (HTS), also known as next-generation sequencing (NGS), is a molecular biological approach that allows for the rapid and cost-effective processing of a large number of DNA fragments in parallel. The possibilities that are opening up using these technologies, but also some of the hurdles and disadvantages with these methods are discussed in a review by Ekblom and Galindo (2011). This review draws attention to the currently limited sequence data availability and the increasing need for data curation and bioinformatic processing.
Mosses and lichens form the macrophytic cryptogams studied in this thesis (**Publication I** and **III**). As with microalgae, light microscopy was used for their identification (maximum magnification of 1000x). If no clear assignment to a lichen species could be made, thin-layer chromatography according to Culberson and Ammann (1979) has been used to detect the characteristic secondary metabolites of the lichen species. This method was necessary to identify individual lichen species of the genus *Cladonia.*

<u>Eukaryotic microalgae</u>

Eukaryotic microalgae are well-known primary biocrust organisms. They are more common in biocrusts of temperate regions (Corbin and Thiet, 2020). Depending on their presumed role in the biocrusts, these algae can be divided into four groups: 1) Biocrust-forming algae, 2) algae attached to soil particles or other algae, 3) photobionts (within lichens), free-living or living epiphytically on lichens, and 4) freshwater algae from aquatic habitats occurring in 'wet' soil (aqueous niches) (Büdel et al., 2016).
Most green algae common in biocrusts belong to the phyla Chlorophyta and Streptophyta. Therefore, the majority of algal species (20 taxa) found in the coastal and inland dune biocrusts belonged to the phylum Chlorophyta. The broad species diversity of Chlorophyta is characteristic of temperate habitats and forest soils (Hoffmann, 1989) and comparable to other studies, for example, in forests of Northern Germany (Glaser et al., 2018). These researchers found that the phylum Chlorophyta was the most species-rich, followed by Streptophyta (81% and 11% of all detected species, respectively).

Chlorophyceae and Trebouxiophyceae (both Chlorophyta) were the overall dominating classes in the studies of this thesis (**Publication I** and **III**). While more species of the class of Chlorophyceae were detected on the dunes of the peninsula Fischland-Darss-Zingst, the species richness of Trebouxiophyceae was slightly higher in the dunes of the Schaabe spit and the inland dune. Species of Chlorophyceae are unicellular and mostly attached to biocrust components, some of them via matrix formation by excreting extracellular polymeric substances (EPS) e.g., *Chlorosarcinopsis* and *Tetracystis*, thereby supporting further biocrust formation. Others form large unicells e.g., *Spongiochloris minor*, that are associated with the biocrust matrix (Büdel et al., 2016). *Tetracystis* cf. *sarcinalis* and *Spongiochloris* cf. *excentrica* were exclusively found in the windwatt at Pramort (**Publication III**) but were reported in different dunes along the Baltic Sea coast (Schulz et al., 2015). Representatives of the genera *Chloroidium, Stichococcus,* and *Myrmecia* (Trebouxiophyceae, Chlorophyta) were almost omnipresent on the Schaabe spit and the inland dune. These genera include species that are known as symbionts of lichens or living epiphytically on lichens (Chiva et al., 2023; Pino-Bodas et al., 2023). A clear assignment of members of the two Chlorophyta classes to a specific biocrust type was not possible.

Filamentous algae belonging to the genus of *Klebsormidium* (Klebsormidiophyceae, Streptophyta) occur in low diversity in the biocrusts but may produce relatively high biomass. They are discussed as key players in biocrust communities because of their filamentous and sticky features which lead to a high physical networking potential between algae and soil particles (Büdel et al., 2016). Due to the wide range of environmental factors tolerated by this genus, it has a cosmopolitan distribution in numerous terrestrial habitats (Karsten and Rindi, 2010) and its frequent presence in biocrust has been proven several times in other studies in central Europe (Glaser et al., 2017; Karsten et al., 2010; Langhans et al., 2009). Three species of *Klebsormidium* (*K.* cf. *flaccidum, K.* cf. *subtile*, and *K. crenulatum*) were found in all observed biocrusts in this thesis. Especially along the dune chronosequences at Darsser Ort and Pramort *Klebsormidium* species were represented in early successional biocrusts stages on the yellow dunes and in those interspersed with mosses on the grey dunes. Such a wide distribution of Klebsormidiaceae could also be confirmed by Glaser et al. (2018) in temperate forests and by Schulz et al. (2015) in coastal dunes of the Baltic Sea. Even if ones found in mature biocrust stages (mature dune at Darsser Ort) species of the genus *Klebsormidium* were predominantly detected in early successional biocrusts in the studies of this thesis.

Terrestrial diatoms are part of a complex microbial soil community that received fairly less research interest than their aquatic equivalents (Geisen et al., 2017). The occurrence of diatoms in biocrusts of the Baltic Sea dunes was evaluated as preliminary work of subsequent ecophysiological experiments on desiccation and temperature tolerance (**Publication II**). The three sampling sites of this study were close to those of **Publication III** (peninsula Fischland-Darß-Zingst) and included early and mature biocrust types. A total of 47 diatom species were morphologically identified in the biocrust samples. All of them were pennate species. Each site showed a similar richness (28-30 species). According to literature, six species have an exclusively terrestrial life cycle. These were *Pinnularia borealis*, *Pinnularia intermedia*, *Hantzschia amphioxys*, *Luticola terrestris*, *Mayamaea fossalis*, and *Nitzschia* cf. *pusilla.* In addition, after inoculation of the field sample material in the laboratory, two further terrestrial species could be identified. These were *Achnanthes coarctata* and *Hantzschia abundans*. *P. borealis* is a truly cryptic species complex, meaning that this is a group of closely related organisms that are so similar in appearance that they are often condensed into a single taxon or several, almost identical, taxa. Pinseel et al. (2020) found in their wide biogeographical study that *P. borealis* is a complex consisting of at least 126 species. Thus, a cryptic diversity in the field samples from the temperate coastal dunes can also be suspected. Terrestrial habitats, like moist to dry soils but also

mosses, are known to be suitable habitats where the *P. borealis* complex can be found. Their frequent occurrence was also reported in Icelandic biocrusts (Pushkareva et al., 2021) and the biocrusts of coastal dunes at the Baltic Sea (Schulz et al., 2015). Terrestrial diatoms seem to be well-adapted to desiccation and extreme cold temperature events (Hejduková et al., 2019; Souffreau et al., 2010), but comprehensive data on their ecophysiology are still missing. There are various mechanisms for diatoms of adapting to extreme habitats such as coastal sand dunes. Raphid pennate diatoms (Figure 9) can actively move within their habitat (e.g., moving vertically in sediments) (Kociolek et al., 2015) by EPS excretion through the raphe (Underwood and Paterson, 2003). This behavior allows for a photoprotective/phototactic movement to survive even in harsh habitats. Hence, these microalgae handle unfavorable conditions by migrating deeper into the sediment to avoid desiccation and UV radiation (Blommaert et al., 2018; Consalvey et al., 2004). A further strategy could be the production of mycosporine-like amino acids (MAAs) as UV-protective substances. This mechanism was reported for marine diatoms (Helbling et al., 1996; Jeffrey et al., 1999). Since MAAs were documented in isolates of terrestrial green algal genera, like *Interfilum* and *Klebsormidium* (klebsormidin A and klebsormidin B) (Hartmann et al., 2020) it seems feasible that terrestrial diatoms could also follow this strategy. However, the accumulation of MAAs as UV-protective substances in terrestrial diatoms has not been experimentally proven up to now and was under investigation in **Publication II**. In this study, *P. borealis* and *H. amphioxys* were the only two cultivated diatoms where MAAs were detected based on the chromatographic and photometric techniques used. The absorbance at 333.5 nm most likely indicates that the detected MAA was Mycosporine-2-glycine. Still, the measured retention time of 6 min did not match that of the corresponding standard (Porphyra-334), which is why this result was not chemically confirmed. Both, mass and nuclear magnetic resonance spectroscopy have to be applied to elucidate the chemical structure of this putative MAA.

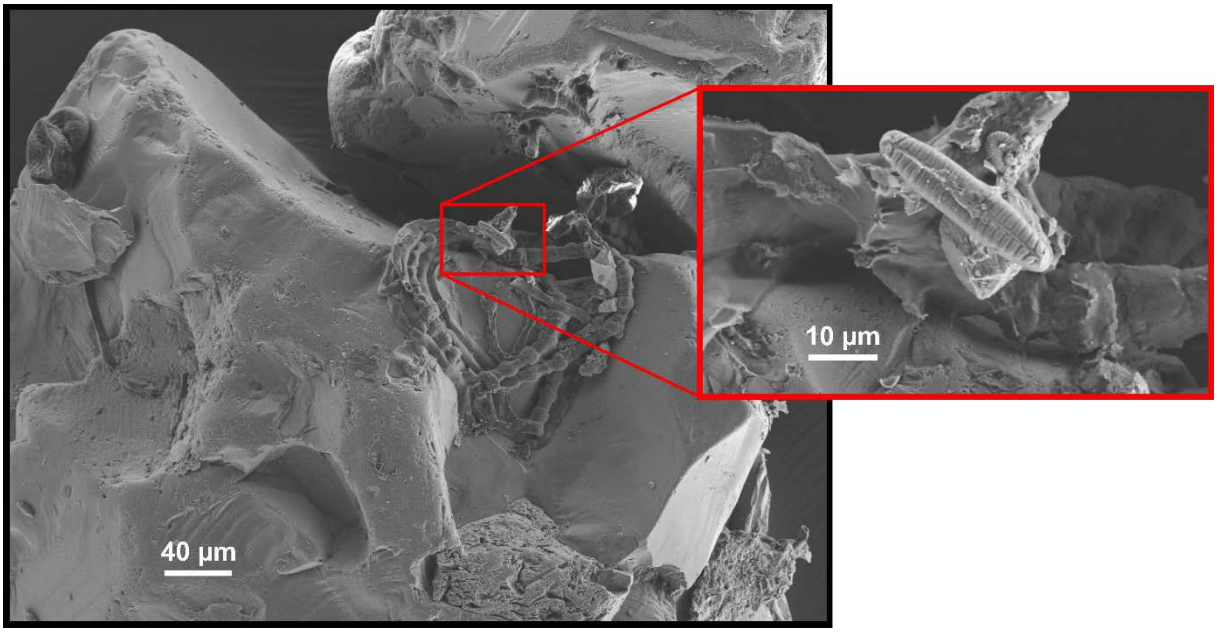


Figure 9: Scanning electron microscopy pictures showing a diatom (*Pinnularia* spec.) attached to a sand gain (sampling site was Pramort, Image: © A. Springer, EMZ, Rostock).

Oxygenic photosynthetic bacteria

Cyanobacteria are well-known biocrust-forming organisms mostly reported from biocrusts in semiarid and arid regions (Danin et al., 1989; Fernandes et al., 2018; Garcia-Pichel et al., 2001; Hagemann et al., 2015; Singh et al., 2014). The diversity of cyanobacteria was studied in this thesis using two different methods. Cyanobacteria were identified microscopically (**Publication I** and **III**) and analyzed via amplicon sequencing of the 16S rRNA gene (**Publication IV**). Morphologically four species within two genera (*Microcoleus* and *Nostoc*) could be identified. Both are frequently reported filamentous cyanobacteria which are considered key genera in biocrusts contributing to initial nutrient inputs into the ecosystem via photosynthesis and nitrogen fixation from the atmosphere (Büdel et al., 2016). *M. vaginatus*, *N.* cf. *edaphicum*, *N*. cf. *linckia*, *N*. cf. *commune* (Figure 10) were found primarily in early successional biocrust stages but were only determined in one mature biocrust sampling plot (grey dune at Pramort). When present cyanobacteria were the dominating biocrust-forming organisms likely together with *Klebsormidium* species. Molecular biological analyses revealed a more detailed resolution of the cyanobacterial diversity within biocrusts. 164 Cyanobacteria-assigned ASVs (amplicon sequence variants, 5.3% of total bacterial sequences) were detected along the Baltic Sea dunes and the inland dune and could be further summarized into 12 families. Comparable to the morphological determination the ASVs assigned to the family Nostocaceae (45 ASVs, 25.5% of total cyanobacterial sequences) dominated within the cyanobacterial community. The ASVs within this family could be assigned to three genera, namely *Calothrix*, *Nostoc*, and *Scytonema*.

The genus *Nostoc* showed the highest relative abundance of the Nostocaceae (21 ASVs, 99% of Nostocaceae-assigned sequences). Schulz et al. (2015) named *Nostoc* as one of the most important biocrust-forming cyanobacteria genera which they found frequently in their study along the dunes of the Baltic Sea coast. Their ability to excrete extracellular polysaccharides and lipopolysaccharides thereby forming a matrix together with soil aggregates favors their colonization in the mobile dune sediment. Therefore, cyanobacteria can be seen as important biocrust-forming microorganisms comparable to the microalgal genus *Klebsormidium* (Cania et al., 2019; Mazor et al., 1996). Besides, Nostocaceae are efficient nitrogen-fixing bacteria (Brankatschk et al., 2013). This ability allows for their colonization, especially in the early stages of biocrust development containing low levels of nutrients. Therefore, they are important primary dune habitat colonizers (Büdel et al., 2016) which are already used for biocrust rehabilitation in China, among other filamentous cyanobacterial taxa (reviewed by Zhou et al., 2020). Along the dune chronosequences, a decline in the relative abundance of Cyanobacteria-assigned ASVs in mature compared to early successional biocrust stages was visible. Earlier studies on biocrust cyanobacteria in Chinese temperate and cold deserts reported a similar trend (Duan et al., 2024; Li et al., 2020). The same applied to a study on a German inland sand flat, describing a significant decrease in the mean species numbers of cyanobacteria during succession (Langhans et al., 2009). A possible reason for this development might be the change in the soil pH with dune succession. With ongoing pedogenesis and soil horizon formation in older dune types the pH decreases due to the leaching of cations and their replacement by H^+ and Al^{3+} ions. Acidic soils seem to be less frequently colonized by cyanobacteria, e.g., Brock (1973) reported a decline and even the total absence of cyanobacteria in habitats with a pH less than 4 or 5. Some exceptions to this generalistic assumption have to be made based on the findings by Whitton and Potts (2002) who described heterocystous cyanobacterial species as the most tolerant to low pH values.

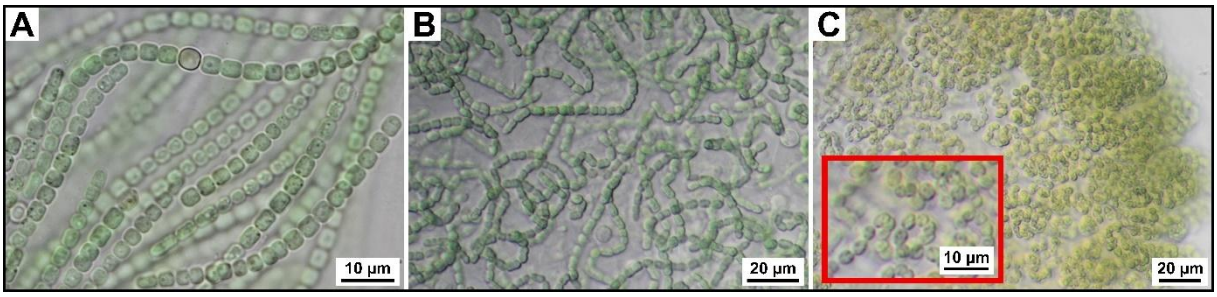


Figure 10: Representatives of the genus *Nostoc*. A=*N*. cf. *linckia*, B=*N*. cf. *edaphicum*, C=*N*. cf. *commune* found in biocrusts of coastal and inland sand dunes. Red frame highlighting *N.* cf. *commune* cells. Microscope images: © T. Mikhailyuk.

Heterotrophic bacteria

The bacterial diversity was studied using HTS methods and reported in **Publication IV**. The ecological functions of bacteria in biocrusts are complex and of increasing scientific interest. The worldwide pattern of bacterial soil microbiomes is reflected in the findings of the bacterial study conducted within this thesis. The most abundant and ubiquitous phyla found in soils include typically Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, Firmicutes, Gemmatimonadetes, Planctomycetes, Proteobacteria, and Verrucomicrobia (Janssen, 2006; Nunes da Rocha et al., 2009). While the taxonomic assignment of the obtained bacterial ASVs revealed the dominance of Actinobacteriota in the biocrusts from the dunes along the Baltic Sea coast, their relative abundance in the inland dune decreased. Therefore, Proteobacteria dominated the bacterial community in this dune habitat. The dominance of these two phyla in biocrusts is comparable with studies by Moreira-Grez et al. (2019) in a Mediterranean semi-arid climate, Steven et al. (2014) in an arid scrubland and Glaser et al. (2022b) from Baltic sand dunes. Changes in the taxonomy between the successional biocrust stages have been determined along all studied chronosequences. While the relative abundance of the two dominating phyla showed no considerable change, the relative abundance of Verrucomicrobiota, Acidobacteriota, and Planctomycetota increased with biocrust succession. The relative abundance of Deinococcota- and Bacteroidota-assigned ASVs in mature successional biocrust stages was decreased compared to early ones. This suggests that bacterial species of these phyla inhabit characteristics that might favor their main occurrence in early biocrust types. Acidobacteriota and Planctomycetota include decomposing bacteria (Dedysh and Ivanova, 2019; Dedysh and Sinninghe Damsté, 2018; Kulichevskaya et al., 2017). Organic matter accumulation in the biocrusts increased with increasing biocrust development in mature dune types (cf. Chapter 2.1.1). The decomposers likely benefit from this nutrient accumulation and energy source and increase in their relative abundance. Further, the genomic potential of cellulose biosynthesis reported from Acidobacteria could enable them to colonize particularly harsh habitats, e.g., sand dunes, since bacterial cellulose can facilitate survival in the soil through biofilm formation, thereby retaining moisture, as reported from Proteobacteria (Ude et al., 2006; White et al., 2006). Deinococcota (45 ASVs, 2.3% of total bacterial sequences) occur almost exclusively in early successional biocrusts (99.7% of Deinococcota-assigned sequences). Their radiation resistance, salt tolerance, and strong resistance to desiccation likely allow their colonization of thin biocrusts in which the organisms are exposed to direct sunlight. Whereas in mature biocrusts it can be assumed that they are shaded by the macrophytic cryptogams growing there (Li et al., 2013; Mattimore and Battista, 1996).

The ASV richness of bacteria was interpreted as the alpha diversity of the community. The trend of an increase in the bacterial richness from early successional stages to mature biocrusts could be identified and was also proven to be statistically significant for study site Pramort (Welch Two Sample t-test, t=-2.9, df=7.8, p=0.02). This finding is in line with other studies on biocrust community structures that reported an increase in alpha diversity with their succession (Duan et al., 2024; Maier et al., 2018; Moreira-Grez et al., 2019). Besides a shift in the bacterial richness between the biocrust types their community composition was more similar in mature biocrusts compared to early ones (**Publication IV** Figure 6). Maier et al. (2018) made a similar observation in biocrusts from the Northern Cape Province, South Africa. Thus, a change from more generalized to specialized organisms along dune succession can be assumed. The successional stage is one key factor influencing the bacterial richness in biocrusts and their composition along the studied dune chronosequences (PerMANOVA, 10.7% explained variance, $p < 0.01$; **Publication IV** Table 1). Further, an overall improvement of the soil (e.g., nutrient and soil organic matter enrichment along with biocrust succession) likely influences the bacterial community composition (Duan et al., 2024). Single environmental parameters investigated, such as sediment pH (as described for cyanobacteria) and water availability, can also be considered decisive factors driving the bacterial community structure in the biocrusts. Chen et al. (2005) demonstrated a positive connection between microbial biomass in a sand dune forest and soil moisture. Moss-dominated biocrusts have a higher water-holding capacity and enhance the moisture content within the biocrusts (Belnap et al., 2013; Chamizo et al., 2016; Sun et al., 2022). Bacteria can benefit from these natural water reservoirs. The water availability varies greatly over the year. These fluctuations in water availability for bacteria greatly impacted their community composition in coastal dunes close to the Mediterranean coast (Wasserstrom et al., 2017), which can also be assumed to apply to the dune chronosequences studied in this thesis. Nutrients such as nitrogen and phosphorus can be a limiting factor in dune ecosystems (Filippelli, 2019). Therefore, bacteria have developed various mechanisms to survive under these nutrient-poor conditions. These include the fixation of atmospheric N (Barger et al., 2016), as briefly described in the context of cyanobacteria earlier, or the decomposition of organic matter. P supply depends on its deposition, the availability of organic material, the geogenic availability, and efficient acquisition and solubilization mechanisms by the bacteria. Common soil bacteria (e.g., *Pseudomonas*, *Azotobacter*) solubilize P in soils (e.g., rhizobacteria producing P-solubilizing indole acetic acid or are associated with mycorrhizal hyphae; Jones and Oburger, 2011 and references therein) and use it for biomass growth (Richardson and Simpson, 2011). Further, the nutrient ratio between N and P has to be considered as a factor influencing their uptake, as well as their overall bioavailability. Kurth et al. (2020) showed that the turnover of N and P strongly correlated when nutrient concentrations were high but the N:P ratio was low and that N mineralization was strongly correlated to P turnover when both elements are easily bioavailable.

Mosses and Lichens

Mosses and lichens dominated the biocrusts of the mature successional stage. Their occurrence also indicated the transition into the grey dune area of the chronosequence (Leuschner and Ellenberg, 2017). A total of 25 moss species were identified in the studies of this thesis. The phylum Bryophyta was significantly more species-rich (22 species) than the phylum Marchantiophyta (liverwort). *Ceratodon purpureus* was the most ubiquitous moss in all studies. This species has an advantage, especially on still partly mobile dunes where the surface undergoes frequent sand deposition, due to

its high tolerance to sand burial (Martínez and Maun, 1999). Such a wide distribution of *C. purpureus* in biocrusts of post-mining sites was also previously demonstrated by Gypser et al. (2016a). Three species of the genus *Hypnum* were found across all study sites. It turned out that these moss species were more restricted to mature and immobile dune areas perhaps due to their lower tolerance to light compared to *C. purpureus* (Ellenberg and Leuschner, 2010). Baltic pine trees (*Pinus sylvestris* L.) and shrubs growing on these dunes along the chronosequences provide partial shade promoting the growth of *Hypnum*. *Dicranum scoparium* was found at all four sampling sites only in later dune successional stages. Similar to *Hypnum*, *D. scoparium* prefers to grow partially shaded (Ellenberg and Leuschner, 2010). Consistent with the results of this thesis, Isermann (2011) reported an increase of *D. scoparium* along a chronosequence of coastal dunes on the island of Spiekeroog and highlighted its dominance in mature dune heathlands. *Campylopus introflexus* dominated the older dune areas along the inland dune transect. This moss species, originally only found in the southern hemisphere, is now spreading as an invasive neophyte also to the northern hemisphere temperate coastal dunes and other sandy habitats, particularly in the Netherlands, Belgium, and Germany (Biermann and Daniëls, 2001). It becomes a threat to protected areas such as the 'Dünengebiet und Halsetal bei Verden-Neumühlen' which is a 'Special Area of Conservation' protected under the Habitats Directive (European Community, 1992). This invasion can seriously affect the endemic cryptogamic community of the prevailing habitat type 2330 (Inland dunes with open grasslands with *Corynephorus* and *Agrostis*). Especially habitat-specific moss species and lichens belonging to the genus *Cladonia* will be further replaced by *C. introflexus*. Isermann (2011) has already detected this invasive behavior on the grey dunesof Spiekeroog. This study reported that the *C. introflexus* increase generally results in overall species-poor communities. *Cephaloziella divaricata* was the most ubiquitous found liverwort among all studied dune chronosequences. Durham et al. (2018) found out that this moss species is a common member of the western Montana (USA) grassland biocrust community, sometimes creating an overall black biocrust. This foliated and very small moss is often overlooked. *C. divaricata* mainly colonizes light-exposed and dry habitats. It prefers acidic, humic soils which are low in their lime content. It often grows alongside the former-named mosses *C. purpureus* and *H. cupressiforme* s. l. among others (Frahm and Frey, 2004). In their study, Gypser et al. (2016a) named *Polytrichum piliferum* as another dominant moss. The studies conducted for this thesis could identify the presence of *P. piliferum* only in two dune sampling sites (inland dune and Pramort: both mature biocrust stages).

38 lichen species were recorded along all four studied dune chronosequences in this thesis. The genus *Cladonia* was most rich in species (22). This genus dominated grey and mature dune types where moss and lichen-dominated biocrusts were most common. *Cladonia* species (e.g., *C. rei* and *C. foliacea*), which favor moderate acidic substrate conditions (pH 4.9-5.6), were found in the grey dune areas while those relying on stronger acidic (pH < 5.6) and sandy habitats (e.g., *C. arbuscular* and *C. gracilis*) grew predominantly on the mature dunes (British Lichen Society, 2022; Landolt et al., 2010). They are all common coastal dune lichens (Isermann, 2011; Remke, 2003). Lichens that prefer to grow on plant debris and litter (e.g., *Lecania cyrtella*, *Myriolecis hagenii*, *Polyozosia persimilis*) were mainly found in intermediate and early grey dunes. *Bacidina etayana* prefers to grow on dune grass litter only (Dolnik, 2005; Wirth et al., 2013). Further, all the litter-inhabiting species mentioned prefer colonizing habitats with subneutrophic (pH 5.7-7) to basotrophic (pH > 7.1) soil conditions. Detailed lists of pH preferences of all determined lichen species can be found in the supplementary material of **Publication I** and **III.** Overall sand-inhabiting lichen species dominated the mature biocrusts along the Baltic Sea coast and the inland dune area.

2.1.3 **Interim conclusion on species diversity and community composition in biocrust from dunes**

Microalgal diversity

- The highest species richness was found in the phylum Chlorophyta (20 taxa). Although the species richness within the Charophyta was lower, the genus *Klebsormidium* can still be seen as the most important biocrust-forming algae, as its representatives formed the dominant microalgal group within the biocrusts.
- No core species community of eukaryotic algae could be used as an indicator to distinguish between the different types of biocrust. Nevertheless, species of the genus *Klebsormidium* were predominantly found in early successional biocrusts.
- Algal species richness decreased with increasing biocrust succession. This trend was not recognizable in the inland dune. The biocrusts on secondary dunes (yellow, intermediate, and early grey dunes) that still experience sand movement showed the highest species richness of microalgae in the biocrust along the successional gradient.
- Six terrestrial diatom species were found at three sampling sites on the Fischland-Darss-Zingst peninsula, based on morphological identification of the biocrust field samples. Those are: *Pinnularia borealis, Pinnularia intermedia, Hantzschia amphioxys, Luticola terrestris, Mayamaea fossalis,* and *Nitzschia* cf. *pusilla*. Two additional species (*Achnanthes coarctata* and *Hantzschia abundans*) were found after inoculating the field material in the laboratory cultures.

Bacterial diversity

- Cyanobacteria:
  - 164 Cyanobacteria-assigned ASVs were determined by DNA sequencing and further assigned into 12 families.
  - Morphological and molecular approaches revealed Nostocaceae to be the dominant family within the cyanobacterial community.
  - *Microcoleus* and *Nostoc* were the dominant genera in early successional biocrust stages, determined by direct microscopy and supported by HTS.
  - Bacteria are important biocrust-forming organisms: Contributing to initial nutrient inputs into the ecosystem (N-fixation) and sediment aggregation by EPS secretion, thereby promoting dune stability.

- Heterotrophic bacteria:
  - Actinobacteriota dominated in the biocrusts from the dunes along the Baltic Sea coast. Whereas, Proteobacteria dominated the bacterial community in the inland dune area.
  - The relative abundance of Verrucomicrobiota, Acidobacteriota, and Planctomycetota increased with biocrust succession. The relative abundance of Deinococcota-assigned ASVs in mature successional biocrust stages was lower compared to early stages.
  - Bacterial alpha diversity (ASV richness) increased from early successional stages to mature biocrusts.

- Key factors influencing bacterial richness and community composition in temperate sand dunes: The successional stage. Further important factors are the soil properties (e.g., nutrient contents, soil organic matter enrichment, sediment pH (as described for cyanobacteria), and water availability).

Macrophytic cryptogamic diversity

- Mosses and lichens form the dominating biocrust type in later stages of dune development along the chronosequences.
- *Ceratodon purpureus* was the most ubiquitous moss among all studied dune chronosequences. Its advantage lies in its high tolerance to sand burial.
- Three species of the genus *Hypnum* were primarily found in mature and immobile dune areas, shaded by shrubs and pine trees, likely due to their lower tolerance to light irradiation.
- *Dicranum scoparium* seemed to be a key moss species in later dune successional stages.
- *Campylopus introflexus* dominated the mature dune area along the inland dune chronosequence. This neophytic moss species might replace endemic cryptogams in the upcoming years, causing overall species-poor communities.
- 38 lichen species were recorded. The genus *Cladonia* was most rich in species (22). The soil pH seemed to be the soil parameter most likely explaining the overall lichen community composition within the mature biocrusts. But further in-depth studies are needed here.

2.2 Synopsis of biocrust's functional traits and resulting ecosystem services

This chapter illustrates the ecological relevance and ecosystem services provided by biological soil crusts. Based on the detailed biodiversity determination of biocrusts, assumptions are made about their potential functions, and selected services are discussed based on the data collected. It demonstrates which of the respective dominant cryptogamic groups have a special share in developing a function during biocrust succession.
The concept of 'Ecosystem Services' developed by the Millennium Ecosystem Assessment (Hassan and Scholes, 2005) strengthens the connection between the human population and ecosystems. Within this concept ecosystem services are assigned into four classes: namely 'provisioning', 'supporting' (e.g., nutrient cycling, soil formation, primary production), 'regulating' (e.g., flood and storm protection, erosion prevention), and 'cultural' services. The services provided by biocrusts can also be found in these categories and their ecological relevance is described in the following.

2.2.1 **Early successional biocrusts**

Phototrophic microorganisms are the early biocrust pioneers in temperate biocrusts. The filamentous structure of biocrust-builders such as microalgae (e.g., *Klebsormidium*) and cyanobacteria (e.g., *Nostoc* and *Microcoleus*) is one of the first mechanisms introducing soil stability to the biocrusts (Belnap and Gardner, 1993). The filaments entrap soil particles causing the first physical structures of the early biocrusts (Mugnai et al., 2018). A second mechanism introducing stability to the biocrust is the excretion of extracellular polysaccharides (EPS). EPS are excreted as sheaths and capsules, or unevenly dispersed as mucilage (Rossi and De Philippis, 2015) binding to soil particles, forming microaggregates, and further a complex extracellular polymeric matrix (EPM). This matrix offers several benefits for the biocrust, such as physical integrity and stability, nutrient accumulation, and moisture retention (Colica et al., 2014; Rossi et al., 2018). Further, the microbial matrix provides various ecosystem services. The EPM positively impacts the prevention of sediment erosion, organic matter and nutrient accumulation (binds and mediates penetration of micronutrients into the cell, and promotes cell-to-surface and cell-to-cell interactions), and the hydrological cycle (Belnap and Büdel, 2016; Fischer et al., 2012; Six et al., 2004; Totsche et al., 2018). Cyanobacteria and microalgae are prominent contributors to this EPM formation (Büdel et al., 2016). They seemed to be particularly relevant in early biocrusts, as at this point of succession they still perform the crust-forming trait without the presence of further macrophytic cryptogams, while in later biocrust succession stages their function is supported or possibly replaced by the presence of mosses and lichens, which also contribute to matrix formation through their filamentous components (e.g., moss rhizoids, lichen rhizines) (Kidron et al., 2010; Weber et al., 2022 and references therein). Cyanobacteria of the sheathed filamentous cyanobacterial genus *Nostoc* were particularly prominent in the biocrusts investigated. Their great contribution to early biocrust formation and stability has already been proven by other scientists (Roncero Ramos et al., 2019; Tamaru et al., 2005). McKenna Neuman et al. (1996) emphasized the advantages of filamentous species over non-filamentous ones when comparing the surface stability of soils. Filamentous species are much more effective at gluing particles together because filaments were present also during periods of dormancy, whereas non-filamentous species mostly form single thick-walled cells under unfavorable conditions not supporting soil stability. Other less acknowledged producers of EPS are members of Actinobacteria and Proteobacteria (Limoli et al., 2015; Martínez-Cánovas et al., 2004). These two were the dominating bacterial phyla along the coastal and the inland dune chronosequence,

respectively. This thesis highlights their important role as pioneers in biocrust formation. As for microalgae, bacterial polysaccharides stick to soil particles, connecting them and building larger aggregates (Huang et al., 2015; Limoli et al., 2015). Thus, biocrust bacteria can also contribute to a reduction in soil erosion caused e.g., by rainfall up to 98% (Kheirfam et al., 2017).

The formation of this matrix has probably the most discussed beneficial effect on the stability of the surrounding sediment. This ecosystem service is particularly relevant in the coastal and inland dunes studied. In **Publication II** the surface stability provided by the biocrusts was measured using a penetrometer. Early biocrusts (near Darsser Ort) and mature biocrusts (Pramort) were compared with each other. The latter were already moss and lichen-dominated while these cryptogams were missing at the other sampling site. Stability increased from early (0.4 and 0.5 MPa) to mature biocrusts (1.1 MPa). Besides the stabilizing function, the organo-mineral matrix works as a hydrated protective coat. This helps the biocrust organisms to tolerate desiccation and freezing more efficiently (Tamaru et al., 2005). Further, it enlarges their tolerance against UV radiation since the sheath of several cyanobacterial species contains UV-screening pigments such as mycosporine-like amino acids (Rossi and De Philippis, 2015) and scytonemin. Its production is a photoprotective mechanism against short-wavelength solar irradiance (Garcia-Pichel and Castenholz, 1991; Karsten et al., 1998). A crucial factor when it comes to biocrust-formation is the availability of water to the organisms. Therefore, EPS secretion-induced soil aggregation can be of critical importance in regulating the delivery and retention of water within the biocrust (Rossi et al., 2018). In the early successional stages of biocrust formation, EPS will swell once they get wetted and cause a pore-clogging effect. Consequently, the water infiltration into the soil is reduced which means that the water collects more on the soil surface and runs off more quickly down the dune slope e.g., during rain events (Eldridge et al., 2020; Kidron et al., 1999; Kidron and Yair, 2008). Thereby, water gets redirected but remains within the biocrusts (Fischer et al., 2012). Sun et al. (2022) could prove that biocrusts had a significantly lower constant infiltration rate and infiltration water amount than bare soil. At the same level of water content, water sorptivity, describing the early stage of water flow into the soil, and diffusion were lower in biocrusts compared to bare soil. This is reflected in a higher water content in biocrusts, indicating an increase in water-holding capacity and water availability of the biocrusts. Gypser et al. (2016b) also observed a decrease in the infiltration rates with increasing biocrust formation on reclaimed soils in temperate regions. These researchers confirmed that cross-linking between sand particles and filamentous green algae caused pore-clogging in the sandy sediment which in turn positively affected water retention in the biocrusts. The onetime-measured water contents in dunes colonized by the early biocrusts studied along the chronosequences showed already higher values than the uncolonized dunes (e.g., **Publication III** Darsser Ort: yellow dune = 3.9% fresh weight (FW) and early grey dune = 8.1% FW).

The lipo- and polysaccharides and further byproducts excreted by the microorganisms can also serve as a nutrient source to other organisms since they consist mainly of carbon-related compounds. Due to the sticky texture of the EPM nutrient-rich dust particles can be caught and efficiently immobilized in the EPM. This makes the EPM a nutrient reservoir for other microorganisms and prevents potential loss through run-off or leaching (Nishanth et al., 2021 and references therein). In addition to nutrient catchment within the EPM microorganisms accumulate, transform, and store nutrient elements such as nitrogen in their biomass (Barger et al., 2016; Castillo-Monroy et al., 2010). Brankatschk et al. (2013) reported that the bacterial impact on nitrogen turnover was enhanced in biocrusts compared to the bare soil in a European inland dune. According to an extrapolation by Elbert et al. (2012), the global N take-up by cryptogamic ground covers (biological soil and rock crusts) amounts to around 0.033 Pg N yr^{-1} corresponding to approximately ~31% of total BNF (biological nitrogen fixation). N-fixing in biocrust is mainly carried out by cyanobacteria and other bacteria (Delmont et al., 2018; Nelson et al., 2021;

Roncero-Ramos et al., 2022; Sellstedt and Richau, 2013) that dominate early successional biocrusts in the studied coastal temperate sand dunes.

2.2.2 Mature successional biocrusts

The mature biocrusts dominating in the immobilized older dune types along the chronosequences are characterized by a high occurrence of mosses and lichens. These macrophytic cryptogams in turn influence the ecosystem function of the surrounding habitat. They give the biocrust additional stability and are therefore the key players in protecting the dunes from erosion at this stage of succession (Martin, 1959).

The occurrence of mosses alters biocrusts' functions concerning their water run-off infiltration balance. While early successional biocrusts dominated by microalgae are known to inhibit infiltration and promote surface runoff, mosses have an even higher water-holding capacity. This first suggests a decrease in the infiltration rate. But contrary to this assumption Gypser et al. (2016b) concluded that with proceeding succession the dry substrate might have been aerated by the rhizoid growth of mosses. These changes in the crustal structure again led to an increase in the infiltration. After passing a threshold of absorption capacity of the mosses infiltration into deeper soil layers was potentially increased by water transport along the moss rhizoids reducing small-scale run-off (Spröte et al., 2010). In line with these results Fischer et al. (2012) found out that at the base of temperate dunes (Germany) where the water holding capacity was highest, infiltration and wettability increased again due to the occurring mosses. Chamizo et al. (2012) also demonstrated the positive effect of increasing colonization by lichens in the biocrusts causing a decrease in water run-off during low-intensity rain events. The described findings are comparable to the measured water contents in the studied grey and mature dunes along the four chronosequences where higher water contents were measured in mature successional biocrust stages compared to the early ones (**Publication I** and **III**). With increasing colonization by the macrophytic cryptogams, a new source of nutrients also forms in the biocrusts. In **Publication I** and **III** an increase in the total nutrient (C_t, N_t, P_t) concentrations within biocrusts with succession could be observed, which is in line with previous studies (Chamizo et al., 2012; Zhao et al., 2010). This finding leads to the conclusion that specific species composition rather than the overall species richness shapes the ecosystem function of nutrient accumulation. Mosses form larger thalli and can accumulate higher amounts of C and N in their biomass than in microalgal biocrusts (Seppelt et al., 2016). Further, thalloid macrophytic cryptogams like mosses grow deeper into the sediment which allows for a 3D expansion of the C-rich organic material and nutrients in the biocrust (Dümig et al., 2013). By accumulating atmospheric carbon, especially mature biocrusts function as carbon sinks storing large amounts within their biomass (Duran et al., 2021; Eldridge et al., 2023; Fischer and Veste, 2018; Kheirfam, 2020). Elbert et al. (2012) estimated the global carbon uptake by cryptogamic ground covers (biological soil and rock crusts) of around ~2.4 Pg C yr^{-1}. The biocrusts by themselves account for around 1% of global net primary production by terrestrial vegetation (~0.6 Pg C yr^{-1}) (Sancho et al., 2016). When taking a closer look at the coastal Baltic areas, the range of N wet deposition is 3-8 kg N ha^{-1} yr^{-1} (Fjæran, 2006; Remke et al., 2009 and references therein). Besides cyanobacteria and other bacteria, lichens of mature successional biocrusts take up atmospheric N. Therefore, *Cladonia portentosa* was used by Remke et al. (2009) as a biomonitor, which takes up wet and dry N deposition. These researchers found out that with increasing N loads on the dunes, lichen-rich short grass vegetation shifts towards species-poor vegetation dominated by the tall graminoid *Carex arenaria.*

2.3 Synopsis of soil formation on temperate sand dunes

In addition to the described successive development of the biocrusts and their cryptogamic communities, soil-forming processes can be observed when studying the dune development along its chronological series. This so-called pedogenesis is based on several soil-forming factors. These factors were summarized in a general equation by Schlichting (1993) assuming that climate, topography, flora, fauna, and humans impact the parent rock material and the organic matter accumulation leading to soil formation.

Soil-forming processes such as desalinization, acidification, and decalcification, over time, lead to the transformation of the rock material, mineral transformation e.g., mobilization of iron, and decomposition of organic matter. The further translocation of the material causes the formation of soil horizons. Cryptogamic colonization on dune surfaces can significantly influence these soil-forming processes during succession, promoting initial pedogenesis along the chronosequence. This chapter will discuss the **second overarching hypothesis** addressed in **Publications I** and **III**. Here, some traits already mentioned as general functional traits (cf. Chapter 2.2) are taken up again and placed in the context of soil genesis.

> **Hypothesis 2:** *With ongoing biocrust succession on the sand dunes along the chronosequences, early soil genesis can be observed in the top sediment layer. These processes are strengthened by the colonization of the uppermost sediment layer by the biocrusts.*

Along all four studied dune chronosequences, physicochemical parameters (pH, electrical conductivity, and total nutrient contents) and the organic matter content, as a biotic trait were examined and interpreted as indicators of soil-forming processes. Along the two dune chronosequences at Darsser Ort and Pramort, additional in-depth pedological analyses on sediment/soil cores (cf. **Publication III** Figure 4) gave an insight into the process of decalcification ($CaCO_3$ content) and the chemistry of Fe-containing compounds potentially indicating mineral weathering. These cores were assigned to soil horizons according to the German classification system 'KA5' (Ad-hoc Arbeitsgruppe Boden, 2005). The cores sampled in the early successional stages of dune development at Darsser Ort and Pramort represented parent material (C-horizon) on which an initial A-soil horizon has formed. These cores were therefore described as 'A + C'. The symbol 'L' indicated a litter layer on top of the mineral material. Additional geogenic (prefixed to main symbol: i = silicon-rich, l = loose soil material) and pedogenic (postposed to main symbol: i = initial, h = humic A-horizon) characteristics were added to qualify the main soil horizons.

As a starting point for soil genesis, the input of nutrients (i.e., the supply of carbon, nitrogen, and phosphorus in their bioavailable forms) is essential to enrich the sediment. Primary producers provide energy in the early processes of soil genesis (Buscot, 2005). Regarding the studied coastal biocrusts, these are photosynthetic microalgae and cyanobacteria. Along all four dune chronosequences, an enrichment with carbon and essential nutrients (N and P) from early to mature biocrusts was detected which is in line with previous studies on biocrusts in temperate forests and along the Baltic Sea coast (Baumann et al., 2017; Schulz et al., 2015 and cf. Chapter 2.2). The pioneer biocrust organisms deliver energy-rich organic material into the soils either in the form of (dead) biomass or by direct exudation of photosynthetic products through their cell walls (Buscot, 2005). The results of the sediment/soil core analyses from Darsser Ort and Pramort demonstrated clearly that the C_t content of the biocrust

was always significantly higher than that of the underlying soil horizons proving that the initial input of organic biomass originates from the biocrusts. This conclusion is also supported by the fact that most of the carbon measured was organically bound (70-100%). Since in the underlying soil horizons (ilC mainly) almost only organically-bound carbon was detected, it can be assumed that the biomass was translocated through the biocrusts in deeper soil horizons, which otherwise barely obtain organic carbon from other sources (**Publication III**). Further, an increase in the N_t concentration in the topsoil layer along the chronosequences was detected. This again illustrates the important function of biocrust organisms in fixing nutrients from the atmosphere (Zhao et al., 2010) and their accumulation in terrestrial ecosystems (Glaser et al., 2018; Pushkareva et al., 2022).

A decrease in the pH was measurable along all chronosequences. While in the early successional dune types the pH ranged between 5.2 and 6.6, the pH in the mature dunes reached values in the acidic range (3.7 to 5.6). This acidification along dune succession indicates the microbial activity within the biocrusts. Biocrust microorganisms in early biocrusts, for instance, excrete protons and organic acid anions to solubilize stable bound nutrients and thereby the nutrients become bioavailable (Bardgett, 2005; Fox, 1995). However, this is only one way biocrust organisms can influence soil acidity. Litter and other dead organic material along the dune chronosequences originate from vascular plants but, especially in mature dunes, from the moss and lichen-dominated biocrusts. These materials can be further processed in two ways. One is partial decomposition (including humification) where organic debris gets transformed into humic substances due to microbial activity (Guggenberger, 2005). Thereby, humification leads to an increasing release of protons causing increasing acidification, especially in the humus-rich topsoils of mature dunes. Another process is the mineralization of the organic matter by soil microorganisms into inorganic components. This leads to the formation of CO_2 and H_2O and bioavailable ions (NH_4^+, NO_3^-, SO_4^{2-}, PO_4^{3-}). These compounds get either returned to the nutrient cycle, bound to soil colloids, or washed out of the soil (Amelung et al., 2018b; Guggenberger, 2005). The aforementioned production of CO_2 and H^+ by microorganisms during respiration further accelerates the decalcification of the dune sediment. The soil horizons of the core samples were low in calcium carbonate (0-2.1 g kg^{-1}). The concentrations are thus significantly lower than those of nearby locations such as the isle of Rügen (14.6-127.8 g kg^{-1}) and Usedom (6.6-7.5 g kg^{-1}) (Baumann et al., 2019). The carbonate content in early dune successional stages is slightly higher than in the older stages. One reason for this is the unweathered shells-containing (calcite) dune sand (Wang et al., 2014).

The mobilization of Fe is a well-known indicator of early soil-forming processes e.g., studied on the island of Spiekeroog (Germany, North Sea) by Pollmann et al. (2020). Along the two dune chronosequences at the Darsser Ort and Pramort generally low total iron (Fe_t) contents of all sediment/soil core samples were detected. If the cores were divided into topsoil and subsoil horizons, the iron content in the upper horizon was higher than in the one below (between 0.3-1.7 g kg^{-1} dry weight (DW) in Ai-horizon; 0.4-0.9 g kg^{-1} DW in ilC-horizon). The average Fe content from poorly crystalline pedogenic Fe oxides (chemically extracted with an NH_4 oxalate solution = Fe_{ox}) was 24 mg kg^{-1} (referring to the topsoil horizons of both sampling sites). Well-crystalline pedogenic Fe oxides (chemically extracted using a dithionite–citrate–bicarbonate solution = Fe_{dit}) only form after the elimination of water as the soil ages (Amelung et al., 2018c; Blume et al., 2010). The average Fe_{dit} content in the topsoil horizons of both sampling sites was 210 mg kg^{-1}. The calculation of different ratios (Fe_{dit}:Fe_t and Fe_{ox}:Fe_{dit}) gives insights into the current status of soil development in the dunes. A slight increase in the Fe_{ox} and Fe_{dit} concentrations can be observed inland along both chronosequences, which confirms an initial soil weathering with dune development. The Fe_{dit}:Fe_t ratio reflects the degree of soil development. Cornell and Schwertmann (2003) name ratios between 0.2 and 0.3 for soils of the

northern hemisphere indicating the start of soil development which also matches the Fe_{dit}:Fe_t ratio at Darsser Ort (0.1-0.3) and Pramort (0.2-0.4).
Fully developed soils get closer to a value of around 1. These findings are in line with Pollmann et al. (2020) who found a significant correlation between this ratio and the soil age of the studied temperate dunes. The Fe_{ox}:Fe_{dit} ratio did not show any decrease, which would be another indicator for soil development along a chronosequence (Cornell and Schwertmann, 2003; Pollmann et al., 2020). Therefore, no soil development along the chronosequences can be determined from this ratio. One reasonable explanation is that the investigated dunes are still relatively young and no further mineral transformation has happened. Another conceivable possibility would be that the quartz-rich sand was not bearing sufficient amounts of weatherable Fe-containing minerals (confirmed by low Fe_t contents). A further supply of pedogenic Fe oxides stopped here and no further development of more crystalline Fe oxides over time could happen. Consequently, no decreasing F_{ox}:Fe_{dit} ratio can be expected in the studied dune chronosequences and therefore this ratio cannot be used as a clear indicator of soil formation in this particular case.

2.4 Synopsis of P-cycling and transformation processes

Phosphorus (P) is essential to all living organisms. Besides its accumulation by biocrust organisms, the microbial communities actively contribute to the transformation processes of this essential nutrient element within the surrounding ecosystem, thereby impacting the bioavailability of P to other (micro)organisms.
This chapter highlights the impact of biological soil crusts on the biogeochemical P cycling. It focuses on the total P accumulation and sequentially extracted P pools as they reflect the bioavailability of P to other organisms and were of major interest in **Publication I** and **III**. The **third hypothesis** of this thesis was:

> **Hypothesis 3:** *Biocrust succession is positively linked to an overall increase in the total phosphorus content within the biocrusts. The proportion of bioavailable phosphorus increases with ongoing succession due to the biocrusts' impact on the P cycle. This leads to a reduction in the proportion of phosphorus in the more stable P pools.*

Phosphorus: Hard to get, hard to use

The weathering of P-containing minerals is one way of P input into the ecosystem (Amelung et al., 2018a; Filippelli, 2019; Kruse et al., 2015). However, the sand dunes along the Baltic Sea coast and the studied inland dune area in Northern Germany contain only small amounts of such minerals (e.g., apatite). Both, the atmospheric wet (PO_4^{3-}) and dry (P_i, P_o) depositions are important ways P reaches the dune ecosystem in which biocrusts are strongly involved. Berthold et al. (2019) summarized the magnitude and influence of atmospheric phosphorus deposition on the Southern Baltic Sea coast over 23 years. The data were collected on the peninsula Fischland-Darss-Zingst. The authors calculated a median daily deposition of phosphate of 56 µg P m^{-2} day^{-1} and an annual median sum of P by atmospheric deposition of 16.7 kg P km^{-2} a^{-1}. At this point, biocrusts' functional traits become once more a key function of further P cycling. Their ability to collect water in the extracellular polymeric matrix and to trap nutrient-enriched aeolian dust from the atmosphere makes the biocrust community an efficient P collector (Jung et al., 2020a; Reynolds et al., 2001). The extracellular polysaccharides, single carbohydrates, lipids, and proteins offer multiple binding sites for metal ions with different affinity and specificity, including P-ions (Greene and Darnall, 1990). These ions mostly remain within the formed extracellular polymeric matrix and are not absorbed into the cell. Thus, these essential ions remain bioavailable while their loss through leaching or wind erosion is reduced (Geesey and Jang, 1990). These mechanisms lead in the first place to an increasing input, retention, and finally an enrichment of P_t in the ecosystem (Baumann et al., 2019; Richardson and Simpson, 2011). This is in line with the finding in **Publication I** and **III** where a constant increase in the P_t content was observed with biocrusts succession. However, this development cannot be transferred to the sediment/soil cores from the dunes at Darsser Ort and Pramort. In this case, P_t contents remained unchanged in both the topsoil and the subsoil along the chronosequences. Baumann et al. (2019) came to the same result in their studies along a dune weathering gradient on the Baltic coast. This is contrary to Walker and Syers's (1976) scheme, which assumes a decline in P_t throughout soil genesis due to the leaching of P over time. Baumann et al. (2019) thought that differences in the mineralogy of the sediments may have caused the rather unchanged P_t contents in their study. Along the studied chronosequence, however, it is more likely assumed that soil genesis had not yet progressed far enough to cause the

weathering of P-containing minerals. This assumption is confirmed by the missing decline of Fe_{ox}:Fe_{dit} ratio along the two chronosequences. Therefore, these findings again highlight biocrusts' ability to initially accumulate P within their biomass, irrespective of the dunes' parent source material (**Publication III**).

While the proportions of P_i and P_o in the total P pool in the topsoil (A-horizon) hardly changed along the chronosequences (Darsser Ort and Pramort), an increase in the P_t content with an increasingly higher proportion of P_o could be measured in the biocrusts with their succession along the two dune gradients. This finding can also be transferred to the dunes at sites Verden and Schaabe (data unpublished) and reflects the presence and biological activity of biocrust microorganisms as well as their residues, thereby stressing the important role of these pioneer colonizers in pedogenesis as stated by Baumann et al. (2017, 2019). Initially, P is expected to be mainly Ca-bound (= more stable bound) (Hedley et al., 1982; Sims and Pierzynski, 2005). In agreement with this knowledge, large parts of the P of early successional biocrusts were found to be bound in the stable P pool (acid extractable P) (Figure 11). Phototrophic microalgae and bacteria of early successional biocrust stages are the first organisms taking action in the transforming processes of phosphorus (Jones and Oburger, 2011). Proton (H^+) release (experimentally tested in vitro cf. Villegas and Fortin, 2002) and the secretion of organic acid anions by microorganisms and macrophytic cryptogams become once more two important mechanisms causing the acidification of the surrounding microenvironment, thereby mobilizing P from Ca-P compounds (Deubel and Merbach, 2005; Jones and Oburger, 2011). Introducing P-hydrolysing enzymes (phosphatases) can further favor this mobilization (Nannipieri et al., 2011). The inorganic phosphate anions mobilized can be taken up and immobilized from the soil solution by microorganisms and vascular plants (Belnap, 2011; Garcia-Pichel and Belnap, 1996). Further, the combination of low pH and the sand dunes' sandy texture reduces the soil sorption capacity, as low concentrations of iron and aluminum minerals can be assumed (Lang et al., 2017). The decrease of Ca-P may result in an increase of Fe/Al-P which are less soluble at low pH but are moderately labile bound (Kruse et al., 2015; Walker and Syers, 1976). This development was observed in all biocrusts along the four chronosequences investigated in this thesis (Figure 11) and is in line with other studies on biocrusts along the Baltic Sea coast (Baumann et al., 2019).

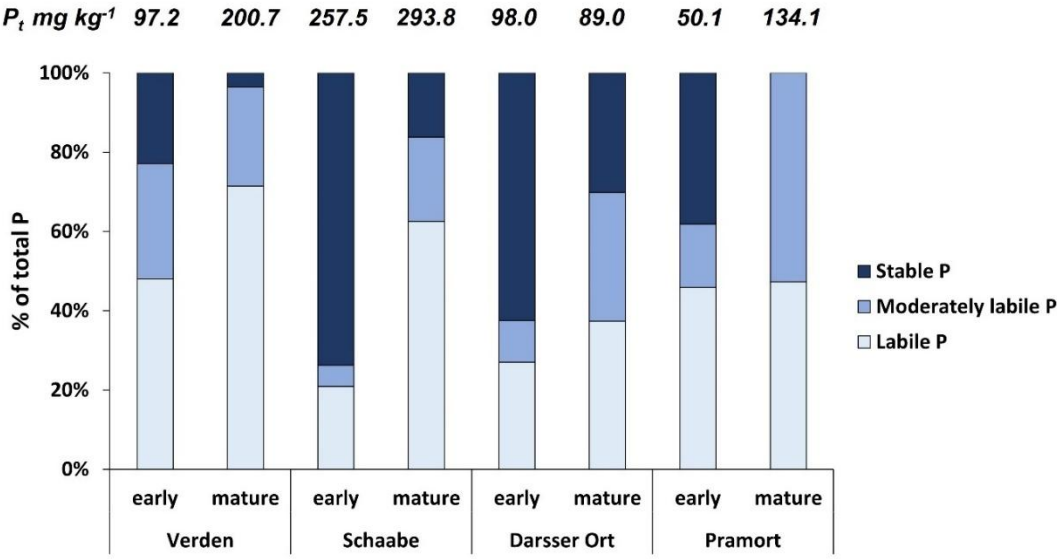


Figure 11: P pools (as determined by sequential P fractionation) as a percentage of total P (P_t) in early and mature biological soil crust types. Data for Verden and Schaabe unpublished, for Darsser Ort and Pramort cf. **Publication III** in the supplementary material.

A similar change in the proportion of P in the different pools could also be observed in the topsoil of the cores from Darsser Ort and Pramort (**Publication III**) which once again speaks for an influence of the biocrust community on the directly underlying soil horizon. The relative proportion of the bioavailable P pool increased with dune succession. This pool was almost exclusively composed of Resin-P_i representing P in the soil solution. A decrease in the proportion of stable bound P accompanied this transformation implying the conversion of more stable P into labile P. Changes in the overall P availability and differences in the binding forms of P within the soil with dune succession and early pedogenesis require specific acquisition strategies e.g., the specific gene expression by the biocrust bacteria, discussed in **Publication IV**. Kurth et al. (2020) demonstrated that in biocrusts with low concentrations in labile P bacteria harboring the starvation-induced pstS gene, a subunit of the high-affine inorganic P transporter of the Pho regulon, was most abundant. The Pho regulon is activated in response to a depletion of inorganic phosphorus. pstS gene-harboring bacteria potentially take advantage of the pst transporter during P scarcity and are better adapted to habitats in which a sufficient supply of phosphate is not ensured (Michigami et al., 2018; Santos-Beneit, 2015).

2.5 General conclusions

Hypotheses 1:

The biocrust species composition changes from thin microalgae to moss and lichen-dominated types along the studied coastal dune chronosequences. Further, an increase in biocrust coverage and biomass is expected.

This hypothesis can be confirmed. Along all four studied dune chronosequences a dune-type dependent, specific phototrophic community composition of the dominating biocrusts was detected.

Hypotheses 2:

With ongoing biocrust succession on the sand dunes along the chronosequences, early soil genesis can be observed in the top sediment layer. These processes are strengthened by the colonization of the uppermost sediment layer by the biocrusts.

This hypothesis can be confirmed. In-depth pedological analyses along two of the four studied dune chronosequences elucidated initial processes of soil genesis, i.e., decalcification, acidification, and the enrichment of the soil with organic matter and nutrients. The formation of pedogenic oxides (Fe compounds) confirmed mineral weathering and the beginning of soil profile development.

Hypotheses 3:

Biocrust succession is positively linked to an overall increase in the total phosphorus content within the biocrusts. The proportion of bioavailable phosphorus increases with ongoing succession due to the biocrusts' impact on the P cycle. This leads to a reduction in the proportion of phosphorus in the more stable P pools.

This hypothesis can be confirmed. While the total P content in the soil horizons below the biocrusts did not show any great difference, a significant accumulation of total P was measured in the changing biocrust types along all dune chronosequences. Further, biocrust microorganisms promoted P transformational processes which led to an increase in the bioavailable P pool at the expense of more stable bound P, especially in the mature biocrusts and the adjacent underlying topsoil horizons.

Considering the findings of all three hypotheses it becomes clear that with biocrust succession, accompanied by dominating species shifts, the community's overall impacts on its close surroundings change as well. The thesis highlights essential ecosystem services provided by biocrusts and focuses on the consequences different biocrust types can have on physicochemical soil parameters, which can initiate and maintain soil development in the long term (Figure 12).

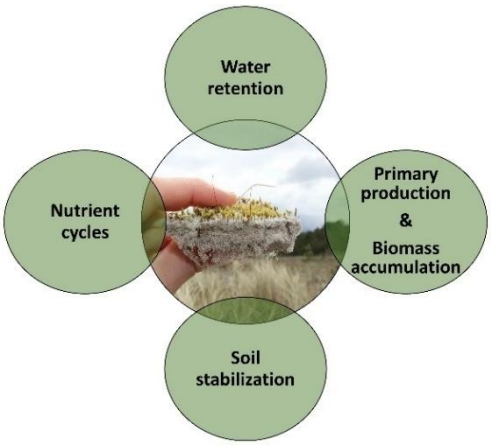


Figure 12: Graphic illustrating the service provided by a biocrust to the dune ecosystem. Image: © S. Kammann.

2.6 Future perspectives and considerations

In conclusion, the studies conducted in this thesis highlight the important ecological traits of biocrust communities within dune habitats. The results emphasize the complexity of ecosystem services supported by biocrust organisms and the influence they can have on the surrounding environment, thereby impacting the dune development and geomorphological processes.
This thesis focuses on the phototrophic community within the biocrusts. Additional essential biocrust builders are fungi and other heterotrophic microorganisms. In a follow-up study, the diversity of these organism groups and a potential change in the species community with biocrust succession in temperate sand dunes should also be investigated to get a holistic picture of the biocrust community. Species interactions should be considered as a determining factor for further community development. Future research approaches could include a seasonal study that investigates the potential changes in the biocrust community in the short term.

The gained knowledge on biocrust key functions creates a baseline for future work, for example, on biocrusts' economic benefits for dune rehabilitation and restoration and subsequent coastal protection. A calculation from 2015 revealed that about 180 km of the flat coast is at risk of flooding in Mecklenburg-Western Pomerania (StALU MM, 2015). The discharge of sediment away from the coast leads, in the long term, to land loss and a landward shift of the shoreline, on average 35 cm yr^{-1} (StALU MM, 2013). Coastal protection is therefore a top priority in these regions. Today, dunes represent a central protection element on the outer coast of Mecklenburg-Western Pomerania. The artificial planting of the dunes with *Ammophila arenaria* promotes better deposition of drifting sand and artificial sand replenishment further strengthens the dunes' stability (Lubke and Hertling, 2001).
At this point, artificial biocrust establishment on sand dunes can be an additional opportunity to promote dune sediment stabilization and hence coastal protection. A review by Zhou et al. (2020) summarized that filamentous cyanobacteria (e.g., *Microcoleus*) are the most suitable microorganisms for the initial growth of artificial biocrust due to their easy cultivation and inoculation. Mosses also seem to be suitable cryptogams for a multi-species approach. Permanent establishment of the biocrusts can be supported by keeping the inoculated soil surface wet during the initial inoculation period, and further installing physical structures that reduce sediment movement. An example of such a restoration attempt in temperate regions is provided by the study of Sommer et al. (2021) These researchers tested the applicability of artificial biocrusts for the restoration of potash tailings piles. Within laboratory experiments, green algal cultures isolated from biocrusts near the piles were used to identify suitable species and substrates ideal for the optimum growth of the algae to form stable biocrusts. A similar experimental approach could follow the basic research carried out in this thesis. Within the scope of such experiments, an optimal artificial microorganism community could be compiled under laboratory conditions that is best adapted to the harsh conditions of sand dunes and can tolerate desiccation, radiation, and sediment burial. Different methodological approaches could be tested to transfer this community onto the dune sediment and promote its establishment. This approach would be followed by a long-term study under real conditions in the dunes to observe the development of these artificial biocrusts. In this field study, parameters such as the surface growth of the biocrusts, their stability, and natural succession in the species community, for example, the colonization of macrophytic cryptogams, should be traced.

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3 Publications

3.1 Publication I

Successional Development of the Phototrophic Community in Biological Soil Crusts on Coastal and Inland Dunes

Sandra Kammann, Ulf Schiefelbein, Christian Dolnik, Tatiana Mikhailyuk, Eduard Demchenko, Ulf Karsten, and Karin Glaser

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Successional Development of the Phototrophic Community in Biological Soil Crusts on Coastal and Inland Dunes

Sandra Kammann [1,*], Ulf Schiefelbein [2], Christian Dolnik [3], Tatiana Mikhailyuk [4], Eduard Demchenko [4], Ulf Karsten [1] and Karin Glaser [1]

[1] Institute for Biological Sciences, Applied Ecology and Phycology, Rostock University, 18059 Rostock, Germany
[2] Botanical Garden, University of Rostock, 18055 Rostock, Germany
[3] Institute for Natural Resource Conservation, Landscape Ecology, Kiel University, 24098 Kiel, Germany
[4] M. G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, UA-01601 Kyiv, Ukraine
* Correspondence: sandra.kammann@uni-rostock.de

Simple Summary: This publication focuses on a comparative biodiversity survey of cryptogamic covers along a dune chronosequence in the Baltic Sea compared to an inland dune in northern Germany. Following these gradients, the cryptogamic vegetation accumulated more and more biomass and nutrients (carbon, nitrogen, and phosphorus). Further, a habitat-specific phototrophic community composition could be revealed. The enrichment of the biotic and abiotic components suggests cryptogamic covers as key players in geochemical processes, supporting sediment moisture and stability. Moreover, it highlights these communities as 'ecosystem engineers' playing a valuable part in nature protection e.g., preventing sediment erosion in coastal dune areas.

Abstract: (1) Biological soil crusts (biocrusts) are microecosystems consisting of prokaryotic and eukaryotic microorganisms growing on the topsoil. This study aims to characterize changes in the community structure of biocrust phototrophic organisms along a dune chronosequence in the Baltic Sea compared to an inland dune in northern Germany. (2) A vegetation survey followed by species determination and sediment analyses were conducted. (3) The results highlight a varying phototrophic community composition within the biocrusts regarding the different successional stages of the dunes. At both study sites, a shift from algae-dominated to lichen- and moss-dominated biocrusts in later successional dune types was observed. The algae community of both 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 taxa along both 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 carbon, nitrogen, and phosphorus in the different biocrust types showed a similar relationship. (4) This relation can be explained by biomass growth and potential nutrient mobilization by the microorganisms. Hence, the observed biocrust development potentially enhanced soil formation and contributed to nutrient accumulation.

Keywords: algae; biocrusts; coastal dunes; lichen; moss; nutrient content; phototroph community composition; successional stages

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1. Introduction

Coastal dunes as a transitional zone between the ocean shore and the terrestrial environment are shaped by harsh climatic and environmental conditions. These include strong seasonal fluctuations in temperatures near the sediment surface, drought, and wind, the latter causing constant sand movement, thereby shaping dunes [1]. Sandy dune soils are characterized by low soil organic matter content along with low nutrient concentrations [2]. Moreover, flooding events and salt spray have a high impact on substrate mobility [1,3].

Therefore, dune formations undergo a continuous succession driven by wind, waves, and storm events, as well as acidification due to precipitation (acid rain), shaping the dune geomorphology. These effects are important close to the sea, while more inland biomass typically accumulates creating a set of heterogeneous dune subsites [1]. The dune areas shaped by these mechanisms represent chronosequences, a geomorphological sequence of dune successions. In the ideal case, chronosequences differ only in the time since the onset of their formation, but all other abiotic factors during pedogenesis remained relatively steady [4]. Therefore, chronosequences are used for studying temporal habitat dynamics, reflecting vegetation and soil development [5]. A dune chronosequence starts 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 [6]. Such a process takes place over a relatively long time scale (100–1000 years [7]). The effects of extrinsic stressors and intrinsic mechanisms (e.g., succession) can drive a dune ecosystem toward a particular assemblage of microbial and vascular plant communities and lead to different dune types characterized by unique geomorphology and vegetation patterns [8]. The establishment of a vascular plant cover is challenging due to the mentioned stressors. That, in turn, facilitates the colonization by stress-tolerant microbial communities, such as cryptogamic ground covers.

Cryptogamic ground covers are characteristic growth forms on top of various terrestrial soil or rock surfaces [9]. 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 surface's uppermost millimeters [10]. Due to the wide range of ecosystem functions, biocrusts affect the inhabiting ecosystem processes and can be closely linked to soil functionality [11,12]. As pioneer microbial communities, they support the initial habitat colonialization by producing organic matter among others [13]. Several studies focused on different mechanisms by which biocrusts can increase soil stability [14,15], which are important when considering soil erosion and blowouts [16]. Fischer et al. [17] refer to the advantage of thicker moss-dominated biocrusts regarding their water-holding capacity compared to thinner biocrusts. A study by Gypser et al. [18] proved this trend. Further, a high water holding capacity has been shown to reduce infiltration though this will depend on soil type, ecological context, and climatic region [11,19].

Phototrophic biocrust organisms are important contributors to the global photosynthetic carbon assimilation within the community biomass [20]. Moreover, biocrust cyanobacteria contribute to global terrestrial biological nitrogen fixation [9,21]. Former studies could also prove the importance of biocrusts in nutrient cycling [22], such as phosphorus [23–26]. The performance of all these collectively mentioned ecosystem functions is strongly related to the dominating biocrust-forming community and the successional stage of the respective biocrust cover [27,28]. A successional development can be seen as a sequence of species colonizing an open space. Thereby, prominent mechanisms interlock, namely facilitation, tolerance, and inhabitation [29]. In addition to species that depend on mechanisms, e.g., the dependency upon earlier species; biocrust succession depends on many environmental factors, namely temperature [30], radiation, topography, soil texture [31,32], microclimate [33], water availability [17,31], and nutrient availability, as well as the effect of seasons [34]. All those factors can either support biocrust development from early to mature thick moss and lichen-dominated communities or limit the further succession of biocrust covers, retaining them in early successional stages. Along with the changing environmental and abiotic variables, and geographical regions, the dominant organisms of biocrusts change and thereby, in turn, biocrust ecosystem functions, too. Biocrust successional development is, therefore, a process over time and in space influenced by multiple factors resulting in a heterogeneity of the community structures [35]. The time frame for biocrust succession was extensively investigated in various studies leading to an obvious outcome [36]. A current review by Kidron et al. [37] critically analyzed available estimates of the biocrust recovery time. The presented systematic measurements and theoretical considerations approve a

relatively short-term recovery of biocrusts (cyanobacterial biocrusts: 5–10 years, lichen- and moss-dominated biocrusts: 10–20 years). The various stages of biocrust succession, caused by the changes in the species composition, allow the establishment of an abstracted categorization system for biocrusts. A study conducted by Büdel et al. [38] distinguished between seven main types of biocrust types along a > 2000 km long transect in Africa which were further categorized into three successional biocrust stages: early, intermediate, and late successional stages. A similar classification system, even though in smaller steps, was published by Williams et al. [39]. In the latter publication, biocrust types were classified by the functional phototrophic 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 [38,40,41]. Much less is known for biocrusts in coastal sand dunes of temperate regions. Fernández-Alonso et al. [42] provided insight into the effects of increasing aridity and biotic cover on soil attributes and functions in coastal dune ecosystems of the Iberian Peninsula. Likewise, Schulz et al. [43] conducted a pioneer biodiversity survey of biocrusts in sand dunes in the Baltic Sea coast. This study highlighted the ecological importance of biocrusts in influencing soil properties, such as increasing total phosphorus concentrations, and their high site-specific diversity of microorganisms. However, the specific dune developmental stage was neglected here. In addition, Schaub et al. [44] focused exclusively on early successional biocrust stages in yellow dunes in the Baltic Sea. Still, information on community changes across biocrust successional stages along the natural dune development is missing, although they can be assumed to affect the ecosystem functionality, nutrient cycling, and further vegetation colonization of coastal dunes significantly.

Therefore, in the present study for the first time, shifts in species composition, biocrust coverage, and biomass accumulation along dune successional gradients were investigated. The biocrust developmental patterns were linked with the dune successional stage along a dune chronosequence in the Baltic Sea compared to that of an inland dune in northern Germany. In order to uncover a link between the biogeochemical cycles of N, C, and P and the biocrust biodiversity correlations between species richness and nutrient status were investigated. It was assumed that (I) the phototrophic biocrust community composition shifts from a thin unstable topsoil layer of algae to stable moss and lichen-dominated 'mature' communities along each dune chronosequence. (II) The locational differences between the coastal and inland dunes will be reflected in the site-specific species composition of the respective biocrusts. A further aim was to characterize and compare the biocrust and sediment characteristics and nutrient contents of the different biocrust types between the sampling sites and along the dune successional stages.

2. Materials and Methods

2.1. Study Sites

Biological soil crust samples were collected in April and May 2020, along two dune succession sequences in northern Germany (Figure 1). Samples from an inland dune area (52.93865, 9.24917) in Verden (Aller, Lower Saxony, Figure 1A) were taken. 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). The second contrasting sampling site was located in the Schaabe (54.60318, 13.38872), a coastal dune spit in the Baltic Sea island of Rügen (Mecklenburg–Western Pomerania, Figure 1B). This spit connects the peninsulas of Jasmund and Wittow. The dune chronosequence under investigation belongs to the landscape conservation area 'Ostrügen'.

Both dune complexes are disturbed by anthropogenic impacts through tourism in the past. Trampling the dunes is prohibited but cannot be excluded. Moreover, even environmental protection measures, such as an adjacent reforestation area to curb further dune movement, might impact the dune development. In May 2020, the German Meteorological Service recorded a monthly precipitation of 14 mm total (an annual total of 543.3 mm)

and a monthly average temperature of 10.7 °C at the 'Arkona' measuring station, which is close to the Schaabe sampling site. In April 2020, the monthly mean temperature for the inland dune in Verden was 9.9 degrees (measured at the Rotenburg station (Wümme); the nearest measuring point was ~24 km away). The monthly precipitation sum, however, could be determined near the inland dune, in Verden–Dauelsen, of 9.7 mm (an annual total of 651.4 mm). Meteorological data is from the DWD Climate Data Center (CDC), The monthly mean of the station measurements of the air temperature at a 2 m altitude in °C for Germany, version v21.3, retrieved on 16 November 2022, and the monthly sum of the station's measurements of precipitation depth in mm for Germany, version v21.3, retrieved on 16 November 2022.

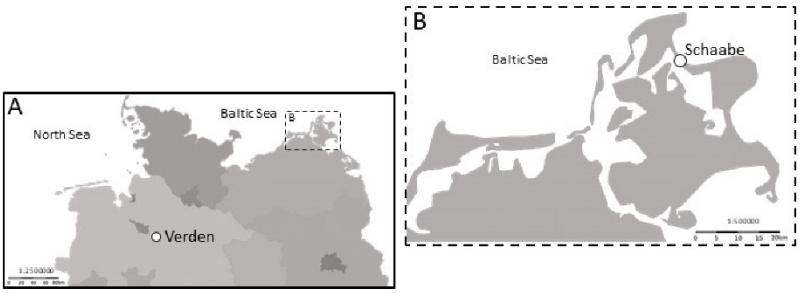


Figure 1. The inland dune in Verden and the island of Rügen in the northern part of Germany (**A**). A close-up of Rügen island (**B**) and the investigated dune sampling site in the Schaabe spit (circle).

2.2. Sampling

2.2.1. Transects

Biocrust samples were taken along one transect per study site. Each transect was established without prior consideration of the existing vegetation. The main focus of the transect was its orientation through a natural dune chronosequence that covered the different dune types. The transect in 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 considered as an interface between a fixed grey dune being frequently repulsed to a more mobile yellow dune phase. This hereinafter is called the intermediate dune (ID) stage and is an abstract recreation, and not a scientifically established term. This transitional dune stage is exemplary of the dynamic processes constantly shaping the dune morphology. The intermediate dune was followed by a grey dune area (GD). With decreasing sand accumulation, increasing sand stabilization, and vegetation cover, supporting organic matter accumulation, this dune type can develop. The transect ended in the mature dune area (MD), which was already overgrown with pine trees. The total length of this transect was 31 m. 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 the crest line of the parabolic dune. Close to the dune crest, the transect ended in a mixed dune forest area (DF) dominated by pine trees. The total length of this transect was 34 m. Along each transect, these described different successional dune stages were selected and further named dune subsites. At each subsite, a plot of 1 m^2 was established and used for further vegetation analyses, biocrust, and sediment sampling. These plots were randomly placed within each described dune type and delimited by a 1 × 1 PVC frame. The plots covered a representative area of the present biocrust community. Each of the sampling plots was further divided into 16 equal subplots (0.0625 m^2) by a grid made out of red rope stretched within the PVC frame (compare Figures 2 and 3).

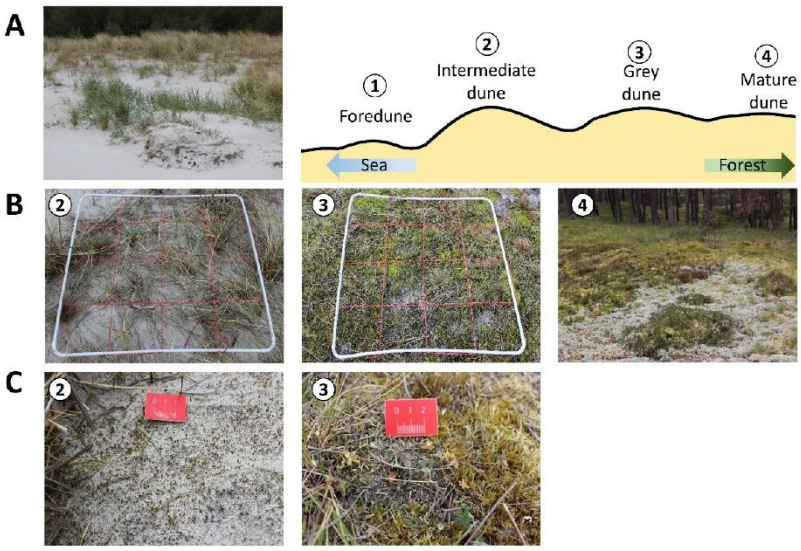


Figure 2. An overview of the transect in the Schaabe spit (Rügen) (**A**). Numbers indicate the sampling plots. Foredune (FD) = 1, intermediate dune (ID) = 2, grey dune (GD) = 3, and mature dune (MD) = 4. Close-ups of the biocrust-holding sampling plots (**B**) and detailed pictures of the dominant biocrust types in the respective plot (**C**). The white PVC frame marks each sampling plot. The red rope within this frame divides it into 16 subplots (0.0625 m^2).

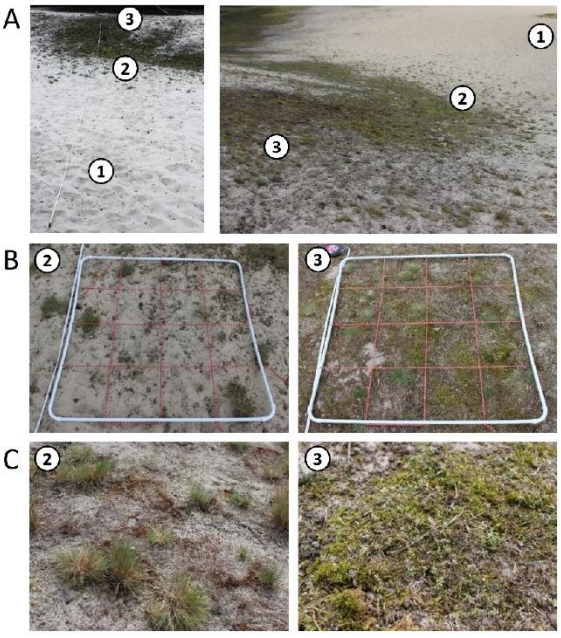


Figure 3. An overview of the transect in the inland dune in Verden (Aller); numbers indicate the sampling plots (**A**). Dune center (DC) = 1, dune slope (DS) = 2, and dune forest (DF) = 3. Close-ups of the biocrust-holding sampling plots (**B**) and detailed pictures of the dominant biocrust types in the respective plot (**C**). The white PVC frame marks each sampling plot. The red rope within this frame divides it into 16 subplots (0.0625 m^2).

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 (Figure 2).

Three subsites were established in the inland dune in Verden (Figure 3). Altogether, five out of these seven plots showed biocrust growth in different successional stages.

2.2.2. Vegetation

In preparation for the vegetation survey, seven different functional groups were defined describing the overall surface coverage (Table S1). These included four biocrust functional groups based on the established categorization systems by Büdel et al. [38], Lan et al. [32], and Williams et al. [39] 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 algal biocrusts became slightly thicker (3–8 mm) and moss-covered, were defined as the intermediate successional biocrust stage (GA/M). Mossdominated biocrusts (MD) and those that were additionally lichenized (MD/L) characterized the mature successional stages of biocrusts. This study assumes the pre-presence of early algal biocrust before the later establishment of mature moss and lichen biocrusts and thus refers to the research results of Lan et al. [32], Williams et al. [39], and Langhans et al. [45]. Vascular plants and litter (dead material, e.g., 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 [46]. A 25 cm × 25 cm (0.0625 m^2) grid of 25 intersections was placed randomly into four of the sixteen subplots per quadrat (Figure S1). Within each subplot, the functional groups were recorded by 25-point measurements according to the approach of Williams et al. [39]. Therefore, a metal pin was dropped next to each intersection and the ground covering the functional group, including bare sediment, was recorded. That allowed 100 point measurements per sampling plot (1 m^2).

2.2.3. 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 m^2) showed a high heterogeneity concerning the respective functional groups. The established 16 subplot grids from the vegetation survey were used again to collect the samples randomly. The grids were arranged in rows labeled with letters (A–D) and columns labeled with numbers (1–4). A random generator was used to decide from which of the 16 subplots biocrusts should be taken. One Petri dish sample was collected from one randomly selected subplot per plot.

Within each plot (1 m^2), nine biocrust samples using Petri dishes were collected in total (one per subplot). Three of them were dedicated to chlorophyll *a* analyses, as well as for algae community cultivation, direct microscopy, and identification (three replicates per sampling plot from each study site in total). Additionally, six biocrust samples were taken for analyses of biocrust and sediment characteristics (water content and organic matter content, and nutrient concentration). The three biocrust samples for chlorophyll *a* analyses and the isolation of cultivable algae were wrapped with aluminum foil and stored in a cooling box for transportation. 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 biocrust-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. In the central plot (DC) in the inland dune and in the foredune (FD) in 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 no biocrusts were visible.

2.2.4. Sample Preparation and Analyses of Biocrust and Sediment Characteristics

For chlorophyll analyses, three subsamples were punched out of each Petri dish using a cork drill (Ø 1.5 cm) to ensure they represented the same area for all samples. Those subsamples were treated as replicates per Petri dish and stored separately in a 15 mL falcon tube and frozen at −20 °C until chlorophyll *a* extraction. Hence, nine chlorophyll *a* measurements represented one sampling plot. This resulted in 63 measurements in total for this study (7 sampling plots × 3 petri dishes (replicates) × 3 subsamples per dish). The remaining biocrust or sediment in each Petri dish was air-dried for further algae isolation and identification and stored in the dark.

In the lab, biocrust and sediment samples used for further analyses were removed from the remaining six Petri dishes per plot. A razor blade was used to separate the visible biocrust or uppermost sediment layer from the underlying sediment. Three of them were used for biocrust characteristically (water and organic matter content) and the remaining three for nutrient (carbon = C_t, nitrogen = N_t, and phosphorus = P_t) analyses. For biocrust characteristically analyses, the biocrust material from each Petri dish was weighed for fresh mass (FM) determination. Afterward, the samples were dried at 105 °C for 24 h and weighed again to determine the dry mass (DW) 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). Each of the samples for nutrient analyses was further sieved (a 2 mm mesh size). From the now homogenized samples, three subsamples each were filled into PVC tubes for further analysis. This resulted again in 63 measurements in total for this study (7 sampling plots × 3 petri dishes (replicates) × 3 subsamples per dish). As a sediment characteristic, the pH of each of the crust-free sediment samples was measured in calcium chloride (0.01 M) solution after one hour (*w/v* ratio 1:4) with a pH meter (METTLER TOLEDO SevenMulti, Gießen, Germany).

2.3. Analyzed Parameters

2.3.1. Nutrient Analyses

Total carbon and nitrogen (C_t and N_t) were determined by dry combustion using the elemental analyzer (UNICUBE® Elementar Analysensysteme GmbH, Langenselbold, Germany). For measurements of algae-dominated biocrusts containing a high amount of associated sand grains, 100 mg was used. For thicker, biomass-rich biocrusts, 50 mg per sample was sufficient. Total phosphorus (P_t) was extracted from 500 mg of air-dried material by microwave-assisted digestion using aqua regia solution (3:1 hydrochloric acid—nitric acid). The concentration in the extract was measured by inductively coupled plasma optical emission spectroscopy at a 214 mm wavelength (ICP-OES Optima 8300, PerkinElmer, Inc. 710 Bridgeport Avenue Shelton, CT 06484-4794, USA).

2.3.2. Chlorophyll a

Chlorophyll *a* (Chl *a*) content was used as a proxy for the photosynthetic biomass (chlorophyll *a* mg m^{-2}) in biocrust (biocrust-holding plots) and sediment samples (plot DC from Verden and FD from Schaabe). The samples were each extracted in a 15 mL falcon tube. A total of 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 [47] and normalized to a square meter (m^2).

$$\text{Chl } a \text{ (g m}^{-3}) = 0.0604 \times (A_{632nm} - A_{750nm}) - 4.5224 \times (A_{649nm} - A_{750nm}) + 13.2969 \times (A_{665nm} - A_{750nm}) - 1.7453 \times (A_{696nm} - A_{750nm}) \quad (1)$$

2.3.3. 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 [48]. Cultures were grown under standard laboratory conditions with a 12 h alteration of light and dark phases and irradiation of 25 µmol photons m^{-2} s^{-1} at a temperature of 20 ± 5 °C. Microscopic study of these raw cultures began in the third week of cultivation. Morphological examinations were performed using an 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 [49] for green microalgae, and on Komárek [50] for cyanobacteria, as well as on some monographs and papers devoted to taxonomic revisions of the taxa of interest [51].

2.3.4. Moss and Lichen Identification

Moss and lichen samples were air-dried after collection. For determination, a microscope with a maximum magnification of 400× was used. Morphological identification of mosses followed Frahm and Frey [52] with taxonomical reference to Hodgetts et al. [53]. Lichens were determined according to Wirth et al. [54] and followed the nomenclature concept provided by Printzen et al. [55]. Morphologically critical species of the genus *Cladonia* were additionally analyzed by thin-layer chromatography, according to Culberson and Ammann [56] in solvent system A.

2.4. Statistical Analyses

All statistical analyses were conducted using R version 4.2.1 (R Core Team (2022) Vienna, Austria). The mean of the replicate samples per quadrat was calculated for further statistical analysis. Analysis of similarities (using the 'anosim' function in R) was performed to test for significant differences in the measured biocrust and sediment characteristics and nutrient contents between the sampling sites and across the transect plots in both dune areas. Data collected for the analysis of vegetation patterns, obtained via the point intercept method, were used to calculate the percentage of areal coverage by each functional group for each sampling plot and visualized as a stacked bar graph. 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 the Bray–Curtis dissimilarity index implemented in R. Correlation of community composition with biocrust and sediment plot characteristics and nutrient contents were statistically analyzed via permutational multivariate analysis of variance (PerMANOVA) (with the 'adonis' function in R) using the Bray–Curtis distance matrix implemented using the vegan R package [57]. Biocrust and sediment characteristics and nutrient parameters that significantly correlated with community composition were added to the nMDS plot. The person correlation (the 'cor' command in R) was further used to test the nutrient contents individually for a possible correlation with the species richness of each phototrophic group. The total species number of each phototroph group (algae, moss, and lichen) per sample was used as the measure of alpha diversity. As a measure of beta diversity, the presence/absence data of the biocrust-inhabiting species were visualized with a Venn diagram using Microsoft Excel 2013 (Microsoft Corporation, Redmond, WA, USA).

3. Results

3.1. Biocrust and Sediment Characteristics, and Nutrient Analyses

The pH of the sediment in the Schaabe spit conspicuously decreased starting from the foredune (6.39) to the mature dune (3.98) (Table 1). A similar trend was observed at the inland dune in Verden. A 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) (Table 1). Hence, the pH values continuously declined from slightly to moderate acidic along both natural dune succession sequences. The organic matter content (OM) in the Schaabe spit increased along the transect when starting at the foredune (uppermost sediment layer*) with very low contents (0.11 ± 0.01% DW). OM accumulated toward the mature dune up to 25.19 ± 7.7% DW in the biocrust (Table 1). For the inland dune, the OM content showed a similar pattern. It started in the biocrust-free sediment of the dune center with an OM value < 1% DW and increased in the biocrusts from 3.3 ± 0.72% DW at the dune slope to 24.03 ± 2.66% DW at the plot close to the dune forest (Table 1). The gravimetric water content in the Schaabe spit ranged between 0.52 ± 0.83% DW (FD, uppermost sediment layer*) and 1.22 ± 0.56% DW (MD, biocrust) (Table 1). As for the pH and OM content, the water content increased along the dune succession gradient toward the mature dune. The same applied to the samples from the inland dune.

Table 1. Overview of all measured biocrust and sediment characteristics (uppermost sediment layer *, as well as biocrust) [1].

Study Site	Dune Area	Sampling Plot	Water Content (% FW)	OM (% DW)	pH ($CaCO_3$)
Schaabe (Rügen)	Coastal dune	FD	0.52 ± 0.83 *	0.11 ± 0.01 *	6.39 *
		ID	0.16 ± 0.05	1.38 ± 0.3	6.13 *
		GD	0.39 ± 0.04	7.14 ± 0.89	5.58 *
		MD	1.22 ± 0.56	25.19 ± 7.7	3.98 *
Verden (Aller)	Inland dune	DC	0.02 ± 0.01 *	<0.1 *	4.49 *
		DS	0.16 ± 0.04	3.3 ± 0.72	3.68 *
		DF	1.73 ± 0.05	24.03 ± 2.66	3.35 *

[1] Water content (in % of fresh weight) and organic matter content (OM, in % of dry weight, after combustion of dry samples at 450 °C) are given in percent. Parameters were measured in triplicates. The pH was only measured once per sampling plot. All data represent mean values ± standard deviation. Site: Schaabe. Dune types: FD = foredune, ID = intermediate dune, GD = grey dune, and MD = mature dune. Site: Verden. Sampling plots: DC = dune center, DS = dune slope, and DF = dune forest.

The total carbon concentration (C_t) along both transects increased following the dune successional gradient inland and reached a maximum of 99.63 ± 4.59 g kg^{-1} in the biocrusts of the dune area close to the forest at the inland dune. The same trend was observed for the total nitrogen (N_t) concentration at both sampling sites (Table 2). Likewise, the total phosphorus (P_t) concentration along both transects increased toward older dune successional stages. The lowest P_t concentrations comparing both sites were measured in the uppermost sediment layer of the dune center (29.89 ± 2.29 mg kg^{-1}) and the biocrusts of the dune slope (71.85 ± 11.44 mg kg^{-1}) of the inland dune. On the spit, the lowest P_t concentration was measured in the uppermost sediment layer of the small foredune (113.9 mg kg^{-1}). Like in the inland dune, P_t concentrations increased toward the mature dune area. The highest P_t concentration at both sites was measured close to the forest (291.25 mg kg^{-1}) in the biocrust of the inland dune (Table 2). No significant difference in the nutrient content between sites could be detected. However, along each dune chronosequence, the nutrient content differed significantly between the varying dune types (inland dune: $p = 0.004$ and coastal dune: $p = 0.001$, anosim).

Table 2. Overview of all measured nutrient contents of the uppermost sediment layer * (if no biocrusts were visible), as well as biocrusts [2].

Study Site	Dune Area	Sampling Plot	C_t (g kg^{-1} DW)	N_t (g kg^{-1} DW)	P_t (mg kg^{-1} DW)
Schaabe (Rügen)	Coastal dune	FD	0.57 ± 0.09 *	0.1 ± 0 *	113.90 ± 12.61 *
		ID	6.63 ± 0.68	0.42 ± 0.11	148.92 ± 22.85
		GD	35.54 ± 10.39	1.3 ± 0.1	173.16 ± 16.34
		MD	84.32 ± 40.69	3.3 ± 1.51	172.23 ± 69.04
Verden (Aller)	Inland dune	DC	1.16 ± 0.36 *	0.2 ± 0 *	29.89 ± 2.29 *
		DS	15.34 ± 3.02	0.81 ± 0.25	71.85 ± 11.44
		DF	99.63 ± 4.59	4.72 ± 0.24	291.25 ± 58.11

[2] Total phosphate (Pt) concentration is expressed as mg kg^{-1} dry weight. Total carbon (Ct) and nitrogen (Nt) concentrations are expressed as g kg^{-1} dry weight. Parameters were measured in triplicates. All data represent mean values ± standard deviation. Site: Schaabe. Dune types: FD = foredune, ID = intermediate dune, GD = grey dune, and MD = mature dune. Site: Verden. Sampling plots: DC = dune center, DS = dune slope, and DF = dune forest.

3.2. *Vegetation Surveys*

Biocrust cover increased along the dune succession gradient at both study sites. The percentage of coverage of each defined biocrust functional group reflected the vegetation dynamics along with the dune succession (Figure 4).

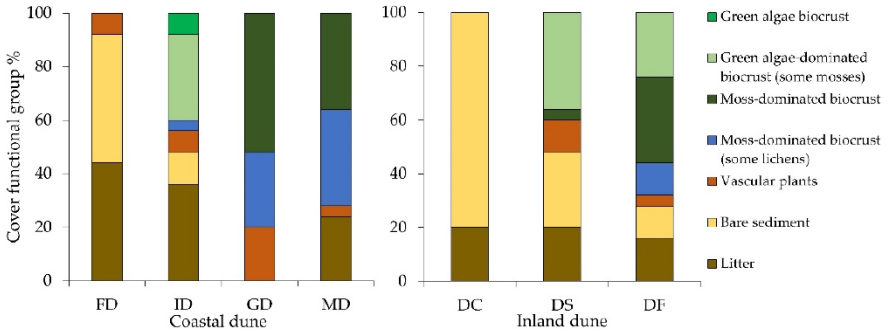


Figure 4. A summary of the vegetation survey. Percentage of the area covered by the different functional groups, as determined by the point intercept method along the two transects. Site: coastal dune (Schaabe). Dune types: FD = foredune, ID = intermediate dune, GD = grey dune, and MD = mature dune. Site: Inland dune (Verden). Sampling plots: DC = dune center, DS = dune slope, and DF = dune forest.

In the Schaabe spit, the first dune type under investigation was a small foredune. No cryptogamic cover was found within this dune type (Figure 4). The surface was mainly bare sediment (48%) or covered by organic litter (44%). Occasionally occurring vascular plants (8%) were *Ammophila arenaria* (L. LINK), which were planted for coastal protection management of dunes. Following the transect inland into the intermediate dune, the earliest biocrust covers were detected. These covers were dominated by green algae, defined as initial biocrusts, smaller mosses, and occasionally lichens growing only on plant litter. Here, biocrusts were the dominant surface cover with 44%, followed by the surface cover of a litter layer (36%) (Figure 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 those dominated by green algae. Additionally, moss-dominated biocrusts associated with lichens covered 28% of the grey dune (Figure 4). In contrast to the intermediate dune, where lichens occurred only occasionally on plant litter, they became more dominant and area-covering in the grey dune. In the mature dune, a thick moss and lichen carpet, characteristic of 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) (Figure 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, such as wind and rain, caused such small bare sediment spots in these dune types.

The proportion of bare sediment 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 (Figure 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%) (Figure 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%) (Figure 4). Additionally, the first lichen development was found in the area close to the forest (12%). However, mature moss-dominated biocrusts were the characteristic functional group within this dune area (32%) (Figure 4).

The chlorophyll *a* content of the biocrusts along the transects at both study sites was associated with the transition in species composition and resulting changes in dominant functional groups. In the inland dune, the chlorophyll *a* concentration was lowest in the dune center (DC = 5.86 mg m^{-2}) and rose to 112.07 ± 20 mg m^{-2} on the dune slope where the green algae-dominated biocrusts 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 in the Schaabe spit. At the beginning of the transect in the foredune, no chlorophyll was measurable in the bare sediment. The moss-dominated biocrusts in the mature dune showed the highest values (287.63 ± 49.07 mg m^{-2}).

3.3. Algae and Cyanobacteria

Within five biocrust samples and one sediment sample, thirteen algae species (nine in the inland dune, twelve in the Schaabe spit), and one cyanobacterium species (the DC plot in the inland dune) were detected using culture-dependent methods followed by morphological identification (Table 3). 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 (eight out of fourteen species). In the Schaabe spit, the intermediate dune plot was most rich in species (eight out of fourteen species).

Twelve species of Chlorophyta belonging to two classes were determined (three members of Chlorophyceae and nine members of Trebouxiophyceae). One species of Charophyta was detected and assigned to Klebsormidiophyceae. One species (*Nostoc* cf. *edaphicum*, Figure 5m) of Cyanobacteria was found. The most frequently detected taxa were *Myrmecia* cf. *irregularis* (Figure 5h) and *Stichococcus* cf. *bacillaris* (Figure 5c). Individuals of both genera were found at two sampling plots (*Myrmecia* cf. *irregularis*: DC and DS; *Stichococcus* cf. *bacillaris*: DS and DF) in Verden and three plots (ID, GD, and MD) in the Schaabe spit. Both species were followed by *Watanabea* cf. *acidophila* (Figure 5e) in four out of six samples. The other species occurred in half or fewer of the biocrust samples. *Nostoc* cf. *edaphicum* was detected once in the intermediate dune in the Schaabe spit. A total of 38.5% of all detected species were detected uniquely. Both study sites had 50% of the identified species in common (Figure S2A). Six of these shared species belonged to the Chlorophyta and one to the Charophyta.

Table 3. Green algal and cyanobacterial species in biocrusts were sampled at six different dune plots [3].

Phylum, Class	Species	Inland Dune			Coastal Dune		
		DC	DS	DF	ID	GD	MD
Cyanobacteria							
Cyanophyceae	*Nostoc* cf. *edaphicum*				■		
Chlorophyta							
Chlorophyceae	*Bracteacoccus* sp.				■		
	Chlorolobion sp.		■				
	Coelastrella sp.				■		
Trebouxiophyceae	*Chloroidium ellipsoideum*						■
	Chloroidium sp.		■				
	Diplosphaera chodatii				■	■	
	Elliptochloris subsphaerica		■				
	Myrmecia cf. *irregularis*	■	■		■	■	■
	Parietochloris alveolaris			■			■
	Stichococcus allas		■	■		■	
	Stichococcus cf. *bacillaris*		■	■	■	■	■
	Watanabea cf. *acidophila*	■	■	■		■	
Charophyta							
Klebsormidiophyceae	*Klebsormidium* cf. *subtile*		■		■		

[3] Site: coastal dune (Schaabe). Dune types: ID = intermediate dune, GD = grey dune, and MD = mature dune. Site: inland dune (Verden). Sampling plots: DC = dune center, DS = dune slope, and DF = dune forest. Dark grey shading indicates the occurrence of the species at that site. Light shading parts indicate no detection of the species at the respective location. Bold font in the first table column is used to highlight the algal phyla under which the corresponding classes are listed.

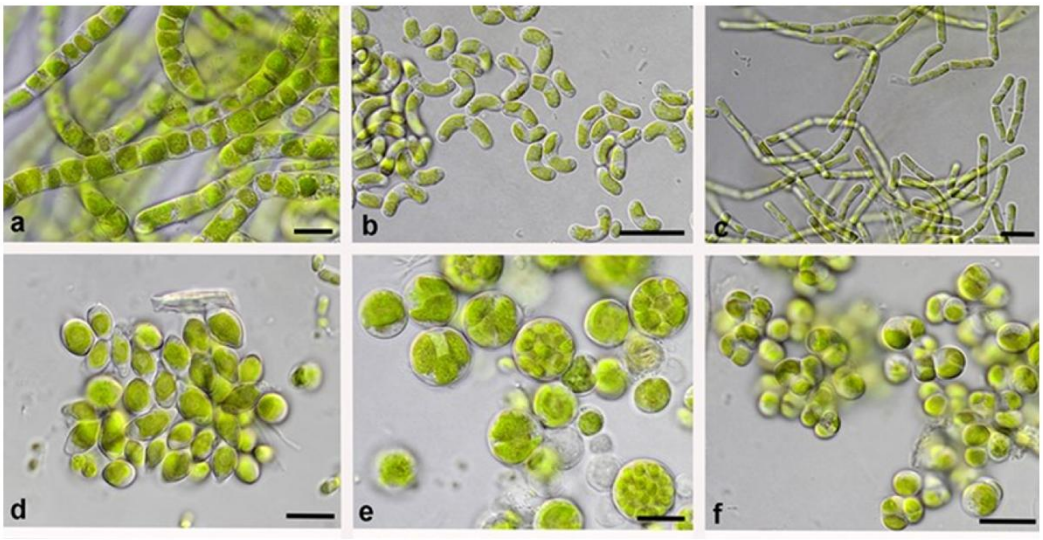


Figure 5. *Cont.*

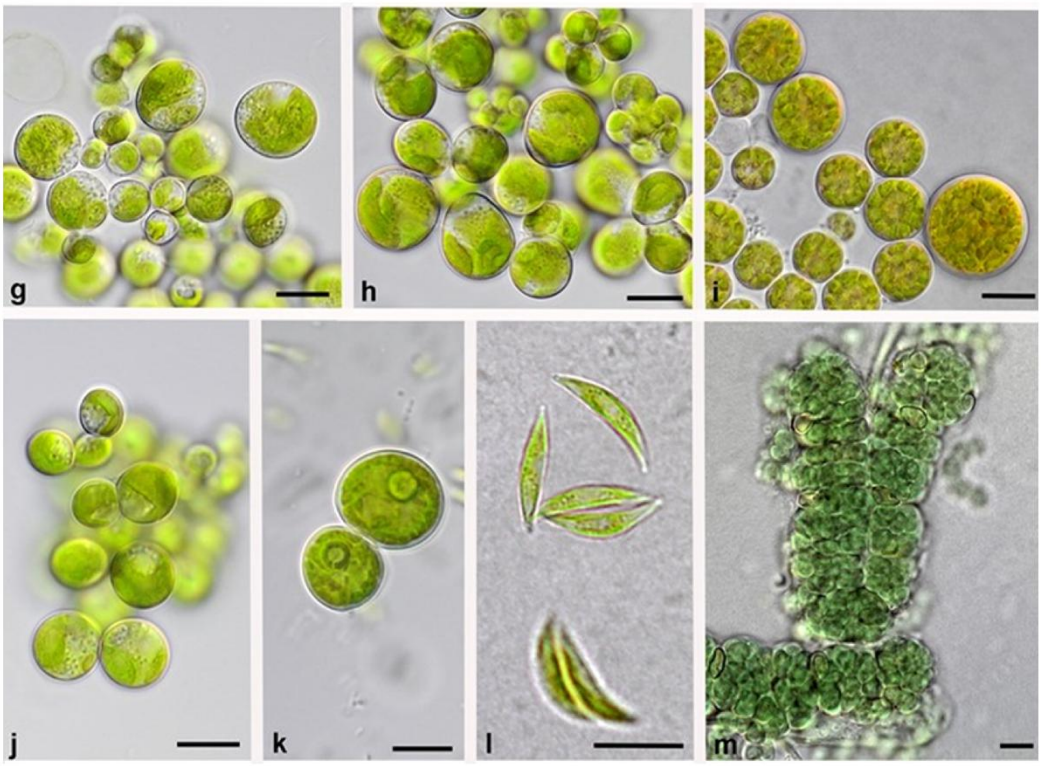


Figure 5. Representative algae and cyanobacteria from different dune succession stages along the two transects. (**a**) *Klebsormidium* cf. *subtile*, (**b**) *Stichococcus allas*, (**c**) *Stichococcus* cf. *bacillaris*, (**d**) *Chloroidium* sp., (**e**) *Watanabea* cf. *acidophila*, (**f**) *Diplosphaera chodatii*, (**g**) *Parietochloris alveolaris*, (**h**) *Myrmecia* cf. *irregularis*, (**i**) *Bracteacoccus* sp., (**j**) *Elliptochloris subsphaerica*, (**k**) *Coelastrella* sp., (**l**) *Chlorolobion* sp., and (**m**) *Nostoc* cf. *edaphicum*. Scale bars are 10 µm.

3.4. Moss Species

Sixteen moss species were detected 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 in the Schaabe spit showed the highest species number of all investigated plots (nine out of sixteen species). The species' richest plot along the inland dune transect was the one close to the forest (Table 4).

Fourteen species of Bryophyta were identified, mostly belonging to the class of Bryopsida and one species belonging to the class of Polytrichopsida. 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, and MD in the Schaabe spit. All other species occurred in two or fewer of the five moss-holding sampling plots. A total of 50% of all detected species were detected uniquely. The study sites showed only two out of sixteen identified species in common (12.5%), namely *Ceratodon purpureus* and *Dicranum scoparium* (Figure S2B).

3.5. Lichen Species

Twenty-seven lichen species were found at four of seven sampling plots in this study. (Table 5). Across all four lichen-holding plots, the species' richness ranged between four and sixteen taxa. The intermediate and grey dune plots in the Schaabe spit had the highest species number of all investigated plots (16 out of 27 species). Along the inland dune transect, the sampling plot close to the forest was the only one on which lichens could be

found. In this plot, four out of twenty-seven overall detected lichen species were observed (Table 5).

Table 4. Moss species in biocrusts were sampled at five different dune plots [4].

Phylum, Class	Species	Inland Dune		Coastal Dune		
		DS	DF	ID	GD	MD
Bryophyta						
Bryopsida	*Brachythecium albicans*			■	■	
	Bryum capillare					
	Campylopus introflexus	■	■			
	Ceratodon purpureus	■	■	■	■	
	Dicranum scoparium		■			■
	Hypnum cupressiforme				■	
	Hypnum cupressiforme var. *lacunosum*				■	■
	Hypnum jutlandicum					■
	Pohlia nutans		■			
	Ptychostomum capillare			■	■	
	Ptychostomum imbrictulum				■	
	Racomitrium elongatum				■	
	Syntrichia ruraliformis	■				
Polytrichopsida	*Polytrichum piliferum*		■			
Marchantiophyta						
Jungermanniopsida	*Cephaloziella divaricata*			■	■	
	Ptilidium ciliatum		■			

[4] Site: coastal dune (Schaabe). Dune types: ID = intermediate dune, GD = grey dune, and MD = mature dune. Site: inland dune (Verden). Sampling plots: DS = dune slope and DF = dune forest. Dark grey shading indicates the occurrence of the species at that site. Light shading parts indicate no detection of the species at the respective location. Bold font in the first table column is used to highlight the moss phyla under which the corresponding classes are listed.

All determined lichen species belonged to families of the class of Lecanoromycetes, and 22 out of 27 species were members of the Lecanorales order. Four different orders were determined in total. *Cladonia furcata* was the only lichen species found in all lichen-holding plots in this study. *Cladonia furcata* and *Cladonia portentosa* were the only lichen species both study sites had in common (Figure S2C). Sand-inhabiting species dominated this survey (19 species). The other eight lichen species only grew on litter and plant biomass. Latter were exclusively found in the intermediate and grey dunes on the coastal dune. All litter layer-inhabiting species, aside from one (*Micarea misella*), settled primarily in subneutophil habitats. Following the coastal dune chronosequence toward the mature dune area, a continuous increase in acidophil lichen species occurred. A detailed table on the pH-characterizable location dependencies can be found in the supplementary material (Table S3).

Table 5. Lichen species in biocrusts were sampled at four different dune plots and are listed by the order of lichen-forming fungi (Mycobiont) [5].

Phylum, Class, and Order (Mycobiont)	Species	Inland Dune	Coastal Dune		
		DF	ID	GD	MD
Ascomycota					
Lecanoromycetes					
Baeomycetales	*Placynthiella uliginosa*		■		
Lecanorales	*Bacidina etayana*				
	Cladonia arbuscula				■
	Cladonia chlorophaea		■	■	
	Cladonia conista			■	
	Cladonia fimbriata		■	■	
	Cladonia foliacea			■	
	Cladonia furcata	■	■	■	■
	Cladonia gracilis				■
	Cladonia humilis		■		
	Cladonia phyllophora				■
	Cladonia portentosa	■			
	Cladonia ramulosa				
	Cladonia rei		■	■	
	Cladonia scabriuscula		■	■	■
	Cladonia uncialis ssp. *biuncialis*	■			
	Evernia prunastri			■	
	Hypogymnia physodes		■	■	■
	Lecania cyrtella		■	■	
	Myriolecis hagenii		■	■	
	Myriolecis persimilis		■		
	Micarea misella			■	
	Parmelia sulcata			■	
Peltigerales	*Peltigera extenuata*		■	■	
Teloschistales	*Athallia cerinella*		■		
	Physcia tenella		■	■	
	Xanthoria parietina		■	■	

[5] Site: coastal dune (Schaabe). Dune types: ID = intermediate dune, GD = grey dune, and MD = mature dune. Site: inland dune (Verden). Sampling plot: DF = dune forest. Dark grey shading indicates the occurrence of the species at that site. Light shading parts indicate no detection of the species at the respective location. Bold font in the first table column is used to highlight the detected lichen phylum. Italic font in the first table column is used to highlight the lichen class under which the corresponding orders (Mycobiont) are listed.

3.6. Biocrust Community Composition

The community composition of moss, lichen, and algae in the biocrusts differed between the sampling sites and along the transects (Figure 6). 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 the Schaabe sites. The earliest stage in the transect of the inland dune (DC) and the coastal dune (FD) had to be excluded from the analyses, as only two algal species and no moss or lichen species were detected. Statistical analyses using PerMANOVA verified that the community composition was significantly shaped by the sampling site (explained variance 42% and p-value < 0.02) and developmental stage of the dunes (explained variance 36% and p-value < 0.02).

The biocrust's gravimetric water content (explained variance 39% and $p = 0.07$), and Chl *a* content (explained variance 33% and $p = 0.08$) tended to correlate with the change in the community composition (PerMANOVA) between the sampling sites and plots. The phototrophic species richness showed the trend to influence especially the total phosphorus content within the biocrust, even though this trend could not be statistically verified as significant. Looking at the phototrophic groups separately, the moss richness tends to be likely influencing the phosphorus content within the biocrust (Figure S3).

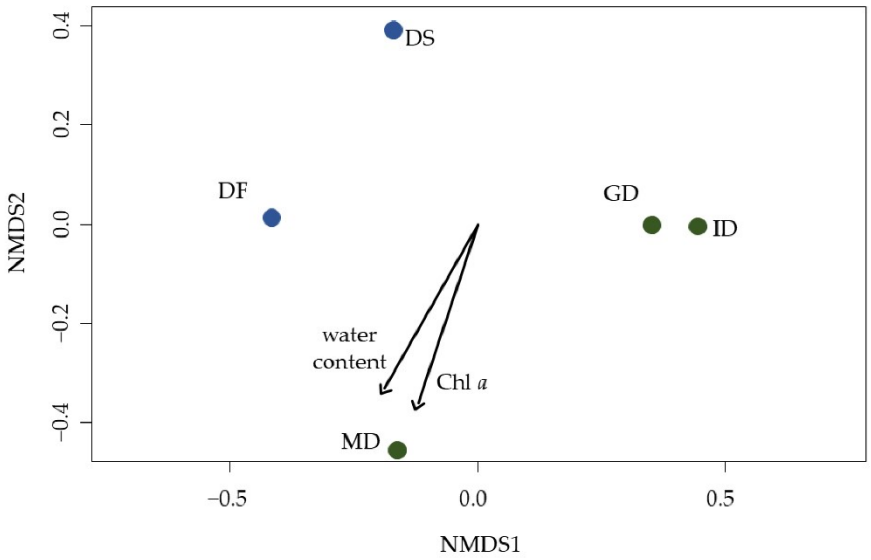


Figure 6. An nMDS plot visualizes the differences and similarities in the community composition of grouped lichen, mosses, and algae between the five sampling sites. Green: coastal dune (Schaabe). Dune types: ID = intermediate dune, GD = grey dune, and MD = mature dune. Blue: inland dune (Verden). Sampling plots: DS = dune slope and DF = dune forest. The black arrows indicate the influence direction of the two significantly correlated biocrust characteristics, namely water content and chlorophyll *a*. Stress = 0.

4. Discussion

4.1. Vegetation

Coastal foredunes and, equally, the center of the inland dunes, are characterized by strong winds resulting in a highly mobile substrate. Additionally, nearshore, higher sediment salinity and air-borne salt spray cause harsh conditions on coastal dunes. Along with a scarcity of nutrients, neither a stable plant nor a biocrust cover could be established at both study sites [1,3,6,58]. Consequently, the organic matter and chlorophyll *a* content were lowest on these mobile dune types. In addition, microorganisms, such as filamentous green algae or cyanobacteria, which might glue sand particles together by excreted exopolysaccharides [16,59,60], were missing. Hence, no coherent topsoil layer can be formed. Consequently, precipitation will easily infiltrate into loose sandy sediment [18]. The earliest successional stages of biocrusts were found in the chronologically following intermediate dune in 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 phototrophic layers. The growth of mosses and lichens could be partially observed as well. However, the mature biocrust establishment was hardly observed in intermediate dunes due to the frequent disturbance by erosive wind forces leading to sand mobility [61] or due to water limitation caused by the low water-holding capacity of the sand [18,19]. Soil moisture can positively affect carbon and nitrogen fixation by microorganisms, as was observed for biocrusts in arid regions [36]. The accumulation of organic carbon by microbial biomass formation plays an essential role in early pedogenesis [62]. Organic carbon accumulation is controlled by the turnover rates of the soil's organic matter [63]. 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 the organic matter within the biocrust has a potential impact on the mechanisms of biogeochemical P cycling in the sediment. Inorganic bound P (e.g., Ca-phosphate minerals) can be solubilized from parent material either by the secretion of organic acids by microorganisms [64] or by an increase in the

pH [65]. Phosphatases, produced by biocrust organisms, are known to hydrolyze organic phosphates releasing P (e.g., from dead cells) [66]. The increase in total P in the biocrusts along both chronosequences can mainly be explained by the increased biomass formation. Increased phototrophic biomass is revealed by the rising Chl *a* content. Depending on the sampling site, season, biocrust communities, and successional type, the Chl *a* content varies clearly. Lange [20] reported a Chl *a* content of 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. [38], the presented study could prove a significant increase in the chlorophyll content in the biocrusts of the early successional stage to the later ones. In a semi-arid desert, Büdel et al. [38] measured a mean Chl *a* value of 118.9 ± 35.8 mg m^{-2} in an area with strong coverage of biocrusts with bryophytes. 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 ± 20 mg m^{-2}). The Chl *a* value of the intermediate dune (161.34 ± 56.51 mg m^{-2}) and grey dune (150.92 ± 26.49 mg m^{-2}) in the Schaabe spit exceeded this value slightly. One reason for these values 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 and sediment organic matter might be caused by the increased establishment of mosses. The Chla *a* values of moss-dominated biocrusts in the presented study (DF inland dune = 210.80 mg m^{-2} and MD coastal dune = 287.63 mg m^{-2}) were significantly higher than those measured by Gypser et al. [35]. These authors reported a mean Chl *a* content of 68.9 mg m^{-2} of moss- and lichen-dominated biocrusts in an artificial temperate sand dune.

Moss-dominated biocrusts took over and covered about half of the investigated plot within the grey dune in the Schaabe spit. These biocrust types formed a denser and more coherent layer on the sediment surface without bare sediment. The growth of lichens increased significantly. The increase in moss and lichen biomass along the chronosequence characterized the transition from the intermediate dune to the established grey dune area [67]. The percentage coverage by the 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 [68]. Therefore, vegetation cover could expand and support the formation of an organic matter layer on the sediment surface [69]. 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 et al. [35], who showed a progressive increase in biomass and the total chlorophyll content from initial to moss- and lichen-dominated biocrusts at post-mining sites in Lower Lusatia, northeast Germany. The mature dune area landwards in the Schaabe spit and, respectively, the area close to the 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 cryptogamic 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 early soil formation [70]. This assumption is consistent with the observations made in the present study and in line with Isermann [69]. Here, the organic matter accumulation originated from annual vascular plants, scrubs, and smaller trees. The observed increase in the biocrust water content could be ascribed to the thick layer of the phototrophic community dominated by mosses and lichens. Such mature biocrusts absorb water into the cellular mucilage using morphological adaptations, such as lamellae and filaments, and thus exhibit a higher water-holding capacity [11,71], thereby stimulating sediment water retention and increasing water availability [72], at least in the top layer. Chamizo et al. [19] additionally 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 agreement with a study by Gypser et al. [18], in which green algae

tended to reduce water infiltration due to the potential pore clogging by algal filaments and their usually high amounts of sticky extracellular polymeric substances (EPS) [16]. Further it was assumed that mosses in later successional biocrust stages probably reduce pore clogging and might have reduced the previous surface 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 [70].

The vegetation survey revealed a successional development of biocrust stages from a thin topsoil layer of algae to a stable moss and lichen-dominated 'mature' community along the two investigated dune chronosequences. An existence of early successional biocrust stages before the development to older stages can be assumed since algae species could still be detected in the older biocrust stages. That confirmed our first hypothesis. 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 and MD = Schaabe) showed the highest proportion of moss-dominated biocrusts compared with the other plots. These results are in line with a described strong zonation from grey to mature dunes regarding the vascular plant communities on the German Wadden Sea coast [69].

4.2. Species Composition Changes

In addition to the general shift in biocrust types (algae, moss, or moss- and lichen-dominated) along the chronosequences, a change in the species composition between the individual dune types was also evident. Only a few species were omnipresent along each chronosequence. Comparing both study sites, locational differences in the community structures (species presence/absence) between the coastal and inland dunes became obvious. While the algal community showed many similarities, the moss and lichen communities differed significantly between the two study sites. Based on these findings, the second hypothesis could be confirmed. the differing locational conditions of both sites were reflected in differing species composition of the biocrusts in sand dunes. Biotic (e.g., litter layer and plant association) and abiotic factors (e.g., storm events, flooding, and salt spray) differ typically for the respective study site. The resulting site conditions can be seen as causes leading to the local differences in the phototrophic species compositions of biocrusts.

4.2.1. Algae and Cyanobacteria

Species belonging to the phylum Chlorophyta were mostly present at both dune chronosequences. High richness of Chlorophyta is characteristic of temperate habitats and forest soils [73]. Comparing the overall green algae and cyanobacteria species richness in the Schaabe spit with the latest studies on biocrust microbial community diversity in this area, Schulz et al. [43] indicated similarities but also conspicuous differences. Even though biocrusts are consistently formed by algae rather than cyanobacteria, species' richness can differ. While Schulz et al. [43] detected 70 cyanobacterial and non-diatom algal taxa in association with biocrusts in coastal dunes in the Baltic Sea, the recent study could reveal only twelve. Since species composition in biocrusts very likely varies with season [34] this might be one reason for the dominance of green algae in the spring biocrusts and cyanobacteria in the autumn biocrusts (October—Schulz et al. [43] and April/May in this study). Schulz et al. [43] showed biocrusts consisting mainly of a few green algae and cyanobacteria in the early successional stages of dune development at their temperate study sites. This is in contrast with studies carried out in arid or semiarid deserts where cyanobacteria were always dominant in early successional biocrusts [12,31,38,74,75]. However, the presented findings are comparable to other studies conducted in temperate areas [76,77]. In temperate forests, Glaser et al. [78] 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) [45].

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 in 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. However, it cannot be excluded that the detected algal species were in 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 ones 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 [79]. Under acidic sediment conditions (pH less than 4 or 5), Brock [80] 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 dune, Schaabe) and from 4.5 to 3.4 (inland dune, Verden). These acidic conditions in the inland dune might limit the growth of cyanobacteria [80]. The biocrusts in the intermediate dune in the Schaabe spit showed only slightly acidic conditions (6.1), and thus few cyanobacteria could grow. In addition to 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 [2]. Considering the shifts in vegetation cover along both dune chronosequences, the oldest successional dune areas were located under or close to 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 [81,82].

The biocrusts on the dune slope of the inland dune mostly consisted of Chlorophyta and representatives of the Charophyta in the Klebsormidiophyceae class. Moreover, this dune's successional stage was the species' richest along the whole chronosequence. These findings were identical to those of the intermediate dune in the Schaabe spit. Here, most algal species could be detected. Representatives of the genus *Klebsormidium* were only found in this dune's successional stage. Many studies point to *Klebsormidium* as a genus, holding species with a wide tolerance range in temperature, water availability, or sun radiation [83–85]. To cope with such extremely changing environmental conditions, Donner et al. [86] assume certain plasticity of the genus morphology as a benefit for adapting to these varying abiotic stresses. These filamentous algae are known as major biocrust-forming taxa [83]. Glaser et al. [78] could prove *Klebsormidium* was the most important biocrust-initiating alga in a temperate forest ecosystem. In an inland dune area in the Netherlands, Pluis [77] found *Klebsormidium* to be the initial green alga 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 the forest in the inland dune and the mature dune in the Schaabe spit, having two of those species in common. Such clear differences between the algal community structure of the initial and later successional biocrust stages were also shown in a sand ecosystem in the northern Rhine valley (Germany). Here, Langhans et al. [45] 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.

4.2.2. Mosses and Lichens

Moss- and lichen-dominated biocrusts were distinctive of older stages of development. In phytosociology [87], 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 a small amount of drifting sand and bring organic litter into the sediment.

Incipient moss and lichen growth could be described on the dune slope of the inland dune and the intermediate dune in 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 the response of mosses to experimental burial by Martínez and Maun [88] could show a high tolerance of *C. purpureus* of up to a 7 cm thick sand layer. This species is the only one that the dune slope in the inland dune and the intermediate dune in the Schaabe spit had in common. Along both chronosequences, *C. purpureus* was observed in transitional dune types, as well as in later dune stages, such as the area close to the forest in the inland dune and on the fixed grey dune in the Schaabe spit. These findings are in line with Gypser et al. [35], who described the growth of *C. purpureus* as an initial moss, as well as dominant in mature moss and lichen biocrusts. Another species only found on the dune slope of the inland dune is *Syntrichia ruraliformis*. This species is highly desiccation-tolerant [89,90]. This trait is favorable for moss growing on dune types that are under constant abiotic stress, such as high irradiation and low water-holding capacity. Surprisingly, this species was not found along the Baltic Sea chronosequence. Nevertheless, it is described as quite common in other sand dunes along the Baltic Coast [91]. In a study in the Curonian Spit, Lithuania, conducted by Jukonienė and Subkaitė [92], *Syntrichia ruralis* var. *ruraliformis* was described as a quite frequent species especially abundant in foredune grasslands. It cannot be ruled out that the species occurred elsewhere in the dunes in the Schaabe spit but not along the investigated transect.

The following later stages of dune succession revealed a shift in community composition along each chronosequence. Pioneer moss species, such as *C. purpureus*, decreased and were supplemented by mosses of later successional stages, such as *Dicranum scoparium* and *Hypnum cupressiforme* var. *lacunosum*. Gypser et al. [35] described *Polytrichum piliferum* as a 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 the forest of the inland dune chronosequence. The mature dune in the Schaabe spit chronosequence was low in moss species richness and was dominated by mosses of the genus *Hypnum*. Comparing the findings of the inland dune in Verden with an official flora mapping in 2015 as part of the habitat's directive (Council Directive 92/43/EEC) in this area, differences in the moss species composition became obvious. This mapping revealed the presence of 17 moss species in the inland dune area. Only seven species were identified in the present study, three identical to the findings in 2015. That could be because the observation areas and the sampling season might have differed from each other. On the other hand, these differences in the present moss species could be an indicator of a general shift in species composition due to habitat succession or abiotic influences (e.g., drought, rainfall frequency, and intensity).

The dune area close to the forest on the inland dune showed the only growth of lichens along this chronosequence. Only four lichen species of the genus *Cladonia* were found here. Those prefer growing on the sand under acidophil habitat conditions, as in this plot. Furthermore, almost no sand-covering plant material was observed, which could have facilitated the settlement of litter-inhabiting lichen species. Along the dune chronosequence in the Schaabe spit, *Bacidina etayana* was found in the coastal dune habitat. This is typical for this species, which is known to grow exclusively on dune grasses [54]. The intermediate and grey dunes were the lichen species' richest dune types. Whereas, in the intermediate dune, lichen species primarily grew on plant litter. Lichen species found in these two dune types, such as *Athallia cerinella*, *Lecania cyrtella*, *Myriolecis hagenii*, *Myriolecis persimilis*, *Physcia tenella*, and *Xanthoria parietina*, do prefer to grow on trees [54]. In the intermediate and grey dunes, tree debris, such as bark or branchlet, was overgrown by these lichen species and provided the favored habitat. As mentioned, in the inland dune, little of such biotic components were found, explaining that none of these species was observed in that

dune habitat. In some cases, lichen–litter interactions tend to form a layer independent from biocrusts and further interactions with the underlying sediment. Such formations have to be carefully separated when describing biocrust growth forms. Later successional dune stages were dominated by representatives of the genus *Cladonia*. *Cladonia* primarily inhabits nutrient-poor soils and forests [54]. The *Cladonia* species found grew most likely in the pH range they favor. Hence, in the grey dune area, lichen species preferring moderate acidophilic site conditions (pH 4.9–5.6), such as *C. rei* and *C. foliacea*, were found. While in the mature dune area, lichen species exclusively favoring a strong acidophil sandy substrate were present (e.g., *C. arbuscular* and C. *gracilis*). Comparing the findings of the formerly mentioned flora mapping in 2015 with the present study, three Cladonia species were found in both surveys. Like the mosses, fewer species were identified in the present study probably for the same reasons discussed earlier.

4.3. The Effect of Biocrust and Sediment Characteristics, and Nutrient Content on Biocrust Community Composition

Biocrusts are often named 'ecosystem engineers' [11,76] for their multiple ecological functions, such as their contribution to soil stabilization and fertilization. Primary production, element solubilization and mineralization, and nitrogen fixation [9,23,93] are processes mediated by microbial activities within biocrusts. A general increase in the nutrient concentration within biocrusts along both transects could be observed, which is in line with previous studies [28,43,94]. These findings indicate that nutrients accumulate within biocrusts and the different functional groups of biocrusts take different weighted parts in this process. In the present study, nutrient contents (C_t, N_t, and P_t) were correlated with the species richness of all investigated phototrophic organism groups (algae, mosses, and lichens) to distinguish between those parts. Although no significant correlation between the overall phototrophic species richness and the different nutrient contents could be observed, more stable biocrusts dominating later dune successional stages are associated with an increase in the total C, N, and P contents along each chronosequence. Considering the three investigated phototrophic groups separately, the impact of the moss community on nutrient enrichment becomes obvious. Due to the higher accumulation of biomass by this phototrophic group, coherence becomes obvious. The results indicate that species composition rather than the overall species richness shapes the biocrust function. Mosses accumulate organic matter and nutrients within their biomass and biocrust-adherent sediment layers. Due to their rhizoids, they are able to penetrate deeper into the sediment compared to lichens and algae. They distribute organic matter and nutrients more spaciously than it is possible for thinner algae-dominated biocrusts [95]. Concerning the moss species richness, a link to the phosphorus cycle can be considered. Phosphorus is an essential element for the growth of all phototropic organisms. The bioavailability of this element in dunes is low due to its strong binding to unweathered minerals [26]. Schulz et al. [43] could reveal phosphorus as a driver for the establishment and cyanobacterial/algal species composition. The later moss community might benefit from the previously established algal biocrust community and binds further available amounts of phosphorus within their biomass. Moreover, the potential for biocrusts to be carbon sinks was investigated in recent studies [96,97]. These results point to another forward-looking ecological function of biocrusts. Their potential influence in reducing atmospheric carbon by inoculation within their biomass highlights their importance in ecosystem conservation and climate change.

5. Conclusions

The study results pointed to a conspicuous shift of the phototrophic biocrust community with the development of the dunes along each chronosequence, as reflected in different successional stages. Furthermore, the different geographical regions revealed a considerable impact on the biocrust species composition, which can be explained by habitat-specific factors. The enrichment of organic matter and nutrient contents along with increased soil moisture and stability are the key functions that originate from the

metabolic activities of the different stages of biocrusts. Consequently, biocrusts strongly shape dune development and contribute to geomorphological processes. In addition, the biocrust key functions offer opportunities for rehabilitation and restoration approaches, such as preventing sediment erosion in coastal dune areas.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/biology12010058/s1, Table S1: Overview of all defined functional biotic and abiotic groups used to determine the dune surface coverage. Abbreviations of these groups, a short description, a color code, and visual examples of each functional group are given. Table S2: Chlorophyll *a* content (mg m^{-2}) for the biocrust or sediment (*) along both dune chronosequences. Table S3: Lichen species in the biocrusts are listed by the order of lichen-forming fungi (Mycobiont). Columns differentiate between lichens' occurrence and characterize the preliminary settled pH range. Abbreviations: e = extreme, v = very, q = quite, and m = moderate. Figure S1: A sampling plot (1 m^2) divided into 16 equal subplots (0.0625 m^2) with a 25 cm × 25 cm (0.0625 m^2) grid of 25 intersections. A metal pin was dropped next to each intersection and the ground covering the functional group, including bare sediment, was recorded. Figure S2: Venn diagrams showing the total species number of (A) algae, (B) mosses, and (C) lichens at the two sampling sites. The number of species that were found at both sites is represented as an overlap between the two circles. Figure S3: Table showing Pearson correlation coefficients to reveal correlations between nutrient contents, which might affect or be affected by the richness of the phototrophic biocrust community. A plot of moss richness in biocrusts over the total phosphorus content in the biocrusts from both sites. The line indicates the best linear fit ($p = 0.115$ (ANOVA)).

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Successional development of the phototrophic community in biological soil crusts on coastal and inland dunes

Sandra Kammann[1], Ulf Schiefelbein[2], Christian Dolnik[3], Tatiana Mikhailyuk[4], Eduard Demchenko[4], Ulf Karsten[1], Karin Glaser[1]

[1] Institute for Biological Sciences, Applied Ecology and Phycology, Rostock University, Albert-Einstein-Straße 3, 18059 Rostock, Germany

[2] Botanical Garden, University of Rostock, Schwaansche Straße 2, 18055 Rostock, Germany

[3] Institute for Natural Resource Conservation, Landscape Ecology, Kiel University, Ohlshausenstr. 40, 24098 Kiel, Germany

[4] M. G. Kholodny Institute of Botany, National Academy of Science of Ukraine, Tereschenkivska St. 2, Kyiv UA-01601, Ukraine

Table S1: Overview of all defined functional biotic and abiotic groups used to determine the dune surface coverage. Abbreviations of these groups, a short description, a color code, and visual examples of each functional group are given.

Category	Short	Description	Code
Vascular plants	VP	Tracheophyta	
Bare sediment/ sand	Ba	No vegetation or biocrust visible, loose sand layer	
Litter	Li	Litter layer i.e. needles, leaves, branches	
Biocrust			
Green algae	GA	Early successional stage, slightly brittle, <3 mm thick, greenish-shimmering	
Green algae-dominated /mosses	GA/M	Stable green crust, occasionally mosses	
Moss-dominated	MD	biocrust dominated by mosses, partly many algae species (mostly green algae), several cm thick/high	
Moss-dominated /lichens	MD/L	MD-type, occasionally lichens (mostly chlorolichens), many algae species (mostly green algae), several cm thick/high	

Figure S1: Sampling plot (1 m^2) divided into 16 equal subplots (0.0625 m^2) with 25 cm x 25 cm (0.0625 m^2) grid of 25 intersections. A metal pin was dropped next to each intersection, and the ground covering functional group, including bare sediment, was recorded.

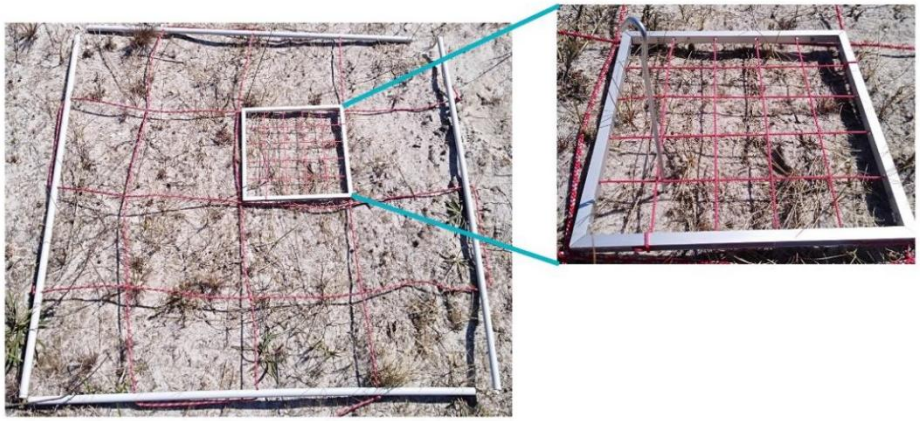


Table S2: Chlorophyll *a* content (mg m^{-2}) for biocrusts or sediment (*) along both dune chronosequences.

Study site	Dune area	Sampling plot	Chl *a* (mg m^{-2})
Schaabe (Rügen)	Coastal dune	FD	0*
		ID	161.34 ± 56.51
		GD	150.92 ± 26.49
		MD	287.63 ± 49.07
Verden (Aller)	Inland dune	DC	5.86*
		DS	112.07 ± 20.0
		DF	210.80 ± 109.01

Figure S2: Venn diagrams showing the total species number of **(A)** algae, **(B)** mosses, and **(C)** lichens at the two sampling sites. The number of species that were found at both sites are represented as an overlap between the two circles.

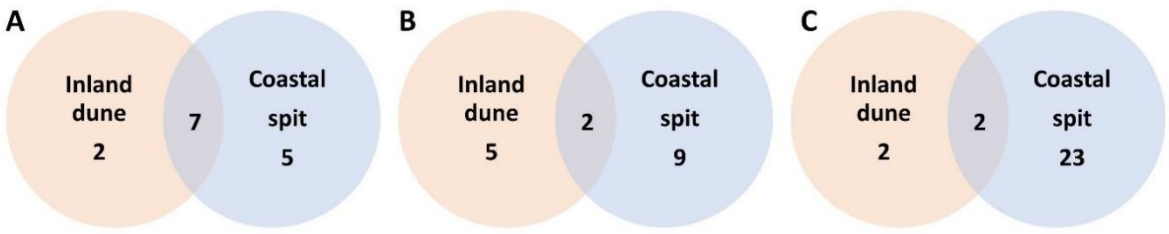
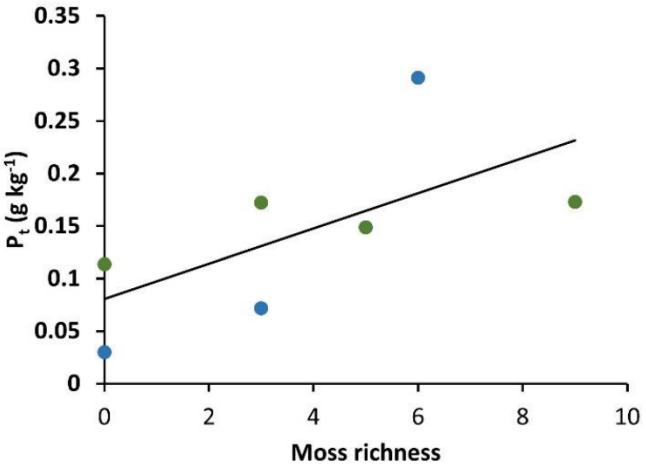


Table S3: Lichen species in biocrusts. Listed by the order of lichen-forming fungi (Mycobiont). Columns differentiating between lichens occurrence and characterizing the preliminary settled pH range; Abbreviations: e=extreme, v=very, q=quite, m=moderate.

Phylum, class, order (Mycobiont)	Species	Occur on	pH range
Ascomycota			
Lecanoromycetes			
Baeomycetales	*Placynthiella uliginosa*	Sand	e.acidoph.-q.acidoph.
Lecanorales	*Bacidina etayana*	Litter	
	Cladonia arbuscula	Sand	e.acidoph.-m.acidoph.-(subneutroph)
	Cladonia chlorophaea	Sand	(e.acidoph.-)v.acidoph.-m.acidoph.
	Cladonia conista	Sand	acidoph.
	Cladonia fimbriata	Sand	q.acidoph.-m.acidoph.-(subneutroph)
	Cladonia foliacea	Sand	(q.acidoph.-)m.acidoph.
	Cladonia furcata	Sand	q.acidoph.-subneutroph
	Cladonia gracilis	Sand	e.acidoph.-m.acidoph.
	Cladonia humilis	Sand	q.acidoph.-subneutroph
	Cladonia phyllophora	Sand	q.acidoph.-m.acidoph.
	Cladonia portentosa	Sand	e.acidoph.-m.acidoph.-(subneutroph)
	Cladonia ramulosa	Sand	v.acidoph.-q.acidoph.
	Cladonia rei	Sand	m.acidoph.-subneutroph
	Cladonia scabriuscula	Sand	m.acidoph.-subneutroph
	Cladonia uncialis ssp. *biuncialis*	Sand	e.acidoph.-m.acidoph.-(subneutroph)
	Evernia prunastri	Sand	v.acidoph.-m.acidoph.
	Hypogymnia physodes	Sand	v.acidoph.-m.acidoph.
	Lecania cyrtella	Litter	subneutroph
	Myriolecis hagenii	Litter	subneutroph.-basiph.
	Myriolecis persimilis	Litter	subneutroph.-neutroph.
	Micarea misella	Litter	v.acidoph.-q.acidoph.
	Parmelia sulcata	Sand	(q.acidoph.-)m.acidoph.
Peltigerales	*Peltigera extenuata*	Sand	q.acidoph.-subneutroph.
Teloschistales	*Athallia cerinella*	Litter	subneutoph.
	Physcia tenella	Litter	subneutoph.-m.basiph.
	Xanthoria parietina	Litter	subneutoph.m.basiph.

Figure S3: Table showing Pearson correlation coefficients to reveal correlations between nutrient contents, which might affect or be affected by the richness of the phototrophic biocrust community. Plot of moss richness in biocrusts over the total phosphorus content in the biocrusts from both sites. The line indicates the best linear fit ($p = 0.115$ (ANOVA)).

	Richness All	Richness Algae	Richness Mosses	Richness Lichens
Ct (g/kg)	0.196	0.021	0.432	0.118
Nt (g/kg)	0.154	0.016	0.408	0.059
Pt (g/kg)	0.441	0.102	0.649	0.396



3.2 Publication II

Ecophysiological performance of terrestrial diatoms isolated from biocrusts of coastal sand dunes

Karin Glaser, Sandra Kammann, Niklas Plag, and Mirko Dressler

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Liang Peng,
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University of Helsinki, Finland
Gang Li,
Chinese Academy of Sciences (CAS), China
Linda Nedbalová,
Charles University, Czechia

*CORRESPONDENCE
Sandra Kammann
sandra.kammann@uni-rostock.de

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Ecophysiological performance of terrestrial diatoms isolated from biocrusts of coastal sand dunes

Karin Glaser[1], Sandra Kammann[2]*, Niklas Plag[2] and Mirko Dressler[3]

[1]Institute for Biosciences, Biology/Ecology, TU Bergakademie Freiberg, Freiberg, Germany, [2]Institute of Biological Sciences, Applied Ecology and Phycology, University of Rostock, Rostock, Germany, [3]Department of Physical Geography, Institute for Geography and Geology, University of Greifswald, Greifswald, Germany

Terrestrial diatoms are widespread in a large variety of habitats and are regularly recorded in biocrusts. Although diatoms have long been known to live in terrestrial habitats, only a few studies have focused on their diversity of ecophysiology. Here we present a study on the ecophysiological performance of five terrestrial diatom cultures from biocrusts, which were collected in sand dunes of the German coast of the Baltic Sea. The sampling sites were selected along a gradient of human impacts on the dunes. The richness of diatom species, roughly estimated from permanent slides, was around 30 species per sampling site. The species abundance was calculated in the same way revealing a high proportion of broken diatom frustules. All diatom cultures established in the laboratory showed no photoinhibition and high oxygen production along a light gradient. The desiccation tolerance differed among the strains, with high recovery observed for *Hantzschia abundans* and *Achnanthes coarctata* and low to no recovery for *Pinnularia borealis* and *Pinnularia intermedia*. The maximum growth rate for most strains was between 25 and 30°C. These temperatures can be easily reached in their natural environments. Nevertheless, during short-term exposure to elevated temperatures, oxygen production was recorded up to 35°C. Interestingly, two of five diatom cultures (*Hantzschia abundans* and *Pinnularia borealis*) produced mycosporine-like amino acids. These UV-protective substances are known from marine diatoms but not previously reported in terrestrial diatoms.

KEYWORDS

light-irradiance curve, growth rate, desiccation, temperature extremes, stress tolerance, biocrust, terrestrial, sand dune

1 Introduction

Sand dunes are the first geological formation along the sea on many natural shores. Coastal dunes are unique ecosystems in the transition zone between terrestrial and marine environments, where interactions between geomorphology, climate, and vegetation create highly dynamic environments (Martínez et al., 2004; Miller et al., 2010). However, dune ecosystems are threatened worldwide by human influences, such as land use and erosion (Hernández-Cordero et al., 2017). Coastal dune growth depends on sediment supply and stability, which are influenced by biotic (vegetation cover) and abiotic factors (wind, waves, and precipitation). Therefore, this ecosystem is vulnerable to declining sediment replenishment or surface degradation. Coastal dunes along public beaches are highly disturbed by trampling, mechanical cleaning, or

permanent structures (e.g., groins for coastal protection) that impede wind-induced natural sand replenishment (Stancheva et al., 2011; Santoro et al., 2012).

Besides these human impacts on the coastal dune system, harsh environmental conditions with a variety of challenging environmental stressors such as strong winds, substrate mobility, nutrient, and soil water scarcity, occasionally extremely high near-surface temperatures, intense radiation, flooding, and salt spray (Maun, 2009; Miller et al., 2010) make the establishment of vascular plants quite challenging. Under these conditions, the growth and development of a closed vascular plant cover is restricted, except for anthropogenically planted marram grass (*Ammophila arenaria* (L.) Link). Under natural conditions, only specialized/stress-tolerant groups of organisms can establish on the dune surface; this includes cryptogamous communities such as biological soil crusts (biocrusts) (Schulz et al., 2016).

Biocrusts are formed by living organisms and their by-products, creating a topsoil layer of inorganic particles bound together by extrapolymeric organic compounds. Biocrusts are found on all continents, in arid, semiarid, and other habitats where soil moisture is limiting and cover of higher plants is sparse (Belnap et al., 2001). In temperate zones, these habitats include, for example, sandy coastal and inland dunes, disturbed areas (windbreaks, burned areas, etc.), or barren soils; biocrusts usually cover all soil areas not occupied by vascular plants and thus comprise up to 70% of the living cover (Belnap et al., 2001). Biocrusts form the most productive microbial biomass worldwide in the so-called 'Earth's Critical Zone', which is the upper approx. 10 mm of soil in most dry areas. In 'new' vegetation-free or disturbed landscapes such as volcanic areas, glacier forelands, etc., biocrusts form the basis for further ecosystem development and succession (Eldridge and Tozer, 1996; Cutler et al., 2008; Yoshitake et al., 2010). Together with other microorganisms such as heterotrophic bacteria, archaea, and fungi, as well as macroscopic lichens and mosses, cyanobacteria and algae comprise the most important phototrophic components of biocrusts (Elbert et al., 2012). Because of their impact on various ecosystem functions, biocrusts can be characterized as 'ecosystem engineers'. The cryptogam community forms water-stable aggregates that play important, multifunctional ecological roles in primary production, nutrient cycling, mineralization, water retention, soil stabilization, and dust binding (Evans and Johansen, 1999; Reynolds et al., 2001; Lewis, 2007; Castillo-Monroy et al., 2010). An overview of these microbiotic crusts clearly shows the important ecological role of these communities for global carbon (C) fixation (about 7% of terrestrial vegetation) and nitrogen (N) fixation (about 50% of terrestrial biological N fixation; Elbert et al., 2012).

Biocrusts in the temperate zone support a diverse algal community (Glaser et al., 2018; Mikhailyuk et al., 2019). Hundreds of different phototrophic species of cyanobacteria and algae (including diatoms) live in association with biocrusts. Terrestrial diatoms are widespread in many terrestrial habitats such as biocrusts, mosses, soil, caves, or artificial environments (Norbäck Ivarsson et al., 2013; Falasco et al., 2014; Kopalová et al., 2014; Schulz et al., 2016; Zhang et al., 2020). They contribute to soil stability by producing extrapolymeric substances, which function as glue for sand particles (Kidron, 2021). Furthermore, terrestrial diatoms are often reported even in high cell counts in biocrusts (Meadow and Zabinski, 2012; Schulz et al., 2016). However, their biodiversity, ecophysiology, and taxonomy are still inadequately characterized (Barragán et al., 2018). Marine diatoms are known to produce mycosporine-like amino acids (MAA) as UV-protective substances in response to increased solar radiation (Helbling et al., 1996; Jeffrey et al., 1999). In detail, there are solid indications that those MAAs are embedded in the silica frustule (Ingalls et al., 2010). MAAs were also recorded from terrestrial algae isolated from biocrusts, like for example *Mesotaenium* and *Klebsormidium* (Remias et al., 2012; Hartmann et al., 2020). It seems likely that terrestrial diatoms also follow this strategy and accumulate MAAs as UV-protective substances. Nevertheless, this fact has not been experimentally proven up to now. Only a few experimental ecophysiological studies on terrestrial diatoms have been undertaken under controlled conditions (Souffreau et al., 2010, 2013; Hejduková et al., 2019). These authors found similar response patterns for different terrestrial diatom species, as reflected in higher tolerances to extreme freezing and desiccation events that were lethal to isolates of freshwater diatom species. All other publications have provided comprehensive species lists and have attempted to find correlations between the occurrence or lack of terrestrial diatom taxa with key environmental factors (Foets et al., 2021). By applying an array of statistical methods (e.g., redundancy analysis), the preferential occurrence or lack of taxa can be explained by specific autecological requirements, such as pH or soil organic-matter content (Antonelli et al., 2017; Foets et al., 2021), yet experimental evidence is mostly missing. Nevertheless, taxa-specific indicator values for undisturbed and disturbed soil habitats, as well as tolerance ranges can at least be estimated from such correlations, and terrestrial diatoms are sensitive to multiple environmental factors such as pH, anthropogenic disturbance caused by farming practices (land-use intensity), and soil moisture and nitrogen contents (Foets et al., 2021). Farming practices play a key role in structuring soil diatom communities (Antonelli et al., 2017; Foets et al., 2021; and references therein), as disturbed areas were found to be less diverse and land uses with different disturbance levels could be differentiated based solely on the community composition. These authors also found that the composition of soil diatom species remained stable throughout the year and that diatoms were always present, in contrast to higher plants. Consequently, terrestrial diatoms could serve as indicator species in soils, similarly to the freshwater-diatom biotic indices used extensively to assess water quality. Recent studies have proven the suitability of diatom species assemblages as bioindicators for human disturbances, heavy-metal contamination, and soil environmental assessment (Wanner et al., 2020; Zhang et al., 2020; Minaoui et al., 2021).

In this study, we present a comprehensive ecophysiological characterization of five diatom cultures originating from biocrusts in coastal sand dunes, accompanied by an insight into the biodiversity of terrestrial diatoms in biocrusts, based on morphological identification. Our study aimed (1) to enhance our understanding of terrestrial diatoms by revealing unknown community structures of a yet-unstudied diatom habitat, the biocrusts in coastal sand dunes; and (2) to obtain insights into the ecophysiological performance of cultured terrestrial diatoms.

2 Materials and methods

2.1 Site description

Biocrusts were collected on October 05, 2021 at three sampling sites along the coast of the Darss-Zingst-Peninsula, Germany

(Figure 1). On that day, a temperature of 12°C and precipitation of 30.5 L m^{-2} were measured at the weather station in Zingst. The three sampling sites were selected according to their degree of disturbance by human activity: the highly disturbed site is located in a camping area (N54.45551, E12.54914); the moderately disturbed site is located at a public beach distant from the next village (N54.44103, E12.77921) in the care and development zone of the 'Vorpommersche Boddenlandschaft' National Park; and the little-disturbed site is located in the core zone of the national park (N54.44327, E12.90223). At the highly disturbed site, the dunes were clearly influenced by human trampling. Most of the area was bare sand and biocrust grew as thin biofilms between trampled paths. At the moderately disturbed site, trampled paths within the dunes were also visible, although it is forbidden to walk in the dunes. Biocrusts were visible as thin biofilm and were more frequently observed than at the highly disturbed site. At the little-disturbed site, no trampling was visible because a wooden boardwalk leads through the dunes. Here, the biocrusts were thicker, and even moss and lichen thalli could develop. A randomly chosen plot of 1 m^2 was established at each of the three sampling sites for further material collection. Biocrusts were sampled by gently pushing a Petri dish into the surface and lifting it with a spatula. Five Petri dish samples were collected per site. These were sealed using laboratory sealing film and transported to the laboratory for further analysis.

The biocrust stability was measured in the field, using a penetrometer (fruit hardness tester FHT-15, tip width 3.5 mm diameter). The penetrometer was pushed at a 90° angle onto the biocrust surface until the biocrust broke. The measurement was repeated five times per sampling site.

In the laboratory, the chlorophyll *a* (Chl *a*) content of the biocrusts was measured as an estimator for photosynthetic biomass. A defined area of 0.5 cm^2 biocrust was picked from the Petri dishes using a cork borer pushed approximately 1 cm into the sample. The biocrust material was incubated in 3 mL 96% ethanol at 78°C for 30 min. The solution was centrifuged and measured spectrophotometrically (Shimadzu UV-2401 PC, Kyoto, Japan) at 632, 649, 665, 696, and 750 nm absorbance. The last served as a control for turbidity (Ritchie, 2008). The extraction with ethanol was repeated until no chlorophyll *a* could be detected in the biocrust samples. Three replicates were measured for each sampling site. Total carbon and nitrogen (C_t and N_t) contents were determined by dry combustion of about 100 mg ground biocrust sample material in an element analyzer (UNICUBE® Elementar Analysensysteme GmbH, Langenselbold, Germany). Total phosphorus (P_t) was extracted from 100 mg of ground material by sub-boiling digestion using an acidic persulfate solution in Teflon® tubes for 24 h at 90°C (Berthold et al., 2015). All samples were neutralized using NaOH after digestion. The neutralized extract was further analyzed spectrometrically for phosphate, using the molybdenum blue method at 885 nm wavelength (Murphy and Riley, 1962). All total element contents were measured in five replicates per sampling site.

2.2 Preparation of permanent slides and morphological identification

Preparation of permanent slides followed the procedure described by Schulz et al. (2016). Briefly, approximately 0.5 g biocrust

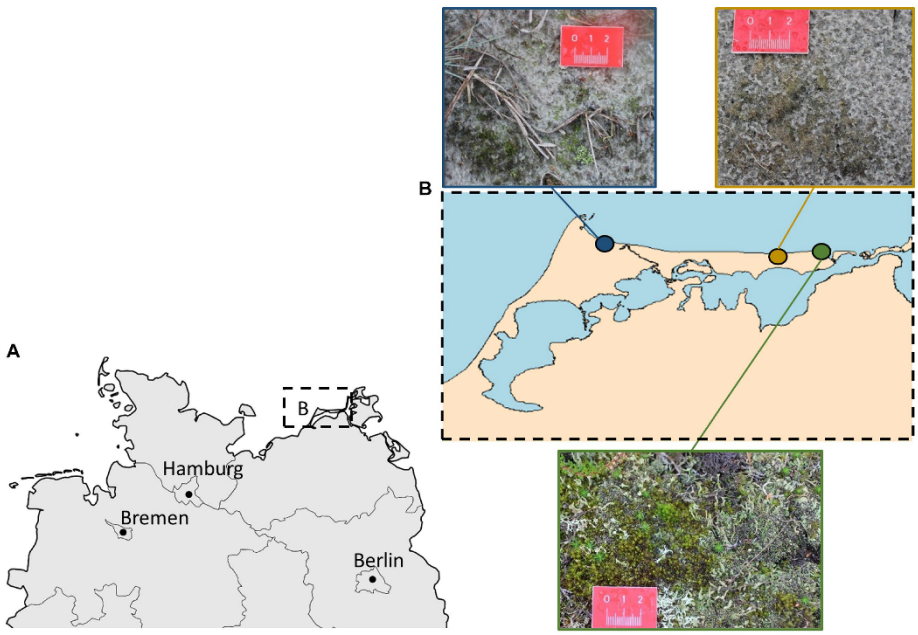


FIGURE 1
(A) The Darss-Zingst Peninsula in northern Germany. **(B)** Overview of sampling sites along the coastline of the Darss-Zingst-Peninsula, including impressions of biocrusts at these sites. Blue: camping area (highly disturbed); yellow: public beach (moderately disturbed); green: core zone of the National Park (little disturbed).

material was mixed with 4 mL distilled water and shaken. Immediately after shaking, 100 µL of overlying water was gently dripped onto glass coverslips, which were first air-dried and then combusted in a muffle oven (Elektra M26) at 550°C for 35 min. After cooling, the glass coverslips were mounted on glass microscope slides using Naphrax®. Diatom species were morphologically identified with the aid of a light microscope (Zeiss Axioplan, oil-immersion Plan-Apochromat objective, aperture 1.4) with 1,000-fold magnification. In total, over 400 valves that were at least 50% intact were counted per sampling site. The proportion of valves at least 90% and 100% intact was also recorded.

2.3 Establishment of diatom cultures

The establishment of terrestrial diatom cultures was challenging. The diatoms stuck tightly to the glass surface of the slides, making it impossible to pick single cells using a micromanipulator under a light microscope. Therefore, the pure cultures had to be developed by repeating transfer steps. Different culture media, both liquid and agarized, were tested to maximize the cultivation success: WC, Diat+Vit.mix (Bacillariophycean medium + vitamin mixture), BG11 (medium for cyanobacteria) and f/2 (enriched seawater medium) (recipes according to SAG). Initially, cultivation in agarized Petri dishes was more successful. After several transfer steps, only five diatom strains remained. They were transferred to liquid media where they could be established as unialgal cultures. These unialgal diatom cultures were cultivated in a Diat+Vit.mix medium at 20°C under low light (50 µmol photons m^{-2} s^{-1}).

2.4 PCR and sequencing for identification

DNA was extracted from the five diatom cultures, following the instructions of the NucleoSpin® Plant II Mini Kit (Macherey and Nagel, Düren, Germany). For identification, the rbcL gene (RuBisCO large subunit) was amplified in a PCR using a commercial PCR-Mastermix (Bioline). The primers Diat-rbcl-iR and Diat-rbcl-F were applied with the respective PCR protocol (Abarca et al., 2014). Sequencing was carried out by a commercial company (Eurofins, Luxembourg), using the same forward primer as for PCR. The sequences were uploaded to NCBI under the accession numbers OR387857–OR387860.

2.5 Desiccation experiment

The experiment followed the procedure described by Karsten et al. (2016). Briefly, the diatom cultures were grown for 1 week on glass-fiber filters (five replicates per strain), which were transferred for the experiment to a desiccation chamber filled with 100 mL silica gel. These were kept at a room temperature of ~25°C. The yield of photosystem II (YII) was recorded during desiccation every 10 min for 4 h as a proxy for the fitness of the cells, using non-invasive pulse amplitude modulation fluorometry (PAM2500, Walz, Germany). After a signal could no longer be measured, the filters were rewetted with 250 µL medium and transferred to another water-saturated chamber. The relative humidity in the chamber was continuously recorded in each second, using a multifunctional data logger (MSR 145 W; MSR Electronics GmbH, Switzerland).

2.6 Photosynthesis-irradiance curves

Photosynthesis-irradiance (PI)-curves of the five diatom strains (four replicates per strain) were measured according to Prelle et al. (2019). Briefly, 3.1 mL of thin log phase algal suspension of each strain and 31 µL sodium bicarbonate ($NaHCO_3$, 2 mM final concentration) were added to four airtight water-tempered (20°C) oxygen electrode chambers (DW1, Hansatech Instruments, King's Lynn, United Kingdom). The oxygen concentration was measured at ten increasing photon flux density levels ranging from 0 to ~1.500 µmol photons m^{-2} s^{-1} of photosynthetically active radiation (PAR), using a non-invasive oxygen dipping probe (DP sensors PreSens Precision Sensing GmbH, Regensburg, Germany). Measurements consisted of a 30 min respiration (dark) phase, followed by a 10 min photosynthesis (light) phase for each light level. The first and last minutes of each phase were excluded from the calculation. After the last measurement, Chl *a* was extracted from the 3.1 mL algal suspension (10 mL, 96% ethanol at 70°C for 10 min) and quantified spectrophotometrically (Ritchie, 2008). The mathematical photosynthesis model of Walsby (1997) was used for fitting and calculation of the maximum rates of net primary production (NPP_{max}), respiration (R), light utilization coefficient (α), photoinhibition coefficient (β), light saturation point (I_k), and the light compensation point (I_c).

2.7 Temperature curve

The photosynthetic and respiratory response of each strain (four replicates per strain) at temperatures between 5°C and 40°C was measured using the same oxygen optode system as for the PI-curves (Karsten et al., 2010). After 20 min incubation in the dark, the respiratory oxygen consumption (10 min in the dark), followed by the photosynthetic oxygen production (10 min under light-saturated conditions at 335 µmol photons m^{-2} s^{-1} PAR) were determined. Measurements were normalized to the total Chl *a* concentration (see procedure above). The model of Yan and Hunt (1999) was used to fit the temperature values, including optimum and maximum temperature.

2.8 Growth rate

The fluorescence of Chl *a* was used as a proxy for biomass to calculate the growth rates of the five diatom strains according to the temperature. The *in-vivo* Chl *a* fluorescence measurements were performed with a self-constructed growth fluorimeter based on the basic electronic unit of an MFMS fluorimeter (Hansatech Instruments, King's Lynn, United Kingdom) according to the protocol of Karsten et al. (1996). Bright-blue light LED emission (Nichia, Nürnberg, Germany) with a peak emission wavelength of 470 nm was selected for excitation of the Chl *a* fluorescence and pulsed with a modulation frequency of 870 Hz. Chl *a* fluorescence was detected as relative units by an amplified photodiode and was separated from scattered

excitation light through a long-pass glass filter (RG 665; Schott, Mainz, Germany) and a bright-red gelatin filter (Lee, Brussels, Belgium). *In-vivo* Chl *a* fluorescence units correlate well to the cell number and the concentrations of organic carbon and Chl *a* in diatoms, as shown by Karsten et al. (1996) and Gustavs et al. (2009). The cultures were grown in disposable plastic Petri dishes with cover lids, in a volume of 20 mL culture medium, and measured every 24 h for 10 days, following the procedure of Gustavs et al. (2009). The light was kept constant at 45–105 µmol photons m^{-2} s^{-1}, following a 16:8 light:dark cycle (Lumilux Deluxe Daylight L15W/950; OSRAM). The cultures were kept in water baths or air-conditioned rooms to ensure constant temperature conditions at five tested temperatures (5, 15, 20, 25, and 30°C), and all diatom strains were measured in triplicate. To ensure constant temperature over the course of the experiment, the light intensities were a bit below saturated conditions, because the light bulbs would otherwise have caused unwanted temperature fluctuations. Growth rates were calculated separately for each replicate, using the phase where the fluorescence signal increased exponentially (Gustavs et al., 2009). For 30°C, no growth rate could be calculated, because decreasing signal intensities were measured during the duration of the experiment. The model of Yan and Hunt (1999) was used to fit the temperature values, including optimum and maximum temperatures.

2.9 Detection of biochemical UV-protective substances

The biocrust biomass was extracted and further processed for HPLC (High-performance liquid chromatography) analysis as described by Karsten et al. (2009). Samples were analyzed with an Agilent HPLC system (Agilent, Waldbronn, Germany), and mycosporine-like amino acids (MAAs) were separated on a Phenomenex Synergi Fusion RP-18 column (Reversed Phase, Polar embedded C18 with TMS endcapping; 4 µm, 250 × 3.0 mm I.D.) protected with an RP-18 guard cartridge (20 × 4 mm I.D., Phenomenex, Aschaffenburg, Germany). The mobile phase contained 2.5% methanol (v/v) in 0.1% acetic acid (v/v) in HPLC water (0.055 µS cm^{-1}) and was run isocratically at a flow rate of 0.5 mL min^{-1} at 30°C column temperature for 20 min. MAAs were detected with a photodiode array detector at 330 nm wavelength, and absorption spectra (290–400 nm) were recorded in each second, directly on the HPLC-separated peaks. MAA standards were run within the sample sequence. Those included Asterina-330 (retention time 3.33 min, absorbance at 330 nm), Shinorine (4.71 min, 334 nm), Prasiolin (9.6 min, 323 nm), Porphyra-334 (5.89 min, 334 nm), Mycosporine-glycine (3.8 min, 310 nm), Klebsormidin A (5.35 min; 323 nm), and Klebsormidin B (5.74 min; 323 nm).

2.10 Statistical analyses

All statistical analyses were done in R, version 4.2.1 (R Development Core Team, 2022) or Microsoft Excel. Significant differences between measured soil parameters for the biocrusts of different sites were calculated in *R*, using one-way ANOVA. Photosynthetic irradiance curves were fitted using the Walsby model in Excel, based on least-square methods (Walsby, 1997). Temperature curves (both growth rate and oxygen production) were fitted using the Yan and Hunt (1999) model in R, also based on the least-square model. The model by Yan and Hunt is a simplified exponential and polynomial model, which represents the plant growth below and above the temperature optimum better than bi-or multilinear models. It has proven to fit the experimental growth data of microalgae well (Losa et al., 2020). Significant differences between oxygen production and consumption along the temperature gradient were calculated using one-way ANOVA followed by a *post-hoc* Tukey test ($p < 0.05$). Confidence intervals for maximum oxygen production, maximum growth rate, and optimum and maximum temperatures were calculated using the command 'confint2' (package nlstools; Baty et al., 2015).

3 Results

3.1 Analyses of biocrust characteristics

The Chl *a* content of the little-disturbed site was much higher (189.17 mg m^{-2}) than for the moderately and highly disturbed sites (72.32 and 76.62 mg m^{-2} respectively; Table 1). Further, the biocrust at the little-disturbed site was significantly more stable (1.12 MPa) than at the other two sites (0.5 MPa at the moderately and 0.4 MPa at the highly disturbed site). The stability of the biocrusts differed significantly between the little-disturbed and the other two sites ($p < 0.05$). The concentrations of total N (3.68 g kg^{-1}) and total C (78.76 g kg^{-1}) were significantly higher ($p < 0.05$) at the little-disturbed site. In contrast, significantly higher ($p < 0.05$) total P concentrations were measured in the biocrust samples from the moderately disturbed sampling site (50.7 mg kg^{-1}).

3.2 Diatom species and relative abundance in biocrusts

In total, we observed 47 diatom species in biocrusts from three sand dunes on permanent slides (Supplementary Table S1). Each site showed a similar richness (28–30 species), all diatom taxa were pennate species. Six of the 47 diatom species could be assigned to a pure terrestrial life cycle, according to the literature. These were *Pinnularia borealis*, *Pinnularia. intermedia*, *Hantzschia amphioxys*, *Luticola terrestris*,

TABLE 1 Biocrust characterization of all three sampling sites.

Study area	Degree of disturbance	C_t (g kg^{-1})	N_t (g kg^{-1})	P_t (mg kg^{-1})	Chl *a* (mg m^{-2})	Stability (MPa)
Camping area	High	9.5 ± 3.6	0.5 ± 0.2	6.8 ± 4.4	76.6 ± 29.0	0.4 ± 0.2
Public beach	Moderate	1.5 ± 0.3	0.2 ± 0	50.7 ± 19.8	72.3 ± 49.9	0.5 ± 0.1
National Park	Low	78.8 ± 23.7	3.7 ± 1.1	19.4 ± 9.4	189.2 ± 24.3	1.1 ± 0.1

Means + standard deviations (stability, C_t = total carbon, N_t = total nitrogen, P_t = total phosphorus, $n = 5$; Chl *a* $n = 3$).

Mayamaea fossalis, and *Nitzschia cf. pusilla*. These six diatom species were abundant in all the biocrust samples: 26% in biocrusts from the national park, 50% in biocrusts from the moderately disturbed area, and 18% in the highly disturbed dune area (Supplementary Table S1). The Simpson diversity index for the moderately disturbed site was lower (0.77) than at the other two sites (0.91 and 0.92). This was mainly because one species, *P. intermedia*, dominated the community at the moderately disturbed site, with an abundance of 45%.

Notably, many diatom frustules were partly disrupted. At the little-and moderately disturbed sites, approximately 48% were at least 90% or 100% intact. At the high disturbed site, only 25% were at least 90% or 100% intact (more details on the exact numbers of totally/mostly intact frustules can be found in Supplementary Table S1).

Most of the diatom species were found at all three sites (Figure 2) but some (~38%) were found exclusively at one site. These unique species were in most cases scarce, whereas the common species for all three sites were highly abundant.

3.3 Identification of diatom cultures

We successfully developed five unialgal cultures of terrestrial diatoms from the sand dune biocrusts. Unfortunately, one culture collapsed during the experiments. This culture (*P. intermedia*) had relatively small cells (smaller than average according to the literature) and those cells became smaller and smaller over time until the culture was no longer viable. This phenomenon is known to occur in some diatom cultures. With each cycle of asexual reproduction, the average size of diatoms in a culture decreases due to the formation of silica frustules, until the species' physical limit is reached. In the case of sexual reproduction, the daughter cells can become larger than the parent cells. However, not all diatoms reproduce sexually under culture conditions. Most likely, our culture collapsed because it reached its lower cell size limit and could not reproduce sexually under our culture conditions. Diatoms in the other cultures did not decrease in average size.

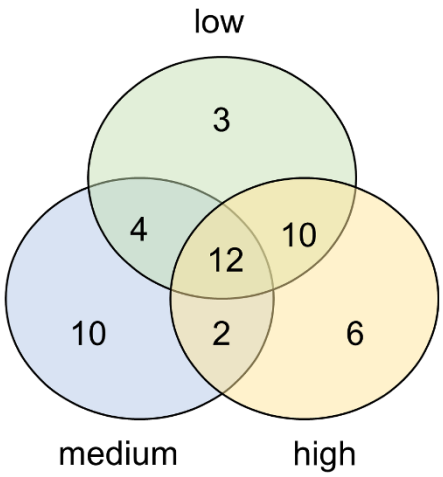


FIGURE 2
Venn diagram displaying the overlapping and unique diatom species present in biocrusts from dunes with high, moderate, or low degrees of human disturbance. Results based on morphological determinations from permanent slides.

We successfully cultivated *Hantzschia amphioxys*-aggr. (#1), *Achnanthes coarctata* (#2), *Hantzschia abundans* (#3), *Pinnularia intermedia* (#4), and *Pinnularia borealis*-aggr. (#6) (Figure 3). *H. amphioxys* and *P. borealis* originated from the highly disturbed site, whereas the other three cultures originated from the moderately disturbed site. The cultures were identified morphologically and also at the molecular level, based on the rbcL gene. The rbcL sequence of *P. borealis* was very similar (99.8% similarity) to the strain TAS17-48-10, which was assigned to clade 3 within the *Pinnularia borealis*-complex (Pinseel et al., 2019). The closest hit for the cultured *P. intermedia* was *P. acrosphaeria*, with 97.7% identity. There are no records of *P. intermedia* in the NCBI databases.

3.4 Desiccation tolerance

The diatom cultures were subjected to desiccating conditions to estimate their desiccation tolerance. After around 4 h, the filters with diatom cultures dried completely in the desiccation chamber (Figure 4). The drop in relative humidity from 40% to ~25% was accompanied by a drop in the yield of photosystem II (YII) to 0%. Few minutes later, the filters were transferred to a water-saturated chamber. *P. intermedia* and *P. borealis* showed only minor recovery to the initial Y(II) after rewetting. *H. amphioxys* recovered to around 40% of its initial Y(II). *H. abundans* and *A. coarctata* performed best, ending with 80% of the initial Y(II) after 24 h (Figure 4).

3.5 Light-dependent photosynthesis

The photosynthetic performance of the diatom cultures was measured as oxygen production along an increasing light gradient. *H. abundans* had a lower NPP_{max}, lower alpha, and lower respiration rate compared to the other four cultures (Figure 5; Table 2). All cultures showed no to only slight photoinhibition up to an irradiance of 1,500 µmol photons m^2 s^{-1}.

3.6 Temperature-dependent photosynthesis

The photosynthetic performance of the cultures showed a broad temperature tolerance (Figure 6; Table 3). The optimal temperature range, where at least 80% of the maximum oxygen production occurred, was about 13°C (Figure 7A). *P. intermedia* had a slightly higher range of about 15°C. In addition, the temperature range (between 10°C and 25°C) of optimal oxygen production for this species was below the range of the other four cultures, which was around 13–18°C to 27–30°C. The respiration of all diatom cultures had a higher optimum temperature (30°C to 35°C) than photosynthesis.

3.7 Temperature-dependent growth rate

The dependence of the growth rate on temperature was similar for *H. amphioxys*, *A. coarctata*, and *P. borealis*. These three cultures

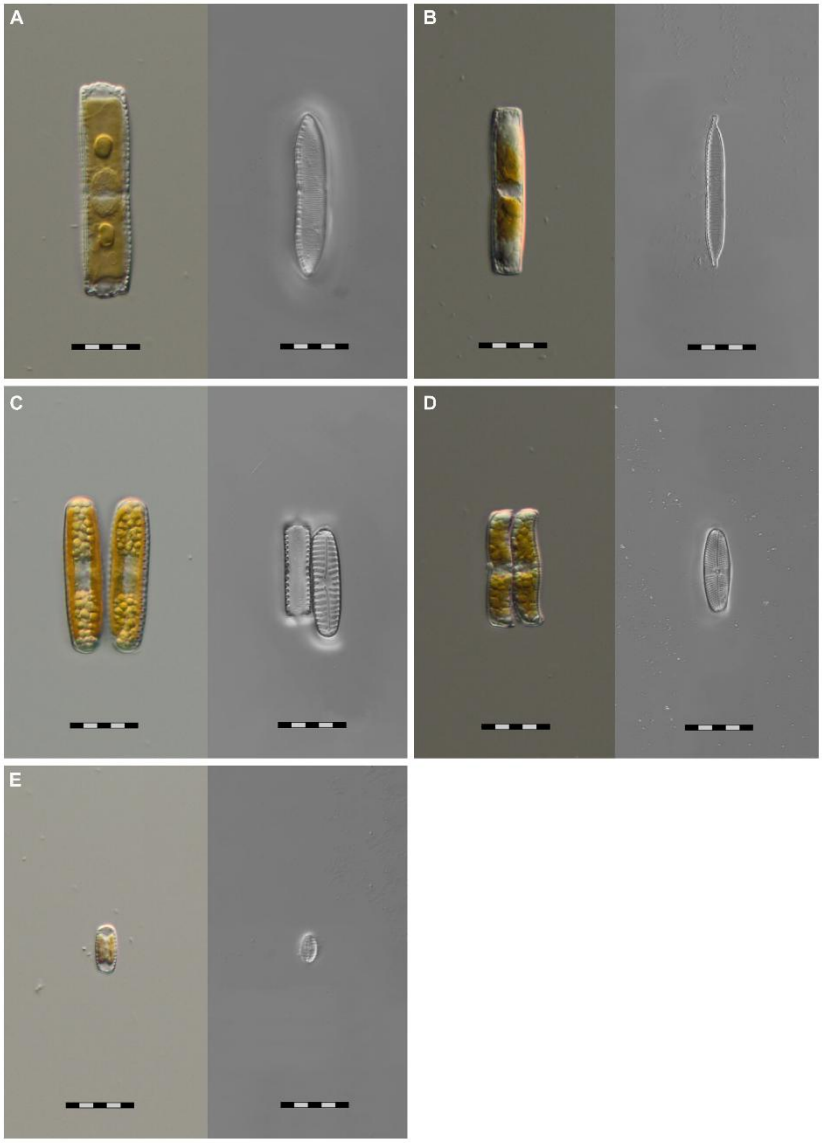


FIGURE 3
Microphotographs of five unialgal living diatom cultures and their frustules, isolated from biocrusts in coastal sand dunes, Mecklenburg-Vorpommern, Germany. Species identification is based on morphological and molecular features. **(A)** *Hantzschia abundans*, **(B)** *Hantzschia amphioxys*, **(C)** *Pinnularia borealis*, **(D)** *Achnanthes coarctata*, **(E)** *Pinnularia intermedia*; scale bar = 20 µm.

showed a similar maximum growth rate of ~0.5 µ day^{-1} (Figure 8; Table 4). *H. abundans* had a higher growth rate than the others. The maximum temperature for growth (Table 4) was highest in *H. amphioxys* (34°C), followed by *A. coarctata* (~31°C), whereas *H. abundans* and *P. borealis* reached their maximum temperature for growth already at 26°C and 28°C, respectively (Figure 7B).

3.8 Biochemical UV protection

In two of five cultures, *H. abundans* and *P. borealis*, the same mycosporine-like amino acid (MAA) was detected (Figure 9). The absorbance of this MAA was 333.5 nm wavelength and had a retention time of 6 min. This was a longer retention time than for our test standards, and therefore the MAA in these diatoms could not be identified.

4 Discussion

Depending on environmental conditions and external influences, biocrusts can reach different successional stages, from a thin algal crust to moss-dominated or lichen crusts (Langhans et al., 2009; Garcia-Pichel, 2023). The biocrusts observed at the little-disturbed site

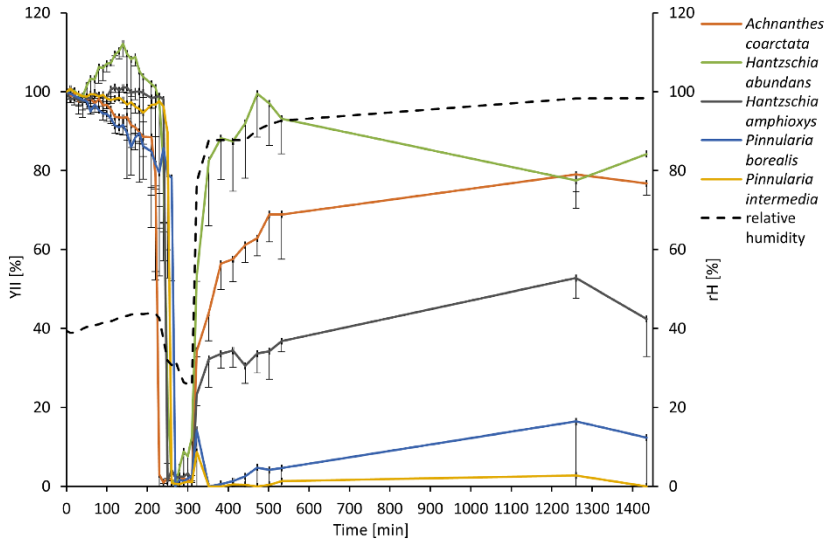


FIGURE 4
Effect of controlled desiccation and rehydration on the effective quantum yield (Y(II)) of PSII to five diatom cultures isolated from biocrusts in sand dunes ($n = 4$, only negative standard deviation is displayed for a better overview). Effective quantum yield values were standardized to the starting Y(II) to 100% for better comparison. The dashed line represents the measurement of relative humidity in the desiccation chamber.

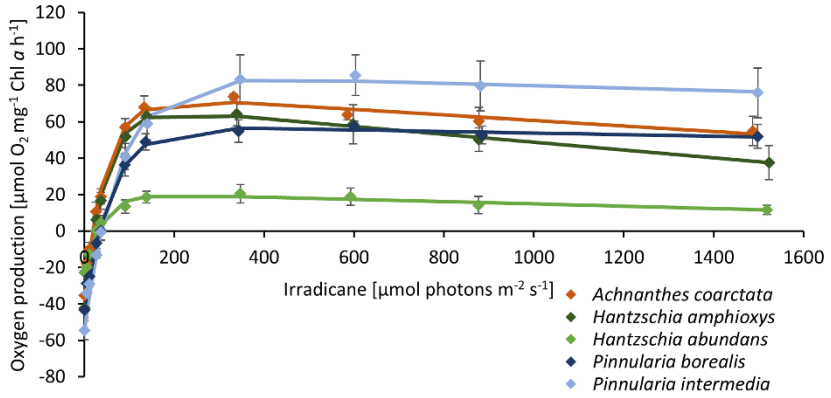


FIGURE 5
Photosynthetic-irradiance curve of five diatom cultures isolated from biocrusts in sand dunes. The points represent the mean of the measured values ($n = 4 \pm$ standard deviation), and the line is the fitting curve after Walsby (1997).

TABLE 2 Parameters of photosynthesis-irradiance (PI)-curves (Figure 4) of the five terrestrial diatom cultures ($n = 4 \pm$ standard deviation) measured at 20°C in Diat+Vit.mix medium.

	Achnanthes coarctata	*Hantzschia abundans*	*Hantzschia amphioxys*	*Pinnularia borealis*	*Pinnularia intermedia*
NPP_{max}	71.27 ± 1.4	19.6 ± 4	64.93 ± 5.1	56.42 ± 3.7	82.84 ± 10.8
alpha	2.3 ± 0.5	1.11 ± 0.9	2.5 ± 0.1	1.72 ± 0.1	1.85 ± 0.2
beta	−0.01 ± 0.01	−0.01 ± 0.004	−0.02 ± 0	0 ± 0.004	−0.01 ± 0.01
Respiration	−35.42 ± 2.5	−22.62 ± 1.2	−42.3 ± 1.6	−43.24 ± 4	−54.56 ± 4.5
I_k	46.29 ± 12.8	38.17 ± 8.9	42.91 ± 8.3	57.96 ± 12.3	74.32 ± 12.1
I_c	18.68 ± 2.2	29.13 ± 4.3	21.51 ± 1.1	32.91 ± 1.6	37.56 ± 2.5

NPP_{max}, maximum rates of net primary production in µmol O_2 mg^{-1} Chl *a* h^{-1}; alpha, light utilization coefficient; beta, photoinhibition coefficient; I_c, light saturation point; I_c, light compensation point.

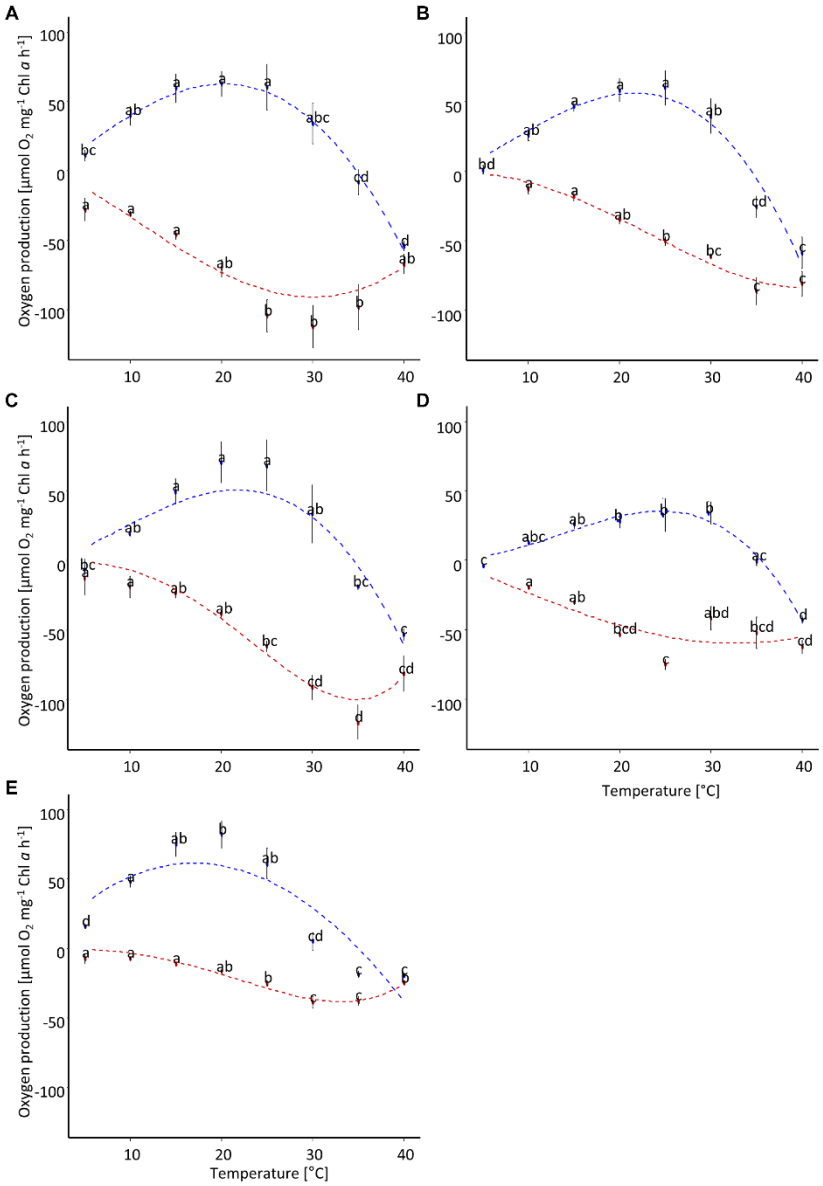


FIGURE 6
Temperature-dependent oxygen production of five diatom cultures isolated from biocrusts in sand dunes. The points represent the mean of the measured values ($n = 4 \pm$ standard deviation), and the dotted line is the fitting curve after Yan and Hunt (1999). Different letters indicate significant differences for photosynthesis (blue) or respiration (red), respectively (ANOVA with *post-hoc* Tukey test). **(A)** *Achnanthes coarctata*, **(B)** *Hantzschia abundans*, **(C)** *Hantzschia amphioxys*, **(D)** *Pinnularia intermedia*, **(E)** *Pinnularia borealis*.

were mostly dominated by mosses, representing a later stage in succession (Lan et al., 2012; Garcia-Pichel, 2023). One reason for this may be the high protection status of the dunes within the national park. The dunes are protected against human trampling and biocrust can form stable layers on the dune sediment, as shown in this study. These stable biocrusts accumulated more organic material, as evidenced by the significantly higher total carbon and Chl *a* contents compared to the other two sites. Phosphorus is transported into the ecosystem mostly by wet and dry deposition (Berthold et al., 2019). Further weathering of phosphorus-containing parent rock material is an important mechanism through which phosphorus becomes available to the biocrust community in the sand dunes (Filippelli, 2002). The significantly higher phosphorus concentration at the moderately disturbed site might be explainable by a selective input of an external P source such as bird droppings, which could have influenced the measurement.

Terrestrial diatoms have long been known, but have received only slight interest from biologists. Recent studies have pointed toward a

TABLE 3 Parameters of oxygen production along a temperature gradient after fitting with Yan and Hunt (1999) model including 5% confidence interval for four diatom cultures ($n = 4$).

	Achnanthes coarctata	*Hantzschia abundans*	*Hantzschia amphioxys*	*Pinnularia borealis*	*Pinnularia intermedia*
NPP_{max}	62.8 (53–72.7)	56.5 (46.8–66.2)	60 (46.6–73.4)	35.6 (29.4–41.9)	64.2 (53.2–75.2)
optimum temperature [°C]	20.3 (17.8–22.7)	21.6 (19.2–24)	22.1 (18.9–25.3)	24.5 (22.3–26.6)	17.1 (13.8–20.5)
maximum temperature [°C]	34.8 (33.6–36)	34.5 (33.3–35.6)	35 (33.5–36.5)	35.5 (34.5–36.5)	35.1 (33.4–36.8)

NPP_{max}, maximumrates of net primary production in µmol O_2 mg^{-1} Chl *a* h^{-1}.

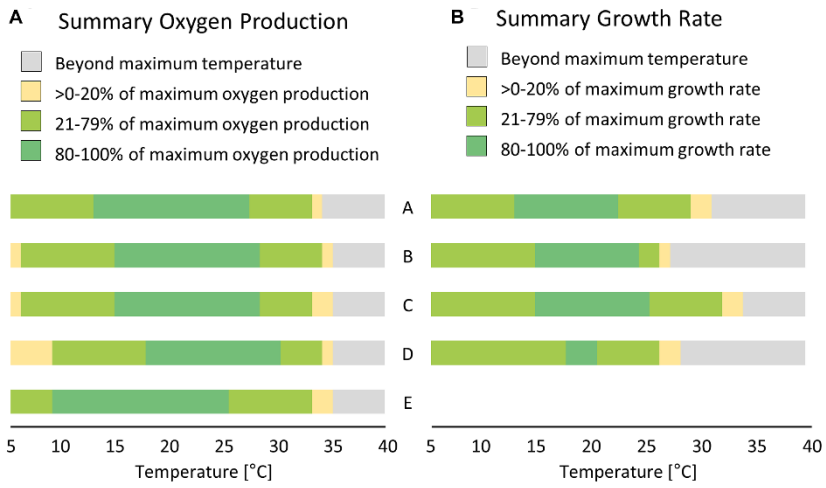


FIGURE 7
Comparison between short-term; [**(A)** few hours, measured as oxygen production] and long-term; [**(B)** few days, measured as growth rate] effects of temperature treatment on five (or four) diatom cultures isolated from biocrusts in sand dunes. Values were calculated based on the fitting results presented in Figures 6, 8. A – *Achnanthes coarctata*, B – *Hantzschia abundans*, C – *Hantzschia amphioxys*, D – *Pinnularia borealis*, E – *Pinnularia intermedia*.

large hidden diversity within morphological species. For example, the species complexes of *P. borealis* and *H. amphioxys* have been divided into several species (Pinseel et al., 2019; Maltsev et al., 2021), which share morphological similarities but can be clearly distinguished by molecular methods. Such studies provide evidence of the gap in our current understanding of terrestrial diatoms.

In our study, we observed 28–30 diatom taxa per sampling site (a total of 47 species at the three sites combined), which is within the common range of species per sample compared to other studies (Van de Vijver et al., 2008; Norbäck Ivarsson et al., 2013; Kopalová et al., 2014; Schulz et al., 2016; Zhang et al., 2020; Fazlutdinova et al., 2021; Foets et al., 2021). However, we observed a large number of marine diatoms (for example *Achnanthes lemmermannii*, *Catenula adhaerens*, *Cocconeis peltoides*, *Navicula germanopolonica*, and *Navicula viminoides*; for ecological preferences of these diatoms see Witkowski et al., 2000; Plinski and Witkowski, 2020). These marine species probably did not live in the biocrusts, and their valves may have been blown onto the beach or transported via sea spray. This idea is supported by our observation of many partly destroyed valves. This would be uncommon if the diatoms were living and reproducing in this habitat. Therefore, it appears that only 4 to 6 species were actually abundant and alive in the biocrust samples. Among these, we found typical terrestrial diatoms such as *P. borealis* and *H. amphioxys*. *P. borealis* is reported worldwide in a variety of terrestrial habitats (Pinseel et al., 2019), even in less-favorable environments such as volcanic soils a few months after an eruption (Fazlutdinova et al., 2021). This species has outperformed other diatom species in surviving frequent and extreme freezing (−180°C) conditions (Hejduková et al., 2019). Nevertheless, it is important to keep in mind that our current understanding of *P. borealis* as a ubiquitous and highly stress-tolerant species might change. Pinseel et al. (2019) found that *P. borealis* is a complex consisting of around eight species. Similarly, *H. amphioxys*, also reported worldwide from a variety of habitats, also seems to be a complex of approximately six species. Single species within a species complex may diverge to different habitats. *A. coarctata* is also occasionally reported from terrestrial habitats, especially since it seems to live in mosses. For example, we cultured *A. coarctata*, which was reported from moss samples in Antarctica (Kopalová et al., 2014). However, we did not observe this species on our combusted slides, which may indicate that it was present in low abundance in our samples. The dominance of *P. intermedia* in the moderately disturbed area was remarkable. We also cultured this species, although we did not succeed in keeping it in culture for long. Notably, *P. intermedia* is only rarely reported and is also missing in the sequence databank. This species was observed from sand dunes (Round, 1957; Schulz et al., 2016) and mosses (Beyens, 1989), but since then has only rarely been reported in terrestrial habitats.

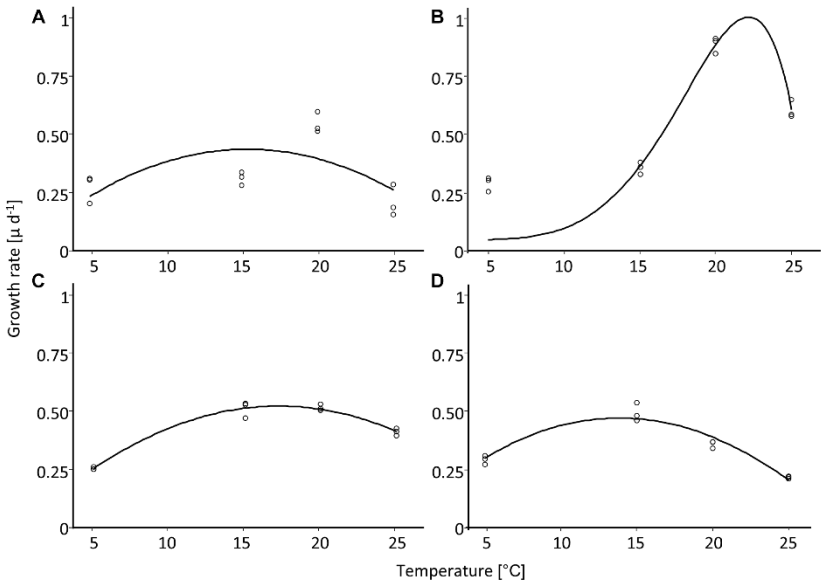


FIGURE 8
Temperature-dependent growth rate of four diatom cultures isolated from biocrusts in sand dunes. Points represent the measured values ($n = 3$), and the line is the fitting curve after Yan and Hunt (1999). **(A)** *Achnanthes coarctata*, **(B)** *Hantzschia abundans*, **(C)** *Hantzschia amphioxys*, **(D)** *Pinnularia borealis*.

TABLE 4 Parameters of growth rate along a temperature gradient after fitting with Yan and Hunt model including 5% confidence interval for four diatom cultures (no results for *Pinnularia intermedia*; $n = 3$).

	Achnanthes coarctata	*Hantzschia abundans*	*Hantzschia amphioxys*	*Pinnularia borealis*
maximum growth rate [μ day^{-1}]	0.44 (0.31–0.57)	0.96 (0.66–1.26)	0.53 (0.51–0.55)	0.42 (0.39–0.46)
optimum temperature [°C]	15.4 (11.4–19.4)	22.2 (21.3–23)	17.2 (16.6–17.9)	13.9 (12.9–14.8)
maximum temperature [°C]	30.6 (22.2–39.0)	26.2 (25.1–27.4)	34.1 (32.1–36.2)	28 (26.7–29.2)

4.1 Indicator value

Freshwater diatoms have long been used as bioindicators in aquatic environments because some species are sensitive to pollution (e.g., high nutrient concentrations) and thus provide valuable information concerning water quality. The idea to use terrestrial diatoms as bioindicators is relatively new, and the criteria for assessment are not yet defined (Antonelli et al., 2017; Barragán et al., 2018). However, this approach seems promising (Wanner et al., 2020; Zhang et al., 2020; Minaoui et al., 2021). For example, a study in suburban soils around Marrakesh, Morocco, supported the idea of using diatoms for indication of high nutrient content, pH, and conductivity (Minaoui et al., 2021). Although our study showed different community patterns, possibly depending on the degree of human disturbance, there was no clear indicator species for low or high disturbance levels. In our case, maybe the high proportion of broken diatom frustules might serve as an indicator for high disturbance levels. Broken frustules indicate that these diatoms had been dead for some time and therefore the frustules became disrupted due to physical forces. These forces can be stronger under regular trampling because in such cases the sand grains would grind the silica frustules. In coastal dunes, such broken frustules could also be carried in from the sea via sea spray. We derive this assumption from our results, but further research is needed to confirm our hypothesis and to establish the proportion of broken frustules as a valid indicator value in the future.

4.2 Ecophysiological performance of soil diatom cultures

Most studies on terrestrial diatoms rely on estimation of morphological diversity based on valves, a well-developed method (Nagy, 2011). Nevertheless, it remains unclear if the valves represent living and reproducing diatom species or if those diatoms were dead, or if the valves were merely blown into place because valves can remain stable for several centuries and are used in paleobiology (Dreßler et al., 2011). Only a few studies on terrestrial diatoms rely on culture techniques. Culturing of terrestrial diatoms is often quite challenging due to unknown requirements and because the diatoms tend to live closely attached to soil particles. Consequently, our study is one of only a few that have examined the ecophysiological tolerance of soil diatoms. Our study showed that the diatoms can use and tolerate a wide range of irradiance intensities. Also, short-term

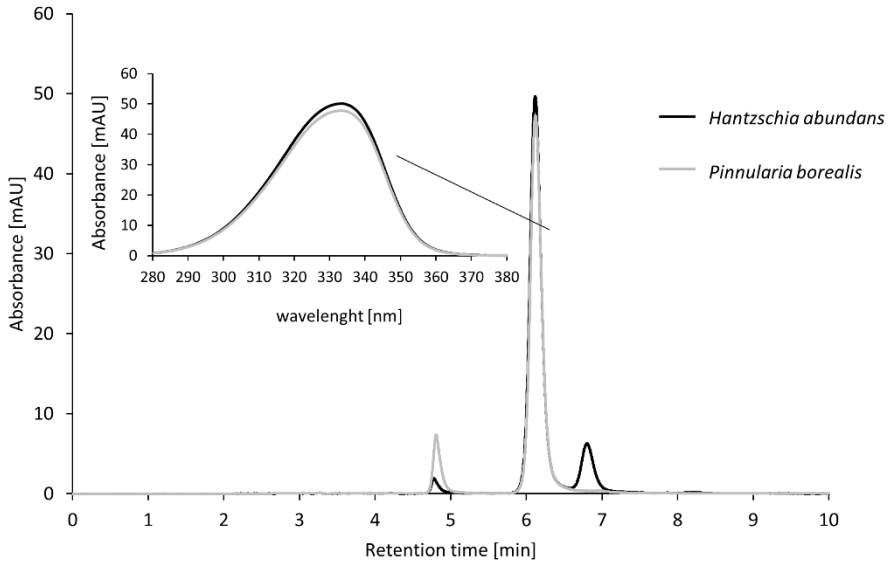


FIGURE 9
High-performance liquid chromatography (HPLC) results for mycosporine-like amino acid (MAA) extraction from terrestrial diatom cultures; two of five diatom strains contained MAAs. The insert shows the absorbance of the strongest peak (maximum absorbance at 333.5 nm).

temperature shifts could be tolerated quite well. Both factors, light intensity and temperature, can change rapidly in terrestrial habitats and over a wider range than in aquatic habitats. However, our observations of slower growth rates during several days of increased temperatures made it obvious that soil diatoms prefer relatively low to moderate temperatures (~15–20°C) and are sensitive to high temperatures (>30°C). In coastal sand dunes, the surface can reach temperatures above 40°C (Maun, 2009). It appears that the diatoms could tolerate such a shift for a short time but need a recovery period with moderate temperatures during the night. Also, other studies have reported that diatoms can tolerate a wide temperature range over the short term (Souffreau et al., 2010).

Terrestrial habitats, especially the sand dunes with their low water-holding capacity, can dry out rapidly during the day. Therefore, terrestrial organisms must deal with periodic desiccation events. Three cultures (*H. amphioxys, H. abundans*, and *A. coarctata*) reached 50% of their initial photosynthetic performance after rehydration. Only the two *Pinnularia* species (*P. borealis* and *P. intermedia*) failed to recover well after the desiccation event. This is somewhat surprising because both *Pinnularia* species are true terrestrial species and can live outside a moss carpet. It might be that our experimental setup was harsh, with a relative humidity below 25%, which does not naturally occur in coastal dunes in Germany. Additionally, the *P. intermedia* cells were smaller than average, which indicates that the culture did not reach its full potential. In general, pennate diatoms, such as those in our five cultures, are mobile and can avoid unfavorable conditions or migrate in a positive phototactic direction (e.g., moving vertically in sediments) under natural conditions (Consalvey et al., 2004; Poulsen et al., 2022). Such a protective vertical movement was not possible for the diatoms during the desiccation experiment. A study on aquatic and terrestrial diatoms also indicated a low desiccation tolerance for diatoms in general when only air-dried (Souffreau et al., 2010). The exceptions in this study were *P. borealis* and *H. amphioxys*, which were able to grow after drying in air for 10 min.

4.3 Mycosporine-like amino acids from diatoms

Mycosporine-like amino acids are frequently reported from marine or brackish water and are mostly attributed to dinophytes and bacillariophytes (Jeffrey et al., 1999). Interestingly, it was suggested that MAAs might be stored in the silica frustules, which would substantially enhance their stability and prevent harmful UV light from penetrating the outer cell layer (Ingalls et al., 2010). We did not test for the location of the MAAs, but this seems to be an interesting strategy, which could potentially also be used by terrestrial diatoms. Studies on marine diatom cultures have reported seven MAAs as the most common: Shinorine, Porpyhra-334, Mycosporine-2-glycine, Palythine, Palythene, Mycosporine-glycine, and Mycosporine-glycine-valine (Helbling et al., 1996; Moisan and Mitchell, 2001). Of these frequently present diatom MAAs, we most likely detected Mycosporine-2-glycine, with an absorbance at 334 nm. This assumption is supported by the retention time for Mycosporine-2-glycine in a methanol/acid mobile phase in HPLC, which is a few seconds longer than for Porphyra-334. In our study, the MAA from the terrestrial diatoms had a slightly longer retention time in the same phase than the Porphyra-334 standard.

Our study contributes the first record of MAAs in terrestrial diatoms. Terrestrial habitats are characterized by high UV radiation compared to aquatic habitats, especially in summer under a clear sky. Terrestrial diatoms are typically pennate with one or two raphes, which allow the diatoms to move, for example, in marine sediments. Therefore, we hypothesize that terrestrial diatoms could move in

deeper sand layers to avoid harmful radiation. This would incur a certain cost: although the diatoms escape the harmful UV radiation, they are less exposed to photosynthetic active radiation. As all the cultures that we tested showed no photoinhibition, protection from harmful UV radiation seems to be a useful strategy to exploit the high radiation on the sand surface for efficient photosynthesis without being harmed by UV radiation.

5 Conclusion

In this study, we evaluated the ecophysiological characteristics of terrestrial diatoms from sand dunes. Although terrestrial diatoms have been known for a long time, only a few studies have investigated their functioning despite their abundance and wide distribution. Our study is one of only a few to provide an insight into the ecology of terrestrial diatoms based on cultures, which is a necessary basis for understanding their ecology and distribution. We observed a wide temperature tolerance of all diatom cultures concerning primary production, but long-term exposure to different temperatures resulted in a lower temperature tolerance concerning growth rates. Desiccation tolerance differed among the cultures, with some showing a high recovery rate after harsh desiccating conditions and others with only low recovery rates. Although terrestrial diatoms appear to be sensitive to warmer and drier summer conditions, the biocrust microecosystem including a moss cushion may reduce the environmental stress for these diatoms.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: NCBI, accession numbers OR387857-OR387860.

Author contributions

KG: Formal analysis, Investigation, Conceptualization, Data curation, Funding acquisition, Project administration, Supervision, Visualization, Writing – original draft. SK: Formal analysis, Investigation, Writing – review & editing. NP: Data curation, Formal analysis, Methodology, Visualization, Writing – review & editing. MD: Data curation, Formal analysis, Methodology, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmicb.2023.1279151/full#supplementary-material

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Green fields mark terrestrial diatoms	Low distrubance site	Medium distrubance site	High distrubance site
Achnanthes aff. *minuscula*	31	27	2
Achnanthes lemmermannii	29	15	33
Anorthoneis pulex			1
Anorthoneis spec.			1
Anorthoneis vortex	1	1	
Astartiella bahusiensis			1
Catenula adhaerens		13	2
Cavinula cf. *weinzierlii*	3		2
Chrysophyte-Cysts	1	9	
Cocconeis aff. *pelta* A		3	
Cocconeis aff. *pelta* B		3	
Cocconeis cf. *hoffmannii*	5	4	1
Cocconeis disculus		2	
Cocconeis nugalas	4	1	2
Cocconeis peltoides	1		29
Cocconeis scutellum	3		
Cocconeis sp. A	49	19	46
Cocconeis sp. B	2	1	1
Delphineis minutissima			1
Delphineis surirella			3
Fallacia aequorea			1
Fallacia cf. *subpygmaea*	3	2	
Fallacia clepsidroides		2	2
Fallacia cryptolyra	1		1
Fallacia florinae	2		
Fallacia pygmaea	1		
Fallacia tenera		1	
Gomphonemopsis exigua		4	
Halamphora cf. *subturgida*		1	
Hantzschia amphioxys	49	6	12
Luticola terrestris		20	
Mayamaea fossalis		1	
Navicula aleksandrae	3	6	
Navicula bozenae		4	
Navicula germanopolonica	6		12
Navicula perminuta		1	
Navicula viminoides	13		13
Nitzschia cf. *pusilla*	4		2
Pennales (nicht bestimmbare Gürtelbänder)	12		1
Pinularia borealis	17		27
Pinularia intermedia	43	183	33
Planothidium deperditum	2		4
Planothidium hauckianum	3		4
Planothidium sp. A	47	39	77
Planothidium sp. B	16	9	27
Planothidium sp. C	53	31	48
Planothidium sp. D	31	1	29
counted microscope fields of view	40	40	60
counted valves	**435**	**409**	**418**
number of taxa	**29**	**28**	**30**
numer of totally intact frustules (100% intact)	**135**	**157**	**79**
number of mostly intact frustules (>90% intact)	**75**	**39**	**27**
number of frustules of aerophilic/terrestrial diatoms	**109**	**189**	**72**
percent of totally and mostly intact frustules	48.3	47.9	25.4
terrestrial diatoms	26.0%	51.3%	17.7%

3.3 Publication III

Successional development of the phototrophic community in biological soil crusts, along with soil formation on Holocene deposits at the Baltic Sea coast

Sandra Kammann, Peter Leinweber, Karin Glaser, Ulf Schiefelbein, Christian Dolnik, Tatiana Mikhailyuk, Eduard Demchenko, Elena Heilmann, and Ulf Karsten

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EDITED BY
Lynne Beaty,
Penn State Erie, The Behrend College, United States

REVIEWED BY
Josef Elster,
University of South Bohemia in ČeskéBudějovice, Czechia
Michael Lakatos,
Hochschule Kaiserslautern University of Applied Sciences, Germany

*CORRESPONDENCE
Sandra Kammann
sandra.kammann@uni-rostock.de

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Successional development of the phototrophic community in biological soil crusts, along with soil formation on Holocene deposits at the Baltic Sea coast

Sandra Kammann[1*], Peter Leinweber[2], Karin Glaser[1], Ulf Schiefelbein[3], Christian Dolnik[4], Tatiana Mikhailyuk[5], Eduard Demchenko[5], Elena Heilmann[2] and Ulf Karsten[1]

[1]Institute for Biological Sciences, Applied Ecology and Phycology, University Rostock, Rostock, Germany, [2]Soil Sciences, Faculty of Agriculture and Environmental Sciences, University Rostock, Rostock, Germany, [3]Botanical Garden, University Rostock, Rostock, Germany, [4]Institute for Natural Resource Conservation, Landscape Ecology, Kiel University, Kiel, Germany, [5]M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine

Harsh environmental conditions form habitats colonized by specialized primary microbial colonizers, e.g., biological soil crusts (biocrusts). These cryptogamic communities are well studied in drylands but much less in temperate coastal dunes, where they play a crucial role in ecological functions. Following two dune chronosequences, this study highlights the successional development of the biocrust's community composition on the Baltic Sea coast. A vegetation survey, followed by morphological species determination, was conducted. Sediment/soil cores of the different dune types were analyzed to uncover the potential impacts of the biocrust community on initial soil formation processes, with special emphasis on biogeochemical phosphorous (P) transformations. Biocrust succession was characterized by a dune type-specific community composition, shifting from thinner algae-dominated biocrusts in dynamic dunes to more stable moss-dominated biocrusts in mature dunes. The change in the biocrust community structure was accompanied by an increase in Chl *a*, water, and organic matter content. In total, 25 algal and cyanobacterial species, 16 mosses, and 26 lichens across all sampling sites were determined. The pedological characterization of these cores elucidated initial processes of soil genesis, such as decalcification, acidification, and the accumulation of organic matter with dune and biocrust development. Furthermore, the chemistry of iron (Fe)-containing compounds such as the $Fe_{dithionite}/Fe_{total}$ ratios confirmed mineral weathering and the beginning of soil profile development. The biocrusts accumulated P over time, while the P content in the underlying sediment did not change. That implies that biocrusts take up P from the geological parent material in the dunes, thereby accumulating available P in the ecosystem, which gets transferred into subsoil horizons through leaching or redeposition. The relative proportion of the bioavailable P pool (56% to 74% of P_t) increased with dune succession. That happened at the expense of more stable bound P, which was transformed into labile P. Thus, the level of plant available P along the dune

chronosequences increased due to the microbial activity of the biocrust organisms. It can be concluded that biocrusts of temperate coastal dunes play a crucial role in maintaining their habitat by accumulating nutrients and organic matter, supporting soil development and subsequent vegetation.

KEYWORDS

biocrusts, chronosequence, dunes, phosphorus, phototrophic diversity, soil development

1 Introduction

The Baltic Sea is geologically relatively young, and so are its coasts. The recent geomorphology of the coastline originates from repetitive glaciations during the Pleistocene period (Niedermeyer and Janke, 2011). The ice shields of the last glaciation, the Weichselian, began to melt about 12,000 years ago, which was the starting point for the altering freshwater and saltwater history of the Baltic Sea. With the advancing melting of the ice shields, the sea level rose, which marked the beginning of the sea-level transgression (Lampe, 2002). The freshwater periods were repeatedly interrupted by saltwater intrusions from the North Sea, which started about 8,000 years ago due to sea level fluctuations and the uplift of land masses. Hereby, the brackish water-dominated Baltic Sea was formed (Lemke, 1998).

Due to today's tideless conditions, erosion and accumulation processes dominate the coastline of the Baltic Sea (Schumacher and Bayerl, 1999; Tiepolt and Schumacher, 1999). Here, the constant impact of wind and waves on exposed coastal areas causes erosion. The eroded material gets transported by coastal-parallel currents and deposited in protected shallow bays. The result is a smoothened and relatively closed coastline, especially along the southern Baltic Sea coast ("graded or equilibrium coast") (Müller et al., 2023), with characteristic geomorphological forms such as sand hooks and spits (Lampe et al., 2011). These coastal forms can be found and studied on the peninsula Fischland-Darss-Zingst.

This peninsula consists of a sequence of Late Weichselian period moraine island cores that are connected by sandy barriers (sand spits). The latter are under ongoing shaping forces causing coastal degradation, sand drift, and accumulation. The Darss is the northwestern part of the peninsula. Mainly due to the shifting of sediment by incoming and outgoing waves in shallow waters, the shoreline expanded in the northern direction of the initial island core. Thereby, an almost triangular foreland ("Neudarss"), showing a sequence of about 120 beach ridges, accumulated over time and today ends in a northeast turning sand hook (Darsser Ort). If no further sand is transported along the coastline to enlarge the hook, this coastline will be ablated again. The western coastline of the Darsser Ort already retreats (approximately 1 m/year) to the east by sediment erosion and is therefore called an abrasion coast. Cliff dunes are created in the process. On the other hand, new beach ridges form in the north and allow the hook at Darsser Ort to expand (Tiepolt and Schumacher, 1999; Lampe and Lorenz, 2010) (Supplementary Figure 1).

Eastwards of the peninsula, the coastline continues with an extensive sand accumulation in shallow water due to the transport of sediment parallel to the coast (Niedermeyer et al., 2011). This area is a wind flat of about 25 km^2. Depending on the wind strength and direction, shallow areas fall dry or are flooded (Karsten et al., 2012). Wind flats typically accumulate sediment particles and hence stabilize coastlines. As at the Darsser Ort, a coastline-parallel orientation of beach ridges can be observed here (Janke and Lampe, 1998; Reimann et al., 2010). Coastal sand dunes have formed on these ridges, resulting in a chronological series of this landform. The source material for these dunes originates from the Pleistocene island cores, which eroded during the sea level rise in the Holocene. After the sea level dropped about 6,000 years ago, this material became accessible again and contributed to the formation of spits, hooks, wind flat, and sand dunes (Schumacher, 2002). Like the coastline, dunes are mobile aeolian landforms that constantly change. The dune geomorphology is based on initial geneses as well as on the following abrasion and accumulation processes due to wind, waves, and storm events. Further inland, in areas where these extreme environmental conditions are declining, a change from mobile to more stable dune types can be observed (Martínez et al., 2004). The resulting sequence of dune types represents a chronological series and allows studies on their formation and development, soil genesis, and vegetation colonization over time (Ranwell, 1960; Isermann, 2011; Pollmann et al., 2020). The abiotic factors during the dune genesis hardly differ from each other. The only difference between the dune types is the time of their formation (Stevens and Walker, 1970; Walker et al., 2010). At the Baltic Sea coast, the successional dune development on a flat coast differs between four to five characteristically dune types, which can be divided into initial, growth, maturity, and decomposition stages (Niedermeyer et al., 2011). The foredune ridge adjoins the beach inland. It is the starting point of an idealistic dune chronosequence and is followed by mobile yellow dunes. Flooding and storms are causing frequent sand movement. In the subsequent grey dunes, phototrophic organisms are already progressively colonizing, thereby stabilizing the dune surface and promoting the formation of a humus layer on the loose sediment. The chronosequence ends in a mature dune area, which is likely to be

forested with scrubs or smaller pine trees (Hesp, 1991; Leuschner and Ellenberg, 2017; Jurasinski and Buczko, 2023). The general trends along such a chronosequence include organic matter accumulation and increasing acidification, as well as decalcification, a decrease in salt stress, and sand transport and deposition (Salisbury, 1952; Hundt, 1985; Giani and Buhmann, 2004; Pollmann et al., 2020). In addition to the constant movement of the sand, extreme temperature fluctuations near the dune surface and drought make this area an extreme habitat (Martínez et al., 2004). On the one hand, living communities settling there have to cope with a low nutrient supply, flooding events, and salt stress (García Novo et al., 2004; Maun, 2009). On the other hand, biotic colonization can significantly influence these geomorphological processes during dune succession, promoting initial soil formation (Williams et al., 2012; Zaady et al., 2014). The colonization of a heterogeneous dune habitat strongly depends on the individual dune types. Driven by extrinsic (e.g., microclimate) and intrinsic (e.g., species competition) mechanisms, dune habitats develop their particular assemblage of microbial and vascular plant communities (Miller et al., 2010).

Cryptogamic vegetation (e.g., mosses, lichens, and fungi) are primary ground covers and characteristic growth forms on top of terrestrial bare soils (biological soil crusts = biocrusts) or rock surfaces (Elbert et al., 2012). They are characterized by an interaction of phototrophic and heterotrophic microorganisms, leading to a complex biotic network. Due to this organismic diversity, biocrusts are involved in ecosystem processes and linked to a wide range of ecological functions (Belnap et al., 2001). The initial habitat colonization of biocrusts is accompanied by an increase in organic matter content (Veste et al., 2011; Dümig et al., 2014) and in soil stability (Fischer et al., 2010; Felde et al., 2018). The latter can be seen as an essential function that biocrusts can provide to highly dynamic ecosystems like coastal sand dunes, which are constantly threatened by soil erosion and blowouts (Belnap and Büdel, 2016). Moreover, it has been shown that biocrusts are likely to influence local hydrological cycles, including absorptivity and water retention (Fischer et al., 2012; Chamizo et al., 2016). In addition, the organisms of the biocrusts are involved in various essential element nutrient cycles, such as carbon (Sancho et al., 2016) and nitrogen (Castillo-Monroy et al., 2010; Elbert et al., 2012; Barger et al., 2016), while the metabolic processes within the phosphorus cycle (P cycle) are far less studied but have progressively received attention in recent years (Richardson and Simpson, 2011; Schulz et al., 2015; Baumann et al., 2019; Kurth et al., 2021). Such complex functions depend on the respective biocrust type and, therefore, its structure, which varies with climate, underlying soil, and disturbance (Belnap, 2006; Sun et al., 2022).

The dominant biocrust-forming community, typical for a specific successional stage and biocrust type, plays a decisive role in the development and performance of its ecological functions (Li and Hu, 2021). Various environmental factors, characteristic of a geographical region, affect the natural successional process of the biocrust community. Prominent among these factors are the availability of water (Fischer et al., 2012), the temperature (Garcia-Pichel et al., 2013), radiation, topography, soil texture (Zaady et al., 2000; Fischer and Subbotina, 2014), microclimate (Veste and Littmann, 2006), and nutrient availability (Bu et al., 2018). The availability of these resources and disturbances impacts the succession (Pickett and McDonnell, 1989) of biocrusts and determines the rates of biocrust formation, which can range from 10 to 1,000 years (Langhans et al., 2010; Williams et al., 2012). The interactions of biocrust types with individual community compositions and morphologies influence the nutrient influx, soil chemistry, and surface microtopography. Therefore, biocrusts can be considered relevant promotors in pedogenesis and dune development (Williams et al., 2012).

Various studies focused on biocrust community development, functions, and changes in arid areas (Büdel et al., 2009; Samolov et al., 2020; Li and Hu, 2021), but less is known about biocrusts in coastal sand dunes of temperate regions (Kammann et al., 2023). Few studies on sand dunes along the Baltic Sea coast underlined the ecological importance of biocrusts in influencing soil properties, causing an increase in total phosphorus concentrations, and emphasized their high site-specific microorganism diversity (Schulz et al., 2015; Mikhailyuk et al., 2019; Kammann et al., 2023). Schaub et al. (2019) identified sand blasting and burial of the biocrust microorganisms as crucial factors in biocrust development on temperate sand dunes. Furthermore, the study showed gains in ecological soil functioning of the sand dunes by initial soil organic matter formation and an accumulation of nutrients, especially on the more protected landward dune slope. The results of these studies led to the first conclusions about the relevant ecosystem functions of biocrusts in dunes for nutrient cycling and further vegetation colonization. Information on community changes across biocrust successional stages along the natural dune development, however, is missing.

In this study, it is assumed that the natural coastal dynamics lead to a successive development of different types of biocrusts on the dunes. Therefore, the intention was to (1) define dominant biocrust types in the different dune successional stages and (2) survey the changes in the biodiversity of phototrophic organisms. In addition to vegetation surveys, (3) pedological investigations focus on initial soil formation processes and the chronosequential changes in dune soils. The P cycle is of particular importance in this context. Hence, a further objective was to (4) determine the P content and sequentially extracted P pools that reflect the availability of P to microorganisms and plants. Easily bioavailable P is expected to (5) accumulate with ongoing dune succession due to biocrusts' impact on the biogeochemical P cycle. Thereby, the biocrust community is assumed to enhance labile P contents due to the conversion of more stable P into labile P.

2 Material and methods

2.1 Study site

Biocrust samples were collected in January 2021, along two dune successional sequences on the peninsula Fischland-Darss-Zingst (Mecklenburg Western Pomerania, Northern Germany; Figure 1A). Both sampling sites are located in the core zone of the national park Vorpommersche Boddenlandschaft, on a flat coast of the Baltic Sea, and differ in their morphology. While the sampling transect at Darsser

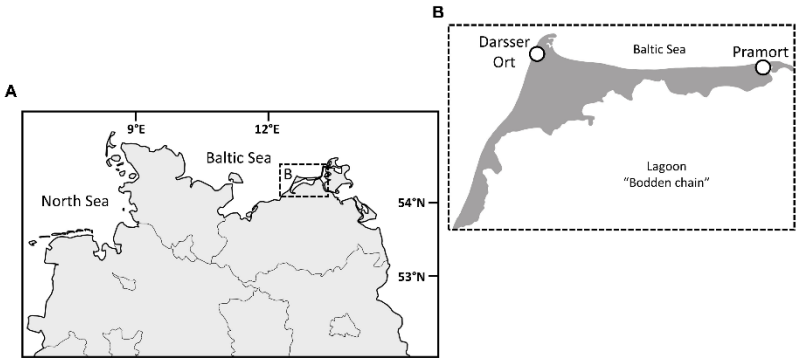


FIGURE 1
The peninsula Fischland-Darss-Zingst in the northern part of Germany **(A)**. A close-up of the peninsula **(B)** and the investigated dune sampling sites, Darsser Ort and Pramort (circle). Copyright: GeoBasis-DE/M-V.

Ort (Figure 1B) is located on a dune cliff (54.472167, 12.499556) endangered by abrasion, the flat coast at Pramort (Figure 1B) forms a sandspit (54.44475, 12.923). Both dune areas are under the strict protection of the national park. Trampling in the dunes is prohibited, but especially at the Darsser Ort, it cannot be excluded.

2.2 Sampling

2.2.1 Transects

Biocrust samples were taken along one transect at both study sites. Each transect followed the natural geomorphological succession (chronosequence) of the respective dune area. At Darsser Ort (Figure 2) it started at the edge of the dune cliff. The dune cliff represented a former grey dune identified visually in the field by visible slight accumulations of iron oxides and humus in the underlying soil horizon [Figure 2A (right)]. Due to erosion processes, this primary dune got eroded, which led to the formation of the dune cliff. As part of a secondary dune formation process, the dune cliff was continuously covered with a large amount of sand due to aeolian transport during storm events. Hence, the dune area today is characterized by a loose sand layer down to a depth of approximately 30 cm without any further visible zonation of the substrate. Due to this trait and the later described vegetational patters, this area of dunes is referred to below as the (secondary-formed) yellow dune (YD). The grey dune area following the geomorphological gradient was divided into two grey dune types. The grey dune area directly following the yellow dune was named the early grey dune area (eGD) since the dune surface was dominated by early microalgae biocrusts, some mosses, and bare sediment. Due to these characteristics, the dune type can be assigned partly to a yellow and partly to a grey dune and therefore reflects a transition zone. In addition, a decline in the marram grass stands (*Ammophila arenaria* (L.) Link) characteristic of the yellow dune was observed here. The part of the grey dune area further inland was defined as a late grey dune area (lGD). A significantly dominant moss cover and the frequent occurrence of lichens led to the differentiation of both grey dune subtypes within the large grey dune area. The transect followed the dune chronosequence further inland and ended in the mature dune area (MD), which was already overgrown with pine trees.

The transect at Pramort started at the eastern accumulation coast of the peninsula, in a periodically submerged wind flat called windwatt (WW). Here, an initial formation of a spit could be seen on the basis of pioneer vegetation (*Ammophila arenaria* (L.) Link) and sand accumulation. After that, the transect crossed a yellow dune area (YD), where microbial and vegetational cover changed. Further inland, a grey dune (GD) area superseded the mobile and higher yellow dunes, finally reaching the mature dune area (MD) (Figure 3), similar to the transect progression at the Darsser Ort.

Along each transect, the described different successional dune stages were selected and further named dune subsites. At each subsite, a sampling plot of 1 m^2 [maxi grid, cf. Figure 3B (2–4)] was established and used for further vegetation analyses, biocrust, and sediment sampling. In total, eight sampling plots at two study sites were under investigation in this study, four per site.

2.2.2 Sample collection and preparation

For sampling, Petri dishes (92 mm in diameter) were pushed gently into the respective biocrust. A metal spatula was then used to lift and further separate the biocrust from the underlying loose sediment. A maxi-grid (1 m × 1 m) divided each sampling plot into 16 equal subplots (25 cm × 25 cm) [cf. Figure 3B (2–4)]. One Petri dish was collected within each subplot.

The yellow dune at Darsser Ort and in the windwatt at Pramort had no biocrusts. To keep the sampling design uniform at each plot, samples were also taken from these two plots using Petri dishes, even when containing no visible biocrusts. At each sampling plot, a set of three samples (equals three Petri dishes) was collected for chlorophyll *a* analyses and for algae community cultivation, direct microscopy, and identification (Table 1). These samples were directly wrapped in aluminum foil and stored in a cooling box for transportation. Three further samples (second set) were taken in the same way, which were later used for nutrient element analyses (C, N, P) of biocrusts (Table 1). For the measurement of biocrust characteristics (water and organic matter content), one additional Petri dish was collected

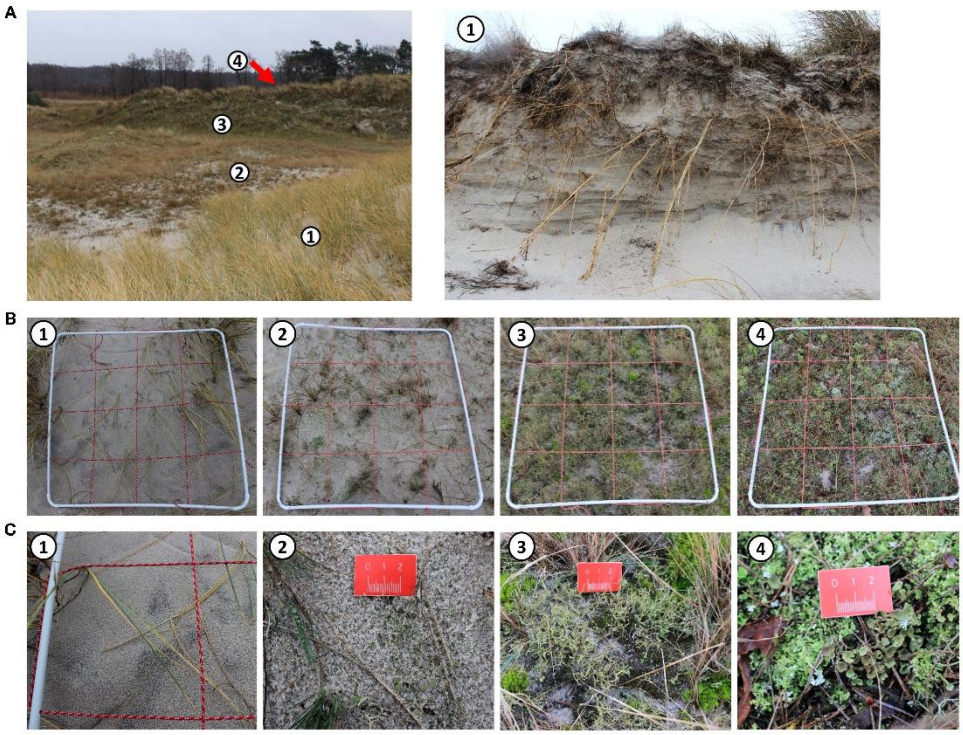


FIGURE 2
Overview of the transect at Darsser Ort; numbers indicate the sampling plots: 1, yellow dune (YD; secondary formed); 2, early grey dune (eGD); 3, late grey dune (lGD); and 4, mature dune (MD). Transect overview (left) and view at the dune cliff from the beach site (right) **(A)** close-ups of the sampling plots **(B)** and detail shots of the top sediment layer and dominating biocrust types in the respective plot **(C)**.

per plot (Table 1). All mosses and lichens detected in the sampling plots were collected by hand and stored in paper bags.

Furthermore, a hand auger (30 cm length, 5 cm diameter) was used for collecting the sediment/soil samples (Figure 4A). The auger was used three times, randomly within the sampling plot. The samples were already visually divided in the field for topsoil horizon and subsoil horizon/sediment layer (cf. Figure 4B, yellow box = topsoil horizon). The sediment/soil core samples were stored in plastic ziplock bags and transported to the laboratory for further chemical analyses. Since before detailed chemical analyses, it cannot be decided to what extent the sediment has already been transformed into soil, the exact naming of the upper and lower parts of the samples in the auger remains open (soil horizon or sediment layer) until the presentation of the results.

2.3 Analyses of biocrusts and sediment/soil characteristics

2.3.1 Biocrusts

In the laboratory, two subsamples were taken using a cork drill (Ø 1.5 cm) from each of the three Petri dishes (first set) planed for the chlorophyll *a* analysis. This tool allowed to punch out a defined biocrust surface area. This resulted in six chlorophyll *a* measurements per sampling plot, i.e., in total, 48 analysis (8 sampling plots × 3 petri dishes (replicates) × 2 subsamples per dish) were done along both transects. These individual samples were each stored in a 15 mL Falcon® tube and frozen at −20°C until chlorophyll *a* extraction. The remaining biocrust material in the Petri dishes was air-dried and further stored in the dark until the subsequent algae isolation and identification.

Chlorophyll *a* (Chl *a*) content was used as a proxy for the photosynthetic biomass (Chl *a* mg m^{-2}) in biocrusts. Even though no biocrusts were visually recognizable in the windwatt (Pramort) and the yellow dune (Darsser Ort), the Chl *a* analysis was performed identically to the protocol for biocrusts. The Chl *a* extraction was conducted after a standard laboratory protocol, and the Chl *a* absorbance at 632 nm, 649 nm, 665 nm, and 696 nm wavelengths was measured using a spectrophotometer (Shimadzu UV-2401 PC, Kyoto, Japan). The Chl *a* content was calculated according to Ritchie (2008) and normalized to a square meter (m^2). A detailed description can be found in Kammann et al. (2023). The biocrusts in the additional three Petri dishes (second set) were separated from the sediment with a razor blade to measure their nutrient element contents. The biocrust samples were sieved (< 2 mm) and subsequently milled to 10 to 20 µm particle size (mortar grinder "Pulverisette 2", Idar-Oberstein Germany) for further homogenization. Total carbon and nitrogen content (C_t and N_t) were determined by dry combustion of about 25 to 30 mg of sample in an elemental analyzer (vario EL cube, Elementar

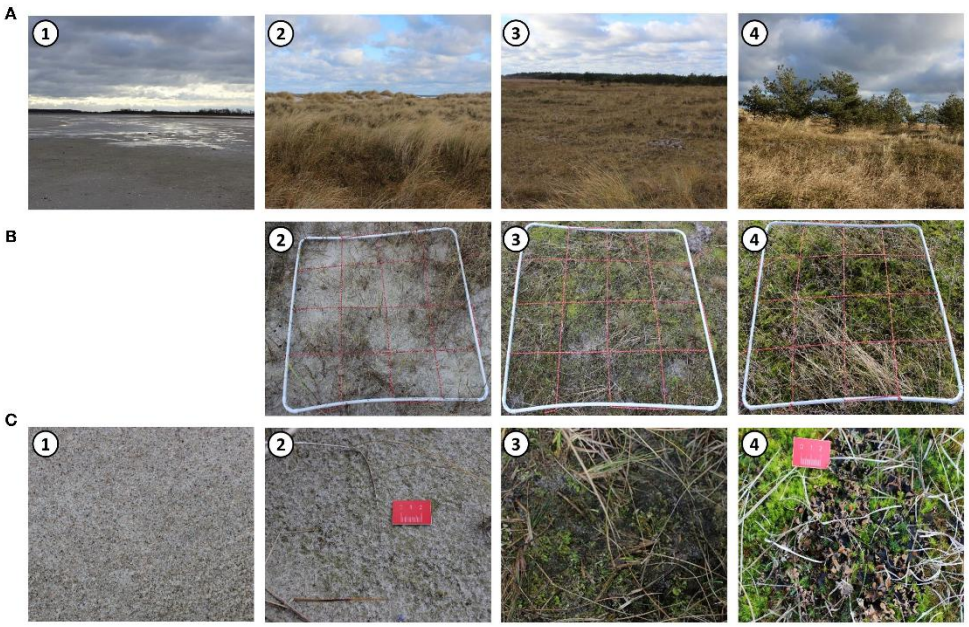


FIGURE 3
Overview of the transect at Pramort; numbers indicate the sampling plots: 1, windwatt (WW); 2, yellow dune (YD); 3, grey dune (GD); and 4, mature dune (MD) **(A)**. Close ups of the biocrust-holding sampling plots **(B)** and detail shots of the top sediment layer and dominating biocrust type in the respective plot **(C)**.

Analysensysteme GmbH, Langenselbold, Germany). Total phosphorus (P_t) was extracted from 500 mg of air-dried material by microwave-assisted digestion using *aqua regia* solution (3:1 hydrochloric acid:nitric acid). The concentration in the extract was measured by inductively coupled plasma optical emission spectroscopy at a 214.914 nm wavelength (Perkin-Elmer Optima 8300 DV, Waltham, MA, USA). At each plot, each parameter was measured in triplicate.

TABLE 1 List of all measured parameters in the corresponding compartments.

Parameters	Sediment/ soil core	Biocrust
pH ($CaCl_2$)	X	
Electrical conductivity (mS cm^{-1})	X	
$CaCO_3$ (g kg^{-1} DW)	X	
Dithionite–citrate–bicarbonate extracted iron (Fe_{dit}) (g kg^{-1} DW)	X	
Oxalate extracted iron (Fe_{ox}) (mg kg^{-1} DW)	X	
Water content (% FW)		X
Organic matter (% DW)		X
C_t, N_t, P_t (g kg^{-1} DW or mg kg^{-1} DW)	X	X
Sequential P fractionation (mg kg^{-1} DW)	X	(X)
Phototrophic community (presence/absence)		X
Chlorophyll *a* content (mg m^{-2})		X

The X indicates the compartment in which the respective parameter was measured.

For analyzing the biocrust characteristics (water and organic matter content), the entire biocrust of the remaining single Petri dish sample was used. After fresh weight (FW) determination, the samples were dried at 105°C for 24 h and weighed again to determine the dry weight (DW). The water content was calculated from these two measurements and expressed as a percentage of total fresh weight (% FW). The sample drying was followed by their combustion at 450°C for 5 h to determine the organic matter (OM) content. Therefore, the sample weight loss after combustion was determined, and the organic matter content was expressed as a percentage of total dry mass (% DW).

2.3.2 Sediment/soil cores

For further analytical determination of basic sediment/soil parameters such as pH, electrical conductivity, and calcium carbonate content ($CaCO_3$), the core material was used. This material was air-dried in the laboratory and sieved to < 2 mm. These basic parameters were determined by routine methods described in Blume et al. (2010): pH electrometrically in 1:2.5 (w/v) suspension with 0.01 M $CaCl_2$; electrical conductivity in saturation extract with de-ionized water by temperature-compensated conductivity measurement device (WTW Microprocessor Conductivity Meter LF196) and $CaCO_3$ content by dissolution with 10% HCl and volumetric CO_2 measurement in a Scheibler calcimeter. Al, Fe, Mn, and P from poorly crystalline pedogenic oxides were extracted from 0.5 g of soil (< 2 mm) using a 0.2 M NH_4 oxalate solution (pH 3) in the dark

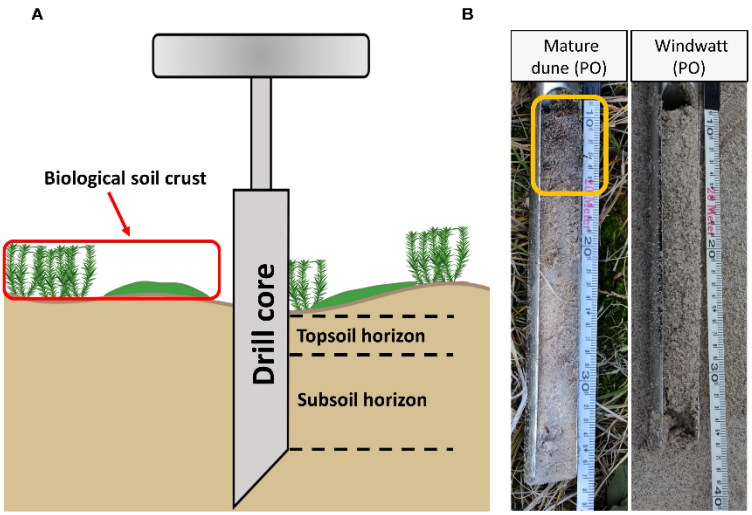


FIGURE 4
Schematic figure of the hand auger application in relation to biocrusts **(A)**. Exemplary representation of two sediment/soil cores sampled at Pramort. Yellow box represents a subdivided topsoil horizon, based on visual inspection and confirmed by chemical analyses **(B)**.

(Schwertmann, 1964). The total amount of Fe, Al, Mn from pedogenic oxides (poorly and well crystallized oxides) was extracted by the dithionite–citrate–bicarbonate (DCB) method after Mehra and Jackson (1958) with slight modifications. In brief, 1 g of soil (< 2 mm) was incinerated at 550°C before being extracted twice with 25 mL citrate–bicarbonate solution and 1 g of Na dithionite at 80°C and washed with a 10 mL 0.1 M $MgSO_4$ solution thereafter. Concentrations of elements in the oxalate extract (Fe_{ox}, Al_{ox}, Mn_{ox}, P_{ox}) and DCB extract (Fe_{dit}, Al_{dit}, Mn_{dit}) were measured by ICP OES. The amount of pedogenic oxides with a higher degree of crystallinity was estimated by subtracting the amount of poorly crystalline oxides from the amount of total pedogenic oxides ($Al_{dit\text{-}ox}$, $Fe_{dit\text{-}ox}$, $Mn_{dit\text{-}ox}$).

The determination of the C_t, N_t, and P_t concentrations followed the same protocol as for the biocrusts. In addition to the total carbon content, the organic carbon content of the sediment/soil core samples was also determined.

2.4 Sequential P fractionation

The method of sequential P fractionation was used to characterize P pools of different solubility in the sediment. Here, the inorganic and organic P fractions in the sediment were characterized according to extractability with increasingly stronger chemicals, which traditionally has been interpreted as an indication of bioavailability for microorganisms and plants. The method was adjusted by Hedley et al. (1982) and applied to the core samples. If these had already been separated into upper and lower layers or horizons in the field, only the upper sediment/soil core samples were examined for P fractions. Exemplarily, biocrusts from two sampling plots along each transect were additionally analyzed. This included 30 mL purified water in the presence of an anion exchange resin (membrane, 2 cm × 6 cm), $NaHCO_3$, NaOH, and H_2SO_4, as described in detail in the Supplementary Material (Supplementary Figure 2; Table 1). The concentration of P_t in the extracts was determined by ICP OES. Concentrations of molybdate-reactive P, which is mostly considered inorganic P (P_i), in each extract was determined using the molybdenum blue method of Murphy and Riley (1962). The concentration of molybdate-unreactive P, here considered organically bound P (P_o, e.g., ADP/ATP, phospholipids), was calculated as the difference between P_t and P_i of each fraction. Resin-P and $NaHCO_3$-P are ascribed to labile P, whereas NaOH-P is considered moderately labile P, and H_2SO_4-P are relatively stable P compounds.

2.5 Vegetation survey

A category system of seven pre-defined functional vegetation groups was designed to describe the overall surface coverage of each sampling plot (Supplementary Table 2). The set of functional groups was based on previous work conducted by Büdel et al. (2009); Lan et al. (2012), and Williams et al. (2017), but was slightly modified. The early successional stages of biocrust development were characterized by thin (1–3 mm) microalgae-dominated biocrusts (MA). Slightly thicker (3–8 mm) microalgae biocrusts, which were additionally partly moss-covered, were defined as the intermediate successional biocrust stage (MA/M). The mature successional stages of biocrusts consisted of moss-dominated biocrusts (MD) and those associated with lichens (MD/L). Moreover, two additional biotic functional groups were established: vascular plants and litter (dead organic matter, e.g., pine needles, leaves, and branches). Bare sediment was the only abiotic functional group.

The point-intercept method of Levy and Madden (1933) was used to record the predefined functional groups. A maxi-grid (1 m ×

1 m) divided each sampling plot into 16 equal subplots (25 cm × 25 cm). Furthermore, a smaller metal grid (25 cm × 25 cm) was randomly placed within four of these 16 subplots (Supplementary Figure 3). Within these four subplots, the functional groups were recorded by 25 point-intercept measurements according to the approach of Williams et al. (2017). At each intersection where two lines crossed, a metal pin was dropped, and the ground covering functional group, including bare sediment, was recorded. This made a total of 100 point measurements per sampling plot (1 m^2).

2.6 Algae isolation, community cultivation, and identification

The air-dried biocrust material, stored in the dark, was further used for the identification of the most frequent and dominant species. Pieces of biocrusts were placed in Petri dishes with Bold basal (1 N BBM) agarized medium to obtain enrichment cultures (Bischoff and Bold, 1963). Cultures grew with a 12-h alteration of light and dark phases and irradiation of 25 µmol photons m^{-2} s^{-1} at a temperature of 20°C ± 5°C. After 3 weeks of cultivation, morphological investigations were performed using an Olympus BX53 light microscope with Nomarski DIC optics (Olympus Ltd, Hamburg, Germany) and a digital camera (Olympus LC30) attached to the microscope. The micrographs herewith recorded were processed by the Olympus software cellSens Entry. Parallel to cultivation, direct microscopy of rewetted samples was performed. Here, the dominant species of algae and cyanobacteria in the original samples were evaluated. Morphological identification of the biocrust organisms was based mainly on Ettl and Gärtner (2014) for green microalgae and on Komárek and Anagnostidis (2005) as well as Komárek (2013) for cyanobacteria. Furthermore, monographs and papers devoted to taxonomic revisions of the taxa of interest were used, such as Lokhorst (1996); Fučíková et al. (2014); Mikhailyuk et al. (2019), and others. Algae and cyanobacteria were presented according to the modern taxonomic interpretations (Guiry and Guiry, 2023). It was not feasible to assess the abundance of each identified taxa within each sample due to the method of enrichment cultivation. To still be able to make a statement about the diversity at each sampling point, the total number of identified algal species per sampling plot, referred to as species richness, was used.

2.7 Moss and lichen determination

Moss and lichen samples were air-dried in the laboratory. A microscope with a maximum magnification of ×400 was used for the determination. Morphological identification of mosses was based on Frahm and Frey (2004), with taxonomical reference to Hodgetts et al. (2020). Lichens were determined according to Wirth et al. (2013) and followed the nomenclature concept provided by Printzen et al. (2022). Some species of the genus *Cladonia* needed a deeper morphological treatment. Therefore, these samples were additionally chemo-taxonomically analyzed by thin-layer chromatography according to Culberson and Ammann (1979) in solvent system A.

2.8 Statistical analyses

The percentage of areal coverage by each functional group recorded in the vegetation survey obtained via the point-intercept method was visualized as a stacked bar graph. Significant differences in the measured biocrust and sediment/soil characteristics, including nutrient contents, were elucidated by performing analyses of similarities ("anosim" function in R) between the sampling sites and across the transect plots in both dune areas. To reflect differences in the overall biocrust community between the different sites and dune successional stages, nonmetric multidimensional scaling (nMDS) using the vegan R package, and the Bray–Curtis dissimilarity index implemented in R was applied. Furthermore, permutational multivariate analyses of variance (PerMANOVA) ("adonis" function in R) using the Bray–Curtis distance matrix were conducted to reveal potential correlations of community composition with biocrust and sediment plot characteristics and nutrient contents (Oksanen et al., 2018). If a significant correlation between the phototrophic community and the sediment/soil characteristics was detected, these parameters were added to the nMDS plot. All statistical analyses were conducted using R version 4.2.1 (R Core Team (2022) Vienna, Austria). The total species number of each phototroph group (algae, moss, and lichen) per sample was considered as alpha diversity. As a measure of beta diversity, the presence/absence data of the biocrust-inhabiting species were visualized within Venn diagrams using Microsoft Excel 2013 (Microsoft Corporation, Redmond, WA 98052-6399, USA).

3 Results

3.1 Analyses of biocrusts and sediment/soil characteristics

3.1.1 Biocrusts

Along both transects, the phototrophic biomass increased from algal biofilms towards more stable and moss-dominated biocrusts (Table 2). At Darsser Ort, the Chl *a* concentration was lowest in the yellow dune (YD = 1.2 mg m^{-2} ± 0.9 mg m^{-2}) and reached a value of 100.3 mg m^{-2} ± 18.9 mg m^{-2} in the early grey dune area where the microalgae-dominated crusts and some mosses were present. In the following late grey dune area, the percentage coverage of biocrusts further increased, and so did the Chl *a* content in the biocrusts (327.1 mg m^{-2} ± 88.4 mg m^{-2}). In the mature dunes, the Chl *a* content reached its highest value (453.8 mg m^{-2} ± 188.0 mg m^{-2}). A similar pattern was observed along the transect at Pramort. The windwatt at the beginning of the transect had no Chl *a* in the bare sediment. In the following yellow dune, Chl *a* was detected as the first sign of early biocrust development (127.6 mg m^{-2} ± 4.2 mg m^{-2}). The moss-dominated biocrusts in the grey and mature dunes had the highest Chl *a* values (GD = 453.2 mg m^{-2} ± 35.4 mg m^{-2}, MD = 482.8 mg m^{-2} ± 125.9 mg m^{-2}).

The gravimetric water content of the biocrusts at Darsser Ort ranged between 7.3% (w/w) in the early grey dune area and 25.3% (w/w) in the biocrusts growing in the mature dune area. At

TABLE 2 Biocrust characteristics of both sampling sites.

Study site	Sampling plot	Compartment	Chl *a* (mg m^{-2})	Water content (% FW)	OM (% DW)
Darsser Ort	YD	Ai	1.2 ± 0.9	3.6	0.0
	eGD	Biocrust	100.3 ± 18.9	7.3	1.0
	lGD	Biocrust	327.1 ± 88.4	12.6	3.7
	MD	Biocrust	453.8 ± 188	25.3	11.0
Pramort	WW	Ai	5.4 ± 1.2	7.9	0.2
	YD	Biocrust	127.6 ± 4.2	5.0	0.3
	GD	Biocrust	453.2 ± 35.4	21.9	5.7
	MD	Biocrust	482.8 ± 125.9	40.9	18.6

Means ± standard deviation for Chl *a* content (n = 3). Ai = initial A-Horizon; no biocrusts in this dune subsites are detectable.

Pramort, the sediment water content along the successional dune gradient was slightly higher than at Darsser Ort. The water content measured in the windwatt was relatively high, at 7.9% (w/w), even though it represented an unvegetated area due to its periodic submersion. While the biocrusts in the yellow dune area exhibited 5.2% (w/w) of sediment water content, the grey and mature dune areas had 21.9% and 40.9% (w/w) moisture, respectively (Table 2).

The biocrust organic matter content (OM) increased along the transect at Darsser Ort. When starting in the early grey dune area, low contents (1.0% DW) were measured. With biocrust development, the OM content rose toward the mature dune, up to 11.0% DW in the biocrusts. The development of the OM content in biocrusts showed a similar pattern at Pramort. The biocrust-free and temporarily submerged sediment of the windwatt had an OM content of 0.2% DW. The OM contents along the successional gradient followed the order: yellow dune (0.3% DW) < grey dune (5.7% DW) < mature dune (18.6% DW) (Table 2).

The contents of nutrient elements (C_t, N_t, P_t) in the biocrusts increased along both transects towards older dune successional stages. The C_t values measured in the biocrusts at Pramort exceeded the values at Darsser Ort by a factor of 2 to 4. Furthermore, the C_t contents at the Darsser Ort increased less steeply (0.9 to 29.9 g kg^{-1} DW) than at Pramort (2.1 to 61.7 g kg^{-1} DW) (Table 3). In the biocrusts, a gradual increase in total nitrogen

TABLE 3 Pedological description and nutrient element contents in biocrusts and sediment/soil cores of both sampling sites.

Study site	Sampling plot	Compartment	C_t (g kg^{-1} DW)	C_{org} (g kg^{-1} DW)	N_t (g kg^{-1} DW)	P_t (mg kg^{-1} DW)
Darsser Ort	YD	Ai+ilC	0.3 ± 0	0.3 ± 0	0.1 ± 0	62.6 ± 1.1
	eGD	Biocrust	0.9 ± 0.1	–	0.1 ± 0	71.8 ± 6.1
		Aih+ilC	1.0 ± 0.2	0.8 ± 0.2	0.1 ± 0	59.1 ± 1.7
	lGD	Biocrust	14.8 ± 2.0	–	0.5 ± 0	99.5 ± 7.4
		Ah	3.5 ± 0.9	3.5 ± 0.9	0.2 ± 0.1	54.2 ± 3.0
		ilC	0.5 ± 0.1	0.4 ± 0.2	0.1 ± 0	53.6 ± 1.9
	MD	Biocrust	29.9 ± 0.3	–	1.4 ± 0	110.4 ± 0.5
		L/Ah	3.9 ± 0.4	3.9 ± 0.4	0.3 ± 0	61.5 ± 18.4
		ilC	1.3 ± 0.2	1.1 ± 0.1	0.1 ± 0	48.8 ± 4.5
Pramort	WW	Ai+ilC	0.4 ± 0	0.4 ± 0	0.1 ± 0	38.1 ± 1.1
	YD	Biocrust	2.1 ± 0.1	–	0.2 ± 0	34.8 ± 0.8
		Ai+ilC	0.5 ± 0.1	0.3 ± 0.2	0.1 ± 0	27.4 ± 1.5
	GD	Biocrust	58.8 ± 28.1	–	2.6 ± 1.1	199.1 ± 84.9
		L/Ah	4.8 ± 1.1	4.7 ± 1.1	0.4 ± 0.1	48.7 ± 2.1
		ilC	0.7 ± 0.1	0.5 ± 0.2	0.1 ± 0	28.2 ± 1.5
	MD	Biocrust	61.7 ± 0.1	–	2.0 ± 0	159.0 ± 3.9
		L/Ah	17.8 ± 4.6	17.7 ± 4.6	0.7 ± 0.3	51.6 ± 11.3
		ilC	1.4 ± 0.2	1.3 ± 0.1	0.1 ± 0	25.9 ± 1.6

Means ± standard deviations (n – 3). DW – dry weight; Ai – initial A-horizon; Ah – humic A-horizon; ilC – silicon-rich, loose soil parent material in C-horizon; L – litter.

(N_t) content was measured along both transects. The N_t concentrations within the biocrusts along the transect at Darsser Ort increased 14-fold from the eGD (0.1 g kg^{-1} DW) to the MD (1.4 g kg^{-1} DW) area. The nitrogen concentrations in the GD (2.6 g kg^{-1} DW) and MD (2.0 g kg^{-1} DW) at Pramort exceed the highest concentration measured at the Darsser Ort MD (Table 3). P_t concentrations in the biocrusts indicated a slight accumulation of P along each transect toward the mature dune area. For biocrust at Darsser Ort, P_t ranged between 71.8 and 110.4 mg kg^{-1} DW). Total P along the Pramort transect ranged between 34.8 and 199.1 mg kg^{-1} DW (Table 3).

3.1.2 Sediment/soil cores

As a first step in pedological analyses, the sediment/soil cores were interpreted in terms of abundant soil horizons according to the German classification system KA5 (Ad-hoc Arbeitsgruppe Boden, 2005). Cores of the yellow and early grey dune at Darsser Ort, as well as the windwatt and yellow dune at Pramort, were initially assigned to parent material (C-horizon) from the sole visual inspection. However, the organic carbon of these samples indicated initial soil A-horizon forming processes, resulting in the description as "A + C". A layer of undecomposed litter on top of the mineral material was indicated by the symbol "L". The cores of the remaining dune plots were already visually divided into soil horizons in the field (Figure 4). Additional geogenic and pedogenic characteristics were added to qualify the main soil horizons.

The C_t and N_t concentrations of the top- and subsoil horizons increased along both transects toward older dune successional stages. It was noticeable that the topsoil horizon C_t concentrations at the Darsser Ort increased significantly less (0.3 to 3.9 g kg^{-1} DW) than at Pramort (0.4 to 17.8 g kg^{-1} DW) (Table 3). At the Darsser Ort, significant differences in the C_t concentration ($p < 0.001$) were detected between the younger dune successional stages (YD and eGD) and the older ones (lGD and MD). At Pramort, significant differences in the C_t concentrations ($p < 0.001$) between all dune stages, except for the windwatt and the yellow dune, were determined. Organic carbon (C_{org}) was detected in all samples and increased clearly in the topsoil horizons along both transects. Although both transects started with almost similar C_{org} concentrations (yellow dune (DO) = 0.3 g kg^{-1} DW; windwatt (PO) = 0.4 g kg^{-1} DW), the values then differed significantly from each other in the mature dune area at Darsser Ort (3.9 g kg^{-1} DW) compared to Pramort (17.7 g kg^{-1} DW). In general, an increase in the C_t and C_{org} carbon content was observed in the top- and subsoil horizons, however, in the latter to a much lesser extent (Table 3). The N_t concentrations of the cores showed a less steep increase along both transects compared to the C_t concentration. The N_t values at Darsser Ort were in the range of 0.1 to 0.3 g kg^{-1} DW, while for Pramort, the values increased from 0.1 g kg^{-1} in the windwatt to 0.7 g kg^{-1} DW in the mature dune area. The concentrations in the topsoil horizons were higher compared to the subsoil horizon, similar to the carbon contents (Table 3). For the significant differences, the pattern for nitrogen is identical to that for total carbon. The total P concentrations of the sediment/soil cores were below 0.1 g kg^{-1}. The P_t concentrations were slightly higher in the topsoil than in the subsoil horizon. The differences between the top- and subsoil horizons were highest in the mature dune areas of both transects. While the P_t values of the windwatt and the yellow dune at the Pramort scarcely differed from each other, significant differences in the P_t content were found between the yellow dune and the grey dune, as well as the mature dune ($p < 0.01$). At the Darsser Ort, on the other hand, there were no significant differences in the P_t concentration between the dune types. The biocrusts generally showed higher C_t, N_t, and P_t contents than the respective soil parent materials in C-horizons (Table 3).

Overall, the iron (Fe) contents of all samples were low, averaging 790 mg kg^{-1} for total Fe (Fe_t), 210 mg kg^{-1} for dithionite-citrate-bicarbonate extracted Fe (Fe_{dit}), and 24 mg kg^{-1} for oxalate extracted Fe (Fe_{ox}). The lowest concentrations of Fe_{dit} and Fe_{ox} were detected in the windwatt and YD samples, and the highest in the mature dune samples. Slightly irregular increases in the Fe_{dit} contents toward the inlands were recognized, which confirmed an advanced degree of weathering of Fe-containing minerals and the formation of secondary pedogenic oxides in this direction. The ratios Fe_{dit}/Fe_t ranged between 0.14 and 0.4. The Fe_{ox}/Fe_{dit} ratios ranged between 0 and 0.2 (Supplementary Table 3).

The topsoil horizons of the sample cores were low in calcium carbonate ($CaCO_3$). However, if a distinction was made between the topsoil and C-horizons, the latter had significantly more carbonate, except for the mature dune at Pramort. The pH ($CaCl_2$) was measured in the sediment/soil cores, if possible, in all divided soil horizons. At both transects, the pH decreased with increasing dune succession. All samples were slightly to strongly acidic, with pH values ranging from 3.6 to 6.2. At the Darsser Ort transect, no difference in the pH between different horizons was measured. However, at Pramort (grey dune and mature dune), the L/Ah horizon tended to be more alkaline than the underlining ilC horizon. The values for the electrical conductivity of the saturation extract in the sediment/soil cores were below 0.75 mS cm^{-1} in all samples, which is a threshold for description of a soil horizon as "saltish" according to Ad-hoc Arbeitsgruppe Boden (2005) (Supplementary Table 4).

3.2 Sequentially extracted P (P pools)

The P_t concentrations in the topsoil horizons were generally very low. The P_t concentrations of sequentially extracted fractions were below the detection limit of ICP OES (≤ 0.05 mg L^{-1}). However, determination of molybdate reactive P was possible, which is considered to be inorganic P (P_i). Whenever the ICP OES values were above the detection limit, they were used to calculate the organic phosphorus (P_o) content of the sample as well.

For the coastal dune area at Darsser Ort, the H_2SO_4 fraction had the highest P concentrations and proportions in the soil samples (27.6 to 35.4 mg kg^{-1}, corresponding to 46.2% to 56.6% of P_t; Table 4). This was the only fraction where P_i and P_o could be distinguished. On the other hand, at Pramort, the labile P fractions (resin-P and $NaHCO_3$-P) exhibited the highest P concentrations and proportions (25 to 45.4 mg kg^{-1}, 56.4% to 74% of P_t; Table 4). Proportions of NaOH-P (moderately labile P_i and P_o, latter only at Pramort MD) ranged

TABLE 4 Concentrations (mg kg^{-1}) of sequentially extracted inorganic (P_i) and organically bound (P_o) phosphorus fractions (mg kg^{-1}) in the topsoil horizon of the sediment/soil cores (n = 3).

Study site	Sampling plot	Labile P	Moderately labile P		Stable P	
		P_i (mg kg^{-1})	P_i (mg kg^{-1})	P_o (mg kg^{-1})	P_i (mg kg^{-1})	P_o (mg kg^{-1})
Darsser Ort	YD	23.3	4.1	b.d.	18.6	13.4
	eGD	21.8	5.4	b.d.	22.7	12.7
	lGD	28.3	3.9	b.d.	13.7	13.9
	MD	39.6	b.d.	b.d.	19.6	13.8
Pramort	WW	31.0	b.d.	b.d.	13.4	10.6
	YD	25.0	b.d.	b.d.	5.5	10.6
	GD	45.4	8.5	b.d.	8.6	14.8
	MD	32.0	10.2	1.2	b.d.	b.d.

Labile P (Resin-P_i + $NaHCO_3$-P_i), moderately labile P (NaOH-P_i + NaOH-P_o), and stable P (H_2SO_4-P_i + P_o). Results on biocrusts can be found in Supplementary Figure 4. b.d. = below detection limit.
Detection limits: ICP OES: Labile P = 0.045 mg P L^{-1} (resin), 0.076 mg P L^{-1} ($NaHCO_3$); moderately labile P = 0.046 mg P L^{-1} (NaOH); stable P = 0.033 mg P L^{-1} (H_2SO_4). Molybdenum blue: Labile P = 0.013 mg P L^{-1} (resin), 0.007 mg P L^{-1} ($NaHCO_3$); moderately labile P = 0.012 mg P L^{-1} (NaOH); stable P = 0.009 mg P L^{-1} (H_2SO_4).

between 0% and 8.7% of P_t at Darsser Ort and 0% and 26% of P_t at Pramort. The distribution of the different P fractions showed the same trends with increasing age and soil development at both transects. An enrichment of more labile (easily bioavailable) P was observed at Darsser Ort. At Pramort, the enrichment became more obvious in the moderately labile P fraction. At the same time, the Ca-bound P concentrations and proportions (H_2SO_4-fraction) decreased. This trend was more pronounced at the Pramort dune chronosequence than at Darsser Ort. For all sediment/soil cores of the Darsser Ort and Pramort transect, the proportions of summed P_i-fractions ranged between 76.7% to 81.1% and 80.8% for 97.2% of P_t, respectively. The proportions of summed P_o fractions were between 18.9% to 23.3% of P_t at Darsser Ort and 2.8% to 25.8% of P_t along the Pramort transect. In the biocrusts of coastal dunes, the P contents were larger by factor three than in the sediment/soil cores. Labile and easily soluble P was absolutely enriched at the expense of Ca-bound P (H_2SO_4-fraction) similar to the finding for sediment/soil cores (Supplementary Figure 4).

3.3 Vegetation survey

At both study sites, a general shift from bare sediment via microalgae-dominated biocrusts in younger dunes to moss- and lichen-dominated biocrusts covers in later dune stages was observed. At Darsser Ort, the biocrusts percentage coverage ranged between 0% and 72% in the different dune stages, while at Pramort it was 0% and 76%. The dominating biocrust cover showed high variability between the different successional dune stages at each site. The following simplified figure schematically illustrates the distribution of the dominant functional groups along an idealized dune succession gradient (Figure 5).

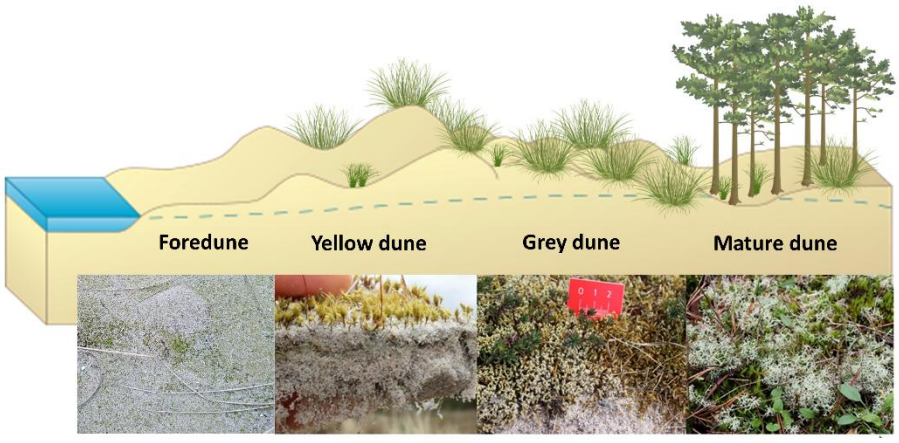


FIGURE 5
Schematic dune succession and pictures of the functional groups dominating the individual dune subsites. Primary dune formation (foredune) is assumed in the scheme. For the dune formation at Darsser Ort, a deviating secondary dune formation at the dune cliff applies. Created with BioRender.com.

At Darsser Ort, the first dune type under investigation was a yellow dune at a dune cliff. This had no cryptogamic cover (Figure 6). The surface was mainly bare sediment (68%) or covered by vascular plants (20%), identified as *Ammophila arenaria* (L.) Link. Organic litter occurred sporadically (12%). When following the transect inland into the grey dune area, the earliest biocrust covers were detected in this dune area. The grey dune area could be visually divided (by dune sand color and vegetation) into an early phase of grey dune succession (eGD) and a later, more stabilized grey dune area (lGD). In the eGD, first biocrust covers dominated by microalgae (44%), defined as initial biocrusts, were detected. Furthermore, smaller mosses and occasionally lichens grew in this early grey dune area as well (4%). Biocrusts were the dominant surface cover, with 60% in the eGD area, followed by patches of bare sediment (20%) and vascular plants (12%) (Figure 6). The late grey dune area showed a change in dominant biocrust functional groups. Moss-dominated biocrusts (36%) and those associated with lichens (28%) covered the lGD area (Figure 6). A thick moss and lichen carpet overgrew the dune surface with further dune succession. This shift in the biocrust functional groups denoted the transition into the mature dune area. The functional groups of moss-dominated (36%) and moss-lichen-dominated biocrusts (36%) were most present in this area (Figure 6). Moreover, patchy accumulations of mainly pine (*Pinus sylvestris* L.) needles, fallen leaves, and other dead plant material covered 12% of the investigated dune surface. Bare sand areas decreased along the dune chronosequence and became rare in the late grey and mature dunes.

As observed at Darsser Ort, the surface coverage of biological soil crusts increased along the succession gradient at Pramort, too. Bare sediment (88%) and organic litter (12%) characterized the windwatt (Figure 6). This wind flat becomes exposed when the wind drives water out of the lagoon. Detected litter was therefore mostly identified as flotsam, remains of reed material, and molluscan shells. The first biocrusts along the chronosequence were detected in the following yellow dune area. This sampling plot was dominated by early microalgae biocrusts (44%). Small mosses associated with microalgae (12%) occurred only near vascular plants (16%), identified as *Ammophila arenaria*. Further inland in the grey dune area, moss-dominated biocrusts became the prevailing biocrust functional group (36%). Moreover, this dune successional stage had the highest variety of biocrust functional groups found at all four subsites (three functional groups out of four) (Figure 6). The following mature dune area was partly forested with pine trees, like the mature dune area at Darsser Ort. Mosses were dominating and interspersed with lichens.

3.4 Biocrust phototrophic community composition

3.4.1 Algae and cyanobacteria

In total, 25 algal and cyanobacterial species have been detected at seven out of eight sampling plots. The richness of species was expressed as the total species number identified per plot. The only plot showing no species was the yellow dune at Darsser Ort. A total of 21 algal species (10 at Darsser Ort, 14 at Pramort) and four cyanobacterial species were detected using culture-dependent methods, followed by morphological identification (Table 5 and Figures 7A–R). Along the Darsser Ort transect, the early grey dune showed the highest algal species richness (six out of 11 species). The yellow dune plot was the most rich in species (seven out of 17 species) at the Pramort transect.

Fourteen species of Chlorophyta dividing into two classes were determined (eight species of Chlorophyceae, six species of Trebouxiophyceae). The phylum of Charophyta was represented by three classes with the Klebsormidiophyceae being the most widespread (five out of seven Charophyta species). Four species of Cyanobacteria were found: representatives of Oscillatoriales and Nostocales. The most frequently detected species were *Interfilum terricola* (Figures 7E, F), *Klebsormidium crenulatum* (Figures 7A, B), and *Tetradesmus arenicola* (Figures 7G–I). *Klebsormidium crenulatum* was the dominant algal species in all plots, if present. If cyanobacteria occurred, these were almost always the dominant species in the respective plot (DO: eGD; PO: WW, GD). The remaining species dominated in two [*Klebsormidium* cf. *subtile* (Figure 7C) and *Nostoc* cf. *linckia* (Figure 7J)] or just one sampling plot. Both study sites had only 12% (three species) of the identified species in common (Supplementary Figure 5A). Biocrusts of different sampling sites are characterized as cyanobacterial (with dominance of *Nostoc*, windwatt, and grey dune of Pramort), green

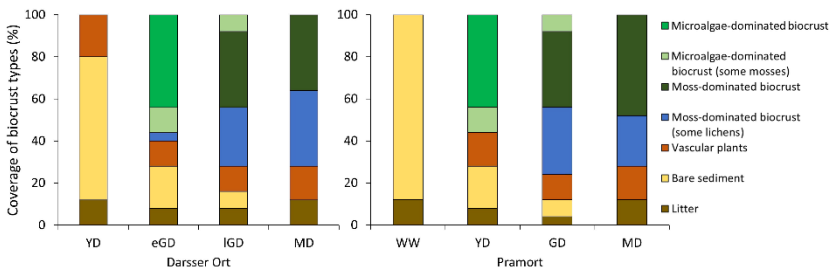


FIGURE 6
Summary of the vegetation survey. The percentage of the area covered by the different functional groups as determined with the point intercept method along the two transects. Darsser Ort; dune types: YD, yellow dune; eGD, early grey dune; lGD, later grey dune; and MD, mature dune. Site: Pramort; dune types: WW, windwatt; YD, yellow dune; GD, grey dune; and MD, mature dune.

TABLE 5 Green algal and cyanobacterial species in biocrusts identified at seven different dune plots using a culture-dependent approach (present species are colored in grey shade).

Phylum, class	Species	Darsser Ort			Pramort			
		eGD	lGD	MD	WW	YD	GD	MD
Cyanobacteria								
Oscillatoriales	*Microcoleus* cf. *vaginatus*	*						
Nostocales	*Nostoc* cf. *edaphicum*							
	Nostoc cf. *linckia*				*		*	
	Nostoc cf. *commune*						*	
Chlorophyta								
Chlorophyceae	*Actinochloris terrestris*							
	Chlorococcum cf. *oleofaciens*							
	Chlorolobion lunulatum							
	Lobochlamys sp.							
	Macrochloris sp.							
	Spongiochloris cf. *excentrica*							
	Tetracystis cf. *sarcinalis*							
	Tetradesmus arenicola							
Trebouxiophyceae	*Chloroidium* cf. *ellipsoideum*							
	Eremochloris cf. *sphaerica*							
	Myrmecia cf. *irregularis*							
	Nannochloris sp.							
	Parietochloris cf. *alveolaris*							
	Pseudochlorella sp.							
Charophyta								
Chlorokybophyceae	*Chlorokybus atmophyticus*							
Klebsormidiophyceae	*Klebsormidium* cf. *flaccidum*	*						
	Klebsormidium cf. *subtile*					*		
	Klebsormidium crenulatum		*	*		*		
	Interfilum terricola							
	Interfilum cf. *massjukiae*							
Zygnematophyceae	*Cylindrocystis* cf. *crassa*							

An asterisk in the grey boxes indicates the dominant species at the respective dune subsite detected during direct microscopy of the environmental samples. Site: Darsser Ort; dune types: early grey dune (eGD), later grey dune (lGD), and mature dune (MD). Pramort; dune types: windwatt (WW), yellow dune (YD), grey dune (GD), and mature dune (MD).

(with dominance of *Klebsormidium*, later grey and mature dunes of Darsser Ort as well as yellow dune of Pramort) or mixed nature (*Microcoleus* cf. *vaginatus* (Figures 7N, O) and *Klebsormidium* cf. *flaccidum* (Figures 7D), early grey dune of Darsser Ort). Mature dune crust of Pramort included only one occasionally occurring green algal species (*Chloroidium* cf. *ellipsoideum*).

3.4.2 Moss species

In total, 16 moss species (Bryophta) were detected at six of eight sampling plots in this study. The mature dune plot at Darsser Ort showed the highest species number of all investigated plots (six out of eight species). The species-richest plot along the Pramort transect was in the grey dune area (Table 6). With the exception of one species from the Polytrichopsida class (*Polytrichum juniperinum*), 14 species have been identified, all of which belong to the Bryopsida class. The remaining two species were assigned to the class of Jungermanniopsida (Marchantiophyta). Four out of all 16 species occurred in ≥50% of all moss-holding sampling plots. Two species (*Cephaloziella divaricata* and *Ceratodon purpureus*) were almost omnipresent; 10 of all detected species were found in one plot only.

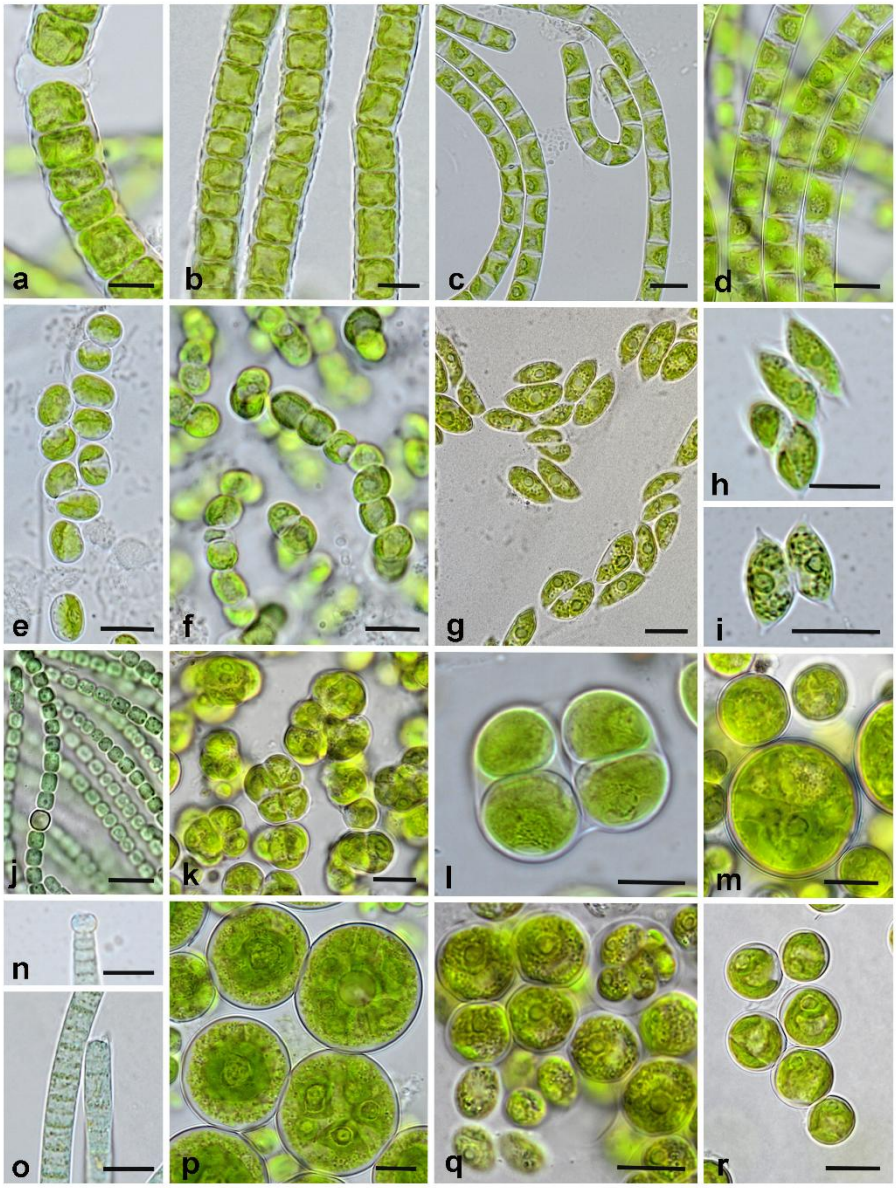


FIGURE 7
Representative algae and cyanobacteria from the biocrusts of Darsser Ort (DO) and Pramort (PO). **(A, B)** *Klebsormidium crenulatum* [**(A)** PO-YD; **(B)** DO-lGD]; **(C)** *Klebsormidium* cf. *subtile* (PO-YD); **(D)** *Klebsormidium* cf. *flaccidum* (DO-eGD); **(E, F)** *Interfilum terricola* [**(E)** DO-lGD; **(F)** PO-YD]; **(G–I)** *Tetradesmus arenicola* [**(G)** PO-WW; **(H, I)** DO-eGD]; **(J)** *Nostoc* cf. *linckia* (PO-WW); **(K)** *Tetracystis* cf. *sarcinalis* (PO-WW); **(L)** *Chlorokybus atmophyticus* (DO-lGD); **(M)** *Spongiochloris* cf. *excentrica* (PO-WW); **(N, O)** *Microcoleus* cf. *vaginatus* (DO-eGD); **(P)** *Actinochloris terrestris* (DO-eGD); **(Q)** *Chlorococcum* cf. *oleofaciens* (PO-GD); **(R)** *Eremochloris* cf. *sphaerica* (PO-WW). Scale bars = 10 µm.

The two study sites showed 37.5% (six species) of the identified species in common (Supplementary Figure 5B).

3.4.3 Lichen species

In this study, 26 lichen species were found at five out of eight sampling plots (Table 7). The late grey dune and mature dune plots at Darsser Ort, as well as the grey dune and mature dune plots at Pramort, hardly differed in the number of lichen species. The early grey dune area at Darsser Ort was the species poorest lichen-holding sampling plot (three of 26 species). All determined lichen species belonged to families of the class Lecanoromycetes, and 24 out of 26 species were members of the order Lecanorales. *Cladonia* was the dominant genus across both study sites. Of the determined species, 19 belonged to this genus; 14 out of the overall detected species were found at both sampling sites (53.9%) (Supplementary Figure 5C). Lichen species that preferred to grow on sandy substrates predominated at both

TABLE 6 Moss species in biocrusts detected at six different dune plots (present species are colored in grey shade).

Division, class	Species	Darsser Ort			Pramort		
		eGD	lGD	MD	YD	GD	MD
Bryophyta							
Bryopsida	*Brachythecium albicans*						
	Ceratodon purpureus						
	Dicranum scoparium						
	Hennediella heimii						
	Hypnum cupressiforme						
	Hypnum jutlandicum						
	Kindbergia praelonga						
	Pleurozium schreberi						
	Pohlia nutans						
	Pseudoscleropodium purum						
	Ptychostomum compactum						
	Ptychostomum moravicum						
	Rhynchostegium megapolitanum						
Polytrichopsida	*Polytrichum juniperinum*						
Marchantiophyta							
Jungermanniopsida	*Cephaloziella divaricata*						
	Lophocolea bidentata						

Darsser Ort; dune types: early grey dune (eGD), later grey dune (lGD), and mature dune (MD). Site: Pramort; dune types: yellow dune (YD), grey dune (GD), and mature dune (MD).

study sites. Only four out of 26 determined species are known to preferably grow on litter. A detailed table on the pH preference of the individual taxa is compiled in Supplementary Table 5. Those litter-preferring species were found in the lGD (DO) and respectively grey dune area (PO) and belong to the subneutrophytic and basidophytic lichen species. Strongly acidophytic species (e.g., *Cladonia macilenta*) were found especially in the mature dune area.

3.5 Relationship between chemical soil properties and biocrust communities

A relationship between nutrient element concentrations in the biocrusts (C_t, N_t, P_t) and their successional stage became obvious. The growth of moss-dominated biocrusts in later successional dune stages led to enhanced biomass production in these dune types. The parallel increase in the Chl *a* content confirmed this observation. Hence, a directly related nutrient element accumulation could be proven. The total species number of mosses and lichens (alpha diversity = α) in the biocrusts differed between the successional dune stages, as visualized in the nMDS plot (Figure 8). A grouping of the early dune successional stages (PO:WW and YD; DO:eGD) relative to the older ones was evident from the biocrust community (PO:GD and MD; DO:lGD and MD). The PerMANOVA showed significant correlations between the community composition of the biocrusts and enrichment with C_t ($p = 0.038$) and P_t ($p < 0.01$) in the topsoil horizons.

4 Discussion

4.1 Analyses of nutrient and sediment/ soil characteristics

In contrast to previous studies, which only examined C_t and N_t element concentrations in individual dune types, this study measured for the first time changes in these element concentrations along an entire dune succession. Thereby, the C_t and N_t contents increased along both successional dune gradients. The C_t concentrations of the biocrusts measured at Darsser Ort (0.9–29.9 g C kg^{-1}) were similar to results from a former study (3.4–48 g C kg^{-1}) conducted on the islands Rügen and Usedom, which are 70 to 100 km further east (Baumann et al., 2019). The C_t contents of biocrusts measured in the grey and mature dunes at Pramort (58.8 g C kg^{-1} and 61.7 g C kg^{-1}, respectively) and Darsser Ort (14.8 g C kg^{-1} and 29.9 g C kg^{-1}, respectively) were similar to biocrusts from temperate forests (23–56 g C kg^{-1}) (Baumann et al., 2017). The biocrusts in the later successional dune stages at Pramort (PO) were more dominated by mosses than at Darsser Ort (DO), as reflected in their higher proportion of organic matter and larger C_t

TABLE 7 Lichen species in biocrusts detected at five different dune plots (present species are colored in grey shade).

Phylum, class, order (Mycobiont)	Species	Darsser Ort			Pramort	
		eGD	lGD	MD	GD	MD
Ascomycota						
Lecanoromycetes						
Lecanorales	*Cladonia arbuscula*					
	Cladonia chlorophaea					
	Cladonia ciliata					
	Cladonia coccifera					
	Cladonia fimbriata					
	Cladonia floerkeana					
	Cladonia foliacea					
	Cladonia furcata					
	Cladonia glauca					
	Cladonia humilis					
	Cladonia macilenta					
	Cladonia novochlorophaea					
	Cladonia portentosa					
	Cladonia ramulosa					
	Cladonia rangiformis					
	Cladonia rei					
	Cladonia scabriuscula					
	Cladonia subulata					
	Cladonia uncialis ssp. *biuncialis*					
	Evernia prunastri					
	Hypogymnia physodes					
	Polyozosia persimilis					
	Scoliciosporum gallurae					
Peltigerales	*Peltigera hymenina*					
Teloschistales	*Physcia tenella*					
	Xanthoria parietina					

Site: Darsser Ort; dune types: early grey dune (eGD), later grey dune (lGD), and mature dune (MD). Site: Pramort; dune types: grey dune (GD) and mature dune (MD).

values (Table 3). Not surprisingly, the C_t concentrations in the biocrusts always significantly exceeded those of the underlying soil horizons because of the organism's biomass and their released metabolites in the biocrust matrix. Furthermore, C_t in the soil samples was almost exclusively organically bound, which can be explained by low proportions of carbonate from marine organisms such as the shells of mussels. This indicates that organic molecules formed in the biocrusts may have been translocated downwards in the soil profiles, pointing to a strong influence of the biocrust community on the underlying soil horizons, which otherwise scarcely receive organic carbon from other sources. The importance of the biocrust community forming the first organic layer at the topsoil horizon becomes obvious. Moreover, fungal hyphae, bacterial communities, and moss rhizomes connect the biocrust with the underlying soil and sediment and support nutrient transfer to these less inhabited compartments (Eldridge and Greene, 1994). An increase in the N_t concentration in the biocrusts along the succession gradients was also observed (Table 3). Likewise, the N_t concentrations in the biocrusts were above those of the underlying soil and sediment samples. Zhao et al. (2010) showed that biocrust-fixed atmospheric N is an important N source for the ecosystem and its vegetation restoration in the Loess Plateau, China, by accumulating between 4 and 13 kg N ha^{-1}, depending on the dominant biocrust type. Further studies confirmed this

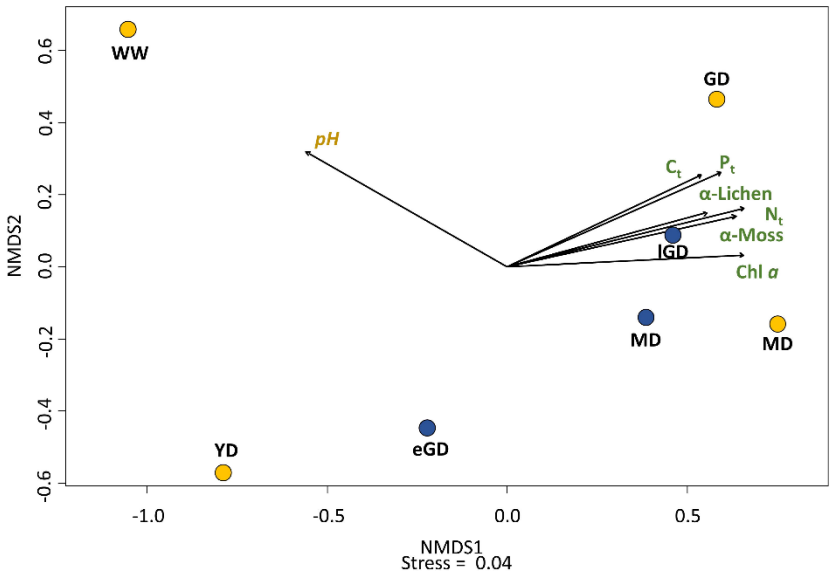


FIGURE 8
The nMDS plot based on the Bray–Curtis dissimilarity index visualized the differences and similarities in the community composition of grouped lichen, mosses, and algae (α-diversity) between the seven sampling sites. Yellow: accumulation coast (Pramort). Dune types: WW, windwatt; YD, yellow dune; GD, grey dune; and MD, mature dune. Blue: abrasion coast (Darsser Ort). Dune types: eGD, early grey dune; lGD, later grey dune; and MD, mature dune. The black arrows indicate the influence direction of the significantly correlated biocrust and sediment characteristics. Stress = 0.04.

biologically mediated terrestrial N accumulation by biocrusts for temperate forests (Glaser et al., 2018) and the Arctic tundra (Pushkareva et al., 2022).

Only very low iron (Fe_t) contents were measured in the topsoil horizons at both study sites. The Fe_t values at all sampling points at Darsser Ort were higher than those at Pramort, suggesting a larger supply of Fe-containing minerals in the parent rock material at this site. The proportion of dithionite-soluble iron (Fe_{dit}) increased along the dune chronosequence, confirming an advanced degree of mineral weathering towards the inland. Cornell and Schwertmann (2003) described the Fe_{dit}/Fe_t ratio as a measure of soil development, and values between 0.2 and 0.3 indicate progressing soil development in the northern hemisphere. The Fe_{dit}/Fe_t ratios measured in this study (DO: 0.14–0.3, PO: 0.17–0.4, Supplementary Table 3) confirmed the beginning of soil development in the dunes. Initial silicate weathering is expected to lead to an increase in oxalate-soluble iron (Fe_{ox}) contents (Cornell and Schwertmann, 2003) with dune succession, as the present study indicated for temperate coastal dunes at the Baltic Sea coast. However, both chronosequences did not show the expected decrease in Fe_{ox}/Fe_{dit} ratio with soil development, according to Cornell and Schwertmann (2003). This result indicates that at least the investigated dunes of the Baltic Sea could be an exception here. Likely, such a development is possible if the supply from weatherable Fe-containing minerals in the parent rock material or the developing soil is sufficiently high for a continuous and subsequent Fe_{ox} supply. If this replenishment stops, the expected development of pedogenic Fe oxides cannot happen over time. Most probably, that was the case in both studied dune areas since the Fe_t supply in the quartz-rich sand might have been quickly exhausted over time. In the case of the younger dune types, advanced weathering of Fe-bearing silicates cannot be expected (Fischer et al., 2010).

The various possible soil-forming processes in the Holocene sands of the dunes were related to decreases in sediment pH in parallel to the calcium carbonate weathering in the sediment/soil cores. The measured carbonate contents at all dune subsites were very low (0–2.1 g kg^{-1}). They were clearly below the values measured on the coast of Rügen (14.6–127.8 g kg^{-1}) and Usedom (6.6–7.5 g kg^{-1}) (Baumann et al., 2019). Likely, the chalk cliffs on Rügen, mainly formed by calcium carbonate-containing limestone, positively influenced the carbonate concentration in the northeast part of the island. Slightly higher carbonate contents in the younger yellow dune stages (Supplementary Table 4) represented the original, almost unweathered parent material, which is shell-containing dune sand. A decrease in the carbonate content with dune succession suggested an ongoing decalcification of the sandy sediment. This observation is consistent with the studies on the Arenosols of dunes on the island Spiekeroog (Giani and Buhmann, 2004; Pollmann et al., 2018). In all previously mentioned studies, the top sediment layers had lower carbonate contents than the subsediment. This observation reflects the metabolic activity of the biocrusts and their impact on soil formation in sandy substrates. Due to CO_2 and H^+ produced during microbial soil respiration (Kuzyakov, 2006) and the excretion of organic acids, biocrusts releasing these substances could potentially promote a more rapid decalcification in the uppermost sediment layer (Fox, 1995; Belnap, 2011), thereby forming a soil horizon. Consequently, carbonate appeared enriched in the deeper horizons of the older dune types, which can be explained as an indication of the original sediment Ca-

carbonate content, perhaps plus precipitates from leached Ca- and hydrogen-carbonate ions. Calcite weathering is a fundamental soil-forming process in all Ca-containing parent rocks, including Pleistocene glacial till and Holocene dune sands (Earle, 2019; Daumantas et al., 2022), and could be tracked in detail along a chronosequence in this study.

The decrease of the pH along the chronosequences is in line with results from the coastal dunes of the North Sea island Spiekeroog (Isermann, 2011; Pollmann et al., 2020). The drop in pH was more pronounced in the topsoil horizon along the chronosequence at Pramort (pH 6.2 to 3.6) than at Darsser Ort (pH 5.0 to 4.3). This indicates that the dunes at Darsser Ort are older than those at Pramort, assuming similar calcite contents and aboveground impacts on the acidity of the sediment, either from the atmosphere or the initial organism colonization. Isermann (2011) measured a pH of 4.6 in early and 3.4 in mature grey dunes. The same applies to a study by Giani and Buhmann (2004), who reported a pH of 4.0 in grey dunes. These analytical data underline the fact that the dunes at Darsser Ort were in a later developmental stage compared to Pramort. The area, initially described as a yellow dune at a dune cliff, is more likely to be an eroded grey dune based on the measured pH (pH 4.9). The dune cliff was continuously covered with a large amount of sand as part of a secondary dune formation process and was therefore designated as a yellow dune in the present study. Isermann (2005) detected that the species richness of vascular plants was greatest at intermediate levels of soil pH along the Baltic Sea coast. The present study was now able to establish such a connection for the algal community in coastal sand dunes of the Baltic Sea since the highest algal species richness was detected in the (early) grey dune stages.

4.2 Total phosphorus and P pools (fractionation)

The total P of the sediment did not decrease, neither in the top- nor the subsoil horizon, with the successional development of the dunes along both chronosequences. This disagrees with the P_t decrease during soil formation, as reported by Walker and Syers (1976). A reason could be that soil formation along both dune successional gradients has not yet progressed far. The P_t concentration of the biocrusts ranged between 35 and 199 mg kg^{-1}, which is slightly less compared to a study by Schulz et al. (2015) (90–310 mg kg^{-1}) along a weathering gradient at the Baltic Sea coast. This difference can be explained by the inhomogeneity of the dune sands with respect to P. The biocrusts accumulated P over time, but the P content in the underlying sediment remained rather constant along the gradient and increased only slightly toward the older dunes, as found at Pramort. This implies that the biocrust community is able to take up essential amounts of P, irrespective of the parent source material on the dunes. With this result, the present study highlights a well-adapted biocrust community that is able to acquire P from different sources in addition to those from the parent material to make P bioavailable. The trapping of nutrient-enriched aeolian dust could be such a potential P source (Reynolds et al., 2001; Chamizo et al., 2012) or P-containing precipitation, which is a quantitatively important nutrient source in the study region (Berthold et al., 2019). Furthermore, it was evident that the P concentration in the topsoil horizons exceeded that in the subsoil horizons. This indicates that some of the P biologically accumulated in the biocrusts has been transferred into the subsoil horizons through leaching or any other redeposition process. Thus, our data confirmed Young et al. (2022), who described this as one of the main mechanisms by which biocrust fertility is transferred downward in the soil.

In the early successional dune stages at Darsser Ort, stable P was identified as the major P pool. This included Ca-bound P, e.g., P in primary minerals such as apatite, P occluded within sesquioxides, as well as stable organic P compounds (Hedley et al., 1982; Sims and Pierzynski, 2005). Moderately labile P, likely originating from P bound to Fe-/Al-oxide surfaces (Hedley et al., 1982), constituted a minor proportion of the P pools at Darsser Ort (Table 4). This can be explained by the low contents of weatherable Fe-containing minerals and already-formed Fe oxides in the aeolian sands. The proportion of labile and bioavailable P compounds continued to increase with dune succession and became the major P pool in later dune types. Such a conversion took place at the expense of the stable P pool, which is in line with the results of Baumann et al. (2019) from a similar study area. In contrast, the labile P was identified as the major P pool in all dune types along the dune chronosequence at Pramort. The relative proportion of P in this pool continued to increase (56% to 74% of P_t) as dune succession progressed (Table 4). The proportion of stable-bound P played only a minor role in the later dune types and was no longer measurable in the mature dune area. This development indicated an accumulation of easily available P in the topsoil horizon, which indicated the microbial activity of the biocrust organisms as assumed in hypothesis (5). It remains to be clarified whether this labile P pool is a P source accessible to other organisms. Hence, it is possible that P was stored in the biocrust organisms and was thus involved in a more closed P cycle. The proportion of organically bound P (P_o) in the biocrusts was higher than in the underlying sediment, reflecting the presence and biological activity of biocrust organisms as well as their organic decomposition products. The low to non-detectable proportion of P_o (0%–1.2% of P_t) calculated for the younger dune types was likely due to the low amounts of organic matter found on these dune types.

4.3 Biocrust characteristics and vegetation survey

The sand dunes on the peninsula Fischland-Darss-Zingst are one example in which microbial diversity changed with soil development during natural succession, which so far has received little attention in this area. In younger dune habitats, which are more endangered by erosive wind forces leading to sand mobility (Martínez et al., 2001), algae-dominated biocrusts predominated. Moss-dominated biocrusts were found in older dune succession stages. The highly mobile dunes nearshore and the airborne salt spray shape environmental conditions where colonization is difficult (Hesp, 1991; García Novo et al., 2004). Consequently, only small to no biocrusts could be formed in mobile dunes. This explained the low chlorophyll *a* values and organic matter content

measured in the windwatt (Pramort) and the yellow dune area at Darsser Ort. The Chl *a* likely changed with sampling site, season, and biocrust communities. As expected, and in agreement with Büdel et al. (2009), a significant increase in the biocrust Chl *a* content from the early successional stage to the later ones was observed. Langhans et al. (2009) measured Chl *a* content between 11 and 295 mg m^{-2} in a temperate sand ecosystem in the northern upper Rhine valley in south Hessen, Germany, which were similar to those of the present study (1 to 483 mg m^{-2}). Whereas Langhans et al. (2009) could not prove an increase in Chl *a* content between initial and stable biocrusts, this was for the first time proven for the biocrust succession on the peninsula Fischland-Darss-Zingst. While the moss-dominated biocrusts grown under temperate climatic conditions reached Chl *a* values up to 483 mg m^{-2}, Büdel et al. (2009) demonstrated significantly lower concentrations in bryophyte-dominated biocrusts in arid regions (120 mg m^{-2}). Further enrichment of the organic matter content along a dune chronosequence was expected, based on the theory of Clements (1916) of habitat alteration and facilitation. The findings of the present study confirmed the assumption of Clements (1916). While in transitional dune areas, the establishment of mature biocrusts was rarely observed, moss-dominated biocrusts took over in the mature dune areas and covered the majority of the dune surface. This dune area is characterized by increased sand stabilization along with less sand accumulation (Martin, 1959) and represents the latest phase of dune succession. The accumulation of organic matter is an indicator of early soil formation (Ampe and Langohr, 2003; Dümig et al., 2014), which is assumed to be based on faster biomass formation and litter input than decomposition within the studied two dune areas. Furthermore, it was proven that biocrusts of mature successional stages were capable of promoting sediment moisture, as reflected by an increase in water-holding capacity and water availability of the thicker moss-dominated biocrusts (Gypser et al., 2016; Sun et al., 2022). Compared to algae-dominated biocrusts, mosses can absorb more water per biomass unit (Gypser et al., 2016) and transfer it via their rhizoids into deeper soil layers (Kidron et al., 2010). Thus, these mature biocrusts fulfill a relevant function for colonization with higher vegetation, which is essential for dune stabilization and finally coastal protection.

4.4 Community composition of the phototrophic species within the biocrusts

Within the present study, the algae species richness was lower compared to other studies conducted in temperate regions. Schulz et al. (2015), for example, detected 70 cyanobacterial and non-diatom algal taxa in association with biocrusts in the coastal dunes of the Baltic Sea islands Rügen and Usedom. Common to both studies was the fact that green algae showed the highest species richness in biocrusts, which is well known from humid terrestrial habitats (Hoffmann, 1989; Glaser et al., 2018). Moreover, 76% (19 species) of the identified algal species composition of the present study is in agreement with those algae from biocrusts of Rügen and Usedom (Schulz et al., 2015; Mikhailyuk et al., 2019). Several rare and taxonomically interesting green algal species common for both studies were found: *Tetracystis* cf. *sarcinalis*, *Tetradesmus arenicola* [described from sand dunes of Germany and Ukraine (Mikhailyuk et al., 2019)], *Eremochloris* cf. *sphaerica*, *Chlorokybus atmophyticus*, and *Interfilum* cf. *massjukiae*. Nevertheless, representatives of the Chlorophyta were never the dominant algal group in all types of dunes studied, for several reasons. Representatives of the genus *Klebsormidium* (Charophyta) as well as the cyanobacterial genera *Nostoc* and *Microcoleus* tend to be the dominant species along both chronosequences. *Klebsormidium* exhibits a wide tolerance to temperature, irradiance, and water availability (Karsten and Rindi, 2010; Holzinger and Karsten, 2013), and their sticky filaments provide optimal traits to glue sand particles together. With this broad ecological tolerance and properties, *Klebsormidium* can easily cope with the harsh conditions in the dunes and coexist in competition with other cryptogamic species, such as mosses and lichens. *Klebsormidium crenulatum* is a typical soil crust-forming alga widespread at coastal sand dunes of the Baltic (Schulz et al., 2015) as well as the Black Sea (Mikhailyuk et al., 2021). *Nostoc* and *Microcoleus* are commonly found in the biocrusts of drylands (Lange and Belnap, 2016). One of *Nostoc's* many survival strategies includes the production of exopolysaccharides, which leads to enhanced soil particle aggregation and the prevention of dune erosion (Büdel et al., 2016). This functional trait makes this genus particularly interesting, such as for coast protection measures. Further, Roncero Ramos et al. (2019) mentioned the potential benefits of *Nostoc* for reclaiming degraded soils by enriching them with organic carbon and nitrogen. Cyanobacteria generally play a crucial role in the enrichment of sandy sediment with nutrients, especially in this nitrogen-poor habitat (Langhans et al., 2009; Zhang et al., 2009). Nevertheless, it must be taken into account that the morphologically determined richness of algae species in enrichment cultures is lower than in nature. Since enrichment cultivation stimulates the growth of only culturable algae, information about the identity of other, often rare species is underrepresented (Langhans et al., 2009). Using molecular biological methods such as eDNA barcoding, it is assumed that more, but still not all species could be identified (Rippin et al., 2018).

Moss- and lichen-dominated biocrusts covered large parts of the later successional dune stages (Tables 6, 7). Leuschner and Ellenberg (2017) described the development of a cryptogamic layer as an indicator of the development of grey dunes. Hence, the cryptogams are not in danger of being buried by sand anymore. Furthermore, these authors assumed cryptogams to stabilize drifting sand grains and to accumulate and transfer organic matter into the underlying soil layers. Martínez and Maun (1999) showed a high tolerance of *Ceratodon purpureus* against burial by up to a 7 cm thick sand layer. Comparable to this, Gypser et al. (2016) identified *C. purpureus* as a characteristic species growing in the initial soils of postmining sites in Lower Lusatia, NE Germany. This is consistent with the fact that *C. purpureus* was the dominant moss species, particularly in the later stages of dune succession at Pramort and Darsser Ort. *Hennediella heimii* was found in the late grey dune of Darsser Ort and the mature dunes at Pramort. The distribution of this halophytic moss species is linked to the natural salinity gradient in coastal habitats. A recent study by Eldridge et al. (2023) provides a detailed insight into the contribution of soil

mosses to ecosystem services, highlighting their value for carbon sequestration and soil, as well as P in soils globally.

The lichen community of the biocrusts at both study sites was dominated by species of the genus *Cladonia*. Those species prefer to grow in sands with acidophilic conditions and were therefore found mainly in the later successional stages of the dune landscape, where pH < 5.5 was measured. It can be assumed that *Cladonia* and other lichen species fulfill important ecological functions in the dune ecosystem. For instance, the lichens within the biocrusts might be involved in the accumulation of available P since the present study points to an enrichment of the labile and easily soluble P fraction at the expense of Ca-bound P (H_2SO_4 fraction) (Table 4). Jung et al. (2020) demonstrated the biogeochemical function of lichens within so-called grit crusts in the bioweathering of P-containing minerals of the underlying soil, since they found a significantly higher total P concentration in the second sediment centimeter (643 mg kg^{-1} average P concentration) than in the first one (211 mg kg^{-1} average P concentration). They interpreted this as P transfer through fungal hyphae that penetrated the material. Another functional trait of lichen-dominated biocrusts might be maintaining resistance to ecosystem invasion (e.g., non-native species or higher shrubs), as shown by Deines et al. (2007) and Serpe et al. (2008) in two shrub-steppes (Northwestern and Southeastern USA, respectively). However, this trait can also be weakened by environmental influences like nutrient enrichment. Even low to medium nitrogen deposition impacts the vegetation in acid coastal dunes of the Baltic Sea, promoting the dominance of taller graminoids (Remke et al., 2009), and, thus, habitats for lichens may decline. Further development of the lichen community on the dunes remains an interesting research topic for the future.

5 Synthesis

This study highlights the successional development of a diverse and changing cryptogamic community along two temperate dune chronosequences of the Baltic Sea coast in conjunction with initial soil formation processes. The results clearly point to a dune-type-dependent, specific phototrophic community composition. While mobile dune types, which initially only provide a small amount of nutrients, are dominated by thin microalgae-dominated biocrusts, older dunes are dominated by mosses and lichens. The processes of earliest soil development on Holocene deposits along the Baltic Sea coast include acidification and decalcification of the sediment. In addition, pedogenic Fe compounds and organic matter are accumulated, along with enrichments in bioavailable plant nutrients such as phosphates. More mature biocrusts accumulated more carbon and P than thinner microalgae-dominated biocrusts due to a higher biomass formation. With this initial phase of soil development, the assumed enrichment of easily soluble and therefore bioavailable P compounds, especially in the mature biocrusts and the adjacent underlying topsoil horizons, could be approved. In conclusion, all these data emphasize the important ecological functions of biocrust communities for dune habitats. Subsequent studies could build on this knowledge and examine, for example, their application in dune stabilization and coastal protection.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

SK: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. PL: Conceptualization, Formal analysis, Methodology, Resources, Writing – review & editing. KG: Data curation, Writing – review & editing. US: Formal analysis, Investigation, Writing – review & editing. CD: Formal analysis, Writing – review & editing. TM: Formal analysis, Visualization, Writing – review & editing. ED: Formal analysis, Writing – review & editing. EH: Data curation, Formal analysis, Writing – review & editing. UK: Funding acquisition, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer ML declared a past co-authorship with the author UK to the handling editor.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1266209/full#supplementary-material

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Supplementary Material

1 Supplementary Tables

Supplementary Table 1. Extractants used for the sequential P fractionation.

P-fraction	Extractants	Procedure	Bioavailable considered as
resin-P fraction	H_2O (in the presence of resin)	30 ml distilled water in the presence of anion exchange resin (6 x 2 cm resin membrane), standard procedure, P was removed from the resin using 45 ml 1 M HCl	Labile P
$NaHCO_3$-P fraction	0.5 M $NaHCO_3$	50 ml 0.5 M $NaHCO_3$, standard procedure, HCO3 of the NaHCO3 extract was cleaved using 37% HCl (10:1, v:v).	
NaOH-P fraction	0.1 M NaOH	50 ml 0.5 M NaOH, standard procedure	Moderately labile P
H_2SO_4-P fraction	1 M H_2SO_4	50 ml 0.5 M NaOH, standard procedure	Stable P

Supplementary Table 2. Overview of all defined functional biotic and abiotic groups used to determine the dune surface coverage. Abbreviations of these groups, a short description, a color code, and visual examples of each functional group are given.

Category	Short	Description	Code
Vascular plants	VP	Tracheophyta	
Bare sediment/ sand	Ba	No vegetation or biocrust visible, loose sand layer	
Litter	Li	Litter layer e.g., needles, leaves, branches	
Biocrust			
Microalgae	MA	Early successional stage, slightly brittle, <3 mm thick, greenish-shimmering	
Microalgae-dominated /mosses	MA/ M	Stable greenish crust, occasionally mosses	
Moss-dominated	MD	Biocrust dominated by mosses, partly many algae species (mostly green algae), several cm thick/high	
Moss-dominated /lichens	MD/L	MD-type, occasionally lichens (mostly chlorolichens), many algae species (mostly green algae), several cm thick/high	

Supplementary Table 3. Iron contents in sediment cores of both sampling sites and as percentage of total Fe (Fet). Fedit = dithionite-citrate-bicarbonate extracted Fe, Feox = oxalate extracted Fe. Site: Darsser Ort; Dune types: YD = yellow dune, eGD = early grey dune, lGD = later grey dune, MD = mature dune. Site: Pramort; Dune types: WW = windwatt, YD = yellow dune, GD = grey dune, MD = mature dune.

Study site	Sampling plot	Compartment	Fe_t (g kg^{-1} DW)	Fe_{dit} (g kg^{-1} DW)	Fe_{ox} (mg kg^{-1} DW)	Fe_{dit} (% Fe_t)	Fe_{ox} (% Fe_t)
Darsser Ort	YD	Ai+ilC	1.0	0.3	29.4	25.7	3.0
	eGD	Aih+ilC	1.3	0.4	27.3	27.0	2.1
	lGD	Ah	1.7	0.2	29.6	14.1	1.9
		ilC	0.7	0.2	33.7	34.2	4.7
	MD	L/Ah	1.2	0.4	32.0	29.5	2.8
		ilC	0.9	0.3	47.3	32.4	5.3
Pramort	WW	Ai+ilC	0.4	0.1	1.0	23.9	0.2
	YD	Ai+ilC	0.3	0.1	1.6	17.2	0.4
	GD	L/Ah	0.6	0.2	33.6	40.6	6.0
		ilC	0.4	0.1	0	21.0	0
	MD	L/Ah	0.6	0.2	35.1	31.4	6.2
		ilC	0.4	0.1	17.2	25.7	4.0

Supplementary Table 4. Sediment characteristics of both sampling sites. Site: Darsser Ort; Dune types: YD = yellow dune, eGD = early grey dune, lGD = later grey dune, MD = mature dune. Site: Pramort; Dune types: WW = windwatt, YD = yellow dune, GD = grey dune, MD = mature dune.

Study site	Sampling plot	Compartment	$CaCO_3$ (g kg^{-1} DW)	pH ($CaCl_2$)	EC (mS cm^{-1})
Darsser Ort	YD	Ai+ilC	0.4	4.9	< 0.75
	eGD	Aih+ilC	2.1	5.0	< 0.75
	lGD	Ah	0	4.6	< 0.75
		ilC	2.1	4.6	< 0.75
	MD	L/Ah	0.3	4.4	< 0.75
		ilC	1.5	4.3	< 0.75
Pramort	WW	Ai+ilC	0	6.2	< 0.75
	YD	Ai+ilC	1.9	5.8	< 0.75
	GD	L/Ah	0.4	5.3	< 0.75
		ilC	2.1	6.6	< 0.75
	MD	L/Ah	0.4	3.6	< 0.75
		ilC	0.2	4.3	< 0.75

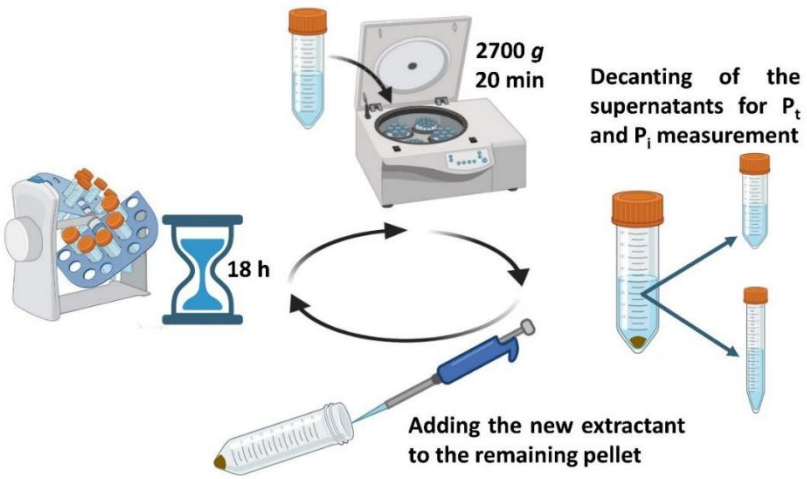
Supplementary Table 5. Lichen species in biocrusts. Listed by the order of lichen-forming fungi (Mycobiont). Columns differentiating between lichens occurrence and characterizing the preliminary settled pH range; Abbreviations: e=extreme-, v=very-, q=quite-, m=moderate.

Species	Occur on	pH range
Cladonia arbuscula	Sand	e.acidoph.-m.acidoph.-(subneutroph.)
Cladonia chlorophaea	Sand	(e.acidoph.-)v.acidoph.-m.acidoph.
Cladonia ciliata	Sand	q.acidoph.-neutoph.
Cladonia coccifera	Sand	q.acidoph.-m.acidoph.
Cladonia fimbriata	Sand	q.acidoph.-m.acidoph.-(subneutroph)
Cladonia floerkeana	Sand	v.acidoph-q.acidoph.
Cladonia foliacea	Sand	(q.acidoph.-)m.acidoph.
Cladonia furcata	Sand	q.acidoph.-subneutroph.
Cladonia glauca	Sand	q.acidoph.-m.acidoph.-(subneutoph.)
Cladonia humilis	Sand	q.acidoph.-subneutroph.
Cladonia macilenta	Sand	e.acidoph.-q.acidoph.-(m.acidoph.)
Cladonia novochlorophaea	Sand	(e.acidoph.-)v.acidoph.-m.acidoph.
Cladonia portentosa	Sand	e.acidoph.-m.acidoph.-(subneutroph.)
Cladonia ramulosa	Sand	v.acidoph.-q.acidoph.
Cladonia rangiformis	Sand	(q.acidoph.-)m.acidoph.-neutroph.
Cladonia rei	Sand	m.acidoph.-subneutroph.
Cladonia scabriuscula	Sand	m.acidoph.-subneutroph.
Cladonia subulata	Sand	q.acidoph.-m.acidoph.-(subneutroph.)
Cladonia uncialis ssp. *biuncialis*	Sand	e.acidoph.-m.acidoph.-(subneutroph.)
Evernia prunastri	Sand	v.acidoph.-m.acidoph.
Hypogymnia physodes	Sand	v.acidoph.-m.acidoph.
Polyozosia persimilis	Litter	subneutroph.-neutroph.
Peltigera hymenina	Sand	neutroph.
Physcia tenella	Litter	subneutoph.-m.basiph.
Scoliciosporum gallurae	Litter	m.acidoph.
Xanthoria parietina	Litter	subneutoph.m.basiph.

2 Supplementary Figures

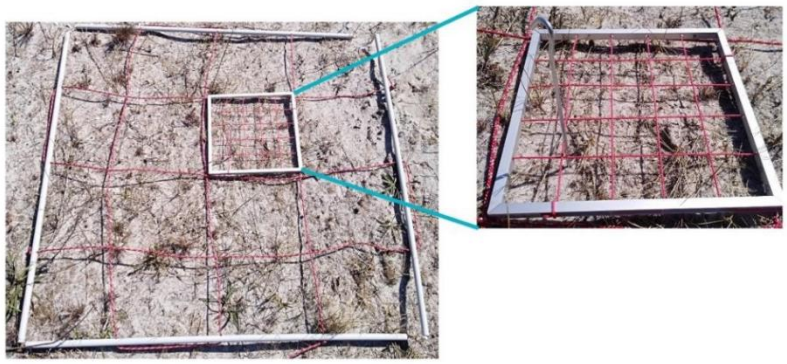


Supplementary Figure 1. Changes in the coastline at the Darsser Ort. The sampling site is located at an abrasion coast marked by a red star.

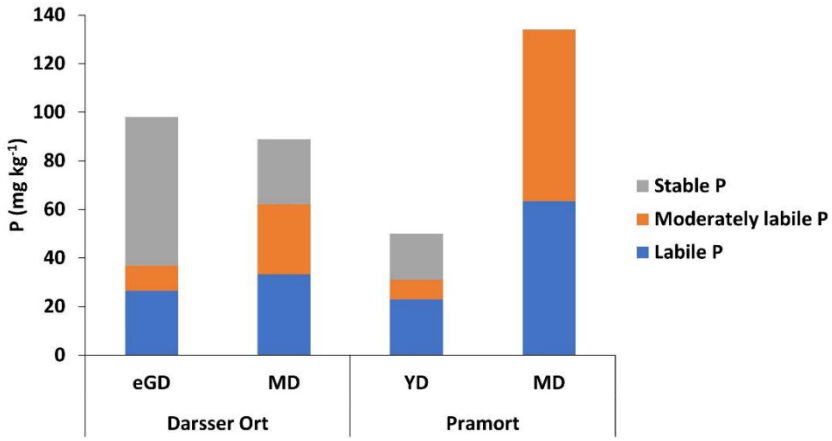


The concentration of P_t of the different extraction fractions was measured in the supernatants by ICP OES Optima 8300 (Perkin-Elmer Optima 8300 DV, Waltham, MA, USA) at 214.914 nm wavelength. The pellet was used for the next extraction step. Concentrations of molybdate-reactive P, which is mostly considered as inorganic P (Pi), of each extract was determined colorimetrically at λ = 882 nm by the method of Murphy and Riley (1962) using a UV/Vis spectral photometer(SPECORD PLUS, Analytic Jena GmbH, Jena, Germany). The molybdate-unreactive P (bound phosphate in extract) was considered as organic bound P (P_o) and was calculated as the difference between P_t and P_i of each fraction. Created with BioRender.com.

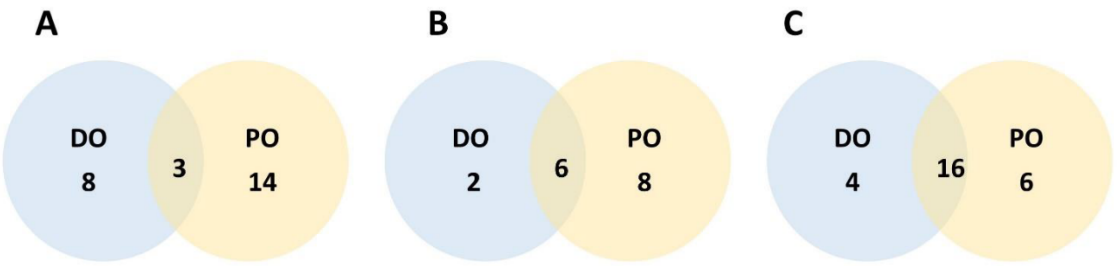
Supplementary Figure 2. Workflow diagram. 0.5 g dry and milled sediment or biocrust material was sequentially extracted. See Table 2 for extractants. The extraction followed a standardized procedure modified by Hedley *et al.* (1982).



Supplementary Figure 3. Sampling plot (1 m^2) divided into 16 equal subplots (0.0625 m^2) with 25 cm x 25 cm (0.0625 m^2) grid of 25 intersections. A metal pin was dropped next to each intersection, and the ground covering functional group, including bare sediment, was recorded.



Supplementary Figure 4. P concentrations in sequentially extracted pools of biocrusts (determined by sequential P fractionation) at two different dune sites. Site: Darsser Ort; Dune types: eGD = early grey dune, MD = mature dune. Site: Pramort; Dune types: YD = yellow dune, MD = mature dune.



Supplementary Figure 5. Venn diagrams showing the total species number of (A) algae, (B) mosses, and (C) lichens at the two sampling sites. The number of species that were found at both sites are represented as an overlap between the two circles. DO = Darsser Ort, PO = Pramort.

3 References

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3.4 Publication IV

Diversity of Bacteria in Biocrusts of sand dunes in temperate regions

Sandra Kammann, Karin Glaser, Christiane Hassenrück, Matthias Labrenz, Ulf Karsten

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Diversity of Bacteria in Biocrusts of sand dunes in temperate regions

Sandra Kammann[1*], Karin Glaser[2], Christiane Hassenrück[3], Matthias Labrenz[3], Ulf Karsten[1]

[1]Institute for Biological Sciences, Applied Ecology and Phycology, University Rostock
[2]Institute for Biosciences, Biology/Ecology, TU Bergakademie Freiberg, Freiberg, Germany
[3]Biological Oceanography, Leibniz Institute for Baltic Sea Research Warnemünde (IOW), Warnemünde, Germany

* Corresponding Author:
Albert-Einstein-Strasse 21, 18059 Rostock, Germany
Telefon: +49 381 498 6342
E-Mail: sandra.kammann@uni-rostock.de
https://orcid.org/0000-0002-8032-3648

Abstract

Biological soil crusts (biocrusts) are microecosystems forming productive layers on the soil surface. While biocrusts in arid or semi-arid regions are well studied, only a few studies focus on temperate ecosystems. Therefore, the present study presents a comprehensive overview of the bacterial diversity in biocrusts from coastal dunes along the Baltic Sea and a contrasting inland dune. It identifies the potential drivers for their community composition. Amplicon sequencing of the 16S rRNA gene revealed the dominance of Actinobacteriota in the biocrusts of the coastal dunes compared with an inland dune where Proteobacteria were prevalent. Comparing early and mature successional stages of biocrust development indicated significant differences concerning alpha diversity (Shannon index). The biocrusts' bacterial richness and community composition were related to the biocrust's successional stage, their physicochemical characteristics, and the underlying sediment. This analysis revealed that the biocrust successional stage is the most important driver affecting bacterial richness and community composition. For the first time, a detailed insight into the bacterial community of biocrusts in temperate sand dunes could be provided. Altogether, these findings deepen our understanding of changes in bacterial species richness and community composition during the succession of biocrusts and how environmental factors can impact on it.

Keywords: biocrust, dune chronosequence, bacterial diversity, succession

Introduction

Biological soil crusts (biocrusts) are known as pioneer colonizers of harsh environments where the establishment of vascular plants is challenging (Belnap et al., 2001). This microbial community of phototrophic and heterotrophic microorganisms such as algae, fungi, and bacteria, is adapted to a huge variety of environmental stressors like substrate mobility, low availability of nutrients and water, high soil surface temperatures, desiccation and UV radiation (Baldwin et al., 1983; Bowker et al., 2018; Bu et al., 2018; Fischer et al., 2014).
Biocrust organisms actively interfere with their surrounding habitat, e.g. through the formation of filamentous cell structures and excretion of adhesive polysaccharides which cause sticky connections between cells and soil particles (Belnap et al., 2016; Cania et al., 2019; Rossi et al., 2018). The uppermost millimeters of the soil get stabilized through this process reducing blowouts of sandy substrate and shaping soil water dynamics (Gypser et al., 2016; Kidron et al., 2014; Sun et al., 2022; van Ancker et al., 1985). Besides this positive effect on soil surface stability and the prevention of erosion biocrusts play a crucial role in the carbon (C) and nutrient cycles, e.g. of nitrogen (N), and phosphorus (P) (Barger et al., 2016; Baumann et al., 2017; Sancho et al., 2016). Elbert et al. (2012) estimated the global carbon uptake by cryptogamic ground covers (biological soil and rock crusts) of around ~2.4 Pg C yr^{-1}. If only the biocrusts are considered, this resulted in a value of ~0.6 Pg C yr^{-1} (corresponding to around 1% of net primary production by terrestrial vegetation) (Sancho et al., 2016). When assessing the global nitrogen uptake by cryptogamic ground covers, these authors calculated around 0.033 Pg N yr^{-1} corresponding to approximately ~31% of total global BNF (biological nitrogen fixation). Biocrust communities also play a key role in the biogeochemical P-cycle, especially by transforming stable P into labile, easily bioavailable P (Baumann et al., 2019). According to biochemical studies, the number of genes involved in P turnover and the enzyme activity of phosphatase is higher in the biocrusts compared to biocrust-free soil (Kurth et al., 2020; Schaub et al., 2019). Further, bioavailable nutrients and soluble carbon derived from biocrusts are likely transferred to the subsoil horizons and deeper sediment layers. Such vertical movements depend especially on the biocrust successional stage and the element being considered (Young et al., 2022).
Biocrusts are studied globally, mostly in arid and semi-arid regions (Fernández-Alonso et al., 2021; Veste et al., 2011), but also in cold deserts (Duan et al., 2024), Arctic and Subarctic regions (Pushkareva et al., 2016, 2021, 2022), as well as more recently in temperate zones (Baumann et al., 2017, 2021; Corbin et al., 2020; Glaser et al., 2017, 2022a). In the temperate climate zone sand dunes are typical ecosystems along the coastlines, such as the Baltic Sea coast and inland dune areas, that are colonized by various biocrust types. Sand dunes provide a harsh habitat for biocrust colonization since the sandy sediment is low in organic matter and nutrients, and flooding events have a high impact on substrate mobility (Martínez et al., 2004; Maun, 2009). While thin algae-dominated biocrusts are found in the more mobile dunes near the coastline, these biocrusts potentially develop into moss and lichen-dominated biocrusts on the older grey and mature dunes further inland. Such a characteristic successional development along dune chronosequences was described in previous publications (Kammann et al., 2023, 2024).
The overall community composition of biocrusts is shaped by various environmental factors (e.g. water availability (Fischer et al., 2012), temperature (Garcia-Pichel et al., 2013), radiation, topography, and soil texture (Fischer et al., 2014; Zaady et al., 2000), microclimate (Veste et al., 2006), and nutrient availability (Baldarelli et al., 2021; Ochoa-Hueso et al., 2016)), but also

by anthropogenic impacts like land use activities and trampling (Rodriguez-Caballero et al., 2018). The interaction of these factors together with the initial parent material and the organic matter content of the substrate greatly influence the microbial diversity and abundance in biocrusts. Subsequently, different types of biocrust are formed at different stages of their development (Kammann et al., 2023, 2024; Lan et al., 2015; Pushkareva et al., 2016). Previous studies investigated the diversity of the phototrophic community components of biocrusts such as lichens (Gypser et al., 2015), mosses (Bu et al., 2018; Eldridge et al., 2023), and microalgae (Büdel et al., 2016; Holzinger et al., 2013; Samolov et al., 2020). The eukaryotic algae of temperate dune biocrusts were intensively studied during the past years and identified as phototrophic key players in the early establishment of biocrusts in such mobile habitats (Mikhailyuk et al., 2019; Schulz et al., 2015). Studies on the heterotrophic community revealed additional insight into the associated fungi (Borchhardt et al., 2019; Glaser et al., 2022b) and protist community (Khanipour Roshan et al., 2021).

The investigation of the biocrust bacterial community is currently increasing significantly since high-throughput-sequencing analyses become more and more common in biodiversity studies (Miralles et al., 2020a; Moreira-Grez et al., 2019; Wasserstrom et al., 2017). These studies showed that Proteobacteria and Acidobacteria were prominent in biocrusts of West Australia (Moreira-Grez et al., 2019), while the bacterial biocrust community of the Oman desert was dominated by Actinobacteria (Abed et al., 2019). In addition, a strong correlation between the N mineralization and the P turnover could be validated in regions with increased labile N and P concentrations (Kurth et al., 2020). Further, the bacterial impact on nitrogen turnover was enhanced in biocrusts compared to the bare soil (Brankatschk et al., 2013). A study by Cania et al. (2019) highlighted the production of exopolysaccharides and lipopolysaccharides as important bacterial traits for initial biocrust establishment regardless of shifts in the bacterial community composition during biocrust development. Other studies investigated the influence of biocrust development on potential shifts in bacterial community composition. Maier et al. (2018) described a shift in the heterotrophic community composition from more generalized to specialized microorganisms during biocrust succession in the Northern Cape Province, South Africa. The observed bacterial gene copy numbers as well as alpha diversity (species richness and Shannon index), were highest in the late-successional biocrust stage, where the most abundant phyla were Bacteroidetes, Proteobacteria, and Actinobacteria. The influence of the biocrusts' successional stages on the structure of soil bacterial communities was confirmed by Miralles et al. (2020a) who described a correlation between different biocrust types, representing different successional stages, and the bacterial community composition in a semi-arid ecosystem in Spain. In line with Maier et al. (2018), the latter scientists confirmed that bacterial alpha diversity was higher in soils colonized by late-successional biocrusts.

Most of these studies were conducted in arid or semiarid environments. Less is known about biocrusts and their interactions with the surrounding habitat in the temperate zone (Corbin et al., 2020; Glaser et al., 2017). Glaser et al. (2022a) conducted a comprehensive study on the assembly of the bacterial community of biocrusts in temperate forests and its interaction with the algal associates. They confirmed that the bacteria in biocrusts are a specialized subset of the overall neighboring soil bacteria (see also Glaser et al. (2022b)). The most abundant phylum in these biocrusts was the Proteobacteria, followed by Actino- and Acidobacteria. The biocrusts' total N and P content, as well as the co-occurrence of mucilage-excreting algae, were revealed as driving factors for the bacterial community composition. Such a recruitment pattern was also observed in biocrusts of sand dunes along the Baltic Sea coast (Glaser et al., 2022b). Similar to temperate forest biocrusts Proteobacteria were most abundant in the sand dune biocrusts.

Nevertheless, there is a lack of further studies that deal in depth with the bacterial community composition in biocrusts and its potential successional shifts in such a mobile and unique habitat as temperate dunes.

Therefore, this study aims to (1) describe the bacterial biodiversity in biocrusts of different successional stages of sand dunes along the Baltic Sea coast in comparison to a contrasting temperate inland dune area. It is assumed that (2) specific functional traits of some bacteria might be favored in mature biocrusts causing a more specialized bacterial community compared to early biocrust stages. Furthermore, (3) the study aims to identify environmental factors driving bacterial community diversity and composition such as soil properties and nutrient contents.

Methods

Study Sites

All four study sites are located in Northern Germany, primarily along the southern Baltic Sea coast, in Mecklenburg-Western Pomerania. One out of four sites represents a contrasting dune area which is located inland, 100 km away from the North Sea coast in Lower Saxony.

The inland dune within the nature reserve 'Dünengebiet und Halsetal bei Verden-Neumühlen' has already been described in detail in Kammann et al. (2023) together with the dune chronosequence on the Schaabe spit on the island of Rügen (Figure 1). Two sampling plots along a transect following the dune successional gradient were under investigation on the inland dune to describe the bacterial biodiversity within the biocrusts. One plot was established on a dune slope (DS) where the first biocrust covers, dominated by early microalgae, were detected. The sampling transect ended in a mixed dune forest area (DF) dominated by pine trees, where the second plot was set. At DF the highest biocrust coverage was determined, characterized by moss and lichen-dominated biocrusts. At the successional transect along the dune chronosequence on the Schaabe spit four sampling plots were established. The plots were established in a foredune, followed by an intermediate dune (transitional zone between yellow and grey dune), a grey dune, and finally ending in a forested mature dune area. A development from early microalgae biocrusts to more stable and thicker moss and lichen-dominated crusts was well visible here.

The two other dune successional gradients were located at the study site Darsser Ort and Pramort on the peninsula Fischland-Darss-Zingst (Figure 1). Both dune areas are protected by the national park 'Vorpommersche Boddenlandschaft'. A detailed description of the sites can be found in Kammann et al. (2024). At both sites, four sampling plots along each chronosequence were set up. The development of the biocrusts is comparable to that of the other two study sites.

What all the sampling sites have in common is that they were geomorphologically formed during the last ice ages in the Pleistocene period (Niedermeyer et al., 2011). Their parent material eroded during the alternation of glacier advances and retreats of the last ice age in the Pleistocene and the following early Holocene period. The eroded sediment was further deposited by wind and waves along the coastline or inland. During this period, the young Baltic Sea coastline became more and more graded (Lampe, 2005; Lampe et al., 2011b, 2011a; Tiepolt et al., 1999).

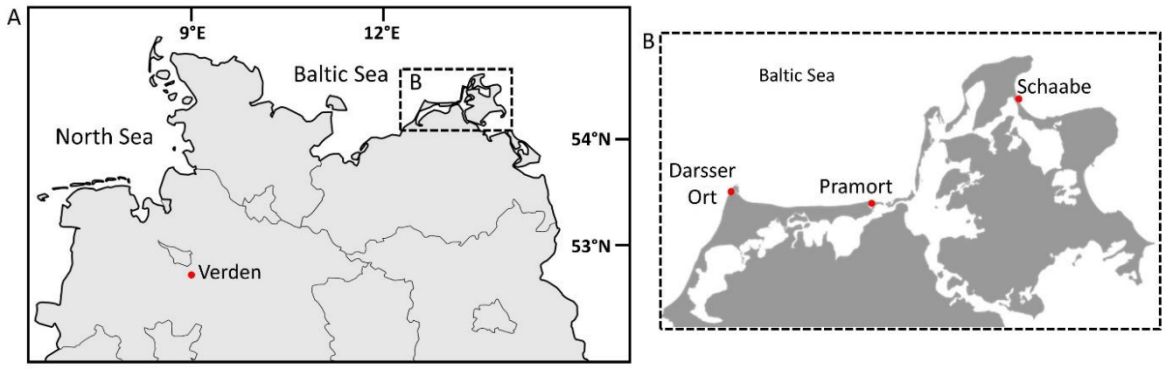


Figure 1: Map showing the four sampling sites under investigation (A). A close-up of the peninsula Fischland-Darss-Zingst with the sampling sites Darsser Ort and Pramort, and the isle of Rügen with the sampling site Schaabe (B).

Sample collection and laboratory analyses

The sampling design at the plots was identical across all transects at the four study sites and can be read in detail in the previous publications (Kammann et al., 2023, 2024). In short: Biocrust samples were taken using Petri dishes and a spatula. Triplicate Petri dishes were taken per sampling plot at each location for subsequent DNA analyses. Samples for DNA extraction were stored in a cooling box during transportation and transferred to a -20°C fridge in the laboratory. The first two plots close to the shore of each of the three chronosequences along the Baltic Sea coast were assigned to early successional biocrust types, while the two following plots further inland were declared mature biocrust types. At the inland dune, the plot at the dune slope represented the early and the second plot in the dune forest the mature biocrust types (Figure 2).

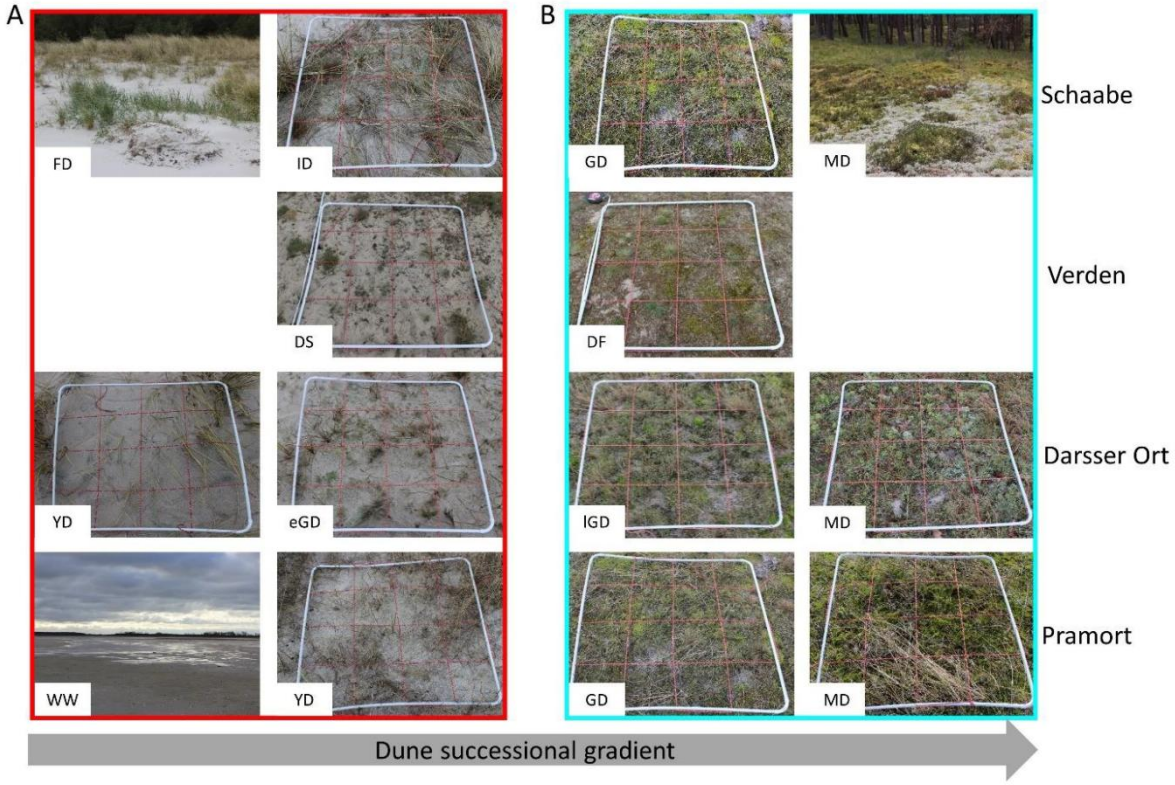


Figure 2: Overview of all sampling plots. Red frame (A): sampling plots assigned to early successional biocrust stages. Blue frame (B): sampling plots assigned to mature successional biocrust stages.
Abbreviation: early successional dune stages; WW = Windwatt, FD = foredune, ID = intermediate dune, YD = yellow dune, eGD = early grey dune, DS = dune slope. Mature successional dune stages; DF = dune forest, GD = grey dune, lGD = late grey dune, MD = mature dune.

Further analyses of physicochemical (water content, pH, total carbon, nitrogen, and phosphorus; Blume et al. (2010)) and biotic characteristics (organic matter content and chlorophyll *a*; Ritchie (2008)) of biocrusts followed standard procedures. Detailed information also on vegetation surveys of biocrust successional development and the phototrophic community are presented in Kammann et al. (2023, 2024).

DNA extraction and amplicon sequencing

According to the company's instructions, total DNA was extracted from approximately 0.25 g of each biocrust sample (triplicates per sampling plot) using the DNeasy PowerSoil Pro Kit (© QIAGEN, United States). Before the DNA was sent to the LGC Genomics GmbH (Berlin, Germany) for sequencing, DNA concentrations were quantified using the NanoDrop UV-Vis Spectrophotometer (Thermo Fisher Scientific, MA, USA). LGC performed PCR amplification and sequencing in a 2x300bp paired-end run using the Illumina MiSeq V3 platform. One set of primers was used for the amplification of the hypervariable V3–V4 region of the 16S rRNA gene (341F: 3'-CCTACGGGNGGCWGCAG-5', 785R: 3'-GACTACHVGGGTATCTAAKCC-5'; (Herlemann et al., 2011; Klindworth et al., 2013)). The primer-clipped sequencing data is available in the European Nucleotide Archive (ENA) under the project number PRJEB56530.

Bioinformatic processing of the 16S rRNA gene data

By generating the sequencing libraries in mixed orientation forward and reverse primers were present in both read 1 (R1) and read 2 (R2). Primers were removed using cutadapt version 3.4 (Martin, 2011), after demultiplexing (performed by LGC Genomics) with a mismatch rate of 0.16 and an overlap of at least 16 and 20 bp for forward and reverse primers, respectively, without indels. Dada2 version 1.22.0 (Callahan et al., 2016) implemented in R version 4.2.2 (R Core Team, 2022) was used to further process the primer-clipped reads, treating reads in different orientations separately. R1 and R2 reads were truncated to 260 and 200bp, respectively, and filtered to a maximum expected error rate of 3, before denoising. Default settings, except that all reads were pooled for the denoising step, were applied for error learning and denoising. After merging the denoised pair-end reads, amplicon sequence variants (ASVs) detected in the reverse-forward oriented part of the data set were reverse-complemented and the resulting two sequence tables generated from the different orientations were combined. Chimera removal was performed with *removeBimeraDenovo* using default settings. ASVs were taxonomically classified with *assignTaxonomy* against the SILVA ribosomal reference database release 138.1 (Quast et al., 2013). Before conducting further statistical analyses ASVs that were present only once in the dataset, those shorter and longer than 400 bp and 431 bp, respectively, as well as those assigned to eukaryotes and archaea, were removed from the data set. More details on amplicon sequence processing are available in Hassenrueck (2022).

Statistical analyses

All statistical analyses were performed in R version 4.2.2. (R Core Team, 2022). Two subsets of successional biocrust types were defined for further analyses (cf. Figure 2). Therefore, all replicates of the respective plots were assigned to one of the two categories 'early vs. mature biocrusts' according to their successional stage before subsequent analyses. Shannon's diversity index was calculated to describe the bacterial alpha diversity using the R package vegan (Oksanen et al., 2018). The differences in biogeochemical parameters among the four sampling sites and between the plots along each dune chronosequence were tested individually with a one-way analysis of variance (ANOVA) and Tukey's HSD post-hoc test (value of $p < 0.05$). The same approach was applied when comparing the alpha diversity indices (bacterial (ASV) richness and Shannon's diversity index) between the sites.

Regression analyses of the pooled data on bacterial richness (one-way ANOVA) and beta diversity of all plots (PerMANOVA using the command *adonis2* in R) on the environmental

factors were performed. The significance of the associations was determined by 9,999 random permutations. All predictors for both types of analyses were assessed independently. Bonferroni correction was applied to adjust the p-values for multiple testing.

Differences in the alpha diversity index and bacterial (ASV) richness between the two grouped successional biocrust stages were calculated using Welch's Two Sample t-test. Normality was assessed using Shapiro–Wilk's test.

Furthermore, Venn diagrams were created to visualize the number of shared and unique ASVs for all four sampling sites using the *ggvenn_pq* command in the R package ggVennDiagram (Gao et al., 2024). The Venn diagram is based on present vs. absent data of each ASV. An ASV was counted as present for the group if it occurred in at least 1 sample of that group.

Community dissimilarities among the sampling plots and four sites obtained by amplicon sequencing were assessed by non-metrical multidimensional scaling (nMDS) applying the Bray-Curtis-Dissimilarity Index based on relative sequence proportions using the R package vegan.

Results

Biocrust developmental stages and elemental contents

The successional development of biocrusts along all studied dune gradients revealed a clear shift regarding the dominance of different biocrust types. More mobile dunes closer to shore, which are typically under the frequent impact of harsh environmental factors (e.g. storms and sea spray), exhibited a patchy growth of thin and light biocrusts dominated by microalgae (10 - 40% coverage). These biocrusts grew mostly close to smaller vascular plants like small marram grass stands (*Ammophila arenaria* (L.) Link) and were assigned to the successional stage of early biocrusts. Along with the gradient, dunes began to change and became more stable, with increasingly flat dune ridges. Biocrusts covered higher percentages of bare ground and were dominated by mosses (35 - 50% coverage). Dunes close to the dune forests were almost fully covered with moss-dominated biocrusts which were also interspersed with lichens. These moss- and lichen-dominated biocrust types were summarized as mature biocrusts. The data table of the percentage coverage of each biocrust type in all specific dunes can be found in Kammann et al. (2023, 2024). Along with biocrust succession, the chlorophyll *a* (Chl *a*) content increased (1.2 - 482.8 mg m^{-2}), indicating a rise in photosynthetic biomass with changing biocrust types (Supp. Table 1). Such an accumulation in biomass is also reflected in a higher organic matter content in mature biocrusts (3.3 - 25.2% dry weight (DW)) compared to early successional stages (<0.1 - 1.4% DW).

The water content was enhanced in mature biocrusts, likely due to the thick layer of the phototrophic community dominated by mosses and lichens, which prevented the water from draining quickly due to their pronounced water-holding capacity. The soil pH was lower for all mature biocrust (3.7 - 6.0) samples compared to early successional stages (4.5 - 6.6) of biocrust development (Supp. Table 1). An increase in the total nutrient element contents of carbon, nitrogen, and phosphorus along each of the four dune chronosequences was measured. These differences in the total P content between the site-specific sampling plots along the dune chronosequences were significant at Pramort (ANOVA, $p = 0.01$) and the inland dune in Verden (ANOVA, $p = 0.02$). The increase in the total P content was less pronounced at the remaining two sites. Overall, the dunes at Darsser Ort showed lower carbon (0.3 - 29.9 g kg^{-1}) and phosphorus (62.6 - 110.4 g kg^{-1}) contents compared to the other three sampling locations (Supp. Table 1).

Taxonomic assignment and community composition of bacteria

Amplicon sequencing using general bacterial primers resulted in 1.3 M quality filtered reads, clustered into 17678 ASVs (amplicon sequence variants). 17618 ASVs of those could be assigned to bacterial phyla, and 60 ASVs were assigned only to the kingdom (non-assigned bacteria).

The taxonomic assignment of the obtained bacterial ASVs revealed the dominance of Actinobacteriota at the three sampling sites along the Baltic Sea coast (Figure 3). The following percentages refer to the total number of sequences per site. These sites were Darsser Ort (20.4%, 1405 ASVs), Pramort (26.4%, 1819 ASVs), and Schaabe (24.2%, 1856 ASVs). At the inland dune, Actinobacteriota were less dominant (12.9%, 636 ASVs) than in the coastal dunes. Instead, Proteobacteria dominated the bacterial community in the inland dune (33.2%, 996 ASVs). At the coastal dune sites, Proteobacteria were the second most abundant phylum. Further, a higher relative abundance of Acidobacteriota (12.3%, 399 ASVs) was only detected

in the inland dune. Cyanobacteria (2.5%, 38 ASVs) and Deinococcota (3.8%, 35 ASVs) were more dominant at the Darsser Ort than at the other three sampling sites (Figure 3).
Within the Actinobacteriota community, Actinobacteria (85.4% of Actinobacteriota-assigned sequences, 1813 ASVs) was the dominant class. Further, Thermoleophilia (9.9% Actinobacteriota-assigned sequences, 552 ASVs) and Acidimicrobiia (4.6% of Actinobacteriota-assigned sequences, 299 ASVs) were present. Within the Proteobacteria community, Alphaproteobacteria (72.8% of Proteobacteria-assigned sequences, 2338 ASVs), and Gammaproteobacteria (27.2% of Proteobacteria-assigned sequences, 1493 ASVs) were present. Within the Acidobacteriota, Acidobacteriae was the dominating class (91.7% of Acidobacteriota-assigned sequences, 615 ASVs).
Cyanobacteria played only a minor role in the biocrusts of the temperate dunes studied. In detail, only approx. 1% of all obtained bacterial ASVs (5.3% of the total number of sequences) were assigned to cyanobacteria. Those could be taxonomically classified into three classes, eight orders, and 12 families. The 12 identified families were relatively dominated by the family of Nostocaceae (36% of all ASVs assigned to the family level). Cyanobacteriia was most dominant at the sampling site Darsser Ort (23% of Cyanobacteria- assigned ASVs).
Changes in taxonomy between successional biocrust stages became obvious in the increase of the relative abundance of ASVs assigned to the phyla of Verrucomicrobiota, Acidobacteriota, and Planctomycetota in mature stages. While the relative abundance of the dominating phyla (Proteobacteria and Actinobacteriota) remained unchanged, the decline in the relative abundance of Cyanobacteria and Deinococcota-assigned ASVs (most visible at Darsser Ort) and Bacteroidota-assigned ASVs (prominent at Schaabe) in mature compared to early successional biocrust stages was most noticeable (Figure 3).

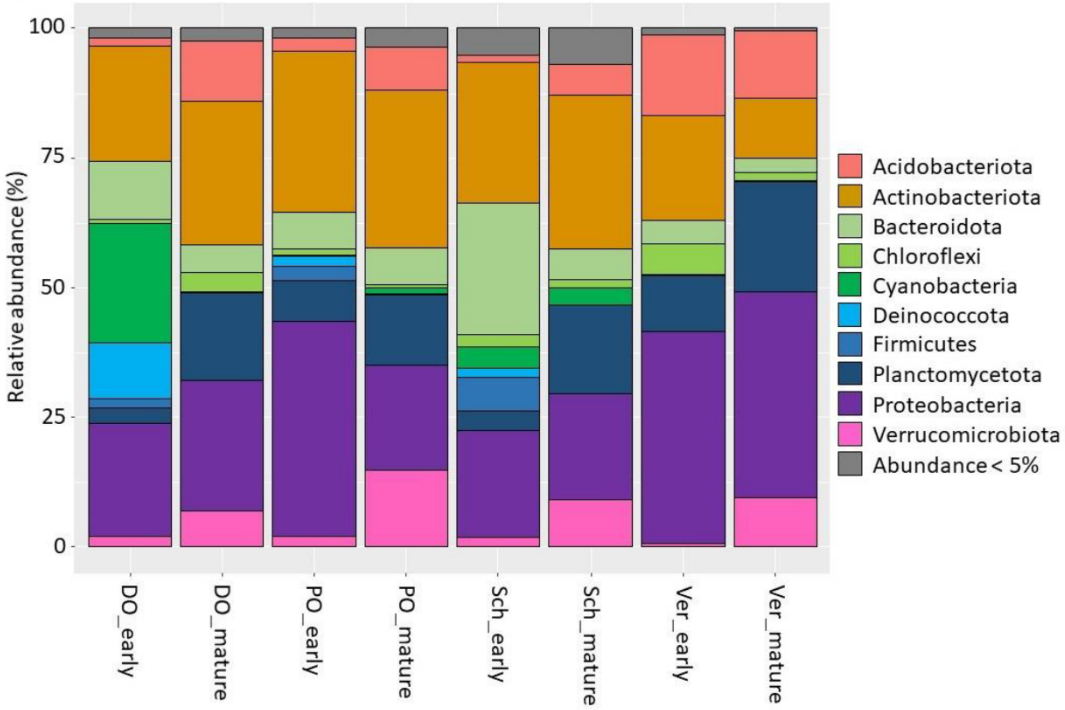


Figure 3: Overview of early and mature biocrusts microbial community composition at each sampling site based on relative abundances of bacterial phyla. Low-abundant phyla or clades with relative abundance < 5% were combined and are shown in grey color.
Abbreviation: coastal dunes; DO = Darsser Ort, PO = Pramort, Sch = Schaabe. Inland dune; Ver = Verden.

Alpha diversity

Bacterial (ASV) richness did not differ significantly between any of the four sampling sites (ANOVA, p = 0.36). Overall, most bacterial ASVs were observed at the sampling site Schaabe (11413 ASVs; Figure 4a). The inland dune (Verden) showed the lowest bacterial richness of all study sites (3836 ASVs). Looking at the ASV richness of all 14 individual sampling plots, the grey dune at Pramort exhibited the highest bacterial richness (5963 ASVs). The Venn diagram revealed the number of shared and unique ASVs of biocrusts between all four sampling sites (Supp. Figure 1). 11% of bacterial ASVs were found in the biocrusts of all four sampling sites. The highest percentage of ASVs (18%) was shared between Pramort and Schaabe, and those two sampling sites and Darsser Ort (17%). Verden had the lowest number of shared ASVs with all other sampling sites (<=2%). The highest number of unique ASVs was observed on the Schaabe spit.

Early and mature biocrusts over all sampling sites shared 44% of the ASVs, while their unique ASVs comprised approximately a similar percentage of the total ASV (27% and 29%, respectively; Supp. Figure 2). Further in-depth analyses focused on the difference between early and mature biocrusts at the different sampling sites (Figure 4b). At Pramort, early biocrusts were significantly (Welch Two Sample t-test, t = -2.9, df = 7.8, p = 0.02) lower in bacterial richness than mature biocrusts. Considering all four sampling sites, the trend of increasing bacterial richness in mature biocrusts compared to the early successional stages is visible (Figure 4b).

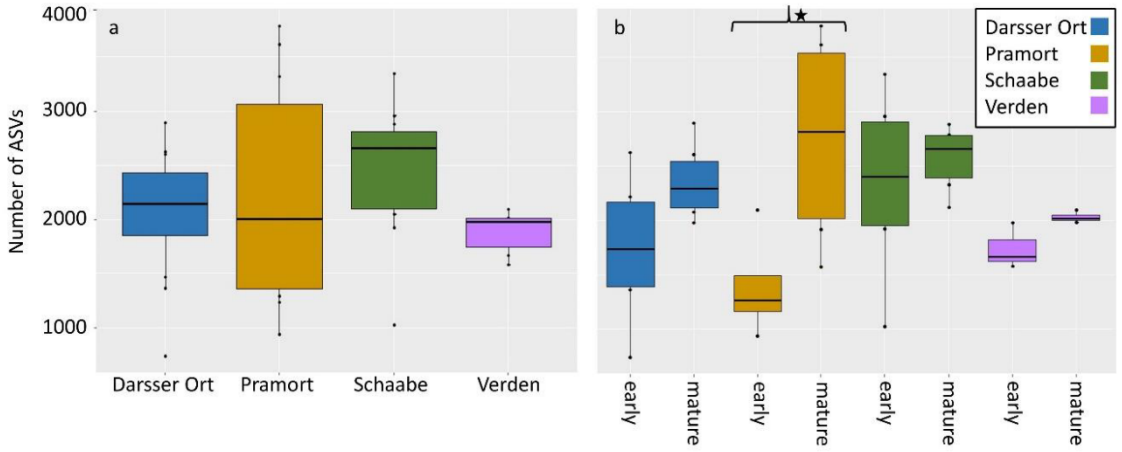


Figure 4: Boxplots showing (a) Bacterial richness as numbers of ASVs (amplicon sequence variants). (b) Bacterial richness as numbers of ASVs in early and mature biocrusts for all sampling locations. Differences in bacterial richness between successional stages were significant at Pramort (Welch Two Sample t-test, df =7.8, p=0.02), marked with an asterisk.

The Shannon's diversity index calculated for the bacterial community did not differ significantly between the sites (ANOVA, p = 0.2). However, larger variations between the two subsets of different successional stages of biocrust development along each dune chronosequence were observed (Figure 5). Welch Two Sample t-test revealed significant differences in the bacterial diversity between early and mature biocrust communities at Darsser Ort (t = -3.3, df = 5.4, p = 0.02) and Pramort (t = -2.6, df = 3.4, p = 0.07).

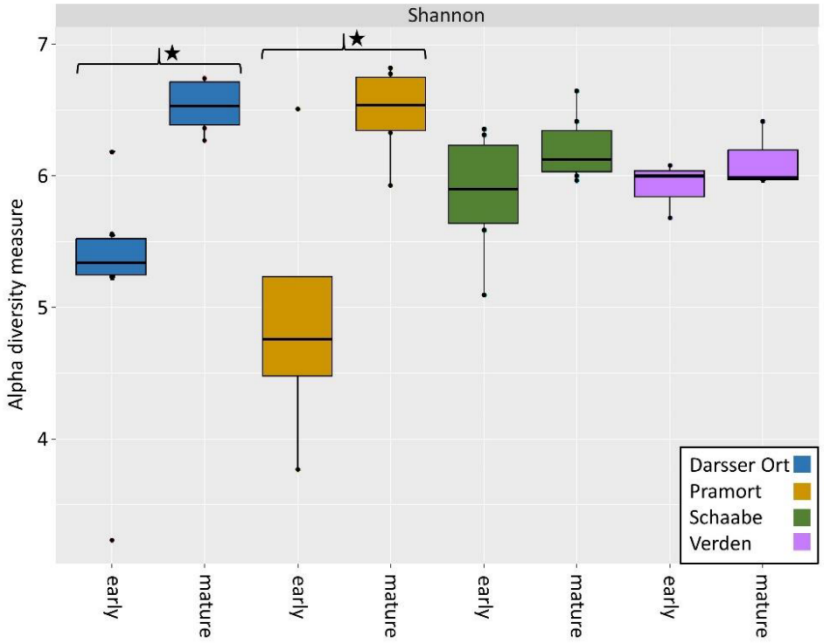


Figure 5: Box plots showing Shannon's diversity index in the biocrusts of different successional stages from all study sites. Significant differences in the alpha diversity index between successional stages at one site are marked with an asterisk.

Environmental factors driving bacterial richness and diversity

Analyses of variance (ANOVA) revealed the biocrust successional stage to be the major driver for bacterial species richness (Table 1).

The non-metric multidimensional scaling (nMDS) indicated a clear clustering of the bacterial biocrust communities into early and mature bacterial biocrust communities (Figure 6). The bacterial community composition from mature biocrusts was more similar to each other and formed a cluster compared to the bacterial community from early biocrusts. The bacterial community composition from early biocrusts was more scattered in the plot meaning those are less similar to each other than the composition from mature dunes. As for the species richness the successional biocrust stage was identified as an important factor shaping not only the alpha diversity but also the community composition of early and mature biocrust stages (PerMANOVA, $R2 = 0.011$, $p < 0.01$; Table 1).

Table 1: Regression of the bacterial richness on environmental factors (based on ANOVA results) and the community composition (based on PERMANOVA results) of bacteria in biocrusts from sand dunes. Signif. codes: ***p < 0.001, **p < 0.01, *p < 0.05, p < 0.1; n.s.—not significant. Subscripted 't' means 'total', C = carbon, N = nitrogen, and P = phosphorus. Predictors were assessed independently. Bonferroni correction was applied to adjust the p-values for multiple hypothesis tests.

	Richness	Community composition
Successional stage	0.03*	0.008**
C_t	n.s.	0.008**
N_t	n.s.	0.008**
P_t	n.s.	0.03*
pH	n.s.	0.008**
Organic matter content	n.s.	0.008**
Water content	n.s.	0.04*

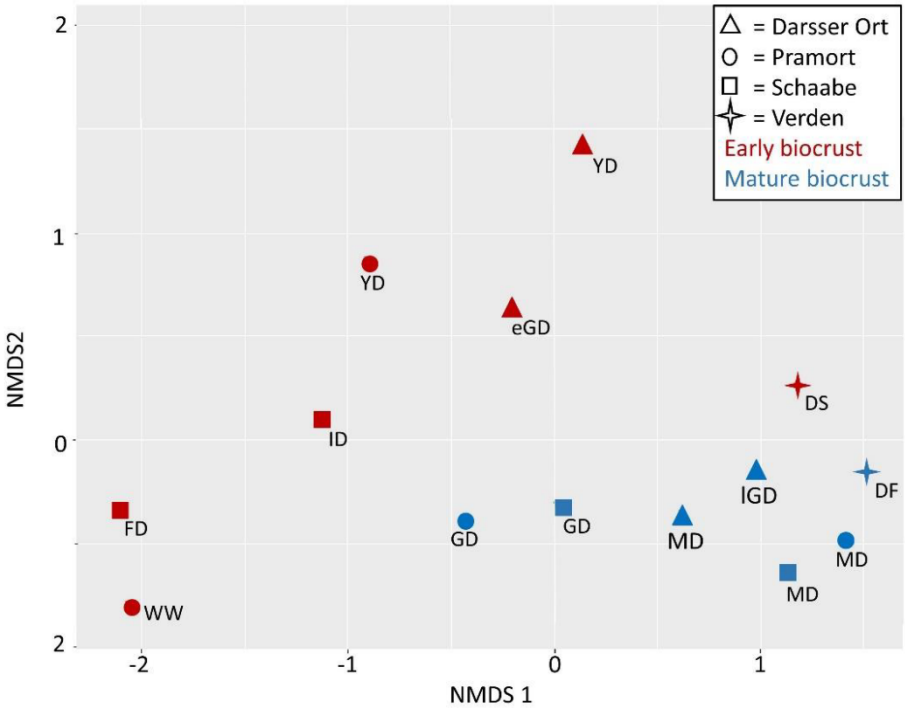


Figure 6: Comparing early and mature successional stages visualized using nMDS, based on the relative abundance of the ASVs in biocrusts; Stress = 0.08.
Abbreviation: early successional dune stages; WW = Windwatt, FD = foredune, ID = intermediate dune, YD = yellow dune, eGD = early grey dune, DS = dune slope. Mature successional dune stages; DF = dune forest, GD = grey dune, lGD = late grey dune, MD = mature dune.

Discussion

Bacterial Diversity of Biocrusts

This study gives an insight into the bacterial diversity of biological soil crusts from temperate coastal dunes. Especially the successional stage of the biocrust is taken into account when analyzing the bacterial community structure. The coastal sand dunes under investigation are dynamic ecosystems representing gradients of biogeochemical parameters e.g. salinity, water content and pH, biomass accumulation, and early processes of soil formation. Such gradients typically go along with natural dune succession forming chronosequences (Jones et al., 2008; Walker et al., 2010).

The development of the biocrust communities of temperate coastal and inland dunes, from early thin microalgae-dominated to moss and lichen-dominated later biocrust types, is closely related to the different stages of succession of the dunes (Kammann et al., 2023, 2024). Concerning the phototrophic biocrust community (microalgae, mosses, and lichens) an increase in the total species richness between early and mature biocrusts was obvious at all four sites (Supp. Figure 3). Such a development seems to apply to the bacterial species richness, too. This observation is in congruence with a previous study from Maier et al. (2018), who studied the impact of photoautotrophic biocrust organisms on microbial abundance, diversity, and physiology in different types of biological soil crusts. They concluded that alpha diversity increases with progressing succession and that the bacterial communities differ significantly between biocrust types. Such a difference was also demonstrated in the present study. Further studies also reported an increase in alpha diversity as succession progresses (Duan et al., 2024; Moreira-Grez et al., 2019). A study by Miralles et al. (2020a) showed comparable alpha diversity values (Shannon index: 5.7 - 6.7) to the present study (Shannon index: 3.7- 6.7). Concerning the overall bacterial ASV richness between study sites, no significant differences could be detected. The geographical distances between the four study locations did not have a strong influence. Longer transects and more separated sampling sites would have probably caused more differences in alpha diversity.

The bacterial microcosm in the soil is typically known to be dominated by nine different phyla: Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, Firmicutes, Gemmatimonadetes, Planctomycetes, Proteobacteria, and Verrucomicrobia (Janssen, 2006; Nunes da Rocha et al., 2009). These phyla are also common in biocrusts, which is confirmed in the studies listed hereafter. Biocrusts in the Mediterranean semi-arid climate (Moreira-Grez et al., 2019) and arid shrubland (Steven et al., 2014) revealed Proteobacteria, Cyanobacteria, and Actinobacteriota, as dominant groups. Abed et al. (2019) came to a similar conclusion and also described the Bacteroidota as a dominant phylum in the arid deserts of Oman. Glaser et al. (2022b) described six abundant phyla in biocrusts from sand dunes in temperate regions, adding Planctomycetes and Verrucomicrobiota to the above-mentioned four phyla. Pushkareva et al. (2022) found that biocrusts in Arctic and Subarctic regions are dominated by Actinobacteriota too, but also by Acidobacteriota and Chloroflexi. The taxonomic composition of the biocrust bacterial community in dunes was comparable to the studies mentioned above. Most similar to the dominant species in the present study are the results of Maier et al. (2018), who studied biocrusts in the Northern Cape Province, South Africa. However, Bacteroidota in the temperate coastal dunes was less abundant in comparison. Additionally contrasting, the relative abundance of Planctomycetes was higher in the present study than in the African biocrusts.

Comparing the bacterial richness between early and mature biocrusts an increase in the alpha diversity of the phyla Acidobacteriota, Planctomycetota, and Verrucomicrobiota was detected. This leads to the assumption that some functional traits of bacteria belonging to these phyla might be favored in mature biocrusts. Genome sequencing of Acidobacteriota conducted by other researchers revealed a variety of genes, for example, those encoding enzymes involved in the carbon cycle (e.g. degradation of complex carbohydrate polymers) supporting the decomposition of organic matter (Banerjee et al., 2016). The higher relative abundance of Acidobacteriota in later successional biocrust types might point to a higher decomposition potential within the mature biocrusts characterized by an enhanced organic matter content. Furthermore, the importance of litter decomposition by Planctomycetota in *Sphagnum*-dominated peatlands was reported by Dedysh et al. (2019) and Kulichevskaya et al. (2017). Both phyla, Acidobacteriota and Planctomycetota, are decomposers in soil and their active participation in the cycling of organic matter has already been proven (Dedysh et al., 2019, 2018). Since the relative abundance of Planctomycetota increased with biocrust succession, it can be assumed that besides Acidobacteriota also Planctomycetota are involved in the transformation of organic matter. The decomposition of organic material is one of the key mechanisms in early soil formation (Schulz et al., 2013) and is commonly enhanced by further organisms within a biocrust such as fungi and archaea (Belnap, 2001). Thus, the formation of a humus layer and early soil formation is supported by bacterial activity. During the process of mineralization organic nitrogen compounds (as part of the organic matter) get decomposed into mineral nitrogen species such as ammonium (NH_4^+). Planctomycetota implies a group of obligately anaerobic, so-called 'anammox' Planctomycetes, that can oxidize ammonium under anaerobic conditions (Jetten et al., 2001; van Niftrik et al., 2012). Apart from denitrification, this anammox process is the only metabolic pathway in which bound nitrogen is transformed back into its molecular form. Thereby, large proportions of the N-rich inorganic compounds are removed from the food chain. Only small fractions of the elemental nitrogen can be refixed by cyanobacteria and algae and reintroduced into the nitrogen cycle as shown by Kuypers et al. (2005) who revealed huge amounts of nitrogen loss from the Benguela upwelling system through anaerobic ammonium oxidation.
Further, cellulose biosynthesis by bacteria can facilitate survival in the soil through biofilm formation, thereby retaining moisture as shown in Proteobacteria (Ude et al., 2006; White et al., 2006) and *Acidobacterium capsulatum* (Acidobacteriota, (Ward et al., 2009)). Such mechanisms can also be essential for survival in the biocrusts of temperate sand dunes and contribute to soil aggregate formation. The formation of soil aggregates due to biocrust activity positively affects soil surface stabilization and is known to increase with dune succession (Forster et al., 1981).

An approximate fivefold increase in the relative abundance of the ASVs assigned to the phylum Verrucomicrobiota can be observed in mature biocrusts. The phylum Verrucomicrobiota is known to be related to several other phyla of bacteria, forming a cluster called a superphylum (PVC), including the former mentioned Planctomycetota (Wagner et al., 2006). Verrucomicrobiota is widespread in soils worldwide (Bergmann et al., 2011; Fuerst, 2019). However, little is known about their composition, diversity, and overall distribution across different soil types. Bergmann et al. (2011) identified that Verrucomicrobiota average 23% of bacterial sequences across North America, South America, Europe, and Antarctica, making them far more abundant than had been estimated before. Interestingly no Spartobacteria-assigned ASVs were detected in the present study. This is surprising because otherwise this verrucomicrobiotal class is described as the most common in soils (Bergmann et al., 2011;

Janssen, 2006; Kielak et al., 2009; Sangwan et al., 2004). Spartobacteria include free-living taxa, as well as endosymbionts associated with nematode worms (Vandekerckhove et al., 2000; Wagner et al., 2006). This symbiosis explains an increasing occurrence of Spartobacteria in temperate grasslands (Janssen, 2006), which are commonly colonized by relatively high levels of nematodes (Fierer et al., 2009). But no such nematode density is to be expected in sandy dune sediments. Therefore, it remains to be investigated in more detail in the future why there has been such an increase in the relative abundance of Verrucomicrobiota in mature biocrusts. About 53% of all Verrucomicrobiota-assigned ASVs belong to the family of Chthoniobacteraceae. Members of this bacterial family can grow with many of the saccharide components of plant biomass and are therefore involved in the transformation of organic carbon compounds in the soil (Sangwan et al., 2004). They potentially join the group previously mentioned bacterial decomposers (Acidobacteriota and Planctomycetota), which also increase in their ASV richness with increasing organic matter accumulation in older dunes.

Cyanobacteria are widespread and known as 'biocrust-builders' due to their excretion of exopolysaccharides (EPS) and lipopolysaccharides (Belnap et al., 1993; Cania et al., 2019; Danin et al., 1989; Mazor et al., 1996). A decrease in the relative abundance of Cyanobacteria-assigned ASVs was detected between early and mature biocrusts. Such a decline is in line with previous studies on biocrust cyanobacteria in Chinese temperate and cold deserts (Duan et al., 2024; Li et al., 2020) and a German inland sand flat (Langhans et al., 2009). Cyanobacteria are well-known biocrust-forming microorganisms described primarily as the dominant phylum in biocrusts of arid regions (Garcia-Pichel et al., 2001; Maier et al., 2018; Roncero Ramos et al., 2019; Samolov et al., 2020). In these habitats, cyanobacteria support the formation of soil aggregates, sediment stabilization, and moisture retention due to their EPS excretion (Danin et al., 1989; Mazor et al., 1996). This function may not only play a central role for dunes in arid deserts but can also be relevant for the stabilization of temperate mobile coastal dunes. As the relative abundance of cyanobacteria in mature biocrusts decreases, the stabilizing function here might be mainly taken over by the dominating phototrophic cryptogams such as mosses, which provide stabilization of the top sediment layer through anchoring structures like their rhizoids (Belnap et al., 2016; Martínez et al., 1999). In addition to soil stabilization by EPS excretion, cyanobacteria have two more general, important ecological functions, namely primary production and nitrogen fixation. The latter function is not realized by all Cyanobacteria species.
75% of all Cyanobacteria-assigned ASVs that could be classified up to the family level belong to the Nostocaceae. Members of this family are efficient nitrogen-fixing bacteria (Brankatschk et al., 2013). However, the overall relatively low abundance of Nostocaceae within the biocrust samples points to a moderate relevance in this functional trait in temperate sand dunes. Potentially either other nitrogen-fixing bacteria have taken over this role, e.g. species of Acidobacteriota (Sellstedt et al., 2013), or nitrogen is supplied by atmospheric precipitation or sea spray. Husbandry contributed most to reduced nitrogen deposition, while the transport sector contributed most to oxidized nitrogen deposition in the Baltic Sea region (Gauss et al., 2021). Thus, nitrogen fixation plays only a minor part and it can be assumed that N is not a limiting nutrient in mature biocrusts. Although outside the scope of the present study, it would be interesting to investigate in more detail which other pathways within the nitrogen cycle are realized by the bacteria of the biocrusts. Li et al. (2020), for example, reported that genes involved in nitrate reduction (assimilative and dissimilatory nitrate reduction, and denitrification) were most dominant in the N cycle of bacterial and moss-dominated biocrusts. Genes involved in nitrogen fixation pathways appeared to be less important in their study. Kurth et al. (2020) demonstrated a strong correlation between nitrogen and phosphorus turnover when nutrient

concentrations were high but the N/P ratio was low. Within the present study in temperate dunes, the N/P ratio was lower in early (mean 4.1) than in mature biocrusts (mean 12.3) suggesting a similar trend. Kurth et al. (2020) also found that N mineralization was strongly correlated to P turnover when both elements are easily bioavailable. Further metatranscriptomic analyses are needed to verify such results in the biocrusts of temperate coastal dunes.

Shift of Bacterial Community Composition in Biocrust Depending on Environmental Parameters

Bacterial richness and diversity are strongly influenced by the successional stage of the biocrust they are associated with, which several studies could prove for cyanobacteria (Büdel et al., 2009; Lan et al., 2012; Langhans et al., 2009). Miralles et al. (2020a) confirmed that the biocrust successional stage was the most important factor, significantly influencing 108 soil bacteria genera within their study, and alpha diversity was higher in soils colonized by later successional biocrust stages. The latter finding is in line with the present results of bacterial community development in the biocrusts. A recent study on cold desert biocrusts revealed that bacterial diversity increased as biocrust succession proceeded (Duan et al., 2024). Accordingly, the improved soil conditions (e.g. nutrient and soil organic matter enrichment along with biocrust succession), influenced the bacterial community composition. This connection can also be assumed in the present study. Nevertheless, it has to be considered, that the successional stages combine specific biotic and abiotic characteristics of the respective biocrust type shaping the bacterial community within. Therefore, the parameter 'successional stage' tends to be co-correlated with several environmental parameters (e.g. pH, nutrients, soil organic matter content; Supp. Figure 4). However, the following discussion considers possible environmental parameters that may have influenced the bacterial composition of the biocrusts.

Further, the water content within the biocrust measured at the time of sampling appeared to be a decisive factor influencing the bacterial community composition in temperate coastal sand dunes. This finding is in line with the results of other studies such as Chen et al. (2005) who showed that the amount of microbial biomass in a sand dune forest ecosystem on the coast of western Taiwan was connected to soil moisture. With further biocrust succession, whereby mosses and lichens become the dominating phototrophic community components, higher water contents in the biocrusts are expected. Mosses absorb water into cellular mucilage thereby exhibiting a higher water-holding capacity resulting in higher water retention and finally moisture content in moss-dominated biocrusts (Belnap et al., 2013; Chamizo et al., 2012, 2016; Sun et al., 2022). Such mosses can act as water reservoirs for the bacteria, which are thus less affected by the short-term absence of water supply (e.g. rain events). A seasonal effect in particular can be seen in the moisture content of biocrusts in temperate regions. Wasserstrom et al. (2017) showed that there was a difference in community composition between the wet and dry seasons, indicating a strong impact of soil moisture on the community composition. If soil moisture was not a limiting factor (during the wet season) for the bacterial community, other parameters such as soil organic matter, pH, and salinity then significantly influenced the community. The sampling and data presented in the present study showed a unique snapshot of the bacterial community of biocrusts growing in the seasonal climate of the temperate zone. Based on the earlier studies mentioned, it it appears to be the logical consequence to

investigate the seasonal effects on the bacterial community of coastal dunes in more detail, for example, as part of long-term monitoring.
Moreover, seasonal patterns of moisture were also reflected in the temporal patterns in soil microbial activity identified in a Chihuahuan desert grassland (Bell et al., 2008). In general, the metabolic activity of most microbial species declined with decreasing soil water potential (Griffin, 1981; Schimel et al., 2007). Brockett et al. (2012) investigated the microbial structure in seven biogeoclimatic zones in western Canada concluding that soil moisture is the major factor influencing microbial community structure and enzyme activities. Consistent with this, water availability was found to affect the soil heterotrophic respiration and nutrient mineralization of a microbial community, as shown by Manzoni et al. (2012). Manzoni et al. (2012) and Bell et al. (2008) assumed that changes in the rainfall pattern, i.e. timing and quantity of precipitation, will greatly impact decomposition rates and processes within nutrient cycling mediated by bacteria. Regarding this assumption, Büdel et al. (2009) concluded that rain frequency and duration of dry periods rather than the precipitation amount are the main factors for biocrust microbial diversity and distribution patterns in Southern Africa. Such patterns still have to be further tested in temperate sand dunes.

The pH is commonly reported as the main driver for soil bacterial diversity and abundance (Fierer et al., 2006; Hartman et al., 2008; Kaiser et al., 2016; Lauber et al., 2009). This was also proven for the bacterial community composition in the biocrust of Arctic and Subarctic regions (Pushkareva et al., 2022) and semi-arid Mediterranean ecosystems (Miralles et al., 2020b).Langhans et al. (2009) studied the community assembly of biocrusts on an inland sand flat in Germany, finding significantly higher genera and species numbers of cyanobacteria and eukaryotic algae in the initial biocrust stages ('light cyanobacterial crust'). In these authors' study, it is assumed that the decline of cyanobacteria in mature biocrusts could be related to the decrease in pH. Cyanobacteria in general seem to be less abundant in acidic soils. Brock (1973) described a decline and even the total absence of cyanobacteria in habitats with a pH less than 4 or 5. However, more recent studies (e.g. Whitton & Potts (2002)) showed that there are exceptions, particularly with heterocystous species which seem to be the most tolerant to low pH values. In line with Langhans et al. (2009) the chronosequences investigated in the present study also showed a decrease in soil pH below 5 in grey and mature dunes in parallel with a decrease in the relative abundance of Cyanobacteria-assigned ASVs.

Conclusion

This work provides a biodiversity baseline for understanding the structure and community composition and functions of the bacterial community in biocrusts along with dune succession in a temperate environment. Although all investigated biocrusts originated from sand dune habitats a pronounced difference in the dominant phyla between coastal and inland dunes became clear. While Actinobacteriota were dominant in the biocrusts of the dunes along the Baltic Sea coast in the inland dune Proteobacteria were most prevalent. When comparing biocrust successional stages the bacterial alpha diversity was higher in mature biocrust compared to thinner early successional biocrusts. Moreover, the bacterial community composition became more similar between mature than between early biocrust stages suggesting a more specialized community in these later successional stages. Results of the regression analyses of the bacterial richness on environmental factors and the community composition suggested that the biocrust successional stage was the most important driver for bacterial richness and community composition in biological soil crusts.

In conclusion, biocrusts in temperate coastal sand dunes seem to be unique habitats for bacterial colonization where these essential photo- and heterotrophic components are potentially key drives in ecosystem functioning.

Data availability statement

Demultiplexed and primer-clipped raw reads have been deposited on the European Nucleotide Archive (ENA) using the brokerage service GFBio and are available under project accessions PRJEB56530. Data concerning environmental data can be found on PANGAEA (Kammann et al., 2022). The scripts for bioinformatic 16S sequence processing are available at https://git.io-warnemuende.de/bio_inf/IOWseq000014.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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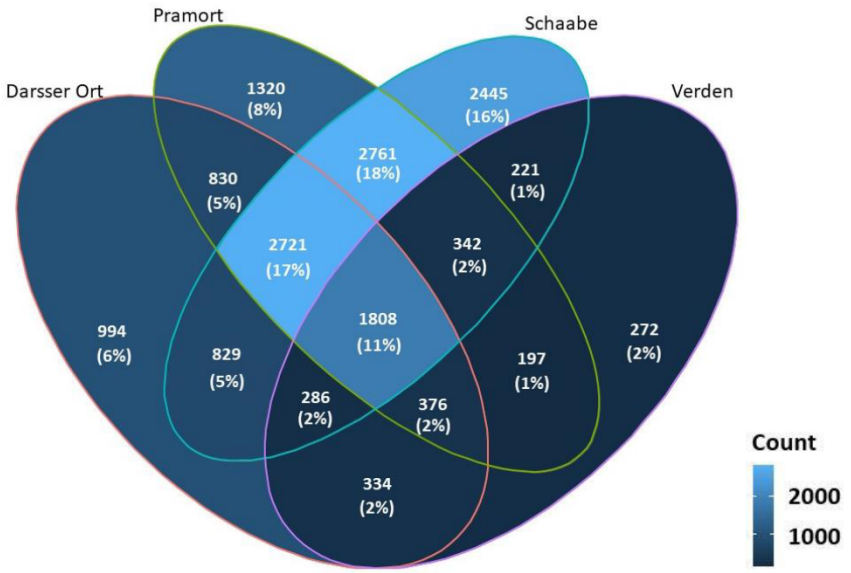
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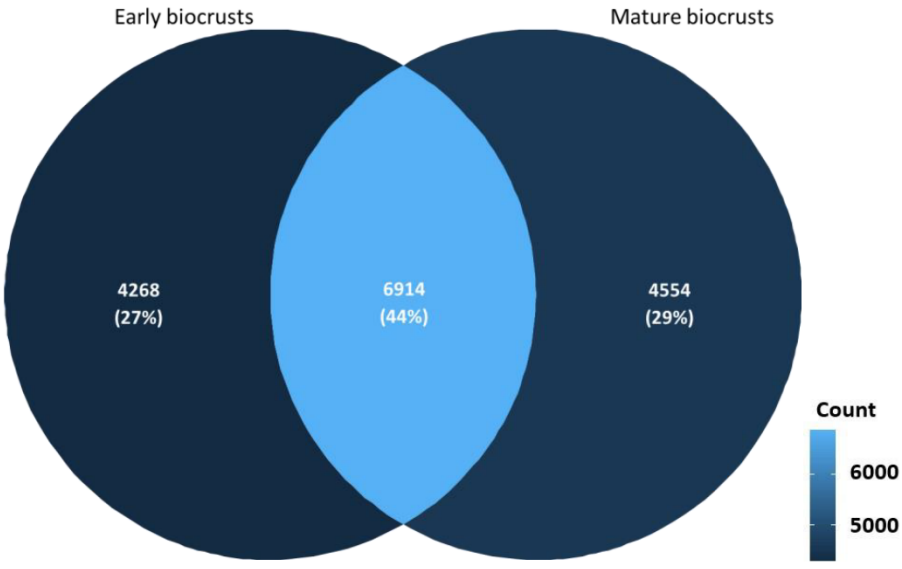
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Supp. Table 1: Characteristics of biocrusts (chlorophyll a (Chl *a*), water content (WC), organic matter content (OM)) and soil chemistry (pH measured in 1:2.5 (w/v) suspension with 0.01 M calcium chloride ($CaCl_2$)) of the study sites and concentration of total carbon (C_t), nitrogen (N_t), and phosphorus (P_t) of biocrusts (FW = fresh weight; DW = dry weight) from four sampling sites. Mean ± standard deviation, n = 3.

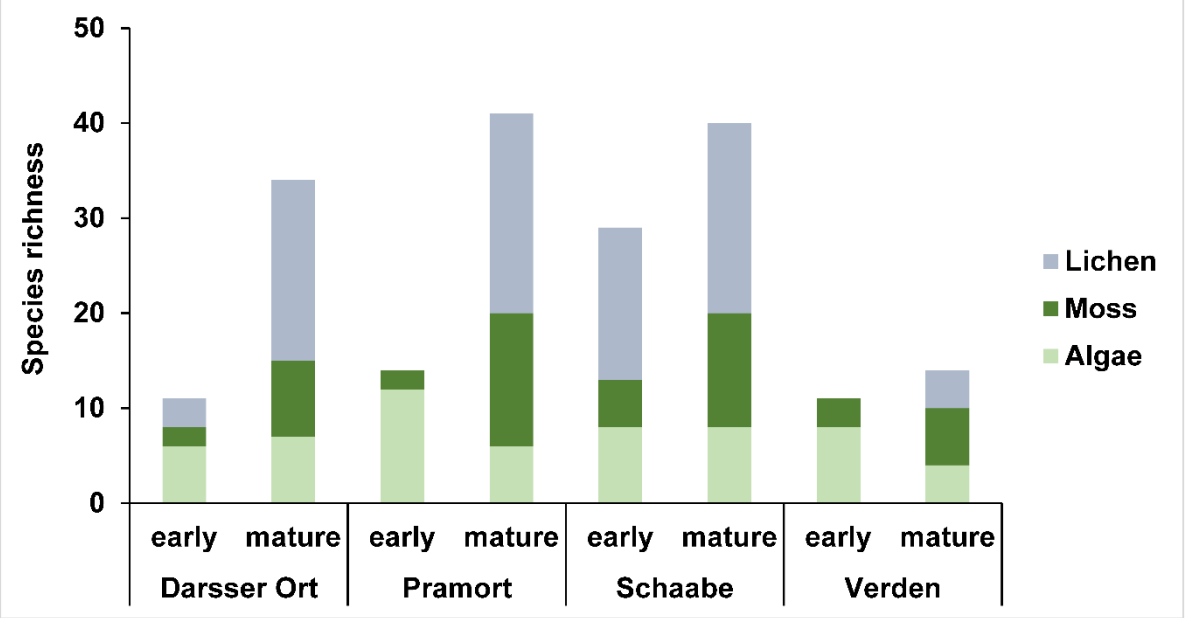
Site	Plot	Biocrust type	Chl *a* (mg m^{-2})	WC (% FW)	OM (% DW)	pH ($CaCl_2$)	C_t g/kg	N_t g/kg	P_t mg/kg
Verden (Aller)	Dune slope	Early	5.9	< 0.1	< 0.1	4.5	15.3 ± 3.0	0.8 ± 0.3	71.9 ± 11.4
	Dune forest	Mature	112.1 ± 20.0	0.2 ± 0	3.3	3.7	99.6 ± 4.6	4.7 ± 0.2	291.0 ± 58.1
Schaabe (Rügen)	Fore dune	Early	0	0.5 ± 0.8	0.1	6.4	0.6 ± 0.1	0.1 ± 0	113.9 ± 12.6
	Intermediate dune	Early	161.3 ± 56.5	0.16 ± 0.1	1.4	6.1	6.6 ± 0.7	0.4 ± 0.1	148.9 ± 22.9
	Grey dune	Mature	150.9 ± 26.5	0.4 ± 0	7.1	5.6	35.5 ± 10.4	1.3 ± 0.1	173.2 ± 16.3
	Mature dune	Mature	287.6 ± 49.1	1.2 ± 0.6	25.2	4.0	84.3 ± 40.7	3.3 ± 1.5	172.2 ± 69.0
Darsser Ort	Yellow dune	Early	1.2 ± 0.9	3.9 ± 0.1	< 0.1	5.2	0.3 ± 0	0.1 ± 0	62.6 ± 1.1
	Early grey dune	Early	100.3 ± 18.9	8.1 ± 0.5	1.0	5.1	0.9 ± 0.1	0.1 ± 0	71.8 ± 6.1
	Late grey dune	Mature	327.1 ± 88.4	18.3 ± 4.6	3.7	4.7	14.8 ± 2.0	0.5 ± 0	99.5 ± 7.4
	Mature dune	Mature	453.8 ± 188.0	20.6 ± 7.0	11.0	4.7	29.9 ± 0.3	1.4 ± 0	110.4 ± 0.5
Pramort	Windwatt	Early	5.4 ± 1.2	9.2 ± 0.9	0.2	6.6	0.4 ± 0	0.1 ± 0	38.1 ± 1.1
	Yellow dune	Early	127.6 ± 4.2	4.6 ± 0.3	0.3	5.6	2.1 ± 0.1	0.2 ± 0	34.8 ± 0.8
	Grey dune	Mature	453.2 ± 35.4	34.6 ± 12.9	5.7	6.0	58.8 ± 28.1	2.6 ± 1.1	199.1 ± 84.9
	Mature dune	Mature	482.8 ± 125.9	47.7 ± 6.0	18.6	3.7	61.7 ± 0.1	2.0 ± 0	159.0 ± 3.9



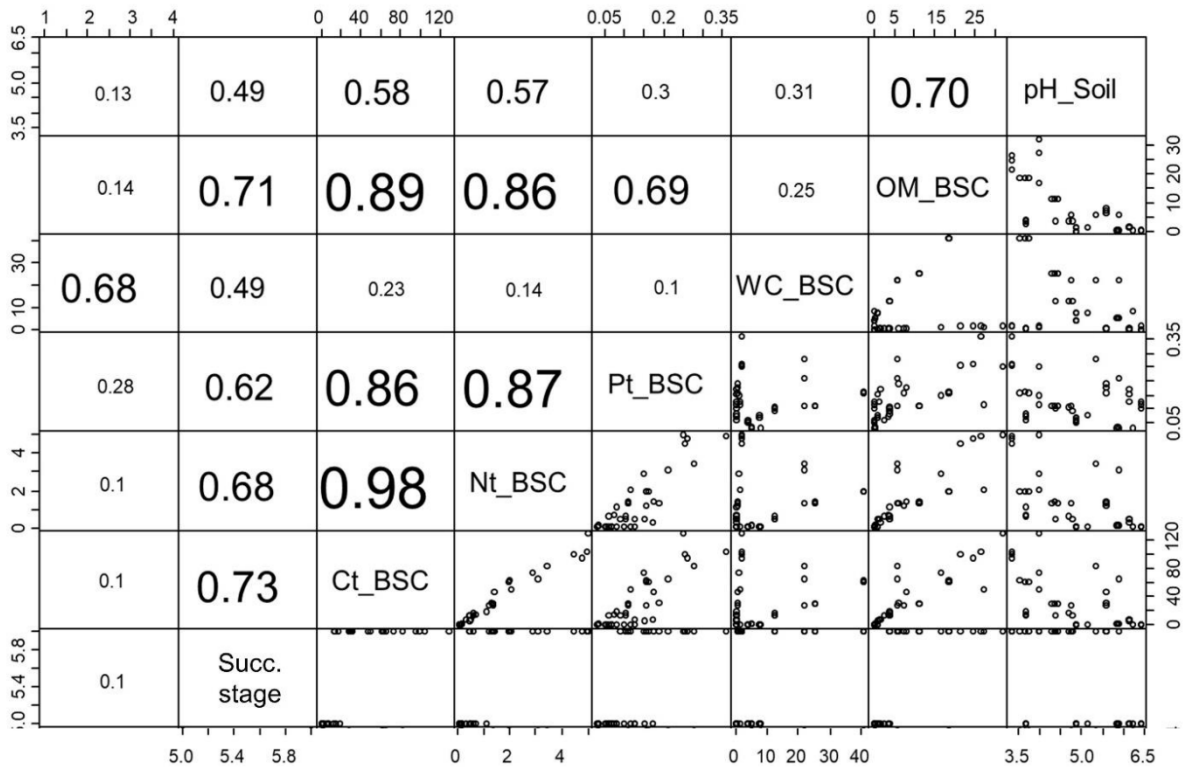
Supp. Figure 1: The Venn diagram shows the number of shared and unique ASVs for all four sampling sites.



Supp. Figure 2: The Venn diagram shows the number of shared and unique ASVs between different biocrust successional stages (reflects biocrust types).



Supp. Figure 3: Bar graphs visualizing the species richness of the biocrust's phototrophic communities. Summary of data published in (Kammann et al., 2023, 2024).



Supp. Figure 4: Pair plot visualizing the relationships among biotic and abiotic variables of the dataset. Each plot shows the relationship between a pair of variables.

Abbreviation: BSC = biological soil crust, Ct = total carbon, Nt = total nitrogen, OM = organic matter content, Pt = total phosphorus, Succ. = successional, WC = water content.

4 Appendices

4.1 Declaration of own contribution to the publications

Author abbreviations: Sandra Kammann (SK), Ulf Karsten (UK), Karin Glaser (KG), Ulf Schiefelbein (US), Christian Dolnik (CD), Tatiana Mikhailyuk (TM), Eduardo Demchenko (ED), Mirko Dreßler (MD), Niklas Plag (NP), Elena Heilmann (EH), Peter Leinweber (PL), Christiane Hassenrück (CH), Matthias Labrenz (ML).

Publication I

Kammann et al. 2023: Successional Development of the Phototrophic Community in Biological Soil Crusts on Coastal and Inland Dunes

SK developed the idea and concept of the fieldwork campaign. Fieldwork was then conducted by **SK** and US. Algae cultivation and determination were performed by TM and ED. US was in charge of the determination of lichen species. CD was responsible for the determination of moss species. Further laboratory analyses were conducted by **SK**. **SK** and KG provided all statistical data. Visualization of data and photomicrographs were created by **SK** and TM. **SK** wrote the original draft. US, CD, TM, UK, and KG reviewed and edited the draft. All authors have read and agreed to the published version of the manuscript. UK was in charge of the supervision.

Publication II

Glaser et al. 2023: Ecophysiological performance of terrestrial diatoms isolated from biocrusts of coastal sand dunes

This manuscript was supervised by KG. KG was responsible for the funding acquisition, developing the sampling design, and conducting the fieldwork with **SK**. Chemical analyses were completed by **SK** and NP. Algae cultivation and laboratory experiments were conducted by NP. MD performed morphological determination of the diatom field samples and cultures. KG provided all statistical data. Visualization of data and photomicrographs were created by KG, NP, and **SK**. The original draft was written by KG. **SK** made major improvements to the original draft. NP and MD reviewed and edited the draft. All authors have read and agreed to the published version of the manuscript.

Publication III

Kammann et al. 2024: Successional development of the phototrophic community in biological soil crusts, along with soil formation on Holocene deposits at the Baltic Sea coast

SK and PL developed the idea and concept of the fieldwork campaign. Fieldwork was then conducted by **SK** and US. Algae cultivation and determination were performed by TM and ED. US was in charge of the determination of lichen species. CD was responsible for the determination of moss species. Further laboratory analyses were conducted by **SK** and EH. **SK** and KG provided all statistical data. Visualization of data and photomicrographs were created by **SK** and TM. **SK** wrote the original draft. US, CD, TM, UK, PL, and KG reviewed and edited the draft. All authors have read and agreed to the published version of the manuscript. UK was in charge of the supervision.

Publication IV (submitted)

Kammann et al.: Diversity of Bacteria in Biocrusts of sand dunes in temperate regions

SK developed the idea and concept of the fieldwork campaign. Fieldwork was then conducted by **SK** and US. DNA extraction was performed by **SK**. 16S rRNA gen sequencing and library preparation was taken over by LGC Genomics GmbH. CH handled the bioinformatic processing of the 16S rRNA gene data. All statistical analyses were conducted by **SK** and KG. Visualization of data was done by **SK**. **SK** wrote the original draft. CH, ML, KG, and UK reviewed and edited the draft. All authors have read and agreed to the submitted version of the manuscript. UK was in charge of the supervision.

4.2 Danksagung

An dieser Stelle möchte ich meinen besonderen Dank nachstehenden Personen entgegen bringen, ohne deren Mithilfe die Anfertigung dieser Dissertation niemals zustande gekommen wäre:

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Besonders danken möchte ich **Niklas,** dem besten Bürokollegen und Pseudo-Dorktoranden aller Zeiten. Du hast sowohl meinen beruflichen Alltag, als auch meine Freizeit unwahrscheinlich bereichert. Ich hab mit kaum jemandem lieber gelacht, als mit dir - WITZIG!

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Danke euch - „Ich mache jetzt real life.“ Grus grus.

'When you know better, you do better'

- Maya Angelou

4.3 Selbstständigkeitserklärung

Ich, Sandra Kammann, versichere hiermit an Eides statt, dass ich die vorliegende Arbeit selbstständig angefertigt und ohne fremde Hilfe verfasst habe. Dazu habe ich keine außer den von mir angegebenen Hilfsmitteln und Quellen verwendet und die den benutzten Werken inhaltlich und wörtlich entnommenen Stellen habe ich als solche kenntlich gemacht.

Rostock, den_____ _____

(Unterschrift)