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# Biological Soil Crusts: An Organizing Principle in Drylands

# Ecological Studies

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Evolution of biological soil crusts during thousands of millions of years of biosphere development of our planet (for detailed legend and explanations see Fig. 25.2);  
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Bettina Weber • Burkhard Büdel • Jayne Belnap  
Editors

# Biological Soil Crusts: An Organizing Principle in Drylands

 Springer

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# Preface

During the last decades, and probably at least partly triggered by the first Ecological Studies volume on this topic (volume 150), biological soil crusts (biocrusts) have quickly gained increasing interest from many audiences, with well above 100 publications per year published during the last few years. Thus, we found that there is now a wealth of new data covering a wide range of different topics on biocrusts and showing that biocrusts can act as “an organizing principle in drylands.” This observation inspired us to use this as the title of this second Ecological Studies volume. This book is divided into seven sections comprising a total of 25 different chapters.

When we selected the authors for the different chapters, we had two intentions in our mind. One was to include many scientists from as many regions of the world as possible, who also used different methodological approaches in order to get a thorough and comprehensive view on the different topics. Second, we also wanted to get a good mixture of younger and well-established researchers. With a total of 61 chapter authors and 28 of them being in the doctoral, postdoc, or associate professor stage, ~46 % of the book authors are in a nonfinal/early stage of their career.

This second book on biological soil crusts would not have been possible without the help of some people in particular, whom we would like to thank here: first of all, we would like to express our sincere thanks to Otto L. Lange, who gave us the opportunity to be editors of this book, who strongly supported us throughout the whole process of development, from the first ideas to the final editions, and who read and gave highly productive feedback to every single chapter of this book. Thank you so much! Second, we also would like to thank all the authors who contributed to the book. We are well aware of the fact that we sometimes asked for rather profound and time-consuming changes during the development of the book chapters. Despite this, all authors remained highly cooperative and motivated, a fact which cannot be taken for granted and which we deeply appreciate. Third, we would like to express our sincere thanks to Dr. Andrea Schlitzberger, who coordinated this biocrust book for Springer. She always was extremely patient and helped

us immediately upon all smaller and larger problems, and it really was a pleasure to work with her. Fourth, we want to thank our supervisors and colleagues, who allowed us to spend so much time and energy on this book and who believed that in the end, we would produce a worthwhile book that would advance this scientific field. Finally, we also would like to express our sincere thanks to our families and partners for their tolerance and support during the endeavor of this second biocrust book.

We sincerely hope this book will help many scientists, land managers, policy makers, and also the environmentally interested public, to receive an overall introduction into the fascinating world of biocrusts and that it will foster many new ideas and scientific projects. Our goal is reached if this book supports understanding of the overall role of biocrusts as an organizing principle in drylands.

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# Contents

## Part I Introduction

- 1 Biological Soil Crusts as an Organizing Principle in Drylands . . . . 3  
Jayne Belnap, Bettina Weber, and Burkhard Büdel
- 2 How Biological Soil Crusts Became Recognized as a Functional  
Unit: A Selective History . . . . . 15  
Otto L. Lange and Jayne Belnap

## Part II Morphology, Composition, and Distribution of Biological Soil Crusts at Different Scales

- 3 Terrestrial Ecosystems in the Precambrian . . . . . 37  
Hugo Beraldi-Campesi and Gregory J. Retallack
- 4 Cyanobacteria and Algae of Biological Soil Crusts . . . . . 55  
Burkhard Büdel, Tamara Dulić, Tatyana Darienko, Nataliya Rybalka,  
and Thomas Friedl
- 5 Bacteria and Non-lichenized Fungi Within Biological  
Soil Crusts . . . . . 81  
Stefanie Maier, Lucia Muggia, Cheryl R. Kuske, and Martin Grube
- 6 Bryophytes Within Biological Soil Crusts . . . . . 101  
Rodney D. Seppelt, Alison J. Downing, Kirsten K. Deane-Coe,  
Yuanming Zhang, and Jing Zhang
- 7 Structure, Composition, and Function of Biocrust Lichen  
Communities . . . . . 121  
Roger Rosentreter, David J. Eldridge, Martin Westberg,  
Laura Williams, and Martin Grube
- 8 Microfauna Within Biological Soil Crusts . . . . . 139  
Brian J. Darby and Deborah A. Neher



9	Composition and Macrostructure of Biological Soil Crusts . . . . .	159
	Claudia Colesie, Vincent John Martin Noah Linus Felde, and Burkhard Büdel	
10	Controls on Distribution Patterns of Biological Soil Crusts at Micro- to Global Scales . . . . .	173
	Matthew A. Bowker, Jayne Belnap, Burkhard Büdel, Christophe Sannier, Nicole Pietrasiak, David J. Eldridge, and Víctor Rivera-Aguilar	
11	Hypolithic Communities . . . . .	199
	Stephen B. Pointing	
12	Remote Sensing of Biological Soil Crusts at Different Scales . . . . .	215
	Bettina Weber and Joachim Hill	

### Part III Functional Roles of Biological Soil Crusts

13	Microstructure and Weathering Processes Within Biological Soil Crusts . . . . .	237
	Ferran Garcia-Pichel, Vincent John Martin Noah Linus Felde, Sylvie Laureen Drahorad, and Bettina Weber	
14	Patterns and Controls on Nitrogen Cycling of Biological Soil Crusts . . . . .	257
	Nichole N. Barger, Bettina Weber, Ferran Garcia-Pichel, Eli Zaady, and Jayne Belnap	
15	Carbon Budgets of Biological Soil Crusts at Micro-, Meso-, and Global Scales . . . . .	287
	Leopoldo G. Sancho, Jayne Belnap, Claudia Colesie, Jose Raggio, and Bettina Weber	
16	Biological Soil Crusts as Soil Stabilizers . . . . .	305
	Jayne Belnap and Burkhard Büdel	
17	The Role of Biocrusts in Arid Land Hydrology . . . . .	321
	Sonia Chamizo, Jayne Belnap, David J. Eldridge, Yolanda Cantón, and Oumarou Malam Issa	
18	Physiology of Photosynthetic Organisms Within Biological Soil Crusts: Their Adaptation, Flexibility, and Plasticity . . . . .	347
	T.G. Allan Green and Michael C.F. Proctor	

### Part IV Interactions Between Biological Soil Crusts and Vascular Plants

19	Interactions of Biological Soil Crusts with Vascular Plants . . . . .	385
	Yuanming Zhang, Asa L. Aradottir, Marcelo Serpe, and Bertrand Boeken	

20	Biological Soil Crusts as a Model System in Ecology . . . . .	407
	Fernando T. Maestre, Matthew A. Bowker, David J. Eldridge, Jordi Cortina, Roberto Lázaro, Antonio Gallardo, Manuel Delgado-Baquerizo, Miguel Berdugo, Andrea P. Castillo-Monroy, and Enrique Valencia	
Part V Threats to Biological Soil Crusts		
21	Effects of Local-Scale Disturbance on Biocrusts . . . . .	429
	Eli Zaady, David J. Eldridge, and Matthew A. Bowker	
22	Biocrusts in the Context of Global Change . . . . .	451
	Sasha C. Reed, Fernando T. Maestre, Raúl Ochoa-Hueso, Cheryl R. Kuske, Anthony Darrouzet-Nardi, Mel Oliver, Brian Darby, Leopoldo G. Sancho, Robert L. Sinsabaugh, and Jayne Belnap	
Part VI Natural and Enhanced Recovery and Management		
23	Natural Recovery of Biological Soil Crusts After Disturbance . . . .	479
	Bettina Weber, Matt Bowker, Yuanming Zhang, and Jayne Belnap	
24	Enhanced Recovery of Biological Soil Crusts After Disturbance . . .	499
	Yunge Zhao, Matthew A. Bowker, Yuanming Zhang, and Eli Zaady	
Part VII Future Research on Biological Soil Crusts		
25	Synthesis on Biological Soil Crust Research . . . . .	527
	Bettina Weber, Jayne Belnap, and Burkhard Büdel	
	Taxonomic Index . . . . .	535
	Subject Index . . . . .	543

# Part I

## Introduction

# Chapter 1

## Biological Soil Crusts as an Organizing Principle in Drylands

Jayne Belnap, Bettina Weber, and Burkhard Büdel

### 1.1 Introduction

Biological soil crusts, including hypoliths (hereafter referred to as biocrusts), consist of microscopic (cyanobacteria, algae, fungi, and bacteria) and macroscopic (lichens, mosses, and microarthropods) poikilohydric organisms that occur on or within the top few centimeters of the soil surface. In regions where water availability limits vascular plant cover, these communities are especially notable, creating an almost continuous living skin that mediates most inputs, transfers, and losses across the soil surface boundary (Fig. 1.1). As these dryland regions constitute up to 40 % of the Earth's terrestrial surface, biocrusts are a major feature of Earth's surface (Fig. 1.2).

Taken together, the various biocrust types form one of the dominant community types on Earth. Despite this, their study has begun only very recently (Chap. 2 by Lange and Belnap). In addition to being among the most dominant community types, organisms similar to biocrust microbes are some of the earliest known terrestrial life-forms, with a possible appearance in the fossil record as early as 2.6 billion years ago (see Chap. 3 by Beraldi-Campesi and Retallack).

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Fig. 1.1 A schematic diagram showing the many ecosystem processes affected by the presence of biocrusts

Cyanobacteria and algae (see Chap. 4 by Büdel et al.), bacteria, and microfungi (see Chap. 5 by Maier et al.) generally create the basic matrix of the biocrust, facilitating the colonization of bryophytes (see Chap. 6 by Seppelt et al.), lichens (Chap. 7 by Rosentreter et al.), and microfauna (see Chap. 8 by Darby and Neher).

At the global and regional scale, the composition and biomass of a given biocrust community depend mostly on climate: at the dry end of the potential evapotranspiration (PET) spectrum, biocrusts are dominated by a low biomass of cyanobacteria, bacteria, and microfungi, with no mosses or lichens present (see Chap. 10 by Bowker et al.). As PET decreases, cyanobacterial biomass increases and bryophytes and lichens appear. Whereas biocrusts are often classified by the type of photoautotrophs present and dominant (see Chap. 9 by Colesie et al.), bacteria, fungi, and micro-invertebrates are also very important components (see Chaps. 5 and 8). However, little is known about how the biomass, species composition, or ecological roles of these organisms change under different environmental conditions. Green algae are also present in biocrusts, but apparently of lower biomass, except in some settings (Chap. 4). Hypoliths dot desert soil surfaces and are colonized by a unique community of microbes, mosses, and lichens (see Chap. 11 by Pointing).

At the local scale, factors other than climate control the type of biocrusts present. Soils are extremely important, as biocrusts prefer soils derived from some parent materials over others, due to their nutrient content or soil texture (Chap. 10). Life at the soil surface in dryland regions exposes biocrusts to various abiotic stresses, including high temperatures, UV, salinity, pH, and low moisture, and thus micro-environments, such as shrub canopies, can also determine the type of biocrust present, as they can moderate these factors (see Chap. 19 by Zhang et al.). However, biocrusts are highly vulnerable to physical disturbance and alteration in climatic conditions, and severe disturbance will alter their species composition or cover, often setting them back to an early successional stage (see Chaps. 21 and 22 by

Fig. 1.2 Drylands of the Earth. Drylands cover ~40 % of the terrestrial land surface

Zaady et al. and Reed et al., respectively). Natural recovery from disturbance is often very slow; thus, techniques for enhancing this recovery are being explored and developed (see Chaps. 23 and 24 by Weber et al. and Zhao et al., respectively). Unfortunately, we have little information on long-term dynamics of recovering communities, either through natural or assisted processes (Chap. 25 by Weber et al.). Remote sensing offers an important tool to gain more detailed knowledge about recovery in the future (see Chap. 12 by Weber and Hill).

As studies on biocrusts continue, there is an ever-increasing understanding of the central role they play in the structure and function of dryland ecosystems. These organisms, such as cyanobacteria and lichens, enhance the weathering of soil from rock, and biocrusts stabilize the resultant soil particles and structure soils by creating soil aggregates (see Chaps. 13 and 16 by Garcia-Pichel et al. and Belnap and Büdel, respectively; Chap. 9). Because biocrusts often determine soil structure and the morphology of the soil surface, they influence hydrologic cycles (see Chap. 17 by Chamizo et al.) and the capture and retention of resources such as soil, organic matter, seeds, and nutrient-rich dust (Chaps. 16 and 19). Biocrusts further enhance soil fertility by fixing atmospheric carbon (C; see Chaps. 15 and 18 by Sancho et al. and Green and Proctor, respectively) and nitrogen (N; see Chap. 14 by Barger et al.) and secreting it to underlying soils, and these contributions appear to be globally significant (Elbert et al. 2012). Biocrusts may also alter the bioavailability of other nutrients such as phosphorus (P; Chap. 19). Combined, the presence of biocrusts enhances soil fertility at the surface relative to underlying or uncrusted soils, as documented in many studies [reviewed in Belnap et al. (2003)]. Because

biocrusts enhance soil fertility and influence local hydrologic cycles, studies show their presence affects the timing and spatial location of the germination and establishment of vascular plants, as well as their nutrition (Chap. 19). Indeed, there are indications that fungi in the biocrust layer create a direct nutrient and C link between biocrusts and vascular plants (Chap. 19). Because of their small size, ease of manipulation, multiple species composition, and multifunctionality, these communities are also now successfully being used as models to test basic ecology theory (see Chap. 20 by Maestre et al.).

## 1.2 Biocrusts as an Organizing Principle, and the Critical Zone, in Deserts

The critical zone concept is becoming commonly used by ecologists and others to explore the defining aspects of a given ecosystem. It is described as the “heterogeneous, near surface environment in which complex interactions involving rock, soil, water, air, and living organisms regulate the natural habitat and determine the availability of life-sustaining resources” (US National Research Council 2001). For mesic regions, this zone is generally measured in multiple meters above and below the soil surface, given the relatively tall plants and deep roots. In drylands, however, the situation is very different. Vegetation is generally sparse and short, with mostly shallow roots, and there is often a large amount of exposed bedrock. Given the criticality of biocrusts in these lands, as well as on Earth’s early land surface before the advent of vascular plants, we and others suggest the critical zone in drylands is now and, for most of Earth’s living history, at, on, or in the top few centimeters of rock or soil surfaces: that is, the zone characterized by the presence of biocrusts, endoliths, and hypoliths, not vascular plant roots (Pointing and Belnap 2012). This view is justified by the central role (discussed above and throughout this volume) that these surface layers play in most ecosystem processes in these landscapes, including (1) mediating almost all inputs and outputs (gases, nutrients, water) to and from the strata above and below the surface; (2) being the zone of high nutrient deposition, transformation, and availability; (3) structuring temporal, spatial, and compositional aspects of the vascular plant community; and (4) facilitating the direct delivery of C, nutrients, and water by biocrusts from the soil interspace to nearby vascular plants. Because of the centrality of biocrusts in these processes, we suggest that they are an organizing principle in dryland ecosystems.

The consideration of biocrusts as an organizing principle in drylands fundamentally alters how we view many ecosystem processes in these landscapes. Traditionally, the scientific community has allocated this structuring role almost exclusively to the more visible aspects of an ecosystem: vascular plants and the larger animals. However, as we will show throughout this volume, there is every reason to question this basic assumption, especially in drylands, and instead begin a careful consideration of the essential organizing role biocrusts can play.

### 1.3 Under-Examined Roles of Biocrusts in Dryland Ecosystems

There are many ways, which have yet to be fully examined, that biocrusts may influence structure and function of dryland ecosystems. Below, we present tantalizing evidence for several of these ideas, although there are certainly many more to be studied.

#### 1.3.1 Islands of Fertility or Oceans of Depletion?

It has long been believed that dryland plants, especially shrubs, create fertile zones around their stems by capturing wind- and waterborne sediments, as well as mining surrounding soils with their roots and then depositing these nutrients via leaf drop, at their base. This results in nutrient levels often being higher under plant canopies than in the interspaces between the plants. On the other hand, it is well known that biocrusts contribute to soil fertility and that undisturbed biocrusts contribute to, and better sustain, fertility than disturbed ones (or bare soil). Biocrusts do this by enhancing soil stability (Chap. 16), by adding newly fixed atmospheric C and N to underlying soils (Chaps. 14, 15, and 18), and by harboring greater microbial and microfaunal populations (Chap. 8, Housman et al. 2007), thus likely increasing nutrient availability via higher decomposition rates. Combining these two sets of observations indicates the possibility of another story: that before wide-scale and high levels of utilization by human-associated activities, especially livestock grazing, well-developed biocrusts occurring in the plant interspace kept soil nutrients levels more or less equal to those under the shrubs. This has been observed in multiple studies comparing grazed and ungrazed areas [reviewed in Allington and Valone (2014); Belnap unpublished data] and the movement of large amounts of sediment, with associated nutrients, after livestock introduction into the Western United States has been documented (Neff et al. 2008). Therefore, human use may have converted much of these landscapes from fairly homogenous, relatively nutrient-rich “mainlands” into the situation found today: that is, generally characterized by highly heterogenous fertility islands surrounded by a sea of depleted soils.

#### 1.3.2 Biocrusts as the Transformative Zone

Dust inputs can substantially increase the fertility of the soil surface, relative to underlying soils, in drylands (Reynolds et al. 2001). In addition, the surface zone of most dryland soils contains the highest levels of N, P, C, and other nutrients compared to underlying soils, due to biocrust (e.g., N and C fixation) and vascular



plant activity (e.g., leaf drop; Belnap et al. 2003). Most rainfall events in deserts are very small: for example, on the Colorado Plateau in Utah, USA, ~70 % of rainfall events are < 5 mm and only 13 % exceed 10 mm (Bowling et al. 2011), and because the proportion of small events increases with aridity (Golluscio et al. 1998), many deserts see almost nothing but small events. Therefore, infiltration of most precipitation events in drylands is limited to the top few centimeters of soils, implying that water-driven input and transformative processes are activated almost exclusively in the biocrusts and far less frequently at depth. Thus, the dominant microbially driven nutrient transformations are decoupled in time and space from vascular plant production (Austin et al. 2004; Schwinning and Sala 2004; Collins et al. 2014). When large rain events do occur, nutrients at the surface are then available to be washed downwards into the plant root zone, especially as biocrusts most often enhance infiltration, at least at the hillslope scale (Chap. 17). Thus, the way in which the species composition of a biocrust influences the spatial and temporal aspects of nutrient input, transformation, and bioavailability may be critical in a more complex way than previously envisioned.

Another phenomenon concerning biocrusts and soil fertility is the mechanism by which the immobile lichens and bryophytes that lack roots obtain P from underlying soils. Phosphorus is an essential macronutrient, and relatively high levels are needed for organismal growth and function (e.g., for ATP production). However, most dryland soils are low in P and that which is present is often bound by carbonates or other elements, making it bio-unavailable. It is not known how lichens and bryophytes access sufficient P once they deplete the soils directly in contact with their tissue. Dust would provide some of this needed P, but is unlikely to provide sufficient amounts on an annual basis (Reynolds et al. 2001). Recent studies show that free-living fungi are likely conduits moving N from interspace soils to plants through the biocrusts in exchange for C from the plant (e.g., Green et al. 2008). Mycorrhizae are well known to deliver P to plants, likely in exchange for plant-derived C. It is well known that lichens secrete copious amounts of the C and N that they fix from atmospheric gases [reviewed in Belnap et al. (2003)]; this has always been somewhat mystifying, as these processes are expensive. This raises the intriguing possibility that either fungi may be delivering P to lichens and bryophytes in exchange for the secreted C (and N) or perhaps the fungi are secreting factors such as phosphatase, to make the P bioavailable to the lichen or bryophyte.

### 1.3.3 Biocrusts Structuring Vascular Plant Communities

Researchers have long observed that invasive plants, whose seeds have large appendages, are often prevented from germinating on a moss–lichen biocrust. A few recent studies have indicated that this may not only apply to invasive plants but to native plants as well (Chap. 19). These studies indicate that whereas all plant species in a given community can establish on bare soils, a few species, all with large appendaged seeds, are absent in soil seed banks and plant communities

covered with cyanobacteria. When soils are covered with lichens and/or bryophytes, many more species, all with large appendaged seeds, are missing from the seed bank and plant community. Thus, the species composition of biocrusts may have a profound impact on the structure of the associated vascular plant community. As biocrusts are often disturbed, there are still many places at the landscape scale where all species can establish, maintaining the larger species pool. The relationship between seed morphology and biocrust composition may set up an interesting spatial and temporal tension between the recovery of disturbed biocrusts that act to screen out more and more species as mosses and lichens colonize and the disturbance of biocrusts that creates bare soil patches where all species can establish. This hypothesis needs to be tested across many more deserts and vascular plant communities to establish how widespread and important this process is in determining the structure and function of dryland plant communities.

### 1.3.4 Biocrusts Creating Biodiversity Hotspots in Drylands

Biocrusts can significantly increase biodiversity for some ecosystems and can be especially important for biodiversity in regions where the numbers of vascular plants are low. This fact has been exemplified many decades ago with the lichen coefficient (Mattick 1953), i.e., the quotient of the number of lichens and vascular plants, which increases from tropical and temperate toward polar regions. But also in some drylands, as the Great Basin Desert, there are relatively few vascular plants, but a rich flora of lichens and mosses. In Idaho, USA, surveys of several different vegetation types show that biocrusts contribute significantly to biodiversity. In a *Chrysothamnus nauseosus*–*Poa sandbergii* community, there were 39 perennial species of nonvascular organisms (31 lichens, 6 mosses, and 2 liverworts), whereas there were only six perennial vascular plant species (Rosentreter 1984). At Orchard Training Grounds in Idaho, USA, the *Artemisia* community had 53 nonvascular biocrust species compared to only six vascular plant species; *Atriplex* community, 23 vs. 5 species; *Chrysothamnus nauseosus* community, 25 vs. 9 species; *Ceratoides lanata* community, 17 vs. 4 species; and *Poa sandbergii*, 25 vs. 4 species (R. Rosentreter, unpublished report, with herbarium vouchers of all the nonvascular biocrust species). In the Colorado Plateau Desert, UT, gypsiferous soils generally support less than five perennial vascular plant species, whereas there are up to 28 lichen and moss species (Bowker and Belnap 2008). Similarly, *Coleogyne ramosissima* communities in this region generally support only shrub and several forb and grass species, whereas there can be up to nine lichen and five moss species (Belnap et al. 2006). In these situations, the presence of well-developed biocrusts may convert biodiversity “cold spots,” based on the number of vascular plants, into biodiversity “hotspots” when biocrust species are included. Also, as we gain more information on lichen and moss species found in biocrusts from understudied regions, this phenomenon may become evermore commonly observed.

Lichens and mosses also significantly contribute to biodiversity in more northern latitudes, even though vascular plant numbers are high relative to drylands. For example, in Spitsbergen, Norway, 184 vascular plants and 1158 species of lichens and bryophytes, most of which were associated with biocrusts, were recorded at one site (Dahlberg et al. 2013). In Greenland, ~450 vascular plants and 1708 species of lichens and bryophytes were recorded; again, most of the lichens and mosses were biocrust species (Daniëls et al. 2013). It is not known if the increased biodiversity conferred by biocrust species results in greater resistance and resilience to disturbance, as has been posited for vascular plant communities (Naeem et al. 2000; Isbell et al. 2015), but this would be worthy of investigation.

### 1.3.5 Challenging the Definition of Lichen Individuals and the Boundary Between Being Heterotrophic and Autotrophic

It is generally believed that most lichen thalli in dryland regions represent individual, slow-growing organisms. However, there have been a handful of studies indicating this may not always be the case. First, a long-term study of lichen dynamics by Belnap et al. (2006) showed that cover values were very dynamic in the short and long term, with cover values changing by up to 10 % from fall to spring (increasing) and spring to fall (declining). Second, recovery from trampling disturbance is not always slow; it depends on the conditions during and following the disturbance (Chap. 23). For instance, several studies in both hot and cool deserts have shown that when biocrust material is removed from a surface, rather than trampled in place, recovery time is much slower (Belnap unpublished data; Chap. 21). Recovery from fires can be rapid in some sites, if fire intensity is low (Bowker et al. 2004, unpublished data).

These observations could be explained by the hypothesis that lichens, rather than being individuals, are connected by a common fungal mat, similar to many mushrooms. Thus, when conditions are unfavorable, the phycobionts of the lichen could sink down into the mat, becoming heterotrophic, and, when conditions become favorable, reform on the surface as phototrophs. Green algae and cyanobacteria are both capable of heterotrophic growth. Many studies have been done on heterotrophic cyanobacteria (e.g., Olson et al. 1999), although most have used marine species. However, Khoja (1973) found that 18 of 24 species tested were able to grow heterotrophically, and 13 of these were cultured from soil. Additionally, Yaeger et al. (unpublished data) found live *Nostoc commune* at 30-cm soil depth from the Colorado Plateau, Utah, USA, and Garcia-Pichel and Belnap (2003) found chlorophyll *a* at 30-cm depth. Far fewer studies have been done on green algae, but some of those tested can grow heterotrophically (e.g., Day and Tsavalos 1996; Ueno et al. 2005; Perez-Garcia et al. 2011). We also know that fungal threads (rhizines) can connect thalli and lichen prothalli (Letrouit-Galinou and Asta 1994).

The presence of a fungal mat connecting what has been considered individual lichen thalli would explain both the rapid appearance and disappearance of lichen thalli seen by Belnap et al. (2006) and the observation that under disturbance circumstances that leave fungal material in place (e.g., trampling, rapidly passing fire), recovery is much faster than when the fungal mat is removed.

## 1.4 Can Biocrusts Be Used as a Vital Sign of Ecosystem Health?

As discussed above and throughout this book, biocrusts influence many aspects of the ecosystems in which they occur. Therefore, they may be good bioindicators of the health of an ecosystem or of a specific ecosystem process. For instance, soil health is critical in sustaining ecosystem function. Because biocrusts influence so many aspects of soils, it may be that evaluation of their cover and composition can be used as an index of soil health, rather than requiring all the different aspects of soil health to be measured separately (Rosentreter and Eldridge 2003). Another example is that, as they are very responsive to temperature and water regimes, they may be excellent indicators of climate changes, regardless of the biocrust type being evaluated. As we are now developing ways to accurately assess biocrust cover and composition using remote sensing techniques (Chap. 12), development of such indices may give us the ability to easily monitor soil/ecosystem health and response to climate change at the regional scale.

## 1.5 Conclusion

As research into biocrusts continues, it is becoming increasingly evident that they perform such important functions in dryland settings that they are likely the critical zone in these settings. Biocrusts modify both the physical and biological environment, thus influencing soil stability, fertility, and hydrology. These changes to the environment then ramify throughout the ecosystem, affecting vascular plants and animals. As research continues on these communities, evermore exciting questions will continue to be raised. In addition, the answering of these questions will likely make it even more clear how central these communities are to the healthy and sustainable function of dryland ecosystems.

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# Chapter 2

## How Biological Soil Crusts Became Recognized as a Functional Unit: A Selective History

Otto L. Lange and Jayne Belnap

### 2.1 Introduction

It is surprising that despite the worldwide distribution and general importance of biological soil crusts (hereafter referred to as biocrusts), scientific recognition and functional analysis of these communities are a relatively young field of science. In this chapter, we sketch the historical lines that led to the recognition of biocrusts as a community with important ecosystem functions. For earlier treatments of relevant aspects of biocrust history, see Friedman and Galun (1974), Cameron and Blank (1966), and Belnap and Lange (2003).

Biocrusts have had multiple names through time. The term “cryptogamic crust” was first coined by Harper (Kleiner and Harper 1972). At that time, there were only two kingdoms, plants and animals, and the dominant organisms in the crust were all classified as nonflowering plants, or cryptogams. However, later taxonomic changes resulted in cyanobacteria and fungi, including lichens, being placed in different kingdoms. As a result, the name “cryptogamic crust” was no longer accurate, and other names were suggested, including microbial crusts (Loope and Gifford 1972), microphytic crusts (West 1990), microbiotic and cryptobiotic crusts (Belnap 1993), and finally, biological soil crusts (e.g., Lange et al. 1992; Belnap and Lange 2001). The name “biological soil crusts” or “biocrusts” has now become universally accepted, as it is taxonomically correct and inclusive of all organisms in the biocrusts, including microfauna. In addition, it clearly separates biological

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crusts from physical or chemical crusts, which is an important distinction, as biocrusts have very different influences on ecosystem properties than other crust types.

## 2.2 Two Lines that Lead to the Recognition of Biocrusts

The idea of biocrusts as a functional ecological community has come from two main scientific branches: botany and soil science. Botanists have long recognized that multiple organisms colonize the soil surface in the open and often dry areas occurring between vascular plants. Later, after the initial taxonomic and phytosociological descriptions were made, soil scientists and agronomists observed that these surface organisms interacted with soils in ways that changed the soil structure. Below, we trace these two lines from the distant past until 1990, when biocrusts became well-known to scientists and the public, at least in some parts of the world.

### 2.2.1 The Floristic, Botanic Approach

#### 2.2.1.1 Lichens

Many lichens common to biocrusts worldwide were among those first described for scientific purposes, including *Psora decipiens*, *Toninia sedifolia*, and *Squamarina lentigera*. In most cases, these species were collected from European dryland habitats where they were found growing on top of the soil. Smith and Sowerby (1803) described *Lichen caeruleonigricans*, the “Black and Blue Lichen” (now *Toninia sedifolia*) (Fig. 2.1), as a lichen that “grows on the ground ... and consists of long branched tufted spongy roots, bearing tufted roundish clustered leaves”. Stahl, in 1877, depicted the long multibranched rhizinae of *Endocarpon pusillum* (Fig. 2.2). This biocrust lichen became an important milestone for lichenology when he performed the first laboratory synthesis of a green algal lichen with this species.

In the nineteenth century, there was the general impression that arid habitats were very poor in lichens (von Humboldt 1859; Zukal 1896), despite many early reports of desert soil lichens either from early explorers or specialized lichenologists. For example, Carl Per Thunberg (who named many South African plants) collected *Psora decipiens* in 1774 (see Doidge 1950), which he published as *Lichen incarnatus* (Thunberg 1823). Other early publications of soil crust lichens from desert and semidesert regions include Nylander (1878) and Steiner (1895) from the Sahara, Fink (1909) from Arizona, Tuckerman (1882, 1888) from North America, and Müller (1880) from Egypt.

The steppes, semideserts, and deserts of south Russia, with their rich soil lichen floras, appear to be one of the first areas to attract extensive studies of ground



Fig. 2.1 “Black and Blue Lichen”, *Toninia sedifolia* [After Smith and Sowerby (1803)]

surface lichens. Peter Simon Pallas (1741–1811), a noted naturalist-explorer who traveled in service of Catherine II of Russia to explore the central Russian provinces, was possibly the first scientist to describe extensive soil lichen covers in the semiarid steppe formation of Kazakhstan (Pallas 1776). He reported that the loamy soil surface was covered by a whitish-gray crust (German “Rinde”) of “Lichen tartareum, tinctorium, candidum, tuberculis, atris Dillenius”, most probably a *Diploschistes* sp. He also observed the crust broke into pieces when dry and was growing together with *Tremella terrestris*, a *Collema* sp. These lichens formed a terrestrial community which, without a doubt, we would call a biocrust today. Much later, Tomin (1926) presented possibly the first key for 36 terrestrial lichen species found in the semideserts of southeast Russia. Most of these species had been collected by Keller (1930), who described several types of communities that we today call biocrusts. Keller also published photographs from this site, which was near Pallas’ site of 154 years earlier (Fig. 2.3), listing 44 soil lichen species or varieties (e.g., *Collema* sp., *Fulgensia fulgens*, *Psora decipiens*, *Squamarina lentigera*, *Toninia caeruleonigricans*, and *Diploschistes scruposus* var. *terrestris*, which probably is *Diploschistes muscorum* or *Diploschistes diacapsis*. His list also included cyanobacteria (*Microcoleus vaginatus*, *Scytonema ocellatum*, *Nostoc commune*) and a moss (*Tortula ruralis*). Keller mentions that growth of these

Fig. 2.2 *Endocarpon pusillum* [After Stahl (1877)]

organisms was supported by a dense layer of soil (“dicke Schicht”); however, he did not recognize that the organisms themselves were creating this dense layer. Thus, despite having described a true biocrust, Keller thought of this layer as the prerequisite to, rather than the result of, biological activity.

The common coexistence of a group of conspicuous and variously colored terrestrial lichens that included *Psora decipiens*, *Toninia sedifolia*, *Fulgensia* sp., and *Diploschistes* sp., together with *Cladonia* and *Collema* sp. on dry calcareous or gypsum soils, was also recognized early by lichenologists throughout Europe, including Arnold (1868–1897), Tirol; Kaiser (1926) and Gams (1938), Central Germany; and Du Rietz (1925), South Norway. After Braun-Blanquet (1928) had stimulated phytosociological classification of plant communities, lichenologists began defining lichen communities, and the grouping above was named “Bunte Erdflechten-Gesellschaft” (i.e., the “colored lichen community”; Reimers 1940, 1950). It is significant that this was one of the very first lichen communities to receive extensive study. For Central Europe, Klement (1955) proposed a general syn-taxonomy of the different types of lichen communities colonizing open soil mainly within local subarid steppe formations within the two main unions of “Toninion coeruleonigricantis” and “Diploschistion terrestris.” These lichen communities were often interpreted by him and by others as relicts from late and postglacial times. There continued to be a rich literature in which these or similar lichen communities were described throughout the world [e.g., Europe, Pause (1997); Australia, Rogers (1972); Israel, Galun (1963); Mongolia, Schubert and

Fig. 2.3 Soil vegetation of the lower Ural and Volga Rivers' area [After Keller (1930)]. Dominating "*Diploschistes scruposus* var. *terrestris*" (probably *Diploschistes muscorum* or *Diploschistes diacapsis*)

Klement (1971); Mesopotamia, Schubert (1973)]. Looman (1964) found a striking similarity between the soil lichen communities of the Great Plains in North America and Central Europe with 16 individual species in common.

### 2.2.1.2 Bryophytes

Similar to lichens, many bryophyte species typically found in biocrusts were taxonomically described in the eighteenth and nineteenth centuries. Several species were included in Linné's *Systema Vegetabilium* (1774), and there are several old reports of bryophytes from dry areas around the world. Examples include the *Conspectus Bryophytorum Orientalum et Arabicorum* by Frey and Kürschner (1991) and Griffith (1849) for Afghanistan, Geheeb (1902) for Syria, and Lorentz (1867) for Egypt and Sinai. Joseph Dalton Hooker collected four Antarctic moss species in 1843–1847 when he participated in James Clark Ross' expedition (Wilson and Hooker 1847), and Skottsberg (1905) was the first to describe moss-dominated tundra of the maritime Antarctic Peninsula.

By the first half of the twentieth century, there were many descriptions and vegetation analyses of habitats with coexisting soil lichens and bryophytes that today would be called biocrusts. In Europe, for example, this includes open patches in local steppe formations where the ground cover was described as communities of “colored soil lichens” growing together with mosses and liverworts on lime or gypsum soil (Du Rietz 1925; Kaiser 1930; Stodiek 1937; Reimers 1940; Bornkamm 1958; Marstaller 1971). There are even phytosociological units defined and named in which bryophytes and lichens are combined, as for instance the “*Caloplaca fulgens*–*Tortella inclinata sinusia*” (Zólyomi 1987). In the last decades, our knowledge of bryophytes of arid areas, including their distribution, sociology, and ecology, has considerably improved [e.g., Afghanistan (Frey and Kürschner 2009), Jordan (Frey and Kürschner 1995), and Saudi-Arabia (Frey and Kürschner 1987)]. In the Judean Desert, Frey et al. (1990) and Frey and Kürschner (1990) observed the close connection between bryophyte communities and the colored lichen communities; they also describe cyanobacteria in the loess soil.

Despite the very early taxonomic description of moss and liverwort communities on dry ground, the older literature does not mention these communities as being part of what we today call a biocrust community. There was also no demonstration or observation of these communities consolidating or protecting the soil surface. This may be because in many hot and temperate arid regions, bryophytes, mosses, and liverworts are generally sparse or even absent, whereas cyanobacteria and lichens conspicuously dominate the biocrusts. According to Scott (1982) and many other authors, the earliest stages of biocrust formation in drylands is the stabilization of the soil surface by filamentous cyanobacteria, followed by colonization of lichens and bryophytes. In contrast, cold-polar area biocrusts are often dominated by mosses that can even create continuous carpets. Temporarily wet areas in the continental Antarctic are typically covered by bryophyte flushes, as described by Rudolph (1963) for Cape Hallett in Victoria Land.

### 2.2.1.3 Cyanobacteria and Green Algae

Ehrenberg (1854) was one of the first to extensively analyze and depict microorganisms in different kinds of soil, and he identified many types of algae. At that time, the term “algae” included both blue–green (cyanobacteria) and green algae. The differentiation between these groups occurred early in the nineteenth century. In 1874, Sachs coined the term “Cyanophyceae” for blue–green algae, and in 1977, Stanier and Cohen-Bazire proposed the term “cyanobacteria” to be used to differentiate between these prokaryote organisms and the eukaryotic green algae. Despite the early separation of these two groups, older studies continued to refer to them collectively as “algae.” Whereas most later studies separate them, phycologists still accept the term “algae” when referring to both groups. Therefore, in our discussion below, we use the terms algae, green algae, blue–green algae, or cyanobacteria, depending on the term used in the study being cited.

The terrestrial species of the genus *Nostoc*, typically occurring in most biocrust communities worldwide, were most likely the first cyanobacteria to attract the interest of plant scientists, as well as the public. During the times of Paracelsus (1493–1541), a heavenly, divine, or devilish origin was ascribed to the frightening gelatinous “Nostoch” colonies that suddenly appeared on the surface of wet soil. These colonies were used for medical purposes (Schmid 1951, see monograph by Mollenhauer 1985–1986). More than 280 years ago, the Italian botanist Micheli depicted a *Nostoc* thallus (Fig. 2.4): “*Linckia terrestris*, gelatinosa, membranacea, vulgatissima, ex pallida et virescente fulva” in his 1729 publication. No one less than Johann Wolfgang von Goethe (1892) provided an early description of *Nostoc* growing on soil (see Schmid 1942). He reported in a handwritten journal entry that in 1785 he had found a large amount of gelatinous lobes (“gallertartige Läppchen”) on the ground in a sandy place after rain. He kept the material in water, and with a magnifying glass he recognized rows of spheres (“Reihen von Kugeln”), which he compared with Micheli’s *Linckia*. Common English names show the anxiety of people about these strange *Nostoc* colonies on soil, calling them fairies’ or witches’ butter, star-slime, star jelly, fallen stars, or will-o’-the-wisp. In Goethe’s tragedy *Faust II* (line 11741/42), Mephistopheles alludes to the captured will-o’-the-wisp (“Irrlicht”) as “disgusting gelatinous dirt” (“ekler Gallert-Quark”). Linné (“*Systema Vegetabilium*”, 1774) used the name *Tremella Nostoc* within his group “*Cryptogamia Algae*,” and Vaucher (1803) finally defined the genus name *Nostoc*. One hundred years after Micheli, a painting by Turpin (1838) depicts a *Nostoc* colony (Fig. 2.5).

In the article “On a substance known as ‘Australian Caoutchouc’”, Thiselton Dyer (1872) reports a strange material resembling elastic bitumen that was found on the ground of an open, sandy place in South Australia. It was thought to be the “mineral” coorongite or gamboge, a petroleum or asphalt-type product, some kind of gum, or a plant secretion of some type. However, microscopic analysis showed diatoms as well as cellular structures that were most probably derived from drying gelatinous algae, all intermingled with sand grains (see Fritsch 1907). Thus, this

Fig. 2.4 “*Linckia terrestris*, *gelatinosa*, etc.”, *Nostoc* species [After Micheli (1729)]

would be an early recognition of a cyanobacterial soil crust according to our present terminology. Takyr soils were described for deserts and semideserts of Central Asia (Bolyshhev and Yevdokimova 1944; Bolyshhev 1952). These are formed in flat depressions which are filled with water during heavy rain and dry out during summer. These are often covered and consolidated by soil algae, mainly filamentous cyanobacteria.

There are many reports in the first half of the twentieth century regarding the diversity, life history, and habitat conditions of algae in different soils and locations. These include North America (e.g., Collins 1909; Martin 1939), England (Bristol Roach 1927), Australia (Phillipson 1935), the Sahara (Killian and Fehér 1939), the Negev (Friedmann et al. 1967), and many others. There is a general and extensive treatment “Soil Algae” (in Russian) by Gollerbakh and Shtina (1969), in which more than 800 relevant publications are cited (see also Cameron 1974).

### 2.2.2 The Soil/Agronomy Scientific Approach

The presence of naturally occurring, nonbiological soil crusts has long been observed by soil scientists and others. In the 1820s in interior Australia, the occurrence of “hard bare soils along the Murrumbidgee River” was documented

Fig. 2.5 *Nostoc thermalis* [After Turpin (1838)]

by Charles Sturt, an explorer [cited in Chartres (1992)]. Studies of these hardened surfaces in semiarid and arid landscapes began in earnest during the 1900s, and it was determined they were mostly physical and/or chemical crusts. Physical crusts are formed by the disruption of soil aggregates by raindrop or compressional forces (e.g., hoof action). When water pools on the soil surface, the fine soil particles are suspended and upon drying, adhere together to form a hard physical crust. Chemical crusts are formed by the deposition of salts or other compounds on the soil surface when soils dry (e.g., Blanck et al. 1926; Schiff and Yoder 1941). Both physical and chemical crusts increase runoff and erosion (Dudley and Kelly 1939). Early in the study of physical and chemical crusts, some soil scientists noted that algae often grew on top of, inside of, or in place of these nonbiological crusts (e.g., Booth 1941; Fletcher and Martin 1948). These authors noted that after rains, soil surfaces often turn green, which alerted them to the presence of the algae. Fletcher and Martin also observed that if one picked up a piece of these crusts (Fig. 2.6), the soil held together and the underside of “these algae-impregnated crusts had a fuzzy appearance with sand grains adhering to what proved to be fungus mycelium”. Both Booth (1941) and Fletcher and Martin (1948) went on to test how the presence of the algae affected local hydrology, and Fletcher and Martin also measured their influence on soil texture, organic matter, and nitrogen. In contrast to physical and chemical crusts, they found the algae decreased runoff and soil erosion and increased the silt,

Fig. 2.6 A piece of rain crust from the soil's surface, Arizona [After Fletcher and Martin ([1948](#))]

clay, carbon, and nitrogen in the soil. This was, therefore, probably the first instance of soil scientists publishing on the presence of algal soil crusts and their influence on ecological processes.

Around the same time as the research into physical and chemical crusts began, agronomists noticed that soil algae could stimulate the growth of vascular plants by increasing soil N (therefore, it was actually cyanobacteria they were investigating). Breazeale ([1929](#)) was one of the first agronomists to intentionally introduce cyanobacteria onto the surface of a crop soil; in this case, he inoculated pots in which Valencia oranges were growing. He found this inoculation increased plant height, plant leaf length, and healthy plant color. Other early work showed the value



of cyanobacteria in stimulating rice production (De 1939) and other crops. Since this time, many studies have been conducted on this topic.

## 2.3 Biological Soil Crusts as a Functional Ecological Unit

Perhaps one of the earliest conceptualizations of the ability of biocrusts to consolidate soil was reported in 1861 by E.F. Klinsmann, a medical doctor. Earlier in this publication, he notes that in 1828, and again at later times, he observed a thick carpet of mixed lichen and algal threads on top and throughout the surface sands of dunes at the Baltic Sea near Gdansk, Poland. His material was sent to F.T. Kützing, who identified the dominant organism as an alga *Stereonema chthonoblastes* A. Br. (Kützing 1849), which was later determined to be a lichen (Kupffer 1924). Its name was changed to *Lecidea uliginosa* var. *chthonoblastes* (A. Braun) Erichsen and then again to *Placynthiella uliginosa* (Schrad.) Coppins & James. However, the description of threads being present in the samples of Klinsmann (1861) makes it likely that cyanobacteria and soil fungi were also present in the material collected. He noted this carpet stabilized blowing sand and facilitated the colonization of other species, starting first with the moss *Ceratodon purpureus* and other lichens and then later followed by vascular plants. The author even discussed the possibility of propagating and spreading this “alga” for dune stabilization, noting it was cheaper than planting grasses which was done at that time.

Subsequent early research showed soil algal growth was an important first step in increasing the fertility and stability of the soils, thus likely enhancing the recolonization of other organisms. One of the first places this was observed was following the volcanic eruption of Mount Krakatoa (Treub 1888), where the disturbed ground was first covered by a layer of blue–green algae before other species colonized the site. Fritsch (1907, 1922) developed an early conceptual model of terrestrial algae and their ecological relevance. He distinguished between subterranean and surface communities, describing the species composition and site morphology for different climatic regimes. His conclusion is very similar to a modern interpretation of algal soil crusts: “The . . . consideration will have shown that the terrestrial Alga possess an equipment which suits it admirably to be a coloniser of inhospitable substrates. Here its small moisture-requirements can probably often be better met than those of any other group of plants. As colonisers these Algae are of importance in three ways: they play a rôle in the erosion of exposed surfaces, by their decay they afford the first available supplies of humus, and especially the more mucilaginous forms afford a moisture-retaining substratum. . . On mobile substrata the filamentous forms are also often of great importance in binding the loose particles together” (Fritsch 1922, p. 232). In later publications (e.g., Fritsch and Haines 1923), the authors conducted field and laboratory experiments to examine the moisture relations of these organisms.

Use of lichens and mosses for sand stabilization was also reported later for several different areas of the world. Possibly one of the first examples of mosses

affecting soil function was noted by Moore (1931), when he observed them, along with lichens, consolidating moving sand on the British Isle of Man (Irish Sea) and preparing the way for the subsequent colonizers. Leach (1931) studied the ability of mosses like *Polytrichum piliferum* and *Polytrichum juniperinum* to act as pioneers on sand habitats in England, analyzing their soil-binding qualities with laboratory experiments. In the USA, Martin and Waksman (1940) showed that soil algae increased soil aggregation and decreased erosion.

In 1955, Vogel provided the decisive insight that the condensed layer at the soil surface, which he observed in South African deserts and which we today call biocrusts, was created by organisms such as lichens and algae. He published what was possibly the first vertical profile of a biocrust, describing it in German as “Bodenkruste” or soil crust (Fig. 2.7). In his illustration, a dust film is shown at the surface, below which lies a layer with *Schizothrix* sp. (cyanobacteria), followed by a layer of fungal hyphae mainly belonging to soil lichens. He provided a description of how these organisms are interwoven with the soil particles, gluing them together into compact layers. The text notes that when broken, fibers with soil particles can be seen dangling from the biocrust pieces. The nitrogen-fixing ability of the soil cyanobacteria is discussed as well. Vogel also posited that these “Bodenkrusten” are of geological importance by preventing soil erosion over the hundreds of square kilometers where he observed them. Thus, with this study, Vogel described 60 years ago most of the important ecological roles we ascribe to biocrusts today.

Studies of the ecological roles of biocrusts began intensifying in the late 1950s and 1960s. For instance, Shields et al. (1957), Tchan (1959), Shields and Durrell (1964), Bond and Harris (1964), Avnimelech and Nevo (1964), Rogers and Lange (1966), Mayland et al. (1966), and Granhall and Henriksson (1969) showed that biocrusts stabilize soils, affect hydrological cycles, and enhance soil nitrogen content. A very early photograph of typical biocrusts from Arizona Upland Desert (Fig. 2.8) was published by R. E. Cameron (1958) in his M.S. thesis. Prompted by finding ways to detect life in extraterrestrial environments, he and others conducted extensive investigations in the distribution and abundance of biocrusts in deserts throughout the world (e.g., Cameron and Blank 1966; Cameron 1969). Cameron and Devaney (1970) also described the successional sequence of soil surface organisms in the Antarctic dry valleys, starting with cyanobacteria and algae, followed by lichens and ending with mosses. Ugolini (1966) observed that initial soil formation exposed after the retreat of an Alaskan glacier occurred under a “mossy crust”. Worley (1973) found three types of “Black Crust” in the Upper Glacier Bay, Alaska, that covered and penetrated into the recently deglaciated soils, observing they protected the soil from erosion. These mats contained the leafy liverwort *Lophozia badensis*, mosses, lichens, and cyanobacteria in differing proportions.

A great deal of work was done on biocrusts in the western USA in the 1970s by scientists working independently or with the International Biome Program. They documented the controls on distribution and many ecological roles of biocrusts, including an influence on nitrogen cycling, soil aggregation, and soil moisture

Fig. 2.7 Profile of the uppermost millimeters of soil crust, Knersvlakte, South Africa [After Vogel (1955)]

Fig. 2.8 Soil algal and lichen crusts, Arizona [After Cameron (1959), by courtesy of University of Arizona]. See also Cameron and Blank (1966)

(e.g., Faust 1971; Kleiner and Harper 1972, 1977; Bailey et al. 1973; Marathe 1972; Loope and Gifford 1972; West and Skujins 1977; Rychert et al. 1978).

The pace of studies increased even more rapidly during the 1980s and early 1990s, especially in Australia, Israel, and the western USA (e.g., Shachak and Steinberger 1980; Graetz and Tongway 1986; Rogers 1989). Research addressed all aspects of the ecological functions of biocrusts, ranging from their contributions to soil fertility, including carbon and nitrogen fixation, their ability to stabilize soils, their response to and recovery from fire and surface disturbance, and their effects on vascular plant establishment and growth. Sufficient research was done to produce at least six review articles within 6 years (Harper and Marble 1988; Dunne 1989;

Isichei 1990; West 1990a, b; Metting 1991; Johansen 1993). These efforts culminated in the first symposium on biocrusts held at the joint American Bryological and Lichenological and Ecological Society of America meetings in San Antonio, Texas, in 1991 (St. Clair and Johansen 1993). This marked a turning point in the acceptance by biologists and ecologists alike of the importance of the biocrust communities in the structure and function of dryland ecosystems. The first compendium volume on biocrust research, "Biological Soil Crusts: Structure, Function and Management," was published in 2001 and reprinted in 2003 (Belnap and Lange 2001, 2003). Since then, there have been two international symposia on Biological Soil Crusts (in Germany and Spain), and the number of researchers involved in this field and the number of papers published have increased exponentially.

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Part II  
Morphology, Composition, and  
Distribution of Biological Soil Crusts at  
Different Scales

# Chapter 3

## Terrestrial Ecosystems in the Precambrian

Hugo Beraldi-Campesi and Gregory J. Retallack

### 3.1 Introduction

Three lines of evidence for ancient life on land are paleosols, microfossils, and MISS (microbially induced sedimentary structures). The three appear in the rock record as old as 3.5–2.7 Ga (Hallbauer and van Warmelo 1974; Rye and Holland 2000; Wacey et al. 2008; Johnson et al. 2010; Noffke et al. 2013). The primitive terrestrial biosphere is plausibly as old as the oldest marine biosphere (Schopf 1983; Schopf and Klein 1992), with both aquatic and terrestrial realms teeming with life 3.5 Ga ago. This result is unsurprising considering the modern ecological capabilities of microbes, which are comparable with fossil analogs and have profound effects in sediments and soils (Belnap and Lange 2001; Navarro-González et al. 2003; Beraldi-Campesi and Garcia-Pichel 2011; Retallack 2012). Functional aquatic and terrestrial ecosystems may be even older than 3.5 Ga, but undisputable biosignatures before that time are ambiguous (Nutman et al. 2010; Papineau et al. 2010), and the timing when life first populated the Earth is still unresolved.

Direct evidence for ancient terrestrial communities comes from the fossil record, and the several limitations of such should be noted. First, it has many temporal gaps, which makes it difficult to appreciate the continuous history of life on Earth (Sadler 1981). Second, not all the rocks have been studied in detail, especially biosignatures preserved in it, so that recent and future discoveries may yield more tangible information about the history of the biosphere (Dutkiewicz et al. 2006). Third, microbial biological diversity of the Precambrian fossil record is

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fundamentally different and more challenging to study than Phanerozoic megafossils (Schopf et al. 2007), which unduly bias orthodox interpretations about the evolution of the biosphere.

## 3.2 Paleosols

The oldest geological unconformity in a sedimentary sequence, which is metamorphically recrystallized in a way that its sedimentary history is almost indecipherable, is ~3.4 Ga old (Fig. 3.1a; Buick et al. 1995). This surface beneath the Strelley Pool Formation has thick (4 m) clayey paleosols (Fig. 3.1b–d), which are deeply weathered, aluminous, and metamorphosed to apophyllite facies, implying high fluid fluxes, secondary mineralization, and an overall alteration after burial (Buick et al. 1995; Hoffman 1995; Ohmoto et al. 2007; Johnson et al. 2009, 2010). Such thick clayey paleosols are very common on basement unconformities of the Archean and Proterozoic record (Table 3.1). Well-developed paleosols as the Neoproterozoic Sheigra paleosol (Fig. 3.1e) are direct records of ancient landscapes, where microbial contribution can be sought. The development of relatively thick paleosols implies stable intracratonic settings where weathering and soil formation prevail and sediment transport is minimal. What stabilized these paleosols to allow such deep chemical weathering could have been life itself, considering evidence of elemental depletions, isotopic composition of carbon, and fossilized structures (Retallack 2001).

The master reaction for weathering in soils is hydrolysis, the incongruent dissolution of feldspars, or other minerals to form clays, by dilute solutions of carbonic acid from dissolution of soil CO<sub>2</sub> in pore waters (Retallack 2001). Such reactions have been demonstrated in many Precambrian paleosols, but could theoretically be created abiotically. However, life has accelerated weathering processes over geological time, and biotic effects are more obvious than abiotic effects. A series of experiments by Neaman et al. (2005) showed that organic ligands are necessary for any significant depletion of phosphorus in modern soils, and such depletions have been demonstrated in paleosols as old as 2.7 Ga (Driese et al. 2011), as well as for geologically younger paleosols (Retallack and Mindszenty 1994; Retallack et al. 2013a, b).

Carbon isotopic composition of biologically produced organic matter is depleted in <sup>13</sup>C ( $\delta^{13}\text{C}_{\text{org}} = -10\text{‰}$  to  $-30\text{‰}$ ), and soil methanogens create extreme depletion ( $\delta^{13}\text{C}_{\text{org}} = -30\text{‰}$  to  $> -90\text{‰}$ ; Schidlowski 2001). Such low values have been reported from Precambrian paleosols as old as 2.7 Ga (Rye and Holland 2000), as well as for geologically younger paleosols (Retallack and Mindszenty 1994; Watanabe et al. 2000; Retallack et al. 2013a, b). Ironically, the carbon content of Precambrian paleosols is very low ( $< 1\text{ wt \%}$ ), about the same as for Phanerozoic paleosols (Tomescu et al. 2009). While low-carbon isotopic compositions reveal microbial primary producers in soils, low-carbon abundance also implies an active decomposition of organics by microbes on the land, which may imply well-

Fig. 3.1 Examples of Precambrian paleosols: (a) One of the oldest paleosols at the 3.42 Ga geological unconformity between the tabletop basalt (basalts dipping to left; white arrow) and Strelley Pool Formation (chert of ridge top; black arrow) 4 miles east of Strelley Pool, Pilbara region, Western Australia (Buick et al. 1995); (b) Another section of the 3.42 Ga paleosol on Double Bar Formation basalts below basal cherty sandstones of the Strelley Pool Formation, Pilbara region, Western Australia (Van Kranendonk 2000; Altinok 2006); (c) Another section of the 3.42 Ga paleosol on Panorama Formation showing felsic tuffs that record ancient volcanism on Steer Ridge, Pilbara region, Western Australia (van Kranendonk 2000; Johnson et al. 2010); (d) A younger 1.8 Ga paleosol with elephant-skin texture (A horizon) above gypsum nodules (arrow-heads) in Stirling Range Sandstone, Barnett Peak, Western Australia (Bengtson et al. 2007);

developed and complex communities, not only of photosynthesizers but heterotrophs as well.

The most common megascopic traces in Precambrian paleosols are irregular subvertical and macroscopic tubular structures, either picked out by drab haloes in red beds (Fig. 3.2a) or preferentially cemented compared with their matrix (Fig. 3.2b, c). These features are formed through pedogenic processes and may be biotically or abiotically mediated. As these macrostructures seem to be embedded within the paleosol profile, it is unlikely that photosynthetic microbes were involved in their formation. Nevertheless, similar alteration features have been observed in modern biocrusts (Retallack 2011). Fungi can also be envisioned as potential candidates for their formation. Examples include the honey mushroom, *Armillaria mellea* (Mihail and Bruhn 2005), or lichen rhizines like those of *Toninia sedifolia* (Poelt and Baumgärtner 1964). The drab-haloed tubular structures are a fossil form called *Prasinema gracile*, best known from Cambrian paleosols (Retallack 2011). The distinctive gray-green haloes of the fine tubules, preserved by burial gleization, are also comparable with drab-haloed root traces in paleosols (Retallack 2001). These tubular structures (Fig. 3.2b) also found analogs among calcareous and siliceous rhizoconcretions in paleosols (Esteban and Klappa 1983). However, unlike root traces in Phanerozoic paleosols, tubular structures in Precambrian paleosols are much smaller and lack several orders of branching and tapering downward.

Paleosols are important pieces of the record of continental evolution because they are widely distributed on all present continents and are represented in the rock record since 3.5 Ga. Most of them contain indirect evidence of biological weathering, biomass accumulation, and potential fossils and ichnofossils (Retallack 2001). Recognizing pedogenic processes is essential for better understanding depositional paleoenvironments and distinguishing those of marine from nonmarine origin. For instance, pedogenic processes recognized in association with Ediacaran fossils, such as *Dickinsonia costata* (Retallack 2013; Fig. 3.2d). Together with the evidence cited below, the long history of paleosols and their likely biotic features attest for well-established, nonmarine, and widespread terrestrial ecosystems by the Paleoproterozoic.

### 3.3 Microfossils

The oldest reported biosignatures occurring in shallow marine to nonmarine strata may be simple “ambient inclusion trails” from basal sandstones of the Strelley Pool Formation in Western Australia (Lowe 1983; Wacey et al. 2008). Higher within the

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Fig. 3.1 (continued) (e) Cross section of the 1 Ga Sheigra paleosol on Lewisian gneiss (bottom) and Staca paleosol on amphibolite (bracket) beneath the Applecross Formation (fluvial facies) of the Torridonian Supergroup, west of Sheigra, northwest Scotland (Retallack and Mindszenty 1994)

Table 3.1 Examples of Archean and Proterozoic paleosols

References	Province	Country	Age
Johnson et al. (2010)	Warrawoona Group	Australia	3.4 Ga
Kimberley and Grandstaff (1986)	Dominion Reef Conglomerate	South Africa	3.1–2.8 Ga
Kimberley and Grandstaff (1986)	Pongola	South Africa	3.0–2.9 Ga
Grandstaff et al. (1986)	Dominion and Pongola Supergroups	South Africa	3.0–2.8 Ga
Reimer (1986)	Kaapvaal Craton	South Africa	3.0–2.5 Ga
Hallbauer and van Warmelo (1974)	Witwatersrand and Ventersdorp Supergroups	South Africa	2.9–2.7 Ga
Macfarlane et al. (1994)	Fortescue Group Mt Roe 1 and 2	Australia	2.7–2.6 Ga
Kimberley and Grandstaff (1986)	Timiskaming Group	Canada	2.7 Ga
Rye and Holland (2000)	Mt Roe 1 and 2	Australia	2.7 Ga
Martini (1994)	Paleosol on ultramafics in the eastern Transvaal	South Africa	2.6 Ga
Watanabe et al. (2000)	Transvaal Sequence	South Africa	2.6 Ga
Pandit et al. (2008)	Tulsi Namla section	India	2.5–2.1 Ga
Aspler and Donaldson (1986)	Nonacho Basin	Canada	2.5–2.0 Ga
Banerjee (1996)	Paleosols BGC–Aravalli boundary	India	2.5–1.9 Ga
Bandopadhyay et al. (2010)	Singhbhum–Orissa craton	India	2.5 Ga
Prasad and Roscoe (1996)	Lower and upper sub-Huronian paleosols	Canada	2.4–2.2 Ga
Kimberley and Grandstaff (1986)	Black Reef Quartzite	South Africa	2.4–2.0 Ga
Gay and Grandstaff (1980)	Huronian SpGp	Canada	2.3 Ga
Farrow and Mossman (1988)	Huronian SpGp	Canada	2.3 Ga
Yang and Holland (2003)	Hekpoort paleosol Pretoria Group	South Africa	2.23 Ga
Gutzmer and Beukes (1998)	Gamagara Fm	South Africa	2.2–2.0 Ga
Jackson (1967)	Gowganda Fm	Canada	2.2 Ga
Retallack (1986b)	Paleosol near Waterval Onder	South Africa	2.2 Ga
Holland and Zbinden (1988)	FlinFlon Paleosol	Canada	1.8 Ga
Driese et al. (1995)	Lochness formation	Australia	1.8 Ga
Gall (1994)	Proterozoic Thelon paleosol	Canada	1.7 Ga
Driese and Gordon-Medaris (2008)	Baraboo Range	USA	1.7 Ga
Zbinden et al. (1988)	Sturgeon Falls paleosol	USA	1.1 Ga
Retallack and Mindszenty (1994)	paleosols from northwest Scotland	UK	1.1 Ga

Fig. 3.2 Terrestrial sedimentary biostructures: (a) oblique cross section of drab-haloed tubular structures (dashed lines) from two successive paleosols (numbered 1 and 2, respectively) in redbeds of the 1.8 Ga Elgee Siltstone, 20 km south of Wyndham, Western Australia (Schmidt and Williams 2008); (b) cross section of a 2.7 Ga paleosol with silicified tubular structures (arrow), and bound by water-laid deposits. Carraman Formation in Nobles Nob mine, 14 km east of Tennant Creek, Northern Territory, Australia (Black 1984); (c) plan view of a sandstone surface of a cracked paleosol (A horizon) as if it were clayey, in the 1.8 Ga Stirling Range Sandstone, Barnett Peak, Western Australia (Bengtson et al. 2007); (d) sandstone surface with elephant-skin texture (*Rivularites repertus*) with three individual fossils of *Dickinsonia costata* (encircled) in the 550 Ma Ediacara Member of the Rawnsley Quartzite, from Crisp Gorge, South Australia (Retallack 2013); scale bar = 1 cm



Formation are shallow marine stromatolites, but the basal sandstones of the Formation unconformably overlay the clayey paleosol developed on basaltic basement (Fig. 3.1b, c), which has been interpreted as estuarine and littoral talus (Allwood et al. 2006). Possible taxonomic affinities of these trails are unknown other than they are small, simple, and very likely prokaryotic (Wacey et al. 2008). Small spheroidal microfossils found in the same formation (Sugitani et al. 2013) may have lived in shallow waters, although nonmarine environments, including fluvial and playa lake environments (Hickman 2008), were also present at the same time and space. In highly oxidized paleosols, where the primary organic matter may not be preserved, casts of putative microfossils may appear as ordered particles along “filamentous” structures that cut across bedding planes (Fig. 3.3a).

*Thucomyces lichenoides* is a striking fossil (Fig. 3.3b, c) forming palisades atop green paleosols in the carbon leader of the Central Rand basin of South Africa, and associated with filamentous (hyphae-like) microfossils (Hallbauer and van Warmelo 1974; Hallbauer et al. 1977; Mossman et al. 2008). *Thucomyces* is now known to be as old as 2.8 Ga (Schaefer et al. 2010) and has been compared with lichens because it has clavate structures above the hyphae-like filamentous mesh and with the endocyanotic living glomeromycotan fungus *Geosiphon* (Schüßler and Kluge 2000). However, there are complex radial and vertical partitions within *Thucomyces* (Hallbauer and van Warmelo 1974; Hallbauer et al. 1977) unlike the central chamber of *Geosiphon*, where the latter hosts symbiotic *Nostoc* filaments. These folded structures are comparable with those in columnar biofilms of hot springs today (Hall-Stoodley et al. 2004). The enigmatic microfossil *Diskagma buttoni* from a 2.2 Ga paleosol in the Hekpoort Formation of South Africa (Fig. 3.3d, e) has also been compared with the living fungus *Geosiphon* given its ellipsoidal central chamber (Retallack et al. 2013b). Suggestive evidence of Archean and Paleoproterozoic filamentous Actinobacteria and fungi may explain the carbon-lean composition of many Precambrian paleosols and may imply the existence of mature biocrusts.

Microfossils recorded from the 2.7 Ga Mount Roe paleosol near Whim Creek, Western Australia, are associated with extremely light-carbon isotopic values suggestive of methanogens that now live in swamp-like environments (Rye and Holland 2000). In this case, the presence of organic matter and microfossils in the same suite of paleosols speaks for a wide distribution of microbial life in widely varied terrestrial environments.

Other Precambrian microfossils have been reported for nonmarine sedimentary paleoenvironments, including deposits of lakes of the ~1.1-Ga-old Torridonian Group in Scotland (Cloud and Germs 1971; Strother et al. 2011), and alluvial settings (Beraldi-Campesi et al. 2014) and paleokarst fill (McConnell 1974; Horodyski and Knauth 1994) of the ~1.2-Ga-old Apache Group in southwestern USA. These microfossils display coccoid and filamentous shapes and likely include both prokaryotic and eukaryotic components. From the sedimentary setting of these microfossils, they were more likely washed in from the surrounding land, rather than introduced from the sea. Aquatic terrestrial environments, such as lakes, also supported large organisms such as the 1.5-Ga-old *Horodyskia moniliformis*, which

Fig. 3.3 Terrestrial microfossils: (a) petrographic thin section of oxidized filaments running across bedding planes (arrow) and more abundant in the lower paleosol than the overlying cross-bedded sandstone of the 1.8 Ga Stirling Range Sandstone on Barnett Peak, Western Australia (Bengtson et al. 2007); scale bar = 10 mm: (b, c) *Thucomyces lichenoides* from 2.8 Ga (Schaefer et al. 2010) Carbon Leader of the Central Rand Group near Carletonville, South Africa (Hallbauer and van Warmelo 1974; Hallbauer et al. 1977); scale bars = 200  $\mu\text{m}$ . (d, e) petrographic thin sections of *Diskagma buttoni* to reveal a thallus group (d) and details of the apical cup (e) from the 2.2 Ga Waterval Onder paleosol of the upper Hekpoort Formation, 2 km east of Waterval Onder, South Africa (Retallack et al. 2013a, b); scale bars = 500  $\mu\text{m}$  and 50  $\mu\text{m}$ , respectively; (f) acritarch with hyphal stalk (*Ceratosphaeridium mirabile*) from the 570 Ma Wilari Dolomite Member, Tanana Formation, Observatory Hill No. 1 well, northern South Australia (Grey 2005); scale bar = 50  $\mu\text{m}$ : (g) *Germinosphaera* sp. indet. from 590 Ma ABC Range Quartzite, SCYW 1a bore, South Australia (Grey 2005); scale bar = 20  $\mu\text{m}$ : (h) *Tappania* sp. from 820 Ma Wynnatt Formation, on Victoria Island, Nunavut (Butterfield 2005); scale bar = 100  $\mu\text{m}$ . Images (a) and (b) are courtesy of Kathleen Grey, (f) of Nick Butterfield and (g, h) of Dieter Hallbauer, all reproduced with permission

has been interpreted as prokaryotic colonies (Knoll et al. 2006), agglutinated foraminifers (Dong et al. 2008), brown algae (Grey and Williams 1990), sponge remains (Hofmann 2001), hydrozoan or bryozoan colonies (Fedonkin and Yochelson 2002), or metazoan fecal strings (Yang and Zheng 1985), but it could also be of fungal affinity (Retallack et al. 2013b). In any case, its presence in paleolake shores (Retallack et al. 2013b) indicates an ample distribution of nonmarine life in the Precambrian.

Another line of evidence for Precambrian life on land is the suggestion of Pirozynski (1976) and Butterfield (2005) that there is a Precambrian record of fungi among the enigmatic microfossil palynomorphs known as acritarchs (Grey 2005; Moczydłowska et al. 2011). Ediacaran (~580 Ma) acritarchs such as *Ceratosphaeridium* (Fig. 3.3f) and *Germinosphaera* (Fig. 3.3g), and Cryogenian-Mesoproterozoic (~850 Ma) fossils such as *Tappania* (Fig. 3.3h), are similar to Glomeromycotan chlamydospores and vesicles. Many of these fossils have attached aseptate hyphal structures, characteristic of Mucoromycotina and Glomeromycota fungi. These fungi today mainly represent saprobiotic and mycorrhizal growth forms, respectively, but it is unclear whether they avoided lake or marine habitats in the distant past. These fossils have not been considered anything but marine until recently, and reevaluation of the sedimentary facies and communities of these fossils is needed.

### 3.4 Sedimentary Biostructures

Although microbial mats developing on coastal carbonate facies (e.g., Demicco and Hardie 1995) can be included in the definition of “biological soil crust” (Belnap and Lange 2001), most modern biocrusts develop on sandy, subaerial, siliciclastic substrates. Many sedimentary deposits of this type, from the Archean onward, display sedimentary biostructures of presumed biotic origin and developed subaerially (Hupe 1952; Lannerbro 1954; Voigt 1972; Eriksson et al. 2000; Prave 2002; Noffke et al. 2013; Simpson et al. 2013; Beraldi-Campesi et al. 2014). These diverse sedimentary biostructures can also be found in modern terrestrial systems, such as supratidal, fluvial, and alluvial settings, and thus indicate that the mechanisms that operate today in forming those structures are similar to those operating billions of years ago. In this regard, it must be said that the main biotic components of this type of modern biostructures are cyanobacteria and particularly filamentous taxa. These bacteria are the primary producers that allow other organisms, such as heterotrophic bacteria and fungi (among others), to become part of the biocrust community and are also essential for the cohesive properties of terrestrial MISS (Garcia-Pichel and Wojciechowski 2009; Beraldi-Campesi and Garcia-Pichel 2011; Retallack 2012).

A striking indication of MISS from dry land was first indicated by Prave (2002), who pointed out that some Precambrian sandstone surfaces show a system of cracks morphologically similar to desiccation cracks in clay stones (Fig. 3.2c).

Comparable features are common in modern biocrusts (Retallack 2012), and comparable gypsic paleosols can be found under paleosols with such cracked surface sandy horizons (Fig. 3.1d). For all these examples, it is clear that clays do not play a dominant role in the formation of sedimentary biostructures (or MISS; Noffke 2010), as the cohesive behavior of a microbial cover does, in this case a biocrust-like community (Beraldi-Campesi and Garcia-Pichel 2011).

Both filamentous and EPS-producing taxa are necessary to form sedimentary biostructures. Filaments can build tight networks among clastic particles and support the biocrust framework, while EPS acts as a gluing agent that keeps particles together, especially if it is well hydrated (Noffke 2010). Aquatic and terrestrial and recent and ancient microbial communities can develop a variety of microscopic and macroscopic features that can be recognized in thin sections and in the field, as listed in Table 3.2.

Table 3.2 Examples of sedimentary biostructures (MISS) and features found in microbial mats and earths from siliciclastic environments

Feature	Observations	References
Cohesive behavior	Ductile rheological behavior of microbial mat layers before and after burial	Fagerstrom (1967), Schieber (1999), Eriksson et al. (2000) and Beraldi-Campesi and Garcia-Pichel (2011)
Collapsed gas domes	Desiccated gas domes that form hemispherical depressions	Beraldi-Campesi et al. (2014)
Desiccation roll-ups	Organo-mineral layers upturned and rolled by desiccation	Beraldi-Campesi and Garcia-Pichel (2011)
Erosional pockets	Formed after fragments of microbial earths or mats have been removed from site	Noffke (2010)
Fairy concentric rings	Formed by small-scale plume degassing or dewatering	Gerdes et al. (1993)
Gas domes and blisters	Formed by upcoming gas pressure underneath sealed microbial mats	Bose and Chafetz (2009) and Beraldi-Campesi et al. (2014)
Gravity or flow-mediated soft deformation	Creases, wrinkles, crinkles, crumples, kinks and furrows, of mm to cm scales	Beraldi-Campesi et al. (2014)
Irregular desiccation crack margins	Unlike pure clay cracks, these have irregular margins	Gerdes (2003)
Laminated leveling structure	"Leveling" of the microtopography due to growth and stabilization of the microbial mat	Gerdes et al. (2000)
Mat chips	Eroded mat fragments transported by flows	Fagerstrom (1967), Pfluger and Gresse (1996) and Schieber 2007
Mat-layer bound small grains and heavy minerals	Accumulation of heavy minerals and micas on bedding planes	Noffke (2009)

(continued)

Table 3.2 (continued)

Feature	Observations	References
Microsequences	mm- to cm-thick sedimentary layers, normally graded, often with organic matter vestiges	Noffke (2010)
Oriented grains	Elongated grains that have been oriented parallel to the bedding plane through microbial baffling	Noffke et al. (1997)
Petees	Ridged structures caused by dewatering along weak planes	Reineck et al. (1990)
Rolled up mats	Organo-mineral layers upturned and rolled by wind or water currents	Simonson and Carney (1999), Schieber (2004) and Eriksson et al. (2007)
Sand/sandstone cracks	Also called earth cracks, are formed by desiccation of microbial mats on sandy surfaces	Picard and High (1973), Sarkar et al. (2008) and Beraldi-Campesi et al (2014)
Sand folds	Organo-mineral layers folded by wind or water flow	Bouougri and Porada (2012)
Sand ridges	Similar to Petee structures but also caused by expansion of biocrust boundaries	Beraldi-Campesi et al. (2014)
Sinoidal structures	Preserved sinuous shapes on ripple marks stabilized by microbial mats	Noffke (2010)
Sponge pore fabrics and vesicular horizons	Gas-produced pores formed within or underneath microbial mats and earths	Noffke (2010) and Beraldi-Campesi et al. (2014)
Tufts, knobs and pinnacles	Protuberances, mm to cm tall, derived from microbial growth and behavior in microbial mats	Gerdes et al. (2000), Noffke et al. (2001), Rosentreter et al. (2007) and Noffke et al. (2008)
Wrinkle marks	Include a wide variety of rugose surface structures due to mechanical and behavioral traits	Hagadorn and Bottjer (1997), Hagadorn et al. (1999) and references therein, Gerdes et al. (2000), Porada and Bouougri (2007) and Shepard and Sumner (2010)

### 3.5 Conclusions

A great variety of terrestrial environments are known in the Precambrian, including soils, peats, ponds, lakes, streams, deserts, and dune fields (Rye and Holland 1998; Eriksson et al. 2004; Retallack et al. 2013a, b). Thus, environmental settings that could potentially become “terrestrial ecosystems” were already in place. Despite sustained uncertainties about these environments being populated or not (Shear 1991; Behrensmeier et al. 1992; DiMichele and Hook 1992; Gray and Shear 1992; Gray and Boucot 1994; Bambach 1999; Blackwell 2000; Corcoran and Mueller 2004; Nesbitt and Young 2004; Gensel 2008), it is clear, through many lines of

evidence, that terrestrial ecosystems were indeed present, full of life, and functional since the Archean (Beraldi-Campesi 2013). The main lines of evidence are (a) paleosols with redoximorphic and concretionary features that are difficult to explain without the presence of microbial life, (b) microfossils found in rock deposits that represent “terrestrial” environments, and (c) sedimentary biostructures that are nonaquatic and microbially mediated. According to this evidence, the studied rock record shows that the period around the Mesoarchean to the Neoarchean (~3.2–2.5 Ga) was especially important for the development of terrestrial ecosystems, not because they could not exist before but because more plausible evidence is found in strata of that age. This “terrestrial” evolution was perhaps linked to supercontinent growth (Santosh 2010) and the associated emergence and diversification of potential new habitats and potential new biota.

The general similarity of some ancient fossils with fungi (e.g., Hallbauer and van Warmelo 1974; Hallbauer et al. 1977; Mossman et al. 2008; Rye and Holland 2000; Retallack et al. 2013a, b) may be of great importance if these turn out to be phylogenetically related. Besides pushing back their antiquity, the existence of fungi in Proterozoic rocks would speak for a greater similarity between ancient and modern biocrusts. Also, the functioning of the ancient terrestrial ecosystems should be reexamined through new insights about the ecological role of fungi in biocrusts and their potential ability to distribute nutrients (or make them available) throughout extensive areas (Collins et al. 2008). It is necessary to continue studying the ancient record of exposed continental masses in order to provide a better appreciation of the impact of life on the development of Earth’s biosphere, especially that involving links between continents and oceans; however, by now, it should be well established in science that Precambrian landscapes were not barren.

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# Chapter 4

## Cyanobacteria and Algae of Biological Soil Crusts

Burkhard Büdel, Tamara Dulić, Tatyana Darienko, Nataliya Rybalka, and Thomas Friedl

### 4.1 Introduction

Cyanobacteria are the oldest photoautotrophic component of biological soil crusts (biocrusts) known (see figure on front page). The oldest record of a fossil soil structure that may be interpreted as a biological soil crust is reported from as early as 2.6 billion years ago, and it presumably was composed of cyanobacteria

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(Watanabe et al. 2000; Beraldi-Campesi 2013, see also Chap. 3 by Beraldi-Campesi and Retallack). Fossil records suggest that eukaryotic algae first occurred on land 480–460 million years ago, while molecular clock estimates suggest an earlier colonization of about 600 million years ago. It is also hypothesized that this colonization of land by eukaryotes was facilitated by a partnership between a photosynthetic organism and a fungus (Heckman et al. 2001). Some of the early eukaryotic algae were able to form biocrusts (see Sect. 4.2.2). In this chapter, we will enumerate, as far as possible, cyanobacterial and eukaryotic algal species that are known so far to either form or occur in biocrusts. We will also discuss appropriate methods to assess their diversity and discuss ecological functions of the cyanobacterial and algal diversity.

## 4.2 Cyanobacterial and Eukaryotic Algal Diversity

### 4.2.1 Role and Diversity of Biocrust Cyanobacteria

From a functional point of view, cyanobacteria of biocrusts can be divided into three different groups: (1) Filamentous cyanobacteria, such as *Microcoleus*, that stabilize soils by gluing soil particles together and thus form soil aggregates due the presence of extracellular matrix (ECM; Figs. 4.1, 4.2, 4.3, and 4.4; see also Chap. 9 by Colesie et al. and Chap. 13 by Garcia-Pichel et al.). Those cyanobacteria are responsible for biocrust formation and are also the most abundant cyanobacteria species in the biocrusts. The formation of filaments in cyanobacteria is an essential feature that enables them to colonize physically unstable environments and to act as successful pioneers in the biostabilization process (Garcia-Pichel and Wojciechowski 2009). Due to the fact that the ECM remains over many years after the trichomes have either moved out of their sheath envelopes or died, the soil-stabilizing effect remains. (2) Cyanobacteria that prefer to live in the biocrust environment, enhancing the ecological role of biocrusts, e.g., through their contribution to C- and N-cycling. Examples are the unicellular *Chroococcidiopsis* (Fig. 4.5), the filamentous *Scytonema* (Fig. 4.4) and *Stigonema* (Figs. 4.6 and 4.7). (3) Cyanobacteria that only stochastically occur in biocrusts and may originate from other habitats, such as the aquatic environment or lichen symbiosis (e.g., *Chroococcus* Fig. 4.8, *Gleocapsa*, *Gleocapsopsis*, *Cylindrospermum*, many *Phormidium* species, *Tolypothrix* Fig. 4.8).

In the first volume of the Ecological Studies series dealing with biocrusts (Belnap and Lange 2003), Büdel (2003) was not able to compare cyanobacteria at the species level at the scale of continents and subcontinents because only 35 cyanobacterial genera from biocrusts were known at that time. Since then, knowledge has increased considerably, and now more than 320 species in over 70 genera are known to occur in biocrusts worldwide. Many studies have included the cyanobacterial species diversity of biocrusts, identified either by morphological

Fig. 4.1 *Nostoc*  
*microscopicum*, biocrust of  
Southern Tunisia

Fig. 4.2 *Nostoc commune*,  
trichomes inside a young  
colony, Negev Desert, Israel

Fig. 4.3 *Microcoleus*  
*vaginatus*, biocrust of the  
Negev Desert, Israel

Fig. 4.4 *Scytonema*  
cf. *ocellatum*, biocrust of  
Israel

Fig. 4.5 *Chroococcidiopsis*  
sp., biocrust of Western  
Cape region, South Africa

(e.g., Langhans et al. 2009; Lewis and Flechtner 2002; Deb et al. 2013) or molecular methods (e.g., Gundlapally and Garcia-Pichel 2006) alone or, ideally, by both methods combined using the so-called “polyphasic approach” (e.g., Dojani et al. 2014). Of the 320 cyanobacteria species reported for biocrusts so far, only about 80 have been reported from at least two of the seven geographical regions distinguished here, while the majority (235 species) are listed only once (see Table 4.1 in the supplementary online material at <http://extras.springer.com/2016/978-3-319-30212-6>). These numbers also include the hypolithic cyanobacterial diversity (see also Chap. 11 by S. Pointing et al.). On a continental scale, biocrust cyanobacteria are relatively well investigated with no major gaps (Fig. 4.9a). However, comparing the diversity of different continents, it immediately becomes obvious that the second smallest continent, Europe, has the highest species number, even though Asia and Africa are the two largest continents with considerably larger



Fig. 4.6 *Stigonema*  
*turfaceum*, biocrust of the  
high Arctic tundra, Canada

Fig. 4.7 Moss associated  
*Stigonema* cf. *hormoides*,  
Antarctic biocrust

amounts of arid and semiarid landscapes (Fig. 4.9b). This certainly does not reflect true biogeography but is rather an effect of the number of group-specialized scientists and the time they have worked on a certain continent. It is also obvious that there is a need for much more biodiversity assessments of biocrusts in the Americas. Knowledge about the actual distribution of cyanobacterial species and their abundance is of a great importance for understanding recent and ancient environmental dynamics. Cyanobacterial diversity influences ecosystem processes by changing the environment on a micro- and macroscale. Also the cyanobacterial diversity in biocrusts, as well as in any other environments, is regulated by many factors, including anthropogenic activities across temporal and spatial scales.

The two filamentous species, the heterocyte-bearing *Nostoc commune* (Fig. 4.2) and *Microcoleus vaginatus* (Fig. 4.3), have been reported for biocrusts of all continents. These may be the core ecosystem “engineers,” forming the early

Fig. 4.8 *Tolypothrix* sp. and *Chroococcus* sp., biocrust from loess sediment, Serbia



biocrusts and contributing the initial soil carbon and nitrogen inputs. Another two filamentous species found in biocrusts of all continents (except Antarctica) are *Coleofasciculus chthonoplastes* and *Trichocoleus sociatus*; both were formerly classified in the genus *Microcoleus*. Also the unicellular genus *Chroococcidiopsis* has been reported from biocrusts of all continents except Europe. Another three species are reported from biocrusts of five continents, i.e., *Nostoc microscopium* (Fig. 4.1), *Schizothrix calcicola*, and *Scytonema myochrous*. The first two of them do not occur in the harsh climate of Antarctica. Ten species have been reported from biocrusts of four continents, i.e., *Aphanothece saxicola*, *Aphanothece muscicola*, *Calothrix parietina*, *Hassallia bysoidea*, *Microcoleus paludosus*, *Nostoc muscorum*, *Nostoc punctiforme*, *Scytonema hofmani*, and *Stigonema ocellatum* (Fig. 4.4). Twenty-four species have been reported from three continents and 48 species from two continents. A list of all biocrust cyanobacteria species worldwide, compiled from the literature, can be found in Table 4.1 of the online supplement of this book, which can be downloaded from <http://extras.springer.com/2016/978-3-319-30212-6>.

#### 4.2.2 Role and Diversity of Eukaryotic Algae in Biocrusts

Based on their presumed role in biocrusts, the eukaryotic algae associated with biocrusts may be distinguished into four functional groups. (1) Crust-forming algae which may actively support the formation of crusts by entrapping soil particles due to their filamentous nature and/or secretion of mucilage, e.g., *Klebsormidium* (Fig. 4.10) and *Zygogonium*. Crust-forming algae occur in lower diversity, but may produce relatively high biomass. (2) Algae which are attached to soil particles and to the crust-forming algae. They are highly diverse and occur mostly in low abundances (Büdel et al. 2009), e.g., *Spongiochloris* (Fig. 4.11), *Neochlorosarcina*

Fig. 4.9 Cyanobacterial species richness on a continental scale (a) and related to continental size (b); the region “Pacific” includes Australia and New Zealand

(Fig. 4.12), and most diatoms (Figs. 4.13, 4.14 and 4.15). (3) A smaller group of green algae that occurs within lichens as symbionts (photobionts), free living within the biocrusts, and/or living epiphytically on lichens, e.g., *Myrmecia* (Fig. 4.16) and *Stichococcus* (Fig. 4.17) (4) Freshwater algae which originate from aquatic habitats, but may occur in the soil, as it can be a “wet” habitat with many aqueous niches,

Fig. 4.10 *Klebsormidium*  
*flaccidum* (Kützing)  
P.C. Silva, K.R. Mattox &  
W.H. Blackwell

Fig. 4.11 *Spongiochloris*  
*minor* Chantanachat &  
H.C. Bold

e.g., *Chlorococcum*, *Chlamydomonas* s.l., *Scenedesmus* s.l. and *Mychonastes* (Fig. 4.18). In biocrusts as well as desert soils, these algae may often be associated with bryophytes because of their higher water content, or they may be present as dormant resting stages.

There are no eukaryotic algae exclusively found in biocrusts; rather, they represent various algal lineages with different levels of ecological specialization. Eukaryotic algae are probably the least studied phototrophic component of biocrusts. The reasons may be that eukaryotic algae are rarely crust-forming species and they exhibit simple morphologies with distinguishing features only expressing

Fig. 4.12 *Neochlorosarcina*  
*negevensis* (Friedmann &  
Ocampo-Paus) S. Watanabe

Fig. 4.13 *Hantzschia*  
*amphioxys* (Ehrenberg)  
Grunow

in unialgal cultures. Using direct microscopy, algal forms other than the filamentous ones are hard to detect because they occur in low abundance or may be present as dormant resting stages, particularly in dry biocrusts. Also, early studies on eukaryotic biocrust algae were based on direct microscopy and, as they encountered many resting stages, may have recorded low algal diversity. Other sources of uncertainty in assessing the eukaryotic algal diversity of biocrusts may come from the fact that soil phycologists often do not pay attention whether the algae were found in “bare soil” or within biocrusts. In addition, molecular methods have

Fig. 4.14 *Luticola mutica*  
(Kützing) D.G. Mann

Fig. 4.15 *Pinnularia*  
*borealis* Ehrenberg

shown that many morpho-species and genera of soil algae are actually of different phylogenetic entities (species and genera), which makes their correct identification using microscopy even more difficult (e.g., Fucíková et al. 2011; Fucíková and Lewis 2012a, b).

The list of species (Table 4.2 in the supplementary online material at <http://extras.springer.com/2016/978-3-319-30212-6>) represents the most current compilation of the literature on eukaryotic algae detected within, or clearly associated with, biocrusts. An overview of the eukaryotic algal diversity reported in this compilation is shown in Figs. 4.19 and 4.20. Eukaryotic algae that are reported from biocrusts were either green algae from both phyla, the Chlorophyta and Streptophyta, or members of one of three lineages of stramenopiles, i.e., the diatoms (Bacillariophyceae), xanthophytes (Xanthophyceae), or eustigmatophytes (Eustigmatophyceae). The identifications used in those studies have almost exclusively been based on morphological criteria observed by microscopy and from material in unialgal cultures. The geographical distribution of eukaryotic biocrust algae is only poorly understood, and there is still an ongoing debate whether microalgae exhibit biogeography or not. Due to their small size and desiccation resistance as well as other harsh environmental conditions, most terrestrial eukaryotic algae may

Fig. 4.16 *Myrmecia*  
*bisecta* Reisingl

Fig. 4.17 *Stichococcus*  
*bacillaris* Nägeli

be easily distributed, e.g., by wind currents, and therefore one may anticipate an ubiquitous distribution for most species. In addition, when compared on a continental scale, the diversity of biocrust-associated eukaryotic algae as compiled from the literature is erratic (Figs. 4.19a, b and 4.20). This is probably reflecting the amount of work spent on samples from a certain continent rather than actual numbers of species diversity and geographic distribution. For example, the eukaryotic biocrust algal

Fig. 4.18 *Mychonastes*  
*homosphaera* (Skuja)  
Kalina & Puncochárová

diversity appears much higher in Antarctica than in the Pacific region (Australia and New Zealand) or South America, as the latter two regions have been clearly neglected so far and require more attention (Fig. 4.19a).

Based on current compilations of literature, i.e., Table 4.2 in the supplementary online material (<http://extras.springer.com/2016/978-3-319-30212-6>) the filamentous species of *Klebsormidium* (Klebsormidiophyceae, Fig. 4.10) and *Zygogonium* (Zygnematophyceae), both from the Streptophyta, are most commonly encountered in biocrusts, especially in sandy soils. The unicellular zygnematophyte *Cylindrocystis* (Fig. 4.21) is the most common unicellular streptophyte green alga (Zygnematophyceae) in biocrusts, probably contributing to crust formation as it forms mucilage. Less frequent is the unicellular genus *Interfilum* (Fig. 4.22).

Biocrust Chlorophyta belong to three classes, the Chlorophyceae, Trebouxiophyceae, and Ulvophyceae; the systematics of the green algae as presented in this chapter follows Friedl and Rybalka (2012). Most biocrust green algae may not actively support biocrust formation but are associated with biocrust components in various ways (e.g., lichen photobionts).

The largest group of biocrust green algae are the Chlorophyceae (21 species, see Table 4.2 in supplementary online material at <http://extras.springer.com/2016/978-3-319-30212-6>). They are recorded from two or more geographic regions. All biocrust Chlorophyceae are unicellular but phylogenetically diverse within the class. They belong to several distinct phylogenetic lineages of the class, the orders Volvocales (syn. Chlamydomonadales) and Sphaeropleales (also called the “DO group”) and are even further distributed on various lineages within these orders. Several biocrust Volvocales form cell packages and may produce mucilage, thus somehow supporting crust formation, e.g., *Chlorosarcinopsis*, *Tetracystis*, *Neochlorosarcina* (Fig. 4.12), and *Borodinellopsis*. Other genera are either inconspicuous tiny coccoids (e.g., *Mychonastes*, Fig. 4.18) or form large unicells, e.g., *Macrochloris* and *Spongiochloris* (Fig. 4.11). Some coccoid members of Volvocales easily form flagellated stages (e.g., *Chlorococcum*); other Volvocales



Fig. 4.19 Eukaryotic algal species richness on a continental scale (a) and related to continental size (b); the region “Pacific” includes Australia and New Zealand

are flagellates in their vegetative stages, e.g., *Chlamydomonas* and *Chloromonas*. The latter occur in immotile stages and are drought resistant by mucilage formation. Just a few members (five species) of the chlorophycean order Sphaeropleales, are common in biocrusts and are widely distributed. Unicellular coccoid *Bracteacoccus* species (Fig. 4.23) are most common in biocrusts, as well as representatives of the

Fig. 4.20 Eukaryotic algal diversity related to class and higher taxonomic ranks and larger eco-regions

family of colony forming Scenedesmaceae, i.e., species of *Acutodesmus*, *Coelastrella*, and *Scenedesmus*.

Members of the Trebouxiophyceae form the second largest group of the Chlorophyta, i.e., 15 genera are reported and are widely distributed. Species of *Chloroidium*, *Coccomyxa* (incl. *Pseudococcomyxa*), *Muriella*, *Myrmecia* (Figs. 4.16 and 4.24), and *Chlorella*-like algae, including the “true” *Chlorella*, *Chlorella vulgaris* (Fig. 4.25), and *Elliptochloris* (Fig. 4.26) were found in almost every type of soil crust and from all geographic regions. However, *Chlorella* in its traditional taxonomic circumscription is of multiple origins and in fact represents several genera, separated from *Chlorella* s.str. only recently. The second most encountered trebouxiophytes are those which form cell packages, i.e., *Apatococcus*, *Desmococcus*, and *Diplosphaera* (Figs. 4.27 and 4.28). The filamentous trebouxiophyte *Prasiola* forms green turf and therefore may also contribute to crust formation in regions with maritime climate. However, it has been reported only from the Alps and Antarctica. Species of *Asterochloris*, *Chloroidium*

Fig. 4.21 *Cylindrocystis brebissonii* (Ralfs) De Bary

Fig. 4.22 *Interfilum terricola* (J.B.Petersen) Mikhailyuk, Sluiman, Massalski, Mudimu, Demchenko, Friedl, and Kondratyuk

(Fig. 4.29), and *Trebouxia* are frequently encountered as photobionts in lichens of biocrusts (Ruprecht et al. 2014).

The Ulvophyceae are the third green algal class commonly found in biocrusts, but just two inconspicuous unicellular or pseudofilamentous genera, *Planophila* and *Pseudendocloniopsis*, were reported from more than just a single geographic

Fig. 4.23 *Bracteacoccus*  
*minor* (Chodat) Petrová

Fig. 4.24 *Myrmecia*  
*biatorellae* J.B. Petersen

region. The branched filamentous *Dilabifilum* is known as a crust-forming alga on different salty soils (solonchak or solonetz).

The second largest group of eukaryotic biocrust algae are the diatoms (e.g., Rumrich et al. 1989) with mostly pennate (elongated cells with bilateral symmetry) forms, i.e., the class Bacillariophyceae (Fig. 4.20). Inconspicuous species of the genera *Hantzschia* (Fig. 4.13), *Luticola* (Fig. 4.14), *Navicula* s.l. (incl. *Fistulifera*), *Nitzschia*, and *Pinnularia* (Fig. 4.15) were very common and may be found

Fig. 4.25 *Chlorella*  
*vulgaris* Beyerinck

Fig. 4.26 *Elliptochloris*  
*subsphaerica* (Reisigl) Ettl  
& Gärtner

associated with almost every soil crust type. Two groups of Stramenopiles algae are common in terrestrial habitats and soils but may also be found in soil crusts.

Members of the class Xanthophyceae are probably restricted to cooler geographic regions with the unicellular coccoid species of *Botrydiopsis* being the most common, but also some filamentous (*Tribonema*, *Xanthonema*) or branched filamentous forms (*Heterococcus*) are frequently found (Fig. 4.20). Rarely also the coenocytic *Botrydium* has been recorded. Eustigmatophyceae have been reported from biocrusts, with only four unicellular genera recovered, i.e., *Ellipsoidion*, *Eustigmatos*, *Gloeobotrys*, and *Vischeria*.

Fig. 4.27 *Diplosphaera*  
*chodatii* Bialosuknia

Fig. 4.28 *Desmococcus*  
*olivaceus* (Persoon ex  
Acharius) J.R. Laundon

Fig. 4.29 *Chloroidium ellipsoideum* (Gerneck) Darienko, Gustavs, Mudimu, Menendez, Schumann, Karsten, Friedl, and Pröschold

## 4.3 Methodological Aspects

### 4.3.1 Sampling

For any assessment of the biodiversity of cyanobacteria and eukaryotic algae in biocrusts, the samples should be as fresh as possible. An appropriate method which leaves the crust mostly undisturbed and yields sufficient material at the same time has recently been described by Büdel et al. (2009). A lower lid of a 10-cm petri dish is lined with several layers of cellulose paper and pressed into the upper 2 cm of the soil crust after which a trowel is pushed below the lid, lifted together with the sample from the surrounding soil, and turned around to carefully remove surplus soil from the sample. For optimal biodiversity assessment, a number of smaller samples [e.g., a sufficient number of samples (test with a saturation curve of species numbers) of 2 cm × 2 cm × 1 cm in size with visible soil crusts] should be pooled (e.g., Gollerbach and Shtina 1969; Kostikov et al. 2001; Novakovskaya and Patova 2013). Wet samples need to be carefully dried (e.g., on cellulose paper) before lab work in order to avoid fungal growth, but on the other hand, drying may hamper the growth of certain algal groups (e.g., Xanthophyceae).

### 4.3.2 Identification, Cultures, and Morphological Approach

For identification of biocrust cyanobacteria in the crust samples by microscopy, small amounts of crust material are soaked in water and separated into two subsamples. Using a dissecting microscope, the first subsample is transferred to a microscope slide and examined under a light microscope. The second subsample is pre-cultured under wet and low light conditions for 3–4 days followed by a light microscopy examination. This will allow growth of cyanobacteria so that they can

be better recognized and identified. In order to start cultures, a small amount of biocrust material soaked in water is checked by microscopy using sterile slides and then transferred to both liquid and agarized media, e.g., BG-11 medium (Waterbury and Stanier 1978), which are known to be well suited for cyanobacteria. Subsequently, they are kept at a temperature of about 20 °C under low light (50--150  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  photosynthetic active radiation) with a light-dark regime of 12:12 h. As soon as colonies are visible, they are checked by microscopy and then purified by transferring them several times onto fresh media. For developing cultures of biocrust cyanobacteria, many of the methods described below for eukaryotic algae can also be successfully employed. For identification of cyanobacteria using morphological criteria, the three volumes of the "Cyanoprokaryota" are recommended, i.e., Komárek and Anagnostidis (1998), Komárek and Anagnostidis (2005), and Komárek (2013).

For eukaryotic algae, direct microscopy of freshly collected soil samples can be useful for an initial survey of algal diversity. However, many eukaryotic algae in the crusts are present in untypical stages (e.g., resting cells), and feature characteristic for genus and species identification may only develop in culture. Therefore, a thorough microscopic investigation of eukaryotic biocrust algae involves several steps following microscopy of the sample, such as developing raw cultures using "wet chambers," agarized enrichment cultures, and, finally, unialgal cultures (Gollerbach and Shtina 1969). The methods do not differ from those used for soil algae except that the biocrust samples need mechanical disruption before starting cultures so that the developing colonies can be better separated from each other. Many studies have used this procedure to determine the biodiversity of soil, e.g., Novichkova-Ivanova (1980), Vinogradova and Darienko (2008), Kostikov et al. (2001). However, employing cultures generally has the risk that those species which may be hard to culture using standard procedures (and they could even be dominant) may be left undiscovered, whereas those species not actively participating in the crust communities (e.g., present just as dormant stages) may be amplified simply because they grow well in culture.

To establish cultures of eukaryotic biocrust algae, some authors use only agarized enrichment cultures (e.g., Peer et al. 2010; Hoppert et al. 2004) or even just direct microscopy of the samples (Büdel et al. 1994; Colesie et al. 2014; Kanda et al. 2002), but mostly a combination of both are applied (e.g., Flechtner et al 1998; Broady 1986; Broady and Weinstein 1998). Raw cultures using distilled water for wetting "wet chambers," introduced by Fritsch and John (1942) for the observation of soil diatoms, facilitate the observation of biocrust algae and induce their growth without selecting certain algae too much. It is important to consider that the nutrient composition of culture media introduces a considerable bias, as certain nutrient compositions will accelerate growth of certain species while inhibiting others. The biocrust is placed in a sterilized petri dish at air humidity up to 80 %. After 2–3 weeks of exposure to a light-dark 12:12 h regime, biofilms will appear on the surface of the biocrust sample to which several cover slips are slightly pressed. The sample surface should be uneven to leave space between the biofilm and the glass cover slip—this will form small chambers in which favorable microclimatic



conditions for algal growth on the cover slip surfaces will occur. The cover slips can be used for microscopy after some time (2–3 weeks) of incubation on the sample surfaces and even allow observation of a succession of algae if the cover slips are used for microscopy after consecutive time intervals. Cover slips can also be put into liquid or on the surface of agarized culture media to start cultures of the algae from these surfaces. Alternatively, small fragments of the biocrust are placed on agarized culture media which should not be too rich in nutrients and devoid of vitamins or any organic compounds to avoid the growth of fungi and bacteria. After incubation for 2–3 weeks, the first small colonies, often formed by a variety of different algae, can already be used for an initial estimate of the algal diversity by microscopy and also for establishing unialgal cultures after several purification steps.

For liquid cultures, fragments of the biocrust are placed in liquid media, e.g., 1–2 g of a crust sample is added to a 50–80 ml sterile medium in 100–150 ml Erlenmeyer flasks. One disadvantage of this method is that algae (e.g., resting stages of freshwater algae), which were in an inactive state in the biocrust and do not belong to the active algal community of the biocrust, can then easily develop in those cultures.

### 4.3.3 Molecular Approaches

Molecular markers may be most promising for assessing biocrust cyanobacteria and eukaryotic algal biodiversity. For cyanobacteria, it was revealed that due to their high physiological plasticity, which allows for their rapid adaptation to various environmental conditions, new morpho- and ecotypes may be developed within short time. This makes the discrimination of species using morphological and ecophysiological characters rather difficult and calls for molecular studies to define species. DNA sequences allow an unambiguous characterization and the comparison with reference sequences (as available from public databases), providing reliable estimates of genetic distances to infer the phylogenetic positions of algae and cyanobacteria. The first cyanobacteria 16S (SSU) rRNA gene sequences have already been determined almost 30 years ago (Giovannoni et al. 1988), followed by corresponding sequences (18S rRNA) for eukaryotic algae, and since then their numbers have ever been increasing up to several thousands in publicly available databases (e.g., NCBI). Due to the large number of available reference sequences, the SSU rRNA genes became the “golden standard,” i.e., the molecular marker of choice for cyanobacteria as well as eukaryotic algae. There are many examples for studies on biocrust cyanobacteria which used 16S rRNA as molecular signatures (e.g., Abed et al. 2010; Zaady et al. 2010; Li et al. 2013; Dojani et al. 2014; Patzelt et al. 2014). However, SSU rRNA alone may not provide sufficient resolution for unambiguous distinction of species, and additional more variable markers (e.g., ITS rDNA) are required. For cyanobacteria, the 16S–23S spacer (ITS) has successfully been used, also because its secondary structure models bear valuable phylogenetic

information for species distinction (e.g., Boyer et al. 2002; Reháková et al. 2007; Siegesmund et al. 2008; Johansen et al. 2011). For eukaryotic algae, i.e., photobionts of lichens associated with soil crusts, the nuclear-encoded ITS rDNA in combination with the chloroplast-encoded intergenic spacer *psbJ-L* has recently been employed for species identification (Ruprecht et al. 2014).

There are two principal ways to apply molecular methods for assessing biocrust algal and cyanobacterial diversity: sequencing of cultured strains isolated from biocrusts and using DNA extracts directly from the biocrusts without culturing (culture-independent approach). For the latter approach, DNA is extracted directly from the fresh biocrust sample followed by PCR amplification, which will result in a mixture of PCR products from the various organisms present in the biocrust sample. They need to be separated by cloning before sequencing, and in order to assess the algal/cyanobacterial diversity most accurately, a larger number of clones need to be sequenced. The culture-independent approach requires PCR primers that selectively amplify certain groups of target organisms, e.g., PCR primers which preferentially amplify cyanobacteria (e.g., Nübel et al. 1997) or green algae (e.g., Hallmann et al. 2013), to enrich the clone libraries with sequences from the target organisms. Several recent studies used cyanobacteria-specific PCR primers for biocrust and/or soil cyanobacteria (Li et al. 2013; Dojani et al. 2014; Patzelt et al. 2014), whereas others studied biocrust cyanobacteria as part of the whole bacterial community using universal bacterial 16S rRNA PCR primers (Gundlapally and Garcia-Pichel 2006; Abed et al. 2010; Zaady et al. 2010; Zhang et al. 2012). Recently, next-generation DNA sequencing (NGS, e.g., using a Roche 454 FLX instrument with Titanium reagents, Steven et al. 2013a; Elliott et al. 2014) provided the ability to determine and read millions of DNA sequences in parallel, making them ideally suited for large-scale biodiversity analyses of environmental biocrust samples. There are already several studies which have analyzed biocrust cyanobacterial diversity based on 16S rRNA gene amplicons obtained with universal bacterial primers (Steven et al. 2013a, b; Elliott et al. 2014; Maier et al. 2014). For eukaryotic biocrust algae, almost all molecular studies have been based on unialgal cultured isolates established from biocrust samples; the culture-independent approach has been used not employing 18S rRNA but other conserved markers as plastid-encoded 16S or 23S rRNA genes (Maestre et al. 2006; Lin and Wu 2014).

As an alternative to the culture-independent DNA sequencing approach for the analysis of microbial biocrust communities, DNA fingerprinting based on PCR amplification has been used, i.e., DGGE (Gundlapally and Garcia-Pichel 2006; Zaady et al. 2010; Zhang et al. 2012), ARISA (Abed et al. 2012) and t-RFLP (Redfield et al. 2002), but so far only for cyanobacteria. DGGE profiling may be appropriate because the characteristic DGGE-banding patterns can easily be compared among many samples. If unique or different patterns are identified, a DGGE band representing a still unidentified species can also be sequenced and identified using sequence comparisons after excised from the gel, but this will yield only rather short sequences (Lin and Wu 2014; Maestre et al. 2006).

For species identifications, the molecular approach is often supplemented by microscopy of the cultures. The latter is still essential for correct identification when no sequences of closer relatives are available in public gene sequence databases (Lewis and Flechtner 2002, 2004; Büdel et al. 2009; Rindi et al. 2011; Flechtner et al. 2013). In general, in the culture-independent DNA sequencing approach, the PCR amplification step is crucial to the diversity assessment. The DNA of the most abundant or any other species may be preferentially amplified and mask the DNA of other less abundant or easy to amplify species and leave the latter species undiscovered. Shorter gene regions may be better amplified compared to longer ones—the lengths of amplicons depend on the type of PCR primers used or species present in the biocrust sample. In addition, biocrust samples may exhibit PCR-inhibiting compounds. It follows that also the culture-independent approach presents various biases. Culture-independent and culture-based approaches may therefore result in different diversities. Consequently, a combination of both approaches is required to assess the algal biodiversity as accurately as possible. In a recent example, results from the culture-dependent and culture-independent approaches were compared, and this pointed out the necessity of employing both techniques because several taxa could be recovered only via one or the other approach (Patzelt et al. 2014; Dojani et al. 2014).

## 4.4 Conclusion

Biocrust inhabiting cyanobacteria and eukaryotic algae are highly diverse, but only few of them are in fact responsible for crust formation. Most cyanobacteria and eukaryotic algae simply use the biocrust habitat but may enhance the biocrust functions by their presence. The main crust-forming cyanobacteria are *Microcoleus*, *Nostoc*, *Scytonema*, and *Stigonema*. In contrast, biocrusts formed by eukaryotic algae, i.e., *Klebsormidium* and *Zygogonium*, are relatively rare. Cyanobacteria from biocrusts are better studied compared to the corresponding eukaryotic algae. Data about the distribution of cyanobacteria and eukaryotic algae are fragmentary and strongly biased towards the intensity of work extended to samples from a certain continent. Also, there is an ongoing debate whether the cyanobacteria and eukaryotic algae exhibit biogeography at all. For microscopic identification of cyanobacteria and eukaryotic algae, it is recommended to develop cultures, but this has the risk that isolating procedures and culture conditions may lead to a strongly biased biodiversity. Therefore, the culture-independent molecular approach is recommended but so far has only been applied a few times, mostly for cyanobacteria. In order to assess the cyanobacterial/algal biodiversity as accurately as possible, the culture-independent and culture-based approaches need to be combined.

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# Chapter 5

## Bacteria and Non-lichenized Fungi Within Biological Soil Crusts

Stefanie Maier, Lucia Muggia, Cheryl R. Kuske, and Martin Grube

### 5.1 Introduction

Microbial fungi and bacteria are ubiquitous, occurring in highly enriched concentrations in biological soil crusts (biocrusts), as compared to the surrounding uncrusted soil. Nevertheless, their diversity can hardly be estimated without molecular biology methods. Only the macroscopic phenotypes of lichen-forming fungal species, which may dominate the landscape in soil crust habitats, allow a more or less secure determination to species level even in the field. Lichens in biocrusts have therefore long been studied (see Chap. 1 by Lange and Belnap) and their diversity and ecosystem services specifically addressed in Chap. 7 by Rosentreter et al. Knowledge on the diversity of non-lichenized fungi in biocrusts is still quite limited, whereas investigation of bacterial communities has received global attention in the past decade. This chapter aims to review the current state of research on bacterial and fungal community composition in biocrusts.

Recent research on bacterial and fungal communities has been conducted in arid and semiarid regions, such as the Colorado Plateau, Chihuahuan Desert, and Sonoran Desert, USA (Garcia-Pichel et al. 2001; Yeager et al. 2004; Nagy et al. 2005; Yeager et al. 2007), the Sultanate of Oman (Abed et al. 2010), and the Gurbantunggut Desert in China (Zhang et al. 2011). In Europe, the bacterial communities of bryophyte and lichen-dominated biocrusts from southern Spain have been investigated (Castillo-Monroy et al. 2011; Moquin et al. 2012; Maier

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et al. 2014). This global assessment allows identification of common and distinguishing characteristics of the bacteria and fungi in biocrusts around the world. Although there are characteristics specific to geographic regions and land masses, many compositional characteristics are similar among the Earth's biocrusts and arid land surface soils.

The present research needs to be put into context with the technological advancements of recent years, which basically allow two approaches. Culture-based approaches have been applied (Garcia-Pichel et al. 2001, 2003; Gundlapally and Garcia-Pichel 2006; Abed et al. 2010; Zhang et al. 2011), providing isolates for in-depth study of biocrust organism genomes and physiology (Yeager et al. 2007; Starkenburg et al. 2011). However, as cultivation techniques only retrieve a small fraction of the total microbial diversity, culture-independent methods have been increasingly used. Community profiling techniques such as denaturing gradient gel electrophoresis (DGGE) and terminal restriction fragment length polymorphism (T-RFLP) were initially used [for bacteria, see Garcia-Pichel et al. (2001), Kuske et al. (2002), Garcia-Pichel et al. (2003), Yeager et al. (2004), Nagy et al. (2005), Gundlapally and Garcia-Pichel (2006), and Castillo-Monroy et al. (2011); for fungi, see Bates and Garcia-Pichel (2009) and Bates et al. (2012)]. Furthermore, 16S ribosomal RNA (rRNA) gene clone libraries were applied [for bacteria, see Yeager et al. (2004), Gundlapally and Garcia-Pichel (2006), Yeager et al. (2007), Abed et al. (2010), and Moquin et al. (2012); for bacteria and fungi, see Steven et al. (2014)]. With the improvement of sequencing technologies such as high-throughput 16S rRNA gene sequence analyses and shotgun metagenome sequencing, there has been a resurgent interest in a wider characterization of the biocrust microbial communities (Steven et al. 2012a, b, 2013a, b, 2014; Angel and Conrad 2013; Davies et al. 2013; Büdel et al. 2014; Elliott et al. 2014; Steven et al. 2015). The complex physicochemical properties of biocrusts, dependence of DNA recovery on the soil type, and PCR bias should be kept in mind as prokaryotic diversity determined by high-throughput amplicon or metagenome sequencing is interpreted (Delmont et al. 2011; Lombard et al. 2011).

## 5.2 Bacterial Biomass and Community Composition

Since biocrusts typically colonize the top 1–2 cm of the soil surface, it is required to study small-scale variations in soil depth. Garcia-Pichel et al. (2003) assessed bacterial biomass and diversity of two stages in biocrust formation (early successional and well-developed late successional) from the Colorado Plateau at a millimeter resolution. According to their results, microbial biomass decreased with depth and increased with biocrust maturity, supporting the view that biocrusts represent “mantles of fertility” in arid regions (Garcia-Pichel et al. 2003).

Cyanobacteria, particularly species in the genus *Microcoleus*, are globally dominant biocrust-forming microorganisms in most arid lands (Garcia-Pichel et al. 2001; Boyer et al. 2002; Belnap and Lange 2003; Pointing and Belnap



2012; see Chap. 4 by Büdel et al.). The production of polysaccharide sheaths aids in formation of centimeter-long filament bundles, and these filamentous Cyanobacteria are thought to act as pioneers in the stabilization process of soils (Garcia-Pichel and Wojciechowski 2009). *Microcoleus steenstrupii* appeared to be the dominant filamentous cyanobacterium in Sonoran Desert biocrusts, but *Microcoleus vaginatus* as well as heterocystous groups (*Scytonema* and *Anabaenopsis*) and an unicellular cyanobacterium (*Synechococcus*) were also present. Yeager et al. (2004) revealed distinct differences in the diazotrophic communities between young and well-developed biocrusts from a cold desert in the Colorado Plateau and a warm desert in southern New Mexico, demonstrating a transition from a *Microcoleus vaginatus*-dominated poorly developed crust to mature crusts harboring a greater percentage of *Nostoc* and *Scytonema* spp. For a detailed account on Cyanobacteria, see Chap. 4 by Büdel et al. Interestingly, Cyanobacteria are not the sole prokaryotes in the biocrusts that harvest energy from light. Up to 6 % of the bacterial community cultured from Canadian biocrusts are aerobic anoxygenic phototrophs belonging to the genera *Belnapia*, *Muricoccus*, and *Sphingomonas* (Csotonyi et al. 2010).

Knowledge about bacteria is rapidly increasing with the convenience of culture-independent sequencing studies. Besides Cyanobacteria, the most common bacteria in the Sonoran Desert comprised members of Proteobacteria (mainly Betaproteobacteria), Actinobacteria, and Acidobacteria. These bacterial phyla are dominant and common in soils and sediments everywhere, in arid as well as wet landscapes (Fierer et al. 2012). All sequences of Betaproteobacteria were close to cultured members of the Oxalobacteraceae (Nagy et al. 2005). Samples from Colorado Plateau biocrusts were numerically dominated by the same top three phyla as found in the Sonoran Desert (Cyanobacteria, Actinobacteria, and Proteobacteria, largely Betaproteobacteria) (Gundlapally and Garcia-Pichel 2006). In particular, *Microcoleus vaginatus* and *Microcoleus steenstrupii* represented the dominant clades of Cyanobacteria (38.4 %). Actinobacteria (particularly the genera *Streptomyces*, *Sphaerobacter*, *Actinomadura*, *Rubrobacter*, and *Nonomuraea*) were common among non-phototrophs. Betaproteobacteria (genus *Massilia* and *Comamonas*) and Bacteroidetes (genera *Flexibacter*, *Spirosoma*, *Flavobacterium*, *Sphingobacterium*) contributed around 10 % each. Remarkably, mycelial genera of Actinobacteria were present (e.g., *Streptomyces*, *Actinoplanes*, *Pseudonocardia*), which are likely to be important during biocrust formation. Moreover, isolates of Proteobacteria and Bacteroidetes produced exopolysaccharides and thereby could also play a role in soil stabilization and biocrust formation (Gundlapally and Garcia-Pichel 2006). The predominance of Cyanobacteria was also demonstrated for the arid deserts of the Sultanate of Oman near Muscat and Adam. Again, *Microcoleus vaginatus* was the most abundant cyanobacterium. Using microscopy, the genera *Scytonema*, *Leptolyngbya*, and *Lyngbya* were also identified (Abed et al. 2010). Taken together, multiple genera of Cyanobacteria, both non-N-fixing genera such as *Microcoleus* and the N-fixing genera *Nostoc*, *Scytonema*, and *Spirirestis*, constitute a major part of biocrust bacterial communities. In addition to the Cyanobacteria, many bacterial phyla that are common to soils are also

present. Similarly, microbial communities that form biofilms on the ventral surfaces and sides of translucent rocks termed hypoliths are dominated by Cyanobacteria and can also support heterotrophic bacteria. Actinobacteria, Acidobacteria, Alphaproteobacteria, and Gammaproteobacteria occur frequently in hypolithic communities (Chan et al. 2012; see Chap. 11 by Pointing et al.). Comparative analyses of the non-cyanobacterial communities at the genus and species level would define relationships among biocrusts from different regions; this has not been conducted but would be an interesting area to pursue. Some differences in microbial community structure of biocrusts have already been observed. In biocrusts from the Colorado Plateau and the Sonoran Desert, Actinobacteria were prevalent (Nagy et al. 2005; Gundlapally and Garcia-Pichel 2006; Steven et al. 2013a, b), whereas this group was absent in biocrusts from Oman (Abed et al. 2010). In contrast, Myxobacteria were detected in samples from Oman but not in those from the Colorado Plateau and Sonoran Desert (Abed et al. 2010). There is, however, no clear explanation for these differences so far.

Besides Cyanobacteria-rich biocrusts, several other subtypes of biocrusts have been recently studied. The bacterial phyla Proteobacteria, Actinobacteria, and Bacteroidetes comprised the majority of the community in lichen-dominated biocrusts from the Tabernas Desert, Spain. Unlike in the studies of Nagy et al. (2005) and Gundlapally and Garcia-Pichel (2006), Alphaproteobacteria represented the dominant class of Proteobacteria. Among the Alphaproteobacteria, the orders Sphingomonadales and Rhizobiales were predominantly observed. Furthermore, 45 genera of the class Actinobacteria were detected. The observation that Actinobacteria are very common and diverse within biocrusts is in line with studies conducted at the Colorado Plateau and in the Sonoran Desert. In lichen-dominated biocrusts from the Tabernas Desert as well as in samples from the Colorado Plateau, a low abundance of Bacteroidetes was found (Maier et al. 2014, Fig. 5.1). In contrast, a 16S rRNA gene library sequencing study of Moquin et al. (2012) on bacterial communities in bryophyte-rich biocrusts from the Sandia Mountains, USA, revealed the dominance of Bacteroidetes (primarily Chitinophagaceae and Cytophagaceae), Acidobacteria, and Proteobacteria (Oxalobacteraceae and Comamonadaceae). Using 16S rRNA gene pyrosequencing, Steven et al. (2013b) demonstrated that biocrust-associated bacterial communities of Arctic permafrost soils were as diverse as in temperate regions. Their samples were numerically dominated by Acidobacteria, Cyanobacteria, Proteobacteria, Planctomycetes, and Verrucomicrobia.

In general, biocrusts that colonize the top few centimeters of the soil from regions around the globe share similar bacterial composition at the phylum level. Comparisons between this biocrust stratum and the soil a few centimeters below the biocrust show less commonality, with distinct differences in biomass and bacterial composition. Steven et al. (2013a, b) demonstrated that community composition in soils with different parent material origin (sandstone, shale, gypsum) differed at small vertical scales of a few centimeters. Cyanobacteria and Proteobacteria had significantly higher relative abundance in biocrusts, whereas Chloroflexi and Archaea were significantly enriched in below-biocrust soils across the three soil

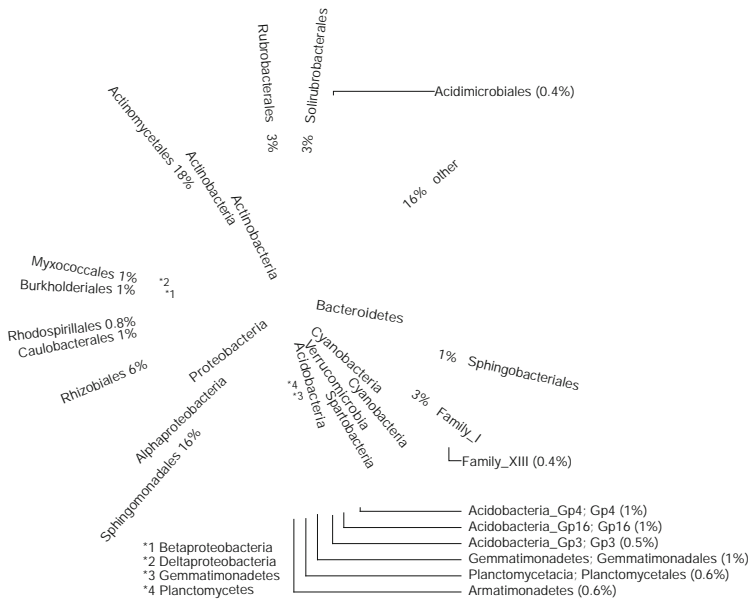


Fig. 5.1 Bacterial community structure of biocrusts from the Tabernas Desert, southeastern Spain. Based on 16S rRNA gene 454 pyrosequencing data; rarefaction with a depth of 1227 reads per sample. 16 % of the sequences could not be assigned to known bacterial taxa (Maier et al. 2014)

types (Steven et al. 2013a, b). As photic zones are generally limited to few millimeters beneath the soil surface, the distribution of Cyanobacteria is rather constrained in deeper layers (Garcia-Pichel et al. 2003). These differences were confirmed by Elliott et al. (2014) for biocrusts in the Kalahari Desert in Southern Africa. According to 16S rRNA gene 454 pyrosequencing, bacterial communities were distinct at the different soil depths, indicating niche partitioning of the microbial community between biocrusts and the subsurface soil. Again, Cyanobacteria (genus *Phormidium*) and Bacteroidetes were significantly more abundant in surface soils (0–1 cm depth), while in below-biocrust soils (1–2 cm depth) Acidobacteria, Actinobacteria, Chloroflexi, and Firmicutes were more frequently detected. This was broadly in line with observations made on samples of the Tabernas Desert, Spain (Maier et al. 2014). The surface soil communities differed from below-biocrust soil communities in having higher abundances of Cyanobacteria and at class level of Actinobacteria and Alphaproteobacteria. Acidobacteria and Verrucomicrobia, among others, as well as Crenarchaeota were overrepresented in the below-crust soil when compared to surface soil (Fig. 5.2).

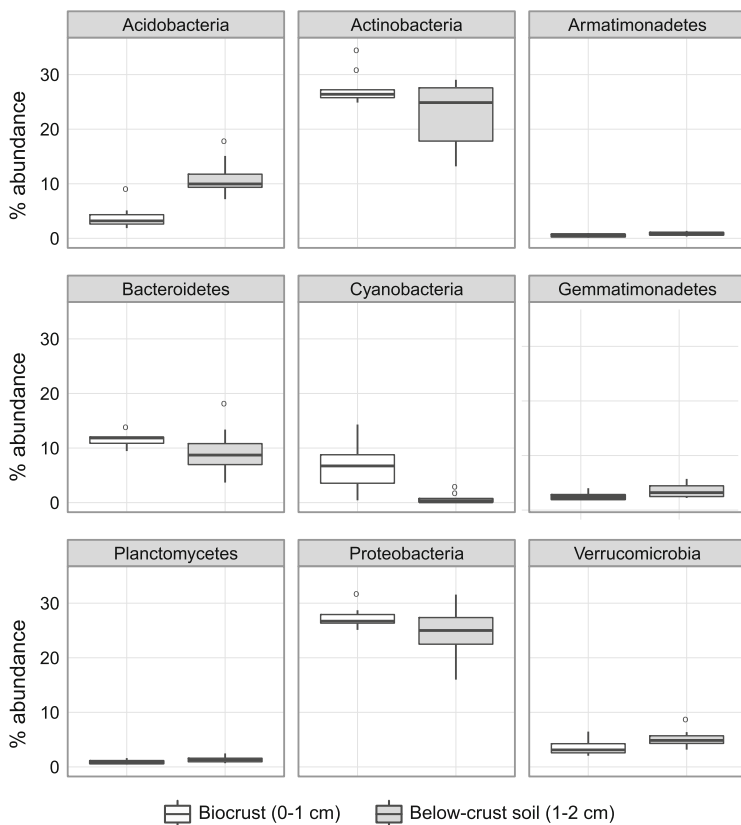


Fig. 5.2 Relative abundances of bacterial taxa in soil layers (biocrust, below-biocrust soil) from Tabernas Desert, southeastern Spain. Based on amplicon 16S rRNA gene 454 pyrosequencing data; rarefaction with a depth of 1227 reads per sample. Boxes represent the interquartile range; median values are shown as line and outliers as dots.  $n = 10$  per soil layer. Acidobacteria, Armatimonadetes, Cyanobacteria, Gemmatimonadetes, Planctomycetes, Verrucomicrobia ( $P \leq 0.05$ ), Actinobacteria, Bacteroidetes, Proteobacteria (not significant), paired t-test or Wilcoxon signed rank test for paired samples if assumptions for parametric tests were not met

### 5.2.1 Impact of Biocrust Age, Soil, and Vegetation Type on Bacterial Community Structure

Variations in biocrust community composition related to differences in biocrust maturity (Garcia-Pichel et al. 2003), soil types (Steven et al. 2013a, b), and distance from plants and/or impact of intermittent water flow have been the focus of some studies. *Microcoleus vaginatus* in biocrusts from the Colorado Plateau was less abundant, and cyanobacterial diversity was lower in gypsum soils compared to biocrusts on sand, silt, and shale soils (Garcia-Pichel et al. 2001). Steven

et al. (2013a, b) showed that Actinobacteria and Proteobacteria were enriched and Cyanobacteria depleted on gypsum relative to sand and shale soils.

The widely spaced plants in arid lands influence the distribution of soil bacteria. The composition of the total bacterial community, particularly Acidobacteria, was significantly different between the plant rhizosphere habitat of bunchgrasses and the plant interspace surface soils colonized by cyanobacterial biocrusts (Kuske et al. 2002). Based on high-throughput 16S rRNA gene sequencing, Elliott et al. (2014) found that vegetation type (trees, shrubs, grasses) influenced bacterial communities of biocrusts in the Kalahari Desert of Southern Africa. In contrast, Nagy et al. (2005) detected no differences in biocrust microbial diversity or composition between biocrusts under plant canopies and those in plant interspaces of the Sonoran Desert using DGGE, indicating a biocrust independence from higher plant resources. Steven et al. (2014) employed rRNA gene sequencing and shotgun metagenomic sequencing to compare the microbial communities inhabiting the root zones of the creosote shrub *Larrea tridentata* and the plant interspace biocrusts in Mojave Desert. The numerically abundant bacterial operational taxonomic units (OTUs) were present in both the biocrusts and root zones, but the relative abundance of those OTUs differed between habitats. The biocrust bacterial rRNA gene libraries were dominated by Cyanobacteria, followed by Proteobacteria and Actinobacteria, whereas the root zones contained about twice as many Actinobacteria and Proteobacteria. Members of the Alphaproteobacteria orders Rhodospirillales and Sphingomonadales were more abundant in the root zones than in biocrusts (Steven et al. 2014).

Steven et al. (2013b) aimed to investigate the impact of naturally occurring intermittent water flow in water tracks, zones of enhanced soil moisture in polar permafrost regions, on bacterial community structure. Cyanobacteria, in particular Oscillatoriales, were more abundant inside the water tracks compared to samples from outside the water tracks. Moreover, Acidobacteria showed responses to wetting pulses in the water tracks.

### 5.2.2 Manipulation Experiments: Response of Microbial Communities to Disturbance and Differing Light or Soil Temperature Conditions

Recently, it has been demonstrated that biocrust bacterial community structures are altered by chronic physical disturbance (e.g., foot trampling) at sites on the Colorado Plateau. A decline in diazotrophic Cyanobacteria such as *Microcoleus vaginatus* in trampled plots was observed using 16S rRNA T-RFLP, whereas the proportion of members of Actinobacteria, Chloroflexi, and Bacteroidetes increased. Furthermore, T-RFLP profiles from trampled biocrusts showed higher variability among replicates indicating an unstable state after disturbance (Kuske et al. 2012).

The influence of light conditions on the establishment of soil surface communities was investigated on pasture soil in microcosm experiments using ribosomal marker gene analyses. The experimental setup included trays filled with pasture soil that were exposed to a 16:8 h light/dark cycle at  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $20^\circ\text{C}$  for 80 days. Trays were covered either with a DS 226 light filter or an opaque filter to simulate dark conditions. At day 0, 20, 40, and 80 samples were taken using a steel sheet in order to separate the two soil layers, soil surface (upper 3 mm), and underlying bulk soil (3–12 mm). Similar phototrophic communities were found at the soil surface and in bulk soil in those microcosms exposed to light, indicating that light can influence phototroph community structure even in the below-biocrust bulk soil. The 454 pyrosequencing results revealed a significant selection for diazotrophic Cyanobacteria such as *Nostoc punctiforme* and *Anabaena* spp. and the green alga *Scenedesmus obliquus*. The soil surface also harbored different heterotrophic bacterial and fungal communities in the presence compared to the absence of light. In particular, a selection for the phylum Firmicutes was observed (Davies et al. 2013).

Angel and Conrad (2013) determined the metabolically active bacterial communities in biocrusts in the Negev Desert, Israel, by incubating samples under light-oxygenic and dark-anoxic conditions after simulated rainfall events. Using stable isotope probing of RNA and 454-pyrosequencing, they showed that the anaerobically growing bacterial communities were at first numerically dominated by members of the order Bacillales, which were later replaced by members of the order Clostridiales. Under aerobic conditions, Sphingobacteriales and Alphaproteobacteria (Rhizobiales, Rhodobacterales, Rhodospirillales and Rubrobacteriales) were more abundant. In dry biocrusts, Actinomycetales were the dominant bacterial order. By the end of the incubation, however, Actinomycetales were rarely detected ( $<1\%$  of the community), indicating complex communities dynamics in biocrusts as these change from dormancy to an active state (Angel and Conrad 2013). Johnson et al. (2012) monitored impacts of increased soil temperature ( $2\text{--}3^\circ\text{C}$ ) and altered precipitation patterns on biocrusts in the cold desert of the Colorado Plateau over 2 years. Increased soil temperature did not affect the cyanobacterial biocrust. However, they found significant declines in the surface soil biomass and chlorophyll a concentration in response to increased frequency of small precipitation treatments. Furthermore, a change of the bacterial community composition at phylum and family level was observed, with the proportion of Cyanobacteria being considerably reduced.

### 5.2.3 Novel Bacterial Species

Only few novel species of Bacteroidetes, Alphaproteobacteria, and Actinobacteria originating from biocrusts have been described so far, including *Dyadobacter crusticola* and *Hymenobacter arizonensis* (Bacteroidetes), *Sphingomonas mucosissima*, *Sphingomonas dessicabilis*, and *Belnapia moabensis*

(Alphaproteobacteria), *Modestobacter versicolor*, and *Patulibacter americanus* (Actinobacteria). All these species originated from Colorado Plateau sites (Reddy and Garcia-Pichel 2005, 2007, 2009, 2013, 2015; Reddy et al. 2006, 2007). Despite their high diversity, representation of biocrust bacteria in culture collections and curated sequence databases is still very limited. Owing to this limitation, most non-cyanobacterial sequences from DNA-based bacterial surveys cannot be reliably named or taxonomically defined. Studies to date have used primarily sequence-based species designations (e.g., operational taxonomic units, OTUs) and/or have binned their sequence data into higher-order taxa such as families and phyla. Discovery and characterization of these dryland-adapted bacterial species is a challenging area for future study.

### 5.3 Non-lichenized Fungi

Biocrusts are niches for specialized free-living fungi, which endure the conditions of desiccation stress. These fungi can play a key role in mediating nutrient exchange between biocrusts and plant vegetation in arid landscapes, an idea which has become known as the fungal loop hypothesis (Green et al. 2008; Collins et al. 2008, see also Chap. 19 by Zhang et al.). However, until now, the study of free-living fungi in biocrusts has been mostly descriptive, with the goal to assess biodiversity and discover the parameters influencing microbial species composition (Bates and Garcia-Pichel 2009, 2010, 2012; Steven et al. 2015).

Fungal communities in biocrusts vary among regions and soil types. Diverse fungal communities have been reported from arid soil lands in the Western USA (Ranzoni 1968) including the Sonoran Desert (States 1978), the cool desert of Arizona, and sagebrush-grassland in South Central Wyoming (Christensen, unpubl.). Greater diversity was reported for fungi than for Cyanobacteria in Colorado Plateau biocrusts (Bates and Garcia-Pichel 2009). Fungal diversity varies with biocrust age and type, and higher fungal diversity occurs in later successional stages than in younger patches (Bates et al. 2012). In addition, qualitative and quantitative changes in fungal assemblages have been reported to be associated with disturbance sites (States and Christensen 2001). Fungal community composition in biocrusts studied so far was dominated by Ascomycota and was highly variable across small spatial distances. Many of them have dark pigmented cell walls and are also known as dark-septate fungi. Consistently, these comprise lineages of the class Dothideomycetes, and in particular representatives of the Pleosporales (e.g., Green et al. 2008; Bates et al. 2010; Abed et al. 2013). Although they are ubiquitous, most of these fungi seem to lack sexual fruiting bodies in biocrusts.

Dark-septate fungi have melanin-rich cell walls, a pigment usually resulting from polymerization of phenolic compounds (e.g., di-hydroxy-naphthalene in many Ascomycetes). This pigment is thought to confer tolerance against multiple abiotic stress factors, including desiccation and UV irradiation (Gostincar et al. 2010).



Pleiosporalean dark-septate fungi are also known to be part of fungal communities associated with plant roots in arid grassland. Their functional analogy to mycorrhizal fungi has been suggested (Jumpponen 2001; Mandyam and Jumpponen 2005), which is interesting as no arbuscular mycorrhizal (AM) fungi have been detected in biocrusts so far (Bates et al. 2010, and references therein). In addition, some arid land soil fungi have been shown to have a vital role as denitrifiers in the N cycle (Marusenko et al. 2013). These functions are well in line with the fungal loop hypothesis.

The hyphomycete genus *Alternaria* seems to be a very common and widely distributed representative in biocrusts (Bates et al. 2010). Coprophilous, moss-, and lichen-associated fungi, including the genera *Acremonium* or *Phoma*, also appear to be main biocrust components (Bates et al. 2012; Steven et al. 2015). In contrast, only few taxa of yeasts are known from biocrusts. Mesophilic yeasts hardly develop in deserts, as they prefer nutrient-rich habitats with high water availability, and only extremotolerant black yeast species present exceptions. The black yeast *Exophiala crusticola* was originally described from the Colorado Plateau and is also present in the Great Basin Desert, USA. Like many other black yeasts, the species can produce both yeastlike cells as well as torulose hyphae (Bates et al. 2006). More yeasts might be present in biocrusts of cool habitats, but this remains to be studied.

## 5.4 Lichens as Microbial “Hubs”

Lichen symbioses are life-forms of fungi that form composite organisms comprising the dominant fungus and a photosynthetic partner (green algae in about 90 % of lichen species, Cyanobacteria in >9 % of lichen species, and <1 % with both as partners). The photobiont is usually sheltered in tight fungal structures. The composite structure, the lichen thallus, is often highly resistant to environmental fluctuations and extremes of cold and heat. Lichens can be prominent components of many biocrusts in habitats with periodic drought and where mechanical perturbation is negligible. In such habitats, lichens often develop species-rich communities which display various life strategies and growth forms. Usually, lichen-dominated biocrusts do not only comprise crustose lichens, i.e., those that tightly seal the soil surface with their entire lower thallus surface. Many other species also develop squamulose phenotypes or forms which elevate their structures above the ground. As lichens are covered in Chap. 7 by Rosentreter et al., we restrict to some general remarks concerning lichens as a niche for other microorganisms.

Owing to their persistence and their morphological diversity, lichen thalli provide a rich diversity of small-scaled niches for microorganisms, in particular fungi and bacteria. While fungi associated with lichens have been studied for a long time, the common presence of bacteria received more attention only recently (Grube et al. 2009 and references therein). Metagenomic and metaproteomic data suggest that these bacteria are involved in complex interactions in the lichen as a “holobiont” (Grube et al. 2015), which may change the view of lichens as a two-tier



relationship between a mycobiont and a photobiont. Since bacteria attach primarily to the surfaces of lichen thalli, their larger morphological structures play a crucial role, also at the interface with soil.

The attachment of lichens to the soil is accomplished by characteristic structures, which have been studied by light and electron microscopy (Asta et al. 2001). Attachment structures range from mycelial felts of narrowly spaced hyphae (rhizohyphae) to rootlike rhizines that are composed of conglutinated hyphae (Poelt and Grube 1993). However, it still needs to be studied to what extent these structures influence the microbial colonization of the soil beneath. The diversity of chemical patterns and phenotypic shapes of upper surfaces of lichen thalli likewise contributes to variations in the microecological environment for associated microbes. Thalli, which detach from the soil surface with peripheric lobes or even develop leaflike or shrubby thalli, create additional habitats between thalli or between thalli and the soil for bacterial and fungal communities. Also, bacteria and fungi can colonize niches between areoles and squamules of crustose lichens. Some observations of these microhabitats are presented in more detail below. While bacteria mostly colonize coherent surfaces of lichens and only few of them may penetrate more deeply (Erlacher et al. 2015), lichenicolous fungi commonly invade the interior of their hosts with their filamentous hyphae to benefit from their symbiotic structures.

### 5.4.1 Life Strategies and Diversity of Lichenicolous Fungi

Lichenicolous fungi comprise all species living in or on lichens beside the thallus-forming fungus. This biological group has been studied extensively throughout the history of lichens. Approximately 1800 species of lichenicolous fungi have been described, but new species are still being discovered (e.g., Lawrey and Diederich 2011). A detailed report on the lichenicolous fungal diversity on soil lichens is beyond the scope here, but we would like to draw attention to some general features. Most lichenicolous fungi are highly specific regarding the hosts (i.e., the lichenized fungal species), which they colonize by means of localized mycelia that eventually develop sexual structures (these are traditionally important diagnostic characters, Fig. 5.3). Some species, however, are able to develop their own symbiotic thalli on their hosts and are then known as lichenicolous lichens. These are also known from soil-inhabiting lichens, where some of these species exploit their lichen host only in early phases of their life cycle, e.g., *Arthrorhapis citrinella* on *Baeomyces rufus* and *Diploschistes muscorum* on *Cladonia* species. In later stages, the thalli of these juvenile parasites become independent from their hosts. Interestingly, algal switching was observed at the onset of parasitic thallus reorganization by *Diploschistes muscorum* (Friedl 1987). Initially, this species lives with the algae of the infected hosts and may later continue thallus growth with another species of algae. This does not seem to be a completely fixed strategy, as we recently observed mature *Diploschistes muscorum* specimens maintaining the photobionts of the host

Fig. 5.3 Examples of lichens infected by different lichenicolous fungi: (a) placodioid lichen crust infected by *Dacampia hookeri*, which itself is infected by the lichenicolous fungus *Stigmidium schaeferi* (arrows indicate the fruiting bodies, perithecia, of the lichenicolous fungus); (b) foliose *Solorina crocea* infected by the lichenicolous fungus *Rhagadostoma lichenicola* (arrows indicate the fruiting bodies, perithecia, of the lichenicolous fungus); (c) sorediate crustose lichen infected by *Arthrorhaphis citronella* (arrows indicate the fruiting bodies, apothecia, of the lichenicolous fungus); (d) *Solorina octospora* infected by the lichenicolous fungus *Dacampia engeliana* (arrows indicate the fruiting bodies, perithecia, of the lichenicolous fungus). Scale bars: (a, b, d) 2 mm; (c) 1 mm

lichen, while others hosted multiple algal types (Wedin et al. 2015). Maintenance of the host's algae has been observed also in other lichenicolous lichens (de los Rios et al. 2002).

Even though lichenicolous species without a distinct thallus organization are usually called non-lichenized, the biology of some species is not entirely clear. The fungus *Tetramelas pulverulentus* (on moss inhabitant *Physconia muscigena*) slightly modifies the host morphology with externally recognizable infection symptoms. This species develops peculiar endokapylic (i.e., mycelia covered by strata of the host) lichenized thalli. Many other species spread infectious hyphae within their hosts and either do not produce any symptoms or become destructive for the host structures. Whether the hyphae of the lichenicolous species infect the algae and/or the fungi or remain without affinity for any of the host's bionts is still unknown in

many cases. Infectious hyphal structures of mycobiont-parasitic species were described by de los Rios and Grube (2000). These structures comprise simple or complex haustoria with fingerlike projections into the host hyphae (observed in *Pyrenidium actinellum* infecting the soil-inhabiting *Peltigera venosa*). Even the growth of hyphae inside of host hyphae has been observed, as for *Dacampia engeliana* infecting the soil-inhabiting *Solorina* sp. Simple haustoria are also present, for example, in species that exploit the algae of their hosts such as known from the genus *Zwackhiomyces* (Grube and Hafellner 1990). Other algal exploiters establish contacts with the photobionts of their host lichens using appressoria (e.g., lichenicolous species in the genus *Arthonia*).

Even more complex cases of interactions, including the phenomenon of hyperparasitism are observed in various manifestations in soil crust lichens. Juvenile lichen-parasitic lichens, such as *Arthrorhaphis citrinella* (lichenicolous on *Baeomyces*, *Cladonia-squamules*, or decaying lichens), are occasionally infected by hyperparasitic non-lichenized fungi (*Stigmidium arthrorhaphidis*, *Cercidospora trypetheliza*, *Cercidospora soror*). Recently, hyperparasitism was also described among lichens: the lichenicolous lichen *Rhizocarpon diploschistidina* parasitizes the lichen *Diploschistes muscorum*, which itself grows as a juvenile parasite on *Cladonia* species (Lumbsch et al. 2011). These few examples demonstrate that the diversity of fungal interactions in soil crusts is a fascinating topic of biology. These specific interactions remain unsolved in pure sequencing studies, as their discovery still requires meticulous microscopic investigation.

#### 5.4.2 Bacterial Habitats in Soil Lichens

Certain species of lichens regularly form interactions with Cyanobacteria, usually *Stigonema* spp., which are commonly present in biocrusts and perhaps more frequently in older successional stages of cyanobacterial crusts. This phenomenon is known since long as cyanotrophy (Poelt and Mayrhofer 1988), which indicates that certain cyanobacterial consortia facilitate the development of lichens. With the development of lichens, multiple new microhabitats now develop to host other bacteria. Using confocal laser scanning microscopy (CLSM), we demonstrated that bacteria associated with biocrust lichens are tightly connected with fungal structures and essentially represent fungal-bacterial interactions (Fig. 5.4). Maier et al. (2014) demonstrated that bacteria colonize the upper cortex in *Psora decipiens* and *Toninia sedifolia* (Fig. 5.4d). Using 16S rRNA gene-targeted fluorescence in situ hybridization (FISH) experiments, bacteria could be seen attached to the hyphal net at the thallus-soil interface of *Psora decipiens*. This pattern agrees with results of Muggia et al. (2013) for other biocrust lichens. In that study, bacterial cells were intermixed with photobiont cells in the lower parts of the lichen thalli and on the surface of the squamules of *Baeomyces placophyllus* and *Psora decipiens* (Muggia et al. 2013). In the inconspicuous thallus structures of *Arthrorhaphis citrinella*, *Baeomyces rufus*, *Imadophila ericetorum*, and

Fig. 5.4 Fluorescence in situ hybridization combined with confocal laser scanning microscopy to visualize bacteria in lichen biocrusts. (a) *Baeomyces rufus*; granulose thallus, which does not display a differentiation in algal layer and medulla, mixed with bacterial colonies. (b) *Immadophila ericetorum*; leprose lichen, no internal organization with green algal layer, bacterial colonies on the upper surfaces shown in the left part. (c) *Psora decipiens*, part of medulla, with bacterial colonization. (d) Thallus cross section of *Toninia sedifolia*, richly developed bacterial colonies on the upper cortex. Merged 4-color images; the 16S rRNA targeted 5' end-labeled Fitc oligonucleotide probe ALF968 was applied to visualize Alphaproteobacteria and Cy3-(indocarbocyanine)-labeled EU388mix to visualize Eubacteria. Calcofluor White was used to stain fungal structures. Colors: Eubacteria red, Alphaproteobacteria yellow in (a–c), pink in (d); autofluorescence of algae green; fungal structures gray. Arrows indicate bacterial cells. Scale bar: 30  $\mu\text{m}$ . The settings for excitation were 405, 488, 532, and 635 nm. The ranges of wavelength set to detect the emission signal of the fluorophores were at 420–480 nm (CFW), 500–550 nm (Fitc), 550–600 nm (Cy3), and 650–700 nm (Cy5)

*Trapeliopsis granulosa*, we also observed associations of bacteria with hyphae and algae, as well as bacteria on the outer surface of the mycobiont-photobiont aggregates (Fig. 5.4a, b). Due to the small-scale variation in ecological parameters in the stratified thallus and soil beneath, the composition of bacteria in lichens may likewise vary at very small scales. The host-specific enrichment of bacteria in lichens and in the subjacent layers of the substrate (the hypothallosphere) has also been demonstrated earlier for rock-inhabiting biocrust-forming lichens (Bjelland

et al. 2010). However, in order to interpret the specificity of bacteria in soil underneath lichens correctly, also the influence of possibly co-occurring non-lichenized fungi needs to be considered, since these free-living fungi could also influence bacterial diversity. Using microscopic observations, we commonly find hyphae of different types beneath soil biocrust lichens (Grube, unpublished data). Interestingly, we also observed that dark pigmented hyphae were poorly colonized by bacteria, whereas hyaline hyphae in biocrusts were frequently associated with small bacterial colonies.

One important factor for the small-scale spatial patterning of bacteria could be the accessibility of air and water within lichen thallus structures. Souza-Egipsy et al. (2002) studied the relative distribution of air- and water-filled spaces in the thallus and lichen-substrate interface using scanning electron microscopy and found correlations with the morphological features of the stratified thalli. According to their study, a water film covered the surface of *Diploschistes diacapsis* and *Squamarina lentigera* after hydration. Microscopic fissures between the areoles in the thalli of *Diploschistes diacapsis* facilitated seeping of water into the thallus without flooding the algal layer. The water then appeared to be retained in the lower part of the medulla. These differences certainly have an impact on the bacterial colonization, which needs to be further explored. In this context it is interesting to note that there are also differences of water conductance within lichen species depending on the geographic origin. According to own observations, the uptake of water is regularly faster in lichens of the Mediterranean provenience compared to those from alpine habitats (Grube, unpublished data).

FISH is an excellent tool to visualize the localization of specific bacteria in their histological and environmental context (Amann and Fuchs 2008). For the first time, Muggia et al. (2013) combined FISH with CLSM to visualize the lichen-soil interface in alpine lichen biocrusts. Their study also highlighted some technical challenges. While some lichen species have compact superficial thalli, the thallus of others is closely connected with the soil (Fig. 5.4a–c). Dry samples are very brittle and thus easily disintegrate into the different compounds during the preparatory work. Muggia et al. (2013) therefore suggested using blocks of thalli with attached soil (up to a few millimeters) for fixation and embedding prior to cutting 30  $\mu\text{m}$  thick sections that are subsequently transferred to poly-L-Lysine-precoated microscope slides for further processing. Their study succeeded to visualize the predominance of Alphaproteobacteria and Acidobacteria in the studied soil crust lichens *Arthrorhaphis citrinella*, *Baeomyces placophyllus*, *Baeomyces rufus*, *Imadophila ericetorum*, *Psora decipiens*, and *Trapeliopsis granulosa*. Acidobacteria appeared to be particularly common in the lower part of and beneath the lichen thallus. This agrees with Grube et al. (2012), who studied the diversity of bacteria associated with the arctic-alpine soil lichen *Solorina crocea* using 16S rRNA pyrosequencing and found high abundances of Acidobacteria, Planctomycetes, and Proteobacteria. The presence of Acidobacteria in these habitats possibly correlates with the fluctuating water conditions and the acidic substrate. In addition to these initial studies focusing on alpine biocrust habitats, Maier et al. (2014) studied the bacterial communities of lichens from the Tabernas Badlands (Almería, Spain) in more

detail. Their results revealed the dominance of Proteobacteria, Actinobacteria, Bacteroidetes, Acidobacteria, and Cyanobacteria.

#### 5.4.3 The Impact of Lichenicolous Fungi on the Lichen-Associated Bacterial Community

As the symbiotic integrity of lichens can be affected by the fungal parasites of lichens, a shift in the composition of the bacterial associates of these lichens might be the consequence. This hypothesis prompted Grube et al. (2012) to study the soil lichen *Solorina crocea*, which is commonly infected by a lichenicolous fungus known as *Rhagadostoma lichenicola* (Sordariomycetes). Forming black-colored perithecia on the living lichen host, *Rhagadostoma lichenicola* is a specialized biotrophic parasite of *Solorina crocea*. The grouped blackish ascomata emerge from the upper surface of the host thallus (Fig. 5.3b). Microscopy reveals a richly branched, dark mycelium beneath the parasite's fruiting bodies in the host plectenchyma. The mycelium extends locally into the internal layers of the nearby regions of the lichen thallus. No specific infection structures with algal or fungal host cells are observed. Apparently, these infections do not immediately impair the host's fruiting body formation nor do they kill the host. However, Grube et al. (2012) found evidence for a shift in the bacterial communities when data were analyzed at the strain level. Strain-specific abundance shifts occurred among Acidobacteria. The consequences for the bacterial community are clearly more pronounced in the course of the infection by lichenicolous lichens, which completely restructure the thallus of the host lichen. By analyses of different infection stages of *Diploschistes muscorum* on the host *Cladonia symphylicarpa*, Wedin et al. (2015) found a decrease in relative abundance of Alphaproteobacteria. Also, Armatimonadia, Spartobacteria, and Acidobacteria were more abundant in *Cladonia*, but Betaproteobacteria increased gradually in relative abundance during the transition to mature *Diploschistes muscorum*. These results from few selected examples offer only a glimpse of the enormous complexity of fungal-bacterial interactions and the parameters regulating their diversity in biocrusts.

### 5.5 Conclusions

High diversity has sometimes been related to stability in ecosystems, and as we have seen here, biocrusts are definitely hotspots of fungal and bacterial diversity. However, as Ives and Carpenter (2007) point out, understanding the diversity-stability relationship needs an evaluation of the environmental drivers affecting both. For developing the complexity of fungal-bacterial life, the biocrust system depends largely on the stability of soil. Once the substrate is disturbed

mechanically, the biocrust community will progressively collapse with increasing physical stress (e.g., induced by wind and water). Thus, mechanical disturbance must be avoided not only to secure known ecosystem services provided by biocrusts (prevention of erosion and water runoff, carbon and nitrogen fixation, etc.) but also to save them as a precious microbial resource of yet unexplored biotechnological interest. Their further exploration requires integrating approaches. Continued and expanded culture-independent approaches still need to be coupled with physiological assessments of cultured isolates to improve our understanding of bacterial and fungal functions (da Rocha et al. 2015).

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# Chapter 6

## Bryophytes Within Biological Soil Crusts

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### 6.1 Introduction

Bryophytes (mosses, liverworts, and hornworts) can play an integral role in biocrust development, ecology, and diversity, yet the role of bryophytes in crusts has received comparatively little attention compared to the roles played by other organisms. In some ecosystems, bryophytes may be a conspicuous component of biocrusts, particularly in the later stages of crust development (Lange et al. 1997), where a diversity of morphological and physiological traits gives them a unique role in biocrust ecology.

Biocrust bryophytes contribute to soil surface stabilization through water entrapment and facilitation of water infiltration (Zhang et al. 2009), whereby reducing surface runoff (Zhao et al. 2014). They also promote soil formation through acceleration of chemical and physical weathering of soil and entrapment of mobile surface particulates (Danin and Gaynor 1991). Bryophytes also influence carbon and nutrient cycling through contributions of organic matter directly to the soil

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(Longton 1992; Melick and Seppelt 1992; Melick et al. 1994) and through indirect effects on soil nitrogen availability (Reed et al. 2012). Many crust bryophytes also provide habitats for invertebrates, algae, cyanobacteria, fungi and lichens (Davidson et al. 1990) and are useful in monitoring landscape health.

## 6.2 Bryophyte Diversity in Biocrusts

Global bryophyte diversity in biocrusts comprises at least 320 species, the majority of which is mosses (>250 sp.), followed by liverworts (>66 sp.). Biocrust bryophyte diversity has been examined most extensively in dryland ecosystems in North America and Australia, but records also exist from Europe, South America, Asia, and Antarctica.

### 6.2.1 Regional Diversity

Globally, the greatest biocrust bryophyte species richness has been recorded in the drylands of the Pacific region (Australia and New Zealand) and in Europe. In North and Central America, biocrust bryophytes are found throughout the Western USA and Northern Mexico in hot desert (Mojave, Sonoran, Chihuahuan) as well as cool desert ecosystems (Colorado Plateau, Great Basin; Fig. 6.1). Early accounts of hot desert bryoflora sampled at sites in the Mojave, Sonoran and Chihuahuan Deserts described species from the families Pottiaceae, Bryaceae, and Grimmiaceae and estimated total species numbers to be <25 (Nash et al. 1977). More recent estimates of the number of bryophyte taxa in hot and cool deserts in these regions, however, place bryophyte diversity above 300 species (two hornworts, 26 liverworts, 262 mosses), the majority being members of biocrust communities (Stark and Whittemore 2000; Brinda et al. 2007).

In Australia, the number of biocrust bryophyte taxa is estimated to be at least 130, including >30 liverworts and >100 mosses (Fig. 6.1). In a study of the distribution and floristics of bryophytes over a 500 000 km<sup>2</sup> area of Australian dryland crusts, Eldridge and Tozer (1996) reported 56 bryophyte taxa (41 mosses, 15 liverworts), dominated by the moss family Pottiaceae and the liverwort genus *Riccia* (Fig. 6.2a). While many bryophytes were ubiquitous in the study area, some were restricted to certain landform types due to the amount and seasonality of rainfall or calcium levels in the soil (Downing and Selkirk 1993).

Biocrust bryophytes are also common in drylands of Europe (90 species) and Asia (28 species), Africa (22 species), and South America (24 species), as well as ice-free soils on Antarctica (14 species, Fig. 6.1). In crusted soils of the Negev Desert, common genera include *Tortula*, *Bryum*, and *Brachymenium* (Lange et al. 1992; Kidron et al. 2002). In the Gurbantunggut Desert in Northwestern China, *Tortula*, *Bryum*, and *Crossidium* are the most common genera found in

Fig. 6.1 Diversity of bryophytes on a continental scale (Graphic Burkhard Büdel)

biocrusts (Zhang et al. 2007; Wu et al. 2009), while on the Loess Plateau, the most dominant genus is *Didymodon* (Zhao et al. 2014). There are over 400 recorded bryophyte species on the Antarctic continent (Green and Broady 2003; Peat et al. 2007), yet only 15 have been reported as forming a component of biocrusts.

Fig. 6.2 (a) *Riccia* sp., a hairy species forming gray, circular thalli; located in the left to central part of the image. In the right hand part an unidentified moss. Biocrust after several months of drought; Queensland, Australia (Photo Burkhard Büdel). (b) *Riccia* spp.; species without hairs (left) and with hairs (right) next to each other; biocrust from Rehoboth, Namibia (Photo Burkhard Büdel). (c) *Riccia* sp. and a leafy liverwort forming part of a biocrust, Caatinga biome, Brasil (Photo Burkhard Büdel). (d) *Campylopus introflexus*, an invasive moss. (e) *Polytrichum piliferum*. (f) *Racomitrium canescens*. (g) *Trichostomum crispulum*, all in the biocrust of an abandoned stone quarry, Germany (Photo Burkhard Büdel). (h) *Bryum argenteum* dominated biocrusts, intermingled with blackish-brown colonies of the cyanobacterium *Nostoc commune*, melt water flush at Canada Glacier, Taylor Valley, Antarctica (Photo Burkhard Büdel)

### 6.2.2 Global Moss Diversity

In both North America and Australia, the moss family Pottiaceae dominates the bryoflora of soil crusts, with Bryaceae usually running a close second (Rosentreter et al. 2007). In Australia, annual and ephemeral species of Funariaceae (*Entosthodon* spp.) may also occur after rainfall events and together with *Fissidens megalotis* often play an important role as first colonizers of disturbed soils prior to the re-establishment of more characteristic soil crust assemblages (Downing and Selkirk 1993; Eldridge and Tozer 1997; Stoneburner et al. 1993). In biocrusts of southern Africa, *Ceratodon purpureus* is a dominant species (Weber et al. 2012), but also species of the genera *Bryum*, *Crossidium*, *Tortula*, and *Campylopus* occur (Büdel et al. 2009).

In Asia, 23 species of biocrust mosses have been reported, where *Barbula*, *Bryum* and *Tortula* are the most common genera. In the Gurbantunggut Desert of Northwestern China, moss crusts occur on calcareous semi-fixed dunes, usually in the swales or on windward faces of dunes. Dominating species in this area are *Syntrichia caninervis* and *Bryum argenteum*, and other commonly observed taxa include *Tortula muralis*, *Crossidium chloronotos* and *Bryum capillare* (Zhang et al. 2007). Of the 15 species of confirmed biocrust bryophytes in Antarctica, all are mosses, the most common genera being *Bryum* (four species) and *Grimmia* (three species).

### 6.2.3 Global Liverwort Diversity

Thallose liverworts, particularly *Riccia* (Fig. 6.2b and 6.2c) and *Asterella*, are abundant in biocrusts on calcareous substrates in the Australian arid and semiarid zones (Downing and Selkirk 1993; Eldridge and Tozer 1997), in some cases, producing crusts composed almost exclusively of liverwort thalli. *Fossombronia* is also an important component of biocrusts, but in southern Australia, it is restricted to higher rainfall ecosystems of temperate to semiarid forests and rangelands (Milner et al. 2011; Eldridge and Tozer 1997). *Riccia* is well known from dryland calcareous substrates but can also be a dominant component of crusts from non-calcareous substrates, e.g. shallow, siliceous soils over granitic inselbergs of Namibia (Bornefeld and Volk 2002) and sandy soils in Namibia and South Africa (Büdel et al. 2009). In North American biocrusts, common liverwort genera include *Cephaloziella*, *Athalamia*, and *Fossombronia* (Rosentreter et al. 2007). Few liverwort taxa have been documented in Asian biocrusts, but where they occur, *Riccia* is most commonly observed. Antarctica, while exhibiting a relatively species-rich liverwort flora of at least 50 species, currently does not exhibit any records of liverworts in crusted soils.

## 6.3 Bryophyte Establishment in Biocrusts

### 6.3.1 Establishment in Dryland Biocrusts

In contrast to temperate areas, where bryophytes may establish early in vegetation successional sequences following disturbance events (Fig. 6.2d-g), in dryland ecosystems, bryophyte biocrusts are generally accepted to be the third successional stage in crust development, after cyanobacterial- and lichen- dominated crusts. Bryophyte crusts are best developed on calcareous fine-textured silt and clay soils, where initial colonization of fungi, cyanobacteria, and microalgae facilitates bryophyte establishment by providing soil stability.

In recent years, research concentrating on the mechanisms that may assist in the restoration and recovery of biological soil crusts has helped elucidate colonization patterns during crust development. Photobionts (cyanobacteria, microalgae) were initially thought to be the first soil colonizers because of the lack of carbon for heterotrophic microbes. However, it is now widely accepted that oligotrophic bacteria and fungi precede colonization by cyanobacteria (Bamforth 2008; Pan et al. 2010; Wu et al. 2010). Filamentous cyanobacteria of cyanobacterial crusts, which follow soil stabilization by oligotrophic bacteria and fungi, exude polysaccharide sheaths which bind soil particles, enhance moisture uptake and increase soil fertility by N-fixation (Bailey et al. 1973; Belnap and Gardner 1993; Campbell et al. 1989; Rosentreter et al. 2007; Zhang et al. 2011a, b; see Chaps. 4 by Büdel et al., 17 by Chamizo et al., and 14 by Barger et al.). Over time, these collective processes act to facilitate bryophyte colonization and later dominance in biocrusts.

Bryophyte establishment on sand dune crusts is less common, as the substrate chemistry and disturbance regime typically favor green algal communities in the upper soil layers (Downing and Selkirk 1993; Rosentreter et al. 2007; Zhang et al. 2011a, b). However, bryophytes are common and abundant in biocrusts on dunes along the southern coast of Australia, where there is an abundance of  $\text{CaCO}_3$  (Moore and Scott 1979). Bryophyte crusts are much less common on siliceous sands of the eastern coast of Australia, potentially because of the relative absence of a calcareous substrate.

### 6.3.2 Establishment in Polar, Alpine, and Antarctic Biocrusts

In polar and alpine regions, crusts may develop in rock interspaces, on exposed soil at the margins of ice fields, or following glacial recession (Fig. 6.2h). Compared to crusts in dryland ecosystems, there have been few studies of alpine or polar biocrusts (but see: Pérez 1997; Gold et al. 2001; Huber et al. 2007). However, in terms of patterns of bryophyte establishment in crusts, many commonalities exist.

In contrast to drylands, polar and alpine regions present particularly unstable surfaces for the formation of biocrusts. Nutrient levels may be low, free water may be



unavailable for plant growth during much of the year, and cryoturbation causes significant disruption of soil integrity. Pioneer colonists such as bacteria, cyanobacteria, algae, and fungi are crucial in stabilizing otherwise mobile surfaces (Wynn-Williams 1986, 1993; Elster 2002). These organisms initiate the basis of an organic- and nutrient-enriched medium on which more complex organisms or secondary colonizers (bryophytes, lichens and small herbs) may establish (Tearle 1986; Greenfield 1989). In alpine regions, species-rich assemblages of cyanobacteria and eukaryotic algae along with Aeolian deposits can contribute to initial pedogenesis in primary stages of crust formation (Peer et al. 2009). Later stages of development in many alpine regions are dominated by lichens, but abundant subsurface bryophyte protonema and rhizoids reveal that bryophytes, while not usually competitively dominant, can contribute to late stage crust diversity (Peer et al. 2010).

In continental Antarctica, where the extent of ice-free soil is a mere 0.8 %, development of biocrusts appears to be limited in extent and composed almost entirely of primary colonizers. There are extensive moss-dominated sites, e.g., Windmill Islands (66°S, 110°E), Botany Bay (77°S, 162°E), and Canada Glacier (78°S, 163°E; Fig. 6.2h), where there is an abundance of nutrients derived largely from former (Windmill Islands) or extant (Botany Bay) penguin or other seabird colonies and ample moisture during the late spring, summer and early autumn period. These areas represent biodiversity hotspots rather than localities with typical biocrust development. More typical biocrust development is rare and dominated by microbial primary colonizers, while secondary colonizers appear to be almost entirely lichens (Seppelt, personal observations).

In the Maritime Antarctic, at Jane Col on Signy Island, unvegetated soil contains a diverse and often abundant reservoir of bryophyte propagules. Similar to the continental Antarctic, this reveals the potential for bryophyte establishment under favorable conditions. Most of these bryophyte propagules originate locally, with a small proportion derived from external or remote sources (Lewis Smith 1993). Most propagules, however, are vegetative diaspores (detached leaves, deciduous stem apices, specialized gemmae, deciduous leaf apices, bulbils), and limited rates of sexual reproduction likely limit the abundance and establishment of crust bryophytes in these regions. In particular, species with spores that germinate under experimental conditions of favorable moisture have only sporadic occurrence in the field. Less than 20 % of the Signy Island bryoflora species regularly produce spores, and the dominant fell-field species produce recalcitrant spores with little germination (Webb 1973).

## 6.4 The Role of Substrate in Bryophyte Abundance and Diversity

Biocrusts can be found on a range of substrates, and substrate chemistry plays a key role in the abundance and diversity of crust bryophytes that occur. Much research has focused on comparisons between species assemblages growing on substrates

either high or low in calcium carbonate, as well as those growing on substrates characterized by high levels of gypsum and dolomite.

#### 6.4.1 Calcareous Substrates

Distinctive calcium carbonate ( $\text{CaCO}_3$ ) bryophyte floras have been described for many parts of the world, clearly demonstrating the dichotomy between bryophytes with an affinity for  $\text{CaCO}_3$  (calciphiles or calcicoles) and those that grow only in the absence of  $\text{CaCO}_3$  (calcifuges). This dichotomy is also apparent in bryophyte communities of biocrusts, where patterns of diversity and abundance are closely related to differences in substrate chemistry.

Bryophytes respond markedly to soil  $\text{CaCO}_3$ , pH, and electrical conductivity (Anderson et al. 1982; Eldridge and Tozer 1997; Ponzetti and McCune 2001).  $\text{CaCO}_3$  in particular contributes to abundance and diversity of bryophytes: biocrusts on calcareous substrates generally support a greater ground cover and species richness of bryophytes than those of non-calcareous substrates (Downing and Selkirk 1993; McCune and Rosentreter 2007). Soil  $\text{CaCO}_3$  levels also influence the ratio of acrocarpous to pleurocarpous mosses, the ratio of thallose to leafy liverworts and the presence of certain bryophyte families, genera and species. In particular, acrocarpous mosses and thallose liverworts have been shown to increase in abundance compared to pleurocarps and leafy liverworts with increasing  $\text{CaCO}_3$  (Downing 1992).

In spite of the differences between bryophyte assemblages on calcareous and non-calcareous soils, these patterns are not universal and may be context dependent. For example, Downing and Selkirk (1993) found that there was no clear dichotomy between calciphiles and calcifuges in Australian biocrusts. Rather, the bryoflora of calcareous substrates was composed of a few exclusively calciphilous species together with many opportunistic, non-substrate-specific species.

$\text{CaCO}_3$  can also interact with other factors such as soil pH to drive patterns of crust development and diversity. In shrub steppe in Oregon, USA, Ponzetti and McCune (2001) recorded considerable differences in dominant bryophyte species and total crust cover between sites with high levels of  $\text{CaCO}_3$  and high pH, and those with lower levels and low pH, concluding that crusts were particularly sensitive to subtle changes in soil chemistry. In semiarid south-eastern Australia, Downing and Selkirk (1993) recorded the highest level of crust development in sites with the highest levels of  $\text{CaCO}_3$  and highest pH. Similarly, in Idaho, North America, Anderson et al. (1982) recorded an increase in cover with increase in pH. However, the opposite has also been the case. Eldridge and Tozer (1997) recorded lower crust cover from sites with high pH and high  $\text{CaCO}_3$  than sites with low pH and high  $\text{CaCO}_3$ .

### 6.4.2 Dolomite and Gypsum Substrates

Dolomite [ $\text{CaMg}(\text{CO}_3)_2$ ] and gypsum [ $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ] substrates often exhibit biocrust bryophyte assemblages that are distinct from  $\text{CaCO}_3$ -dominated substrates. Biocrusts on gypsum substrates are typically rich in species number and have a high percentage of ground cover, and individual species can be useful indicators of soil chemistry (Belnap et al. 2001). In Australia, *Riccia albida* has been described by Scott (1982) as a species which grows in abundance on gypsum-rich soils of north-western Victoria, where it forms dense crusts of white, gypsum-encrusted thalli. In Spain, Guerra et al. (1995) identified 21 species of bryophytes from gypsiferous sites, which they suggest may provide refugia for many rare species. Here, Pottiaceae was the dominant moss family, accounting for 18 species, whereas only one thallose liverwort, *Riccia crustata*, was recorded. A study by Peer et al. (2009) of biocrusts in the mountains of Hohe Tauern (Austria) included one site with greywacke, dolomite and marble substrates, another with non-calcareous substrates including phyllites, mica schists, and quartzite. Ten mosses and four liverworts were recorded, all species with a wide altitudinal range and substrate tolerance, but in many of these sites, bryophytes were outcompeted by a dominant lichen flora.

### 6.4.3 Interactions Between Substrate Chemistry and Aridity

In general, the number of bryophyte species recorded from biocrusts on calcareous substrates decreases with increasing aridity. Such patterns can also be accompanied by a significant change in bryophyte assemblages, including ratios of acrocarps to pleurocarps and thallose to leafy liverworts. Eldridge and Tozer (1997) recorded 20 bryophytes (15 mosses in 12 genera, 5 liverworts in 2 genera) from semiarid areas of eastern Australia along a rainfall gradient decreasing from 500 mm per annum in the East to 220 mm per annum in the West. Species richness was directly correlated with annual rainfall and declined from East to West. These authors also determined that there was a significant negative correlation between annual rainfall and pH, indicating that with increased aridity, there was a corresponding increase in alkalinity and  $\text{CaCO}_3$  content, both of which likely contribute to reductions in bryophyte diversity.

## 6.5 Adaptive Strategies of Biocrust Bryophytes

Bryophytes within biological soil crusts exhibit a diverse range of adaptations that permit them to tolerate and survive in unfavorable and often extreme environments. Many of these traits are related to performance, growth, and reproduction in

habitats where they must cope with desiccation, temperature extremes, and high radiation on short- or long-term timescales, all of which represent major obstacles to survival. Crust bryophyte phenotypes thus represent trade-offs among these competing processes. Plant habit, specialized leaves and leaf surfaces, hygroscopic leaf movements, physiological and biochemical adaptations, niche specificity, longevity and, for some species, short life spans are important to survival and colonization.

Crust bryophytes typically inhabit the soil-atmosphere interface region within the boundary layer of the ground surface, a microhabitat that functions to minimize water loss to the air through convective processes. Morphologically, they are plants of small stature (shoots typically < 15 mm height) that grow in a clonal habit. This dense growth form of tightly packed stems increases boundary layer resistance, maximizes transfer and absorption of water in the capillary spaces among and within shoots and minimizes water loss to the surrounding environment (Proctor 1982; Sveinbjornsson and Oechel 1992). In soil layers immediately below the moss, subsurface features (rhizomatous shoots, protonemal filaments, rhizoidal filaments, tubers) aid in asexual reproduction and colonization.

At the shoot level, most arid and semiarid biocrust species are small, with small leaves. Leaves may be tightly overlapping (e.g. *Bryum argenteum*) or exhibiting distinctive hygroscopic movements that maximize water absorption (e.g. *Syntrichia* spp., *Tortula* spp.). Specialized surface features such as hairpoints, incurved margins, surface papillae, glossy reflective costae, and surface filaments serve to trap and retain moisture as well as retard water loss (Wu et al. 2014; Zhang et al. 2009; Zhang et al. 2011a, b). Some thalloid liverworts, such as *Asterella*, *Plagiochasma*, and *Riccia*, enroll on drying, exposing the often darkly pigmented and protective scales on the under surface of the thalli (Scott 1982). High amounts of lipids stored in leaves and stems, together with anthocyanin and carotenoid pigments, may aid thermoregulation, freeze tolerance, and long-term survival.

In arid regions, persistent desiccation, limited temporal water availability, and skewed sex ratios in natural populations restrict reproductive frequency of crust bryophytes (Stark and Castetter 1987; Benassi et al. 2011; Stark et al. 1998; Bowker et al. 2000; see Sect. 6.6). Several adaptive strategies allow crust bryophytes to maintain reproductive outputs in spite of these limitations. First, propagule banks may exist in upper soil layers. Bryophyte propagule banks have been described from a variety of habitats from deserts (Smith 2013), temperate grasslands (During 1987), and temperate wetlands (Eckstein 2006) to polar (Lewis Smith 1987) and alpine regions (Peer et al. 2009). They are critical sources for colonization following natural (Furness and Hall 1981; Miles and Longton 1982) and anthropogenic disturbance (Bisang 1995; Hassel and Söderström 1998). Bryophyte soil propagule banks in arid and semiarid landscapes remain largely unstudied (see: During 1987; During and Moyo 1999; Smith 2013) but likely contribute to bryophyte diversity and abundance. In Australia, a number of arid zone mosses (Pottiaceae, Gigaspermaceae, Funariaceae) and hepatics (*Riccia*, *Asterella*, *Fossombronina*) regularly produce spores that can form a component of propagule banks, while others produce rhizoidal tubers or perennating underground stems (*Gigaspermum*).

The relationship between propagule bank diversity and surface bryophyte diversity, however, may not be linear or simple to predict. Low elevation dryland propagule banks of high species richness have been shown to produce surface bryophyte communities of low species richness (Nash et al. 1977), illustrating that the mechanisms of maintaining diversity in subsurface soil banks may operate differently to that of surface communities (Smith 2013).

Adaptive life history strategies are another means by which biocrust bryophytes persist long-term in dry and unfavorable habitats. Although many biocrust bryophytes are long-lived, slow-growing perennials that rarely reproduce sexually, others exhibit very short life spans, a strategy which may function to increase annual reproductive output. Species with a short life span, the annual shuttle life strategy described by During (1992), may be extremely successful in producing few, but often very large, spores (up to 160  $\mu\text{m}$  or more) with the potential to remain viable for many years.

## 6.6 Biocrust Bryophyte Physiological Ecology

### 6.6.1 Water and Temperature Relations

Crust bryophytes are poikilohydric organisms, for which internal water content is wholly dependent on water content of the surrounding environment. In general, they are adapted to capitalize on precipitation when it occurs (their only opportunities for growth) and remain in a state of suspended metabolism during all other times (Tuba et al. 1996; Proctor 2001). When precipitation events occur, shoots become hydrated and remain physiologically active for the duration of the precipitation event (Mishler and Oliver 2009; Coe et al. 2012a), after which tissues dry and enter a desiccated state.

The ability to withstand various degrees of drying duration and intensity, from which full physiological function can be recovered, is termed desiccation tolerance (DT). DT is a multifaceted suite of physiological and molecular traits that encompasses mechanisms of preserving tissues as they dry, maintaining tissues while desiccated and ensuring recovery of cellular functionality upon rehydration. As shoots dry, cellular components are packaged and protected by polysaccharides and proteins (Smirnoff 1992; Buitink et al. 2002; Oliver et al. 2005). While desiccated, biocrust mosses often lose virtually all cellular water and can dry to 5–10 % dry mass and water potentials of  $-100$  MPa in the most desiccation-tolerant species (Proctor et al. 2007a, b). In this state, shoots can remain dry for periods of 190 days or more (Stark et al. 2005). Upon rehydration, membrane repair is initiated, and synthesis of proteins unique to the hydration process recovers within minutes (Oliver 1991). The genetic basis for DT has been shown to involve late embryogenesis abundant (LEA) proteins that protect cellular constituents while tissues are desiccated and as they rehydrate (Oliver et al. 2004). The mechanistic basis for gene expression during a wet-dry cycle likely includes polysomal retention of mRNA

transcripts during dehydration (Wood and Oliver 1999) and their rapid transcription into proteins upon rehydration (Oliver 1991).

Crust bryophyte species exhibit varying degrees of DT, and most are described as displaying either constitutive or inducible DT. In constitutive DT species (e.g. *Syntrichia caninervis*, *Syntrichia ruralis*), the cellular and molecular mechanisms that provide DT are present irrespective of environmental conditions, and plants will typically display the same degree of DT even if the surrounding environment causes different degrees of desiccation stress (Oliver et al. 2005). Conversely, species displaying inducible DT (e.g. *Physcomitrella patens*, *Pterygoneurum lamellatum*) fully activate DT processes only after conditions of desiccation stress are imposed. If the surrounding environment remains moist, plants 'deharden' and do not display DT phenotypes (Stark et al. 2013). Recent evidence suggests that in inducible DT species, the degree of DT displayed is directly related to the speed at which tissues dry: compared to shoots that dry rapidly (<3 h), shoots that dry slowly exhibit higher photosynthetic performance and rates of regeneration upon rehydration (Greenwood and Stark 2014). Speed of drying for crust bryophytes in dryland systems is related to temperature, degree of cloud cover following a precipitation event, microhabitat (under shrub vs. open interspace) or shoot density in a colony.

Crust bryophytes exhibit a large range of temperature tolerance but also can be very responsive to temperature changes while physiologically active. In dryland ecosystems, selective pressures to tolerate temperature extremes are high, and in the desiccated state, dryland crust mosses can withstand temperatures from  $-2.5^{\circ}\text{C}$  to  $120^{\circ}\text{C}$  (Malek and Bewley 1978; Hearnshaw and Proctor 1982; Stark et al. 2009). While hydrated, however, moss tissues are far more vulnerable to both low and high temperatures. In hydrated crust mosses, optimal temperatures for photosynthesis range from  $10^{\circ}\text{C}$  to  $20^{\circ}\text{C}$  (Furness and Grime 1982; Alpert and Oechel 1987). At temperatures  $>30^{\circ}\text{C}$ , photosynthetic capacity becomes compromised (Grote et al. 2010; Coe et al. 2012b), and, depending on species, lethal damage to shoots occurs at temperatures between  $42^{\circ}\text{C}$  and  $51^{\circ}\text{C}$  (Meyer and Santarius 1998; Proctor and Pence 2002).

Tolerance of desiccation and extreme temperatures comes at the expense of growth and reproduction in crust bryophytes. Annual shoot growth increments can be 0.3 mm or less (Stark et al. 1998), inter- and intra-annual growth are both highly dependent on precipitation regime (Coe and Sparks 2014) and rates of sexual reproduction are typically very low.

### 6.6.2 Reproductive Ecology

Reproductive strategies and trade-offs in crust bryophytes often have been the subject of extensive study over the last decade. Nearly all crust bryophytes are dioecious, producing shoots that express either male (antheridia) or female (archegonia) sexual structures at maturity. Disparate sex ratios, where one sex is observed more frequently than the other, are widespread in dioecious bryophytes, and in

dryland ecosystems, bryophyte sex ratios are almost always skewed toward females. In fact, the crust moss *Syntrichia caninervis* exhibits the most disparate sex ratio (14 females to 1 male) among all land plants (Bowker et al. 2000; Stark et al. 2009). But sex expression and sexual reproduction are also both rare in dryland crust bryophytes. Several lines of evidence suggest these phenomena are related to differential costs of sexual structures in males and females as well as sex-based adaptations to disturbance regimes in dryland ecosystems.

For one, sex-expressing male shoots are often restricted to shade microsites with higher resource availability (e.g. under a shrub), whereas females are commonly observed in exposed plant interspaces (Stark et al. 2005). This results in a characteristic pattern of spatial segregation of the sexes and as a consequence, reduced sexual reproduction, as the transfer of liquid water between male and female gametophytes is required for fertilization. Using biomass as a metric, the cost of pre-fertilization reproductive effort expended by males is an order of magnitude higher than that of females (Stark et al. 2000), indicating it is energetically more expensive for a shoot to produce antheridia compared to archegonia. One explanation for male-expressing shoots to occur in such a low frequency thus relates to the relative abilities of mature shoots to produce either male or female gametangia. The “Shy Male Hypothesis” proposed by Stark et al. (2010) postulated that male and female shoots occur in equal frequency in nature, but males simply produce sex structures less frequently.

Disparate sex ratios and low sexual reproduction in crust bryophytes may also relate to the differential stress tolerance of male and female shoots. In *Syntrichia caninervis* exposed to drought conditions, female shoots appear to regenerate more rapidly and be less susceptible to microbial infection in controlled conditions, but these patterns do not necessarily manifest in the field (Stark et al. 2005). There is also evidence in *Tortula inermis* and *Grimmia orbicularis* for abortion of sporophytes from female shoots following episodes of desiccation stress (Stark 2001; Stark et al. 2007), which suggests these sexual structures may be particularly demanding for gametophytes to support unless environmental conditions are favorable. When subjected to high-temperature (120 °C) events, males from under shrub microsites displayed higher levels of thermotolerance compared to females from interspace regions (Stark et al. 2009). This has been thought of as evidence for selection to tolerate natural wildfires that burn hottest in shrub regions compared to plant interspaces (Stark et al. 2009). Environmental, developmental, and physiological factors all play a role in sexual segregation and patterns of sex expression in crust bryophytes, all of which lead to the disparate sex ratios and low rates of sexual reproduction ubiquitously observed in populations in nature.

### 6.6.3 Ecological Roles of Biocrust Bryophytes

Bryophytes within biological soil crusts play important ecological roles in many ecosystems. In drylands, they are dominant crust members in many high (>610 m)



and low desert habitats, where they can account for 30 % or more of cover within crusts (Thompson et al. 2005). Crust bryophytes influence soil stability through growth of fine rhizoids and protonemal mats during regeneration and contribute to soil formation through modification of the hydrologic and thermal environment of sandy soils as well as through capture and accretion of soil particles (Carter and Arocena 2000). Crust bryophytes also influence soil fertility by intercepting dust particles, whereby increasing dry atmospheric deposition of nutrients (Belnap 2003), and by facilitating development of microorganism communities that increase the nutrient status of crusts (Zhao et al. 2014). Dryland bryophyte nitrogen and phosphorus ratios often correlate with soil availability of these nutrients (Ball and Guevara 2015), and environmental stress in the form of alterations in precipitation regime has been shown to cause moss mortality, with consequences for changes in ecosystem nitrogen cycling (Reed et al. 2012).

Crust bryophytes influence carbon cycling in dryland ecosystems as well. Peak photosynthetic activity for many dryland crust mosses is in the winter months, due to favorable temperature and water status. These times of the year are when net ecosystem exchange can also be highest, even though (in the case of many North American drylands) dominant shrubs may be dormant. These observations suggest that crust bryophyte photosynthetic activity can control the overall carbon balance of some dryland ecosystems (Zaady et al. 2000; Jasoni et al. 2005).

As the global climate changes, dryland systems are among those that are likely to be most responsive to environmental change (Brown et al. 1997; Weltzin et al. 2003; Reed et al. 2012). Increased temperatures, elevated atmospheric CO<sub>2</sub>, and changes in precipitation regime are all likely to impact the physiology, ecology, and distribution of dryland biocrust mosses. Increased temperatures, particularly high thermal stress events occurring during heat waves, are likely to reduce physiological performance in biocrust mosses and reduce viability, especially if they increase in frequency. However, the degree to which high-temperature events will be a large factor in future distributions depends on local hydrology, as they will only impose physiological stress if mosses are hydrated. In contrast, changes in precipitation are likely to cause rapid and potentially irreversible changes in moss viability and persistence in biocrusts. Even subtle changes in intra-annual precipitation have been shown to dramatically alter long-term C fixation and viability (Reed et al. 2012) with consequences for biocrust structure and function.

## 6.7 Concluding Remarks

Bryophytes are conspicuous components of biocrusts in the Northern and Southern Hemispheres, particularly in dryland systems, where they are represented by many species in relatively few families. Morphological and physiological attributes contribute to their adaptations to extreme environmental conditions in these habitats, where they take on an array of ecological roles. Much remains to be done to understand the basis of persistence and survival strategies in crust bryophytes, as



well as how functional plant traits influence ecosystem scale processes. From a diversity perspective, surveys of bryophyte propagules that may remain hidden in the soil for long periods may be critical to assessing potential biocrust biodiversity. Although rarely applied, molecular screening may assist biodiversity assessment, particularly with regard to ecosystem management of arid and semiarid lands. Finally, much could be gained by wide-ranging integrated collaborative studies examining interspecific interactions among crust and soil members that will enhance our understanding of biocrust ecology and soil biodiversity.

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# Chapter 7

## Structure, Composition, and Function of Biocrust Lichen Communities

Roger Rosentreter, David J. Eldridge, Martin Westberg, Laura Williams, and Martin Grube

### 7.1 Introduction

Lichens are symbiotic associations between a fungal partner (mycobiont) and one or more photosynthetic partners, either green algae or cyanobacteria (photobiont), living in a close physiological integration that forms a thallus. The mycobiont provides the basic lichen structure, and the alga provides the nutrition through photosynthesis. Like many other biological components of biological soil crusts (biocrusts), lichens are poikilohydric, meaning that they do not actively regulate water uptake or loss, but gain it from, and lose it to, the environment passively. When desiccated, their metabolic activity ceases and they undergo a transient cryptobiotic phase until metabolism can resume with changing environmental conditions. The particular characteristics of soil as a substrate may include high light intensities, poor water availability, and often an unstable surface to grow

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on. Such a poikilohydric strategy is perfectly suited for life within biocrusts where environmental conditions vary dramatically between the extremes of inundation and drought.

Lichens form a diverse and often colorful part of biocrusts in all parts of the world (see Fig. 7.1 and Chap. 10 by Bowker et al.) and can be the dominant

Fig. 7.1 Soil crust lichen richness (a) at the continent scale and (b) in relation to continental area. S Amer South America, Pac Pacific (Australia, New Zealand), Ant Antarctica, Afr Africa, Eur Europe, and NC America North and Central Americas and includes Greenland. Source: Büdel (unpublished data)



life-form in many soil surface communities. Their ability to tolerate severe abiotic stresses such as desiccation, extreme temperatures, and high light intensities makes them ideally suited for relatively resource-limited environments that support well-developed biocrust communities: polar regions, high mountains, arid and semiarid deserts, and xerothermic steppe. In temperate regions, lichens also form important biocrust communities. For example, in Europe, lichen-rich biocrust communities can occur where human activity has created or maintained environments and landscapes largely free of vascular plant vegetation through, for example, grazing by cattle or intense mining or military activity. Lichens can also be important as pioneer species in more ephemeral crusts establishing in areas with open soil created by either natural events such as rockslides or human activities such as road cuttings and forest clearings.

Lichens perform many critically important ecological functions such as altering the physicochemical properties of soil, by, for example, enhancing soil stability and altering water infiltration and retention (Eldridge et al. 2010; Chamizo et al. 2012), increasing fertility through nitrogen fixation and carbon sequestration (Maestre et al. 2010; Elbert et al. 2012; Delgado-Baquerizo et al. 2013), and interactions with other organisms (e.g., hosts for parasitic fungi and food for various invertebrates such as snails, mites, and insects but also for larger animals such as reindeer Seaward 1988; Lalley et al. 2006; Li et al. 2006). While lichens are recognized as a key component in many biocrusts, there remain substantial gaps in our understanding of the taxonomy and diversity of the lichens. In this chapter we summarize some important aspects of lichens in biocrusts and highlight the need for taxonomic research on these organisms.

## 7.2 Structure and Morphology of Lichen Biocrusts

Biocrusts include the full range of lichen types including gelatinous, crustose, squamulose, foliose, and fruticose forms (Eldridge and Rosentreter 1999). The relative importance of these forms can change in relation to average annual rainfall and evaporation (aridity) and substrate type (see Büdel et al. 2009; Chap. 9 by Colesie et al.). A general introduction to the morphology and anatomy of the lichen thallus can be found in Büdel and Scheidegger (2008). Here we will focus on some aspects of lichen morphology that are relevant to their ability to form biocrust communities.

### 7.2.1 The Importance of Fungal Hyphae

Lichens attach themselves to the substrate by penetrating the soil with their fungal hyphae. These hyphae are generally assumed to be restricted to the surface of their substrate. However, the hyphae of saxicolous lichens have been shown to penetrate

the spaces between mineral particles to a depth of up to 12 mm (Bjelland and Ekman 2005; Chen et al. 2000), suggesting that fungal hyphae of biocrust lichens may be capable of deeper penetration into substrates that are substantially looser than rock. Observations of the dense aggregations of rootlike rhizines and rhizoids (e.g., Poelt and Baumgärtner 1964; see Chap. 3 (Fig. 3.3) by Beraldi-Campesi and Retallack), common in many biocrust communities such as those of the genera *Endocarpon*, *Catapyrenium*, and *Psora*, support this notion. This is also true for some Antarctic soil crust-forming species such as *Acarospora gwynii* (8 mm depth) and *Caloplaca citrina* and *Lecanora expectans* (24 mm depth; Colesie et al. 2013). Indeed, Belnap et al. (2001) demonstrated that hyphae of *Psora cerebriiformis* can penetrate to depths of 14 mm. These dense clumps of deeply penetrating rhizines help to aggregate soil microaggregates into macroaggregates, increasing the resistance of biocrusts to wind and water and mechanical deformation (see Chap. 16 by Belnap). They also increase soil surface roughness, which may further improve resistance to wind and water erosion (Eldridge and Rosentreter 1999).

### 7.2.2 The Role of the Lichen Photobiont

Photosynthesis in lichens is performed by either green algae or blue-green algae (cyanobacteria). About 86 % of lichens have green algal photobionts (chlorobionts), creating chlorolichens, and about 10 % have cyanobacterial photobionts (cyanobionts), creating cyanolichens. In addition, about 3–4 % use both cyanobacteria and green algae as their photobionts (Honegger 1991). In the latter case, cyanobacteria are usually found in specific structures called cephalodia, where they are mainly responsible for nitrogen fixation and, consequently, have an elevated frequency of heterocysts (Hyvärinen et al. 2002). Despite the primacy of the photobiont, very little is known about the specificity of fungal–algal association in biocrust lichens. In general, green algae of the genus *Trebouxia* have been found to be the dominant photobiont of biocrust chlorolichens. Very little is known about physiological interactions between lichens and algal colonies outside the thallus structures. Chlorolichens are known to grow in close proximity to cyanobacterial colonies in a wide range of relationships, from facultative to obligate (cyanotrophy, sensu Poelt and Mayrhofer 1988).

Despite the diversity of algal species present in biocrusts, lichen mycobionts appear to be highly specific. For example, studies by Ahmadjian et al. (1980) and Ahmadjian and Jacobs (1981) showed that, although the biocrust lichen *Cladonia cristatella* and rock-dwelling *Rhizoplaca chrysoleuca* formed thalli when associated with several photobionts, at least in vitro, development was retarded when distantly related photobionts were used. Similarly, Schaper (2003) demonstrated the extremely photobiont-specific nature of certain lichenized fungi, with a proper lichen thallus developing only when associated with a specific partner. However, the degree of algal specificity of biocrust lichens does not contrast with those lichens growing on other substrates (Wirtz et al. 2003; Pérez-Ortega et al. 2012).

Interestingly, the soil lichen *Psora decipiens* has been shown to be associated with a wide range of chlorobiont species (Ruprecht et al. 2014). We assume that the ability to form associations with a wider range of locally available photobionts may be an important trait that increases the distribution and survival of biocrust lichens growing in environmentally extreme habitats, such as the Antarctic Peninsula (Romeike et al. 2002; Jones et al. 2013). This could account for its widespread global distribution and its ability to tolerate a wide range of environmental conditions ranging from alpine areas to deserts.

Photobiont pools may exist in areas that allow many species to take advantage of locally adapted species or haplotypes, and some species have even evolved to steal their photobionts from other lichen species. A noteworthy example of this is the soil lichen *Diploschistes muscorum*, which parasitizes different *Cladonia* species by developing apothecia in the *Cladonia* squamules and associating with its photobiont *Asterochloris irregularis*. Consequently the *Cladonia* structure breaks down, resulting in free-living *Diploschistes thalli*. In mature thalli of *Diploschistes*, the photobiont is exchanged for *Trebouxia showmanii* (Friedl 1987). *Toninia sedifolia* and *Fulgensia* species are often found growing together and appear to share the same photobiont pool of *Trebouxia* strains (Beck et al. 2002). Indeed, ascospores of *Fulgensia bracteata* have been found to germinate on the thallus of *Toninia sedifolia* and the invading hyphae gain access to the photobiont (Ott et al. 1995).

## 7.3 Composition of Biocrust Lichens

### 7.3.1 Distribution of Biocrust Lichens

Biocrust lichens are found on all continents (Fig. 7.2a), although richness seems to be largely independent of continent area (Fig. 7.2b). As with any other organism, the distribution of biocrust lichens ranges from highly localized to globally ubiquitous. Many biocrust species are ubiquitous and have a broad geographic distribution. Species such as *Psora decipiens*, *Toninia sedifolia*, and *Fulgensia bracteata* are often very common components of lichen-dominated biocrusts worldwide (Timdal 1986, 1987). However, morphological variation in *Toninia sedifolia* at different biocrust sites is difficult to interpret and may obscure the presence of different, closely related species. Similarly, *Psora decipiens*, thought to be taxonomically well defined (Schneider 1979; Timdal 1986), is now known to exhibit variation both in morphology and chemistry, and this variation has not been thoroughly studied using molecular techniques. It is likely, therefore, that the considerable variation within this particular lichen taxon could be sufficient to warrant the description of new species. Such variation is also apparent in many other biocrust lichen species and raises the question whether they are also associated with variation in ecophysiological traits of the species. In this context,

Fig. 7.2 Images of lichen-dominated biocrusts. (a) The Great Alvar on Öland, Sweden showing shallow soils on limestone pavement with, e.g., *Diploschistes muscorum*, *Toninia sedifolia*, *Toninia physaroides*, *Psora decipiens*, *Fulgensia bracteata*, and *Collema* spp. (b) *Artemisia* shrub-steppe near Boise, Idaho, USA, on deep loess soils with *Diploschistes muscorum*, *Fulgensia bracteata*, and *Psora montana*. (c) Crusted loamy soils near Deniliquin, NSW, Australia, with *Xanthoparmelia reptans*, *Neofuscelia pulla*, and *Lecidea ochroleuca*. (d) *Tabernas* badlands near Almeria, Spain, with well-developed biocrusts on gypsum-calcareous soil dominated by *Squamarina lentigera*, *Diploschistes diacapsis*, *Buellia zoharyi*, and *Acarospora nodulosa*

taxonomists often stress the concept of cryptic species (i.e., species that are not characterized by distinct phenotypic characteristics). This, however, may reflect merely an ignorance of subtle phenotypic traits that have been overlooked or inadequately studied.

The abundance of some biocrust taxa may exhibit skewed distributions across their geographic range due to differences in their ecological response to idiosyncratic environmental cues. One species with a skewed distribution is *Solorinella asteriscus*, a xerothermic continental species that typically occurs on loess soils. Its sporadic occurrence in continental valleys in Norway and dry valleys in the Canadian Alps and Italy does not reflect a global rareness, because it is relatively common in semiarid steppe grasslands in Asia, and also occurs in isolated pockets in moderate continental climates in urban and peri-urban environments in Europe (e.g., Bratislava, Slovakia). It is likely that populations of this species, which were isolated during the Late Glacial and Holocene periods, are also genetically distinct, although their scarcity in Central Europe may also be related to the loss of available habitats due to human activity (Farkas and Lökös 1994).

Other biocrust species have very limited geographic distributions and, to date, are known only from the locations where they were first described. For example, the

squamulose coralloid lichen *Protopannaria alcornis* (Jorgensen 2001) is an endemic biocrust lichen known from only two specimens from the subantarctic Kerguelen Islands. It is difficult to establish the realized niche of this species because comparable habitats on other subantarctic islands are difficult to survey and therefore have been poorly sampled. The high number of currently endemic lichens worldwide probably reflects the poor state of floristic research rather than true endemism per se. For some species, local or regional endemism has been adequately established through substantial regional collections. For example, *Tephromela siphulodes* is a species with a distinct, three-dimensional growth form and has only been found on soils in high-altitude alpine areas in Nepal (Poelt and Grube 1993a). Similarly, *Lecanora himalayae* and *Lecanora chondroderma* are well-described species from the same area, but are absent from other alpine habitats (Poelt and Grube 1993b). In Mediterranean habitats, some white-colored *Buellia* species, known as the *Buellia epigaea* group, have a wide distribution in the Northern Hemisphere, but three species of the group (*Buellia dijana*, *Buellia georgei*, and *Buellia lobata*) are only known from Australia (Trinka et al. 2001). The preceding discussion about lichen distribution and endemism indicates that considerable work is required to determine the true distribution of many of our biocrust-forming lichen taxa.

While many scientists acknowledge the close links between biocrusts and the condition or health of dryland ecosystems (Klopatek 1993; Rosentreter and Eldridge 2002), biocrusts and their component lichens and bryophytes are rarely recorded during field-based assessment (West 1990). In the mid- to late 1980s, Australian rangeland scientists pioneered a range of techniques to determine the health of landscapes that placed more emphasis on soil and landscape function rather than relying, as previously, on the status and condition of the vascular plant community (Tongway and Smith 1989). The resulting “soil surface classification system” used biocrust cover as an important measure of the capacity of the soil to carry out two functions: resist deformation and cycle nutrients.

### 7.3.2 Richness and Abundance of Biocrust Lichens

A global assessment of biocrust lichen richness is difficult to conduct. Part of the reason for this lies in the difficulties associated with the term “biocrust.” Although this term and its synonyms (biological soil crust, cryptogamic crust, cryptobiotic crust, microphytic crust) are widely used by ecologists, its application for a well-described group of lichens is problematic. Biocrusts have been defined as a community of organisms that are an intimate part of binding soil surface particles into a crust. However, fruticose (shrubby) lichens (e.g., *Chondropsis semiviridis*) do not form true crusts (Eldridge and Greene 1994), and it is doubtful whether vagrant (syn. vagrant) lichens (e.g., *Xanthoparmelia chlorochroa*), that are associated with soils and biocrusts, have a role in crust formation or whether the thallus itself represents a biocrust without the underlying soil. Here we avoid this ontological

issue by adopting a wider concept of biocrusts, which also includes lichen taxa that develop more complex thallus forms when growing on soils (i.e., terricolous lichens). A key of terricolous species in Italy includes 439 species (Nimis and Martellos 2004). Extrapolating globally, we expect that the worldwide number of species may be beyond 1000. Unpublished data on lichen richness (Büdel et al. 2014, pers. comm.) indicates a described lichen richness of about 550 taxa (Fig. 7.2a).

The composition of the lichen flora in biocrusts varies considerably with differences in soil physical and chemical properties, climate, and vegetation community (see Chap. 10 by Bowker et al.). Although lichens are often a prominent or even dominant component of biocrusts, it is often difficult to compare species richness between different areas because the taxonomic status of some ubiquitous species is under revision (e.g., *Buellia* spp., Trinka et al. 2001). Advances in the molecular taxonomic techniques and improved DNA sequencing could result in range extensions for some species or the splitting of globally distributed taxa into different species or subspecies.

In general, biocrust lichen richness tends to be higher in environments such as deserts, arctic, and alpine areas, where competition from vascular plants is low. Cool habitats, in particular, seem to support a large diversity and biomass of lichen taxa (Eversman 1995), possibly because the balance of photosynthesis and respiration between the symbiotic partners maximizes the opportunity to form complex thallus structures. Several studies have shown that large-seeded grass species, such as cheatgrass, *Bromus tectorum*, are inhibited by biocrusts (Serpe et al. 2006, 2008). In arid and semiarid environments, competition from vascular plants is generally low, either because the distribution of vascular plants is also low or lichen crusts inhibit vascular seed germination (Prasse and Bornkamm 2008; Serpe et al. 2006). In more mesic environments that support larger populations of herbivores, there is often positive feedback between increased soil moisture, fluctuations in vascular plant cover, and the response of biocrusts to these altered levels of bare soil (see Chap. 19 by Zhang et al.).

### 7.3.3 Taxonomy and Identification of Biocrust Lichens

Biocrust lichen taxonomy is still in its relative infancy compared with vascular plant taxonomy. For example, in a study of lichen species richness by a number of lichen experts at four sites in Europe (Austria, Germany, Spain, and Sweden, Büdel et al. 2014), about 9 % of all lichens collected remained unidentified at the species level even though these areas have previously been studied intensively. Given this uncertainty in identification, we would expect that even more remote and poorly studied biocrust communities would yield many new lichen species.

Similar to many other organisms associated with biocrusts, lichens are also often difficult to identify. In contrast to most prokaryotes and many other microscopic eukaryotes, however, lichens have macroscopic structures with characters that

allow the recognition of species or at least their classification to higher (taxonomic) ranks. Many terricolous macrolichens found in biocrusts are characterized by large, leaflike thalli. These biocrusts are easily recognizable but include “difficult” genera that are hard to identify at species level because they are morphologically variable and have few external characteristics. Genera typical of this group are found in the families of Aspiciliaceae, Acarosporaceae, Lichinaceae, and Verrucariaceae. In addition, the high substrate specificity typical for many lichens may not be strictly maintained on soil substrates. Some species normally found on rocks may occasionally be found on compacted or gypsiferous soils, and in alpine environments, corticolous (bark-inhabiting) species are sometimes found on soil (e.g., *Evernia divaricata*). The taxonomic significance of such substrate shifts is relatively unknown, but a reasonable hypothesis is that the variable composition of soils could facilitate the adaptation of species to alternative substrate types.

The accurate identification of biocrust lichens generally requires expert knowledge that goes beyond the information presented in formal lichen texts. Specific problems of identification arise when biocrust lichens lack reproductive structures needed for determination. Molecular techniques and DNA sequencing of individual thalli may help to improve the identification of species. Such a DNA bar-coding approach to the identification of lichenized fungi, however, will only be useful after basic data on the genetic variation of species have been collected (e.g., Del-Prado et al. 2010; Kelly et al. 2011; Pino-Bodas et al. 2013). Unfortunately, such information is virtually unknown for the majority of biocrust lichens. Moreover, microlichens often occur mixed together in a rich tapestry rather than occurring as discrete individuals. Without knowledge of the species, it is difficult to recognize which structures belong to separate species, and molecular approaches that do not consider these problems will undoubtedly lead to confusing results.

### 7.3.4 A Morphospecies Approach to Biocrust Lichen Identification

The notion that similar morphology reflects similar functions (or susceptibilities) in ecosystems could improve our understanding of biocrust function, leaving taxonomic intricacies aside. Ecological studies are often conducted by assessing “morphological groups” (sensu Eldridge and Rosentreter 1999), rather than fully resolving diversity at the species level. Morphological groups are groups of superficially similar species that are difficult to differentiate in the field, but which possess similar morphologies (e.g., “green leafy lichens” or “gelatinous lichens”) and often function similarly (Eldridge and Rosentreter 1999). In many cases, morphological groups are surrogates for functional groups (Pike 1978; Rosentreter 1995). For example, the gelatinous lichen genera *Collema*, *Leptogium*, and *Leptochidium* of shrub-steppe communities in the western USA all fix nitrogen



and provide a similar degree of protection from surface soil erosion (Anderson et al. 1982; Brotherson et al. 1983).

The concept of functional groups is well illustrated by the susceptibility of biocrusts to trampling, which is seen as a major factor threatening soil crust communities worldwide. Some lichen species appear more tolerant of trampling than others (Rogers and Lange 1971). This is probably due to differences in their morphologies, as foliose or fruticose forms seem to be more susceptible than crustose and squamulose forms (Eldridge and Rosentreter 1999). Morphological groups of lichens can also provide valuable insights into the health and recovery of ecosystems. For example, in a study across more than 0.6 million km<sup>2</sup> of eastern Australia, Eldridge and Koen (1998) found that the presence of the “yellow foliose” morphological group, which was comprised of foliose lichens of the genera *Heterodea*, *Xanthoparmelia*, and *Chondropsis*, was consistently correlated with stable, productive landscapes with little evidence of accelerated erosion.

Biocrust color has been shown to be a useful morphological trait to indicate the role of biocrusts in nitrogen cycling. For example, the later successional, dark cyanobacteria-dominated biocrust is known to be more closely involved in nitrification and denitrification than the earlier successional light forms (Barger et al. 2013; Rosentreter et al. 2007). While light cyanobacterial crusts are generally dominated by cyanobacteria of the genus *Microcoleus*, dark biocrusts contain nitrogen-fixing cyanobacteria (e.g., *Nostoc*, *Scytonema*) and often the nitrogen-fixing lichens *Collema tenax* and *Collema coccophorum*. Some lichen morphologies may be indicative of moisture type and inundation conditions. Gel-like cyanolichens (e.g., *Collema*) depend on liquid water for activity. Some chlorolichens may be activated by humidity alone. Thus, they are likely to be relatively intolerant of inundation and found therefore in exposed situations (Lange et al. 2001). Water vapor alone, however, is insufficient to activate some chlorolichens such as *Acarospora gwynii*. The ability of chlorolichens to be activated by water vapor may be an adaptation to very low liquid water availability (Colesie et al. 2014). Moderately cool habitats with high levels of humidity are often dominated by fruticose lichens. Their productivity under such conditions seems to be the result of high photosynthetic rates compared to respiration. The markedly different response of lichens to environmental conditions thus provides useful information on environmental quality.

## 7.4 Functional Roles of Biocrust Lichens

The important functional roles of biocrust lichens related to the physiological or chemical properties are already highlighted in several chapters of this book, including soil stabilization (see Chap. 16 by Belnap), weed abatement, lowering or raising of the albedo of the soil (see Chap. 12 by Weber and Hill, and Chap. 22 by Reed et al.), provision of microhabitats for invertebrates (see Chap. 8 by Darby and Neher), and nitrogen fixation (see Chap. 14 by Barger et al.). However, the



assignment of particular species or morphological groups to such categories is an important task if we are to be able to assess the ecosystem value of particular soil crust communities.

Different photobionts influence the capacity of biocrust lichens to undertake different functions. For example, cyanolichens fix nitrogen which makes them efficient pioneers on degraded soils (Eldridge 1998). They preferably grow at sites of lower potential radiation (Pinho et al. 2010) and tend to have a lower photosynthetic efficiency compared to chlorolichens (Wu et al. 2013). But the soil crust lichen *Collema tenax* has been shown to reach higher values than most soil crust chlorolichens and to be saturated at light intensities as high as  $1500 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (Lange et al. 1998; Lange 2003). Soil biocrusts may also help to maintain resistance of ecosystems to invasion. In the western USA, lichen-dominated biocrust communities have been shown to reduce the invasibility of shrublands by large-seeded Eurasian weeds such as *Bromus tectorum* (Deines et al. 2007; Serpe et al. 2008; Reisner et al. 2013, see Chap. 19 by Zhang et al.). Before the introduction of European livestock, a combination of low levels of disturbance in dry times and the presence of a stable lichen-dominated biocrust have kept weedy flammable grass species at low levels. With an increase in human- and livestock-induced soil disturbance, European annual grasses have proliferated, increasing the extent and intensity of wildfire in areas which had not coevolved with frequent fire.

Recent research in the Orchard Combat Training Center south of Boise, Idaho, USA, has focused on the role of biocrust diversity on ecosystem functions, particularly the capacity of different biocrust taxa, including lichens, to withstand disturbance from livestock trampling and military vehicles (Table 7.1). Sites with a high richness of biocrust taxa have been shown to support only a sparse cover of flammable grasses whereas low-richness sites are dominated by flammable grasses (Rosentreter, unpublished report to the Idaho Army National Guard, Nov. 2014). Apart from their suppressive effect on large-seeded, annual plants, biocrusts may also facilitate the succession of other plant communities by, for example, fixing nitrogen, providing a niche for specialized microbes, or stabilizing the soil by trapping resources such as organic matter and water (Maestre et al. 2008). They also moderate the flow of water into the soil (see Chap. 17 by Chamizo et al.).

In order to convince land managers, practitioners, farmers, politicians, and the general public of the ecosystem role provided by biocrust lichens, it may be more useful to consider a functional group approach to lichen identification rather than one based on a traditional species approach. This emphasizes the extent to which they are critical for providing ecosystem goods and services rather than merely how many individual species they support. These roles and functions include, but are not limited to, erosion prevention and soil stabilization, which are of increasing concern in relation to environmental change and global warming (see Chap. 22 by Reed et al.). In some ecosystems, soil lichens form food for ungulates as well as invertebrates, and absorption of environmental pollutants by lichens can result in transfer into the food chain (Skuterud et al. 2005).

Table 7.1 Biological soil crust taxa recorded in the Orchard Training Center, Idaho, their life-form, functional role, and tolerance to disturbance

Species and authorities	Life-form	Functional role	Disturbance rating
<i>Bryum argenteum</i> Hedw.	Bryophyte	Soil stabilizer	H
<i>Bryum argenteum</i> Hedw. var. <i>lanatum</i> (P. Beauv.) Hampe	Bryophyte	Soil stabilizer	H
<i>Caloplaca cerina</i> (Ehrh. ex Hedwig) Th. Fr.	Bryophyte	Detritus binder	M
<i>Ceratodon purpureus</i> (Hedw.) Brid.	Bryophyte	Soil stabilizer	H
<i>Crossidium</i> sp.	Bryophyte	Soil stabilizer	H
<i>Didymodon vinealis</i> (Bridel) Zander	Bryophyte	Soil stabilizer	H
<i>Pterygoneurum ovatum</i> (Hedw.) Dix.	Bryophyte	Soil stabilizer	H
<i>Riccia frostii</i> Aust.	Bryophyte	Soil stabilizer	M
<i>Syntrichia caninervis</i> Mitten	Bryophyte	Soil stabilizer	H
<i>Syntrichia ruralis</i> (Hedwig) F. Weber & D. Mohr	Bryophyte	Soil stabilizer	H
<i>Microcoleus</i> sp.	Cyanobacterium	N fixer, soil stabilizer	H
<i>Acarospora schleicheri</i> (Ach.) A. Massal.	Lichen	Soil stabilizer	L
<i>Buellia punctata</i> (Hoffm.) Coppins & Scheid.	Lichen	Detritus binder	M
<i>Arthonia glebosa</i> Tuck.	Lichen	Soil stabilizer	M
<i>Aspicilia aspera</i> (Mereschk.) Tomin	Lichen	Soil stabilizer	L
<i>Aspicilia filiformis</i> Rosentreter	Lichen	Soil stabilizer	VL
<i>Aspicilia mansourii</i> Sohrabi	Lichen	Soil stabilizer	L
<i>Aspicilia</i> sp.	Lichen	Soil stabilizer	L
<i>Caloplaca jungermanniae</i> (Vahl) Th.Fr.	Lichen	Detritus binder	M
<i>Caloplaca tominii</i> Savicz.	Lichen	Soil stabilizer	H
<i>Caloplaca</i> sp.	Lichen	Detritus binder	M
<i>Candelariella aggregata</i> M. Westb.	Lichen	Detritus binder	M
<i>Candelariella rosulans</i> (Müll. Arg.) Zahlbr.	Lichen	Soil stabilizer	M
<i>Candelariella vitellina</i> (Hoffm.) Müll. Arg.	Lichen	Soil stabilizer	M
<i>Candelariella</i> sp.	Lichen	Soil stabilizer	M
<i>Cladonia pocillum</i> (Ach.) Grognot	Lichen	Soil stabilizer	M
<i>Cladonia pyxidata</i> (L.) Hoffm.	Lichen	Soil stabilizer	M
<i>Collema tenax</i> (Sw.) Ach.	Lichen	N fixer	M
<i>Collema coccophorum</i> Tuck.	Lichen	N fixer	M
<i>Diploschistes muscorum</i> (Scop.) R. Sant.	Lichen	Soil stabilizer	L
<i>Endocarpon pusillum</i> Hedwig	Lichen	Soil stabilizer	H
<i>Lecanora floweriana</i> H. Magn.	Lichen	Detritus binder	M
<i>Lecanora muralis</i> (Schreber) Rabenh.	Lichen	Soil stabilizer	M
<i>Lecidea laboriosa</i> Mull. Arg.	Lichen	Soil stabilizer	L
<i>Lepraria</i> sp.	Lichen	Soil stabilizer	H
<i>Leptochidium albociliatum</i> (Desm.) M. Choisy	Lichen	N fixer	L

(continued)

Table 7.1 (continued)

Species and authorities	Life-form	Functional role	Disturbance rating
<i>Massalonia carnosa</i> (Dickson) Körber	Lichen	N fixer, soil stabilizer	L
<i>Physconia enteroxantha</i> (Nyl.) Poelt	Lichen	Soil stabilizer	L
<i>Physconia muscigena</i> (Nyl.) Poelt	Lichen	Soil stabilizer	L
<i>Placidium squamulosum</i> (Ach.) Breuss	Lichen	Soil stabilizer	H
<i>Placynthiella icmalea</i> (Ach.) Coppins & P. James	Lichen	Detritus binder	H
<i>Psora montana</i> Timdal	Lichen	Soil stabilizer	M
<i>Psora tuckermanii</i> R. A. Anderson ex Timdal	Lichen	Soil stabilizer	L
<i>Texosporium sancti-jacobi</i> (Tuck.) Nadv.	Lichen	Soil stabilizer	L
<i>Thelenella muscorum</i> var. <i>octospora</i> (Nyl.) Coppins & Fryday	Lichen	Soil stabilizer	L
<i>Trapeliopsis bisorediata</i> McCune & Camacho	Lichen	Soil stabilizer	L
<i>Trapeliopsis steppica</i> McCune & Camacho	Lichen	Soil stabilizer	L
<i>Toninia ruginosa</i> (Tuck.) Herre	Lichen	Detritus binder	L

N fixer: fixes nitrogen; soil stabilizer: binds surface sediments using a range of mechanisms, generally hyphae or physical protection; detritus binder: stabilizes organic material. VL very low, L low, H high, and VH very high. Disturbance rating based on a soil crust index (Rosentreter and Eldridge 2004)

### 7.4.1 Sampling Biocrust Lichen Communities

Qualitative studies of lichen diversity often involve the collection of specimens in a somewhat haphazard sequence, over landscapes that are often of ill defined, or with no specific number, size, or extent of plots. The landscapes sampled are often of variable complexity and sampling is conducted with variable effort (Nash and Sigal 1981; Will-Wolf 1998). This opportunistic sampling, however, has resulted in the collection of data from ecologically interesting sites such as within ecotones, undisturbed areas excluded from grazing, or biodiversity hot spots (Wetmore 1985; Neitlich and McCune 1997). Consequently, there may appear to be some bias in the collection of these data (McCune et al. 2000).

Biocrust lichen research has advanced considerably in the past two decades with a greater attention to systematic sampling. Intensive sampling of different patch types within landscapes is now standard practice, with stratification of sampling sites in relation to vascular plant community composition, soils, and climate. For example, Root and McCune (2012) recorded 99 biocrust lichen species within fifty nine 0.4-ha plots. Of these, one-third were observed only once. The use of morphological, functional, or taxonomic group approaches has also improved field-based assessment of biocrust communities, allowing researchers to increase the consistency and statistical power by lumping taxa that are morphologically similar into groups (Ponzetti et al. 1998; Ponzetti and McCune 2001; Eldridge and

Rosentreter 1999). The use of morphological groups for biocrust lichens minimizes the errors associated with overlooking small or otherwise inconspicuous species or species which are frequently intertwined and decreases the sampling variance by increasing statistical power. It also increases the repeatability of cover or abundance estimates (Ponzetti et al. 1998). Using morphological groups in the field will, however, invariably underestimate true alpha diversity (Ponzetti and McCune 2001).

## 7.5 Lichens in Biocrusts: Concluding Remarks

A number of knowledge gaps compromise our ability to fully understand how lichens function and how they affect their environment. First, biocrust lichens are still poorly studied, resulting in an underestimation not only of their abundance and diversity, but a lack of understanding of how they interact with their environment and the extent to which they influence the provision of ecosystem goods and services. Some disciplines have developed lists of key indicator species that are useful for assessing the health of ecosystems (e.g., aquatic algae; McCormick and Cairns 1997). Extending this concept to biocrust lichen (and bryophyte) taxa would be a valuable contribution to the field of biocrust ecology. Second, any studies of biocrust lichens must take into account the physicochemical differences in substrates that are likely to affect their diversity and functionality. Third, a more comprehensive understanding of biocrust lichens must consider the degree to which they interact with associated microbiota. Only recently, for example, have bacterial communities associated with biocrust lichens been examined in detail using relatively modern techniques (see Chap. 5 by Maier et al.). Fourth, little is known about functional redundancy in biocrust lichen taxa and the physiological responses of different taxa to a range of perturbations. This can only be solved when taxonomic work has advanced to the stage where the majority of taxa are readily identified and can be studied *in situ* or where techniques are available for studying *ex situ* communities (e.g., Maestre et al. 2012). Finally, the study of biocrust lichens is hampered by the lack of consistent, rigorous methodologies, which are exacerbated due to the small size of the target organisms.

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# Chapter 8

## Microfauna Within Biological Soil Crusts

Brian J. Darby and Deborah A. Neher

### 8.1 Introduction

A variety of microfauna inhabit the biological soil crusts (biocrusts) of arid soils from all parts of the globe, including the southwestern USA (Bamforth 2004, 2008; Darby et al. 2006, 2007a, b; Neher et al. 2009), the Negev Desert of Israel (Jones and Shachak 1990; Pen-Mouratov et al. 2011), the Tengger Desert of northern China (Liu et al. 2011; Li et al. 2011), Australia (Robinson et al. 2002), and Antarctica (Bamforth et al. 2005; Sohlenius et al. 2004; Schwarz et al. 1993; Colesie et al. 2014). The objective of this chapter is to review the literature on microfauna associated with biocrusts and identify the major microfaunal groups that inhabit biocrusts, the functions they perform in the biocrust ecosystem, when they are most active, where they are located in the soil and biocrust profile, and how they are affected by surface disturbances and altered abiotic conditions. We conclude by proposing three research priorities that are most necessary to improving our understanding of the ecology of biocrust microfauna.

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## 8.2 Who Are the Microfaunal Inhabitants of Biocrusts?

### 8.2.1 Protozoa

Protozoa may be the least understood of the biological soil crust consumers because they are small and numerous, but difficult to quantify, observe, manipulate, and identify taxonomically. Most protozoans are generally considered bacterivorous, or predators of other protozoans and small invertebrates, but many species are known to feed on fungal spores and hyphae, and it is likely that many also feed on cyanobacteria in biocrust systems. Predation of cyanobacteria by protozoans is prevalent (Dryden and Wright 1987), but most reports are from aquatic species and it is not clear how many cyanobacteria-feeding species occur in biocrusts. Ghabbour et al. (1980) suggested that protozoans from desert soils (particularly a species of *Acanthamoebae*) consumed the cyanobacteria *Anabaena* spp. and *Nostoc* spp. in a liquid culture and contributed to the reduction of chlorophyll- $\alpha$ , but there was no definitive evidence that this was not due to grazing from the nematode microfauna also present. Protozoan predation of bacteria, spores, and other protozoans is generally by phagocytosis or engulfing of the whole cells, while predation of filamentous fungal hyphae and cyanobacteria can be either through phagocytosis of the cells/filaments or by a more specialized piercing mechanism. Filose pseudopods (in the case of certain amoebae), or specialized internal structures (in the case of some flagellates and ciliates), pierce fungal hyphae or cyanobacterial filaments to access the prey cells' cytoplasm. This method of feeding by piercing has been found in diverse protozoans, such as in the amoeboid genus *Vampyrella*, the flagellate family *Viridiraptoridae*, and the ciliate family *Grossglockneridae*, but it remains to be determined how many of these species are to be found in biocrust systems.

Much of the ecological research on biocrust protozoa distinguishes between mobility groups, which include "amoebae," "flagellates," and "ciliates." These mobility groupings are not monophyletic groups, nor do they necessarily perform distinct functions, but this does not necessarily mean that mobility groupings are invalid methods of understanding the ecology of biocrust protozoa. Protozoa live within a network of water films and water-filled pore spaces, which constrains the size and number of organisms that can inhabit soil and organic matter. Presumably, small, amoeboid protozoa are able to occupy smaller pore sizes that are slow to dry out compared to larger, rigid-bodied protozoans like ciliates. If true, this would have significant implications for which species can be physiologically active in different levels of soil moisture. The difficulty that comes with counting, observing, and identifying protozoa also impedes our ability to distinguish specific niches or feeding habits of different protozoan species. Desert amoebae have been distinguished at finer mobility forms to differentiate between amoebae with (1) extended pseudopodia, (2) limax amoebae (see Fig. 8.1a, roughly cylindrical in shape, resembling a slug) with a single leading pseudopod and no subpseudopodia, (3) limax amoebae with eruptive cells, and (4) flattened, fan-shaped cells

Fig. 8.1 Biological soil crust biota. (a) *Limax* (snail-like) amoebae (arrow points in the direction that the amoebae are moving). (b) Stylet-bearing fungivorous/omnivorous nematode of the genus *Tylenchus* (arrow points to needlelike stylet that is used to pierce fungal hyphae and filamentous cyanobacteria). (c) Bacterial-feeding nematode of the genus *Acrobeles* in an active, hydrated form (arrow points to probolae). (d) Bacterial-feeding nematode of the genus *Acrobeles* in a coiled, anhydrobiotic form. Images by B. Darby

(Rodriguez-Zaragoza et al. 2005; Zaragoza et al. 2007). Some studies have been able to further identify individual species belonging to some functional groups (Bamforth 1984, 2004, 2008; Bamforth and Bennett 1985; Bamforth et al. 2005; Robinson et al. 2002). The results of these meticulous studies at finer resolution have led to the observation that biocrusts contain numerous species of non-encysting protozoa (like *Thecamoebae*), which may suggest that biocrusts serve as microrefugia with pockets of adequately moist pores for some protozoa (Robinson et al. 2002).

### 8.2.2 Nematodes

Nematodes are not as abundant as protozoa in either numbers or biomass, nor are they as phylogenetically diverse as protozoa, but we have a greater understanding of nematode ecology in biocrust habitats, mostly because we can count, identify, and manipulate nematodes easier and with a finer level of taxonomic resolution. However, most of our understanding of feeding habits and life history traits of

specific nematode species is still based on generalizations made at the taxonomic level of family or genus. One of the outstanding questions of biocrust nematode ecology is whether the species that are found in biocrusts have similar or different feeding habits of comparable species of the same genus in non-biocrust habitats. Nearly every component of the biocrust food web has some potential nematode predator. For the purposes of estimating general trophic links in the nematode community, species of nematodes are typically grouped into one of several feeding types identified largely on the basis of the size and shape of feeding apparati (Yeates et al. 1993). One of the most distinguishing factors is the presence or absence of a stylet (see Fig. 8.1b), a fine, needlelike piercing apparatus of organisms that pierce (rather than fully engulf) their prey. There are five types of nematodes: herbivores, fungivores, bacterivores, predators, and omnivores. Herbivores have a fine-apertured stylet with a length depending on whether the species tends to be an endo- or ectoparasite. Fungivores have a fine-apertured stylet that is typically short. Bacterivores do not have a stylet and instead have an open buccal cavity with various types of lips surrounding the anterior opening, from smooth and low-rounded to very elaborate, branched processes extending from the lips (called probolae, see Fig. 8.1c). Predators (order Mononchida) have a large, open stoma (oral opening), often with a prominent tooth or row of denticles (Fig. 8.2). There are two main types of omnivores that deserve to be acknowledged in biocrust systems. Nematodes in the orders Tylenchida and Aphelenchida have fine-apertured stomato-stylets and can potentially pierce filaments to feed on the cytoplasm of fungi, fine root hairs, moss rhizoids, and cyanobacteria (Fig. 8.3a). Nematodes in the order Dorylaimida have a broad-apertured odontostylet and can feed on fungi, cyanobacteria, and other microinvertebrates including nematodes, tardigrades, and rotifers. Previous outlines of nematode feeding habits advised against assigning the name of omnivore whenever possible, due to the ambiguity of the designation. However, they also acknowledged the significant “gaps in knowledge of feeding in the smaller tylenchids and many dorylaims” (Yeates et al. 1993). The nematodes that are most likely to consume cyanobacteria are those with a piercing/sucking stylet (such as those traditionally identified as fungivores or predator/omnivores) rather than those with an open buccal cavity (otherwise called bacterivores). This is supported by some of the earliest studies that documented nematode feeding habits as they demonstrated that feeding on algae (both green algae and cyanobacteria) was just as prevalent as feeding on fungal hyphae among the small Tylenchidae (Wood 1973a, b). Because cyanobacteria are such a significant portion of the biocrust soil food web, we consider it prudent to assume for now that many nematodes in genera thought to be primarily fungivorous in temperate ecosystems may also feed on cyanobacteria in biocrust systems (Fig. 8.3b).

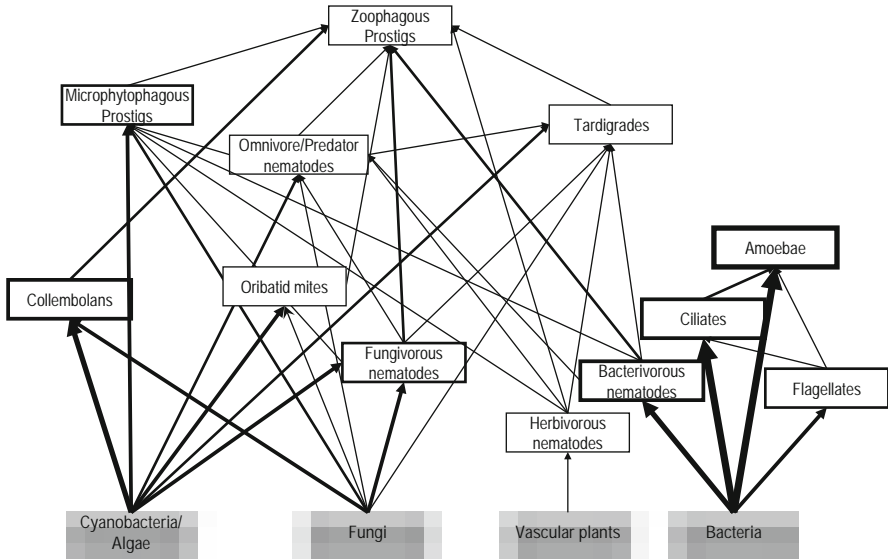


Fig. 8.2 Biocrust consumer food web. The consumer food web as based on the microfauna found in a Moab, Utah, biocrust system in southwestern USA (Darby et al. 2011; Neher et al. 2009). The width of the arrows linking prey to their consumer is proportional to the biomass nitrogen of that trophic link, and the width of the border around the consumer text box is proportional to the amount of inorganic nitrogen (N) being released from the consumer functional group [according to the results of the model as computed by Hunt et al. (1987) for the Moab, Utah, biocrust food web]. In contrast to a typical short-grass prairie soil food web, the biocrust food web: (1) has more N cycling through and from protozoans and (2) has more N cycling through and from the functional groups that are otherwise thought to be fungivorous (if, indeed, these functional groups are also capable of feeding on cyanobacteria, which is a reasonable but yet unconfirmed assumption)

### 8.2.3 Tardigrades and Rotifers

Tardigrades and rotifers are also among the microinvertebrates that one might find inhabiting the water films of a biocrust sample. Both tardigrades and rotifers are sometimes found exclusively on the surface of biocrusts as most species are extremely desiccation tolerant. Rotifers are filter feeders that primarily prey on small cells (e.g., bacteria, flagellates, and small unicellular algae), but probably not on filamentous cyanobacteria or large protist cells that are larger than their mouths. Tardigrades may be algivores, fungivores, cyanovores, or predators (on other microinvertebrates) depending on whether they have a piercing/sucking stylet or an open buccal tube. Compared to nematodes, there is less doubt that tardigrades feed on cyanobacteria (Fig. 8.3c), but it remains unclear which species of cyanobacteria are acceptable prey items and whether cyanobacteria are necessarily preferred over other potential foods (such as moss, fungi, or green algae).

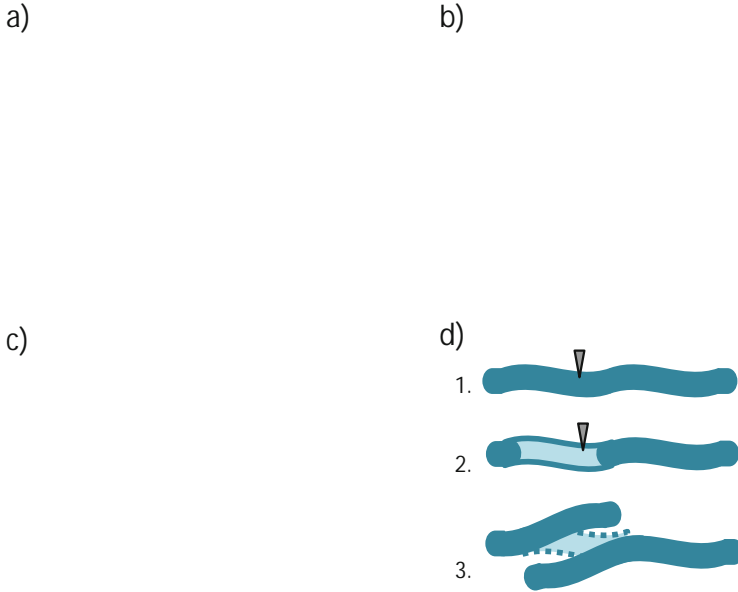


Fig. 8.3 Feeding on cyanobacteria. Digital images of microfauna feeding on cyanobacteria. (a) *Aphelenchoides* sp. feeding on *Microcoleus vaginatus* in monoxenic culture, (b) dark green/cyan pigmentation in the intestines of an *Aporcelaimidae* extracted from soil, (c) tardigrade *Haplomacrobiotus utahensis* feeding on *Microcoleus vaginatus*, (d) schematic of the regrowth of evacuated cyanobacterial filaments after being fed on by a piercing and sucking stylet-bearing nematode or tardigrade. First, the stylet-bearing nematode or tardigrade pierces the cyanobacterial filament with its piercing stylet (represented by the triangle). Second, the organism sucks out the cytoplasm of the segments adjacent to the initial stylet piercing. Finally, the ends of the filaments regrow into and out of evacuated segments, effectively creating two new ends from which the cyanobacteria grows

#### 8.2.4 Microarthropods

A variety of animals that do not require thin films of water, including arthropods and mollusks, also inhabit biocrusts around the world (Shepherd et al. 2002; Colesie et al. 2014; Shachak and Steinberger 1980). Microarthropods such as mites and collembolans inhabit primarily air-filled pore spaces (unlike the water-film fauna that include protozoans, nematodes, tardigrades, and rotifers) and are typically more mobile than water-film fauna (both vertically and horizontally) across larger spatial scales (Shepherd et al. 2002). Like nematodes, the feeding habits of most microarthropods are predicted based on observations of closely related taxa and on the morphology of feeding structures. Most biocrust collembolans are microphytophages, feeding on cyanobacteria, fungi, and detritus, but some are also facultatively predaceous on smaller microinvertebrates such as nematodes. However, biocrust mites can feed on diverse food items such as cyanobacteria, fungi,

nematodes, detritus, mammals, carrion, arthropods, lichens, pollen, and plants (Neher et al. 2009). Larger invertebrates, including mollusks such as snails and macro-arthropods such as ants and pseudoscorpions, can also be significant components of some biocrusts (Li et al. 2011). Unlike microfauna, which are thought to have minimal impact on the physical structure of soil and biocrusts, arthropods like ants have been shown to alter the physical architecture of soil and biocrust hydrology (Chen and Li 2012; Li et al. 2014). Predators of microarthropods form the link between the soil microinvertebrate fauna and the aboveground insectivores. Snails graze lichens, cyanobacteria, and mosses of rocky surfaces (Jones and Shachak 1990; Shachak and Steinberger 1980).

### 8.3 What Microfauna Do in Soil Crust Ecosystems

Microfauna in biocrusts perform many of the same functions that microfauna perform in grassland or forest systems. This includes regulating their microbial prey populations, cycling nutrients by stimulating microbial growth and excreting waste nutrients as soluble inorganic or low molecular weight organic form, dispersing spores or vegetative microbial cells that are viable and not fully crushed during digestion, and serving as prey for macrofauna at higher trophic levels in the soil food web (Neher 2001; Freckman 1988). However, the relationship between microfauna and autotrophic (and in some cases diazotrophic) cyanobacteria in the soil food web is one of the primary questions that remains regarding the role of microfauna in biocrust systems: that is, how many microfauna consume cyanobacteria, and what is the significance of this trophic link for the biocrust food web? The nutrients that microinvertebrates mobilize are thought to depend on the elemental ratio of their prey (Hunt et al. 1987). For example, a nematode that feeds on fungi with a relatively high carbon(C)/nitrogen(N) ratio is thought to be N limited and therefore will mineralize more C by respiration than N by waste release. Additionally, the ecosystem function that would be affected by grazing would be the decomposition performed by fungal extracellular enzyme activity. However, if this same nematode species can also prey on N-fixing cyanobacteria with a low C:N in a biocrust system, then we would expect the nematode to be relatively C limited and would instead mineralize more N as a waste product instead of C by respiration. Additionally, the ecosystem function that would be affected by grazing would be photosynthesis and N-fixation from the cyanobacteria. These possibilities have not been demonstrated experimentally with nematodes, but they have been shown for protozoa feeding on *Azotobacter chroococcum* (Nasir 1923; Cutler and Bal 1926) and *Collembola* feeding on arctic cyanobacterial mats (Birkemoe and Liengen 2000). In both cases, the experimenters found that N-fixation increased with intermediate levels of grazing from their microfaunal predator.

To demonstrate the potential effect of biocrust fauna on nutrient cycling, N cycling through the biocrust food web was estimated for a field site in a cool desert location in the southwestern USA (Darby et al. 2011; Yeager et al. 2012; Zelikova

et al. 2012), based on the approach of Hunt et al. (1987) and de Ruiter et al. (1993). The desert food web was constructed based on best estimates of feeding habits known for the organisms found at this site and accounted for the findings of grazing on cyanobacteria by stylet-bearing nematodes and tardigrades, as well as microphytophagous mites and collembolans. Biomass of micro- and mesofauna at this site was obtained from 2-year mean abundances of all functional groups previously measured at Colorado Plateau (Darby et al 2011). To facilitate comparison, and conform to published conventions, biomass per gram of dry soil was converted to biomass per area (to 10 cm depth) assuming a bulk density of  $1.0 \text{ g cm}^{-3}$  (Belnap 1995), and biomass N was estimated as 5 % of total dry biomass. Feeding preferences and physiological parameters were assigned according to Hunt et al. (1987) with the following exceptions. First, the generation time of omnivore nematodes in the order Dorylaimida was set to 50 days per year, representative of the slower-growing omnivore-predators in the desert such as Aporcelaimellus and Qudisianematidae (Wood 1973a, b). Second, the generation time of all protozoa was decreased from 6.67 days to 2 days, which is a conservative estimate of the maximum growth rate (0.5 per day) of these desert protozoa (Darby et al. 2006). Finally, microphytophagous prostigmatid and oribatid mites, collembolans, tardigrades, and tylench- and dorylaim-type omnivores were assumed to prey on cyanobacteria with the same preferences as on saprophytic fungi (Neher et al 2009; Wood 1973a; Yeates et al 1993). Microarthropods were assumed to be active and growing for 365 days per year because they are thought to be active even in dry, air-filled pores. Nematodes and protozoa were assumed to be active and growing for 40 days per year (Hunt et al. 1987). This model predicted that belowground soil fauna produce  $311 \text{ mg N m}^{-2} \text{ year}^{-1}$  inorganic N and  $97 \text{ mg N m}^{-2} \text{ year}^{-1}$  organic N from feces (Table 8.1) or  $3.0 \text{ kg N ha}^{-1} \text{ year}^{-1}$  inorganic N and  $1.0 \text{ kg N ha}^{-1} \text{ year}^{-1}$  organic N from feces. Like in temperate grassland systems, most of the inorganic N comes from protozoa and bacterivorous nematodes grazing on bacteria (Fig. 8.3). However, what is unique in this system is that a large portion of biologically fixed N from cyanobacteria would be mobilized by microfauna under the assumption that fungivorous functional groups also prey on cyanobacteria. This is a reasonable but unconfirmed assumption, which is why detailing the actual feeding habits of desert microfauna is so important to understanding overall ecosystem function.

Another significant function of microbe-feeding microinvertebrates is the dispersal of viable microbial spores and cells to new locations. In the case of biocrusts, this would include fungal spores and bacterial cells that are not crushed or enzymatically degraded by a predator that feeds by engulfing its prey. However, this would not include filamentous prey items (such as fungal hyphae and filamentous cyanobacteria) that are consumed by predators that feed by piercing their prey (Fig. 8.3). Even though piercing-type predators of filamentous cyanobacteria, such as nematodes or tardigrades, would not disperse vegetative cells, it may still be possible that these predators may nonetheless alter the distribution of filamentous cyanobacteria in biocrusts. As predators such as tardigrades pierce a cyanobacteria filament and suck out the cytoplasm, they leave a gap of evacuated cytoplasm. As



Table 8.1 Faunal contributions to nitrogen cycling

Functional Group	Biomass (mg N m <sup>-2</sup> )	Inorganic (mg N m <sup>-2</sup> year <sup>-1</sup> )	Feces (mg N m <sup>-2</sup> year <sup>-1</sup> )	Death (mg N m <sup>-2</sup> year <sup>-1</sup> )
Zoophagous	35.6	0.76	0.90	0.60
Microphytophagous	88.4	1.99	3.56	1.57
Oribatid	33.1	0.50	0.89	0.39
Collembolans	1070.7	24.14	43.10	18.97
Tardigrades	9.6	0.03	0.06	0.03
Dorylaim omnivore nemas	88.6	0.19	0.30	0.11
Tylenchid omnivore nemas	541.6	2.21	5.71	1.30
Herbivore nemas	2.7	0.007	0.03	0.004
Bacterivore nemas	1861.8	33.25	26.08	5.87
Amoebae	2406.7	161.14	11.01	(48.13)
Ciliates	1185.1	79.95	5.47	(23.88)
Flagellates	98.6	6.90	0.47	(2.06)
Total (mg N m <sup>-2</sup> )	7422.5	311.08	97.61	102.91

Nitrogen (N) cycling results from soil food web model [adapted from Hunt et al. (1987)], including standing biomass and nitrogen contributions to inorganic substrates and organic substrates through feces and death. Death of amoebae, ciliates, and flagellates was computed as for other organisms (inverse of generation time) but is presented in parentheses because they are thought to not die naturally but rather continue to divide. Thus, contributions to substrate from death may be much less than modeled and limited to environmentally induced mortality rather than natural turnover

the adjacent cells grow and extend into the gap, they sometimes extend past the opposing end, which results in lateral branching, creating twice as many ends from which the cyanobacteria can grow (Fig. 8.3d). This phenomenon was observed in laboratory cultures on flat agar surfaces, but it is unclear if it occurs similarly in a more complex natural environment.

8.4 When Are Microfauna Active?

The water-film fauna that are restricted to water-filled pores are often constrained to brief windows of activity in biocrusts. Most biocrust microfauna have diverse cryptobiotic (“hidden life,” Crowe and Cooper 1971) capabilities that allow them to enter temporary dormant stages such as anhydrobiosis (to survive life without water, Crowe and Crowe 2000), cryobiosis (to survive freezing), and anoxybiosis (to survive life without oxygen, although this is less common in surface biocrusts). As soils dry, microinvertebrates enter anhydrobiosis by converting storage carbohydrates into low molecular weight cellular protecting sugars, such as trehalose (Crowe 2002; Madin and Crowe 1975). Specimens that have entered anhydrobiosis are often seen in a coiled, anhydrobiotic state (Fig. 8.1d). Entering and exiting

anhydrobiosis is metabolically costly (Crowe et al. 1977; Madin et al. 1985), and the frequency and duration with which microinvertebrates must endure hydration cycles is thought to affect their fitness in a biocrust habitat. The microinvertebrate species that exist in surface biocrusts must be able to tolerate frequent wetting/drying cycles, brief periods of activity following hydration events, prolonged periods of drought, and extreme temperatures while anhydrobiotic. The surrounding soil conditions, such as texture, depth, and cover, can influence the severity of the abiotic stresses. Soil pores dry out more quickly at the surface than at depth, in coarse relative to fine soils, and in soils with very low organic or vegetative cover than soils with higher cover. As a result, the biocrust microinvertebrate community composition differs somewhat between soils of different depth, texture, and cover (Darby et al. 2010), as does the mobility of microfauna after rain events (Whitford et al. 1981; Parker et al. 1984).

## 8.5 Where Are Microfauna Found in Biological Soil Crusts?

Perhaps the best characterized aspect of biocrust microfaunal ecology, more so than their feeding habits or life history traits, is the overall abundance and distribution of organisms relative to soil depth, cover type, successional stage, and proximity to vascular plants. Microfauna can generally exist wherever sufficient microbial prey exists, and this usually matches the distribution of plant biomass or organic matter. This means that microfauna are associated with diverse types of biocrusts even in relatively extreme environments or with little moisture, such as sand savannas (Neher et al. 2003), desert biocrusts (Belnap and Phillips 2001; Shepherd et al. 2002), tropical inselbergs (Vaculik et al. 2004), and Antarctic soils, glaciers, and hypoliths (Sohlenius et al. 2004; Schwarz et al. 1993; see Chap. 11 by Pointing). In arid systems, nematodes can be found as deep as 11–12 m (Freckman and Virginia 1989), but the peak abundance of microfauna in soils covered by biocrusts is usually within the top 10–20 cm. In most soils, protozoa, nematodes, and microarthropods are more abundant in the surface 0–10 cm than in the next 10–20 cm or 20–30 cm (Darby et al. 2006, 2007a, b, 2010; Housman et al. 2007; Neher et al. 2009). However, the proportion of microfauna that are anhydrobiotically inactive is inversely proportional to soil moisture or relative humidity, and relative humidity in soils below 10 cm is generally greater than in surface 0–10 cm soils. Thus, the abundance of active, hydrated water-film fauna may actually be greater below 10 cm than above 10 cm depth because even though microfauna are generally more abundant above 10 cm than they are below 10 cm, most of them are inactive at the surface (Darby et al. unpublished results). This is potentially significant because if the autotrophic biocrust components are most active at the surface during brief periods after rain events, but the heterotrophic consumers are most active at depth in between rain events, then this means that

productivity and consumption is potentially decoupled in both space and time. The full implications of this spatial and temporal decoupling have not been explored experimentally.

The second most determining factor of the abundance and distribution of microfauna is the distribution of vascular plants. Microfauna are generally more abundant and taxonomically diverse close to plant rhizospheres than in the inter-space between plants (Darby et al. 2010; Housman et al. 2007). This is generally true for all ecosystems, but it is easier to quantify in arid systems with more sparsely distributed vascular plants. Furthermore, microfauna are more abundant and taxonomically diverse beneath and associated with late-successional stage “dark” lichen and moss biocrusts than when associated with early-successional stage “light” cyanobacteria biocrusts (Darby et al. 2006, 2007a, b, 2010). This can reasonably be explained, as greater productivity and microbial prey biomass is found in lichen and moss biocrusts than in cyanobacteria crusts. It has also been observed that nematode communities are more “ecologically mature” in late-successional stage biocrusts than early-successional stage crusts (Darby et al. 2007a, b). A greater proportion of the individuals associated with late-successional stage crusts are “K-strategists” (sensu Pianka) that are late to develop and have low reproductive output, slow generation times, and longer life spans (Bongers 1990). However, the persister-type “K-strategist” nematodes that are associated with late-successional stage crusts also tend to be higher trophic levels (such as predators and omnivores). We cannot necessarily distinguish whether predatory K-strategist nematodes are associated with late-successional stage biocrusts due to increased biomass and autotrophic productivity going into the soil food web, or because late-successional stage biocrusts tend to ameliorate temperature and moisture fluctuations that promote persister-type nematode species. Similarly, physical trampling of surface crusts reduces the biomass and architectural complexity of the lichen, cyanobacteria, and moss cover. This is associated with reduced abundance and species richness of nematodes relative to that of non-trampled biocrusts (Darby et al. 2010). However, we are not yet able to determine whether the effect of physical trampling on reducing nematode abundance and richness is due to the reduced biomass of microfloral prey items or because of the altered hydrology and reduced architectural complexity and pore size distribution of the trampled biocrust surface.

## 8.6 How Are Microfauna Affected by Surface Disturbance and Altered Climate?

The effect of altered climate on crust microfauna is a complex interaction of temperature, moisture, and the seasonality of these changes. Most microfauna can tolerate relatively high temperatures (>40–50 °C) if they gradually enter their anhydrobiotic state, but cannot tolerate being hydrated at high temperatures.

Similarly, many microfauna can tolerate frequent wetting and drying cycles in moderate temperatures, but they incur significant mortality if these wetting and drying cycles are at high temperatures ( $>35\text{--}40\text{ }^{\circ}\text{C}$ ). Thus, we predict that neither increased temperature during drought nor decreased moisture during warm seasons is necessarily going to alter microfaunal communities if they are already dormant. Instead, the combination of altered temperature and moisture is likely to be more influential than either alone. However, empirical evidence of the effect of altered temperature and precipitation on microfaunal communities is likely to come only after long-term experimentation (Darby et al. 2011). The primary literature does not have sufficient empirical evidence of the influence of altered climate on desert soil fauna community composition and their role in soil ecosystem functioning, so instead we rely on model predictions. Hunt and Wall (2002) addressed this challenge in temperate food webs by asking the question “how many species does it take to maintain ecosystem function?” They compared food web dynamics run to steady state after deleting each of the 15 functional groups, one at a time. They found that only two functional group deletions (i.e., bacteria and saprophytic fungi) resulted in the extinction of other groups, and only three functional group deletions (i.e., bacteria, saprophytic fungi, and herbivorous nematodes) resulted in a 10 % alteration in some index of ecosystem function (i.e., nitrogen mineralization or primary production). They concluded that “the results suggest that ecosystems could sustain the loss of some functional groups with little decline in ecosystem services, because of compensatory changes in the abundance of surviving groups.” However, we suggest that the wholesale loss of entire functional groups is an unlikely scenario from climate change predictions. Instead, the more likely changes appear to be subtle and sometimes idiosyncratic shifts in the relative proportions (or species composition) of existing functional groups (Sohlenius and Bostrom 1999; Todd et al. 1999; Convey and Wynn-Williams 2002). Intolerant species that are lost from a functional group are often replaced by what appears to be redundant species of a similar functional group (Todd et al. 1999; Bakonyi and Nagy 2000). Thus, rather than addressing the question “how many species does it take to maintain ecosystem function,” it would be more prudent to ask, “what happens to ecosystem function after a directional shift in species and functional group composition?”

To address the question “what happens to ecosystem function after a directional shift in species and functional group composition?” we first have to identify a likely directional shift in community composition and the functional significance of that change. In the case of biocrusts, we have observed that nematodes are affected more negatively by these abiotic stresses than amoebae (Darby et al. 2011). Because nematode body size is an order of magnitude greater than amoebae, they are expected to respire less per unit of biomass than amoebae (West et al. 1997, 1999; Ryszkowski 1975). Thus, nematodes contribute proportionately more to nitrogen cycling through dissolved organics (Wright 1975a, b), while amoebae contribute more to nitrogen cycling through excretion of inorganic nitrogen (Hunt et al. 1987). In sum, climate changes of increased temperature and summer precipitation could decrease the abundance of nematodes more than that of amoebae and shift the balance of nitrogen cycling by reducing the relative contributions of

dissolved organics and increasing the relative contributions of labile inorganics. This is significant because ammonium, the form of inorganic nitrogenous wastes by nematodes and protozoa, can be oxidized rapidly in this system (Johnson et al. 2005) and exported through leaching of nitrate (Johnson et al. 2007). Future research should be careful to compare the balance of organic and inorganic nitrogen in desert soils and determine whether changes in soil microfauna affect these substrate pools (Belnap et al. 2005).

## 8.7 Future Directions and Research Priorities

In the last decade we have learned much about the microfauna in biocrusts, including who are the main taxa and functional groups, what important functions they perform, when they are most active, where they exist in relation to depth and vegetative cover, and how they are affected by physical disturbance and abiotic stresses. We have identified three areas of research that we believe will be most beneficial in leading us toward a more complete understanding of the importance of microfauna in biocrust systems: (1) identify specific feeding behaviors of individual species, (2) increase the taxonomic resolution of ecological studies to the level of species, and (3) identify the ecologically relevant genetic and genomic aspects of microfaunal adaptations to the biocrust habitat.

### 8.7.1 Feeding Behavior

For most families and genera in biocrusts, we have a reasonable idea of what potential prey items they could consume (largely based on the size and shape of feeding structures), and what some of their sister species likely consume (largely based on published reports of feeding trials or tissue analysis), but we most likely do not know what the biocrust species actually consume. The two main pieces of information that need to be distinguished for each species are (1) the full breadth of acceptable prey items and (2) the subset of preferred prey items. Accomplishing this goal will require multiple different empirical approaches, such as culturing assays with feeding trials (Wood 1973a, b), molecular gut content probing (Treonis et al. 2010), stable isotopes (Darby and Neher 2012), and phospholipid fatty acid signatures (Buse et al. 2013; Ruess et al. 2005). This is important information because even though each functional group of biocrust fauna is represented by multiple species, we have no way to confirm whether or not these species are truly functionally redundant as we do not know if there are actually more subtle feeding preferences. This is especially true for taxa that are broadly considered omnivorous (e.g., stylet-bearing nematodes of Dorylaimida and some Tylenchidae). In many of these cases, we do not know whether omnivorous genera represent many species who themselves are all omnivorous, or if they represent many species who

themselves are all specialists but on different trophic levels, so that the genus as a whole appears omnivorous.

### 8.7.2 Increased Taxonomic Resolution

Most studies of biocrust microfauna are performed at the taxonomic resolution of family or genus. This provides enough information on the broad feeding or functional groups that are present but does not provide enough information to distinguish between biocrust and underlying soil species, nor does it allow comparison of species composition across studies in geographically distinct locations. We still do not know whether the species of a particular genus inhabiting biocrusts of one site are the same species of that genus inhabiting the soil beneath the biocrust or even if they are the same species of that genus inhabiting biocrusts at a different site. There is a clear possibility that many of the species found in biocrusts have yet to be described (as in Pilato and Beasley 2005). To further our understanding of the ecology of biocrust food webs, there is a need for future ecological studies to aim for species-level taxonomic resolution in their enumeration of biocrust microfauna. This is challenging, but molecular techniques such as high-throughput amplicon sequencing (Bik et al. 2012; Darby et al. 2013; Steven et al. 2014) are making high-resolution enumerations rapid, accessible, and informative. Various methods of specimen preservation are available to allow for the recovery of both molecular and morphological information (Yoder et al. 2006). Thus, species-level taxonomic resolution can be obtained by combining, from the same specimen, both molecular sequence data and virtual morphological vouchers by digital multifocal imaging (De Ley and Bert 2002). The cumulative benefit of increasing taxonomic resolution to the species level will be to allow more reliable comparison of species composition between communities of different study sites or of different habitats (e.g., biocrust versus underlying soil) within a site.

### 8.7.3 Ecological Genomics

The effects of abiotic stresses on biocrust microfaunal communities have been studied mostly by the application of acute short-term experimental treatment (such as heat, desiccation, and UV radiation). However, the chronic, long-term implications of abiotic stresses on biocrust microfauna community composition have not been well studied, nor have we been able to quantify the consequences of changes in community composition on ecosystem processes. We believe this is largely because our understanding of the genetic and genomic adaptations of biotic and abiotic stress on biocrust microfauna lags behind that of the research on biocrust microflora (Zelikova et al. 2012; Steven et al. 2014). This is a significant research need, because the role of microfauna in ecosystem-wide functioning is

linked to the physiological traits that allow biocrust microfauna to survive in this unique habitat. If we can understand how biocrust microfauna are adapted to the biocrust habitat at a genetic and genomic level, then we may be better able to predict the ecosystem implications of changes in species composition. For example, the relative composition of waste nutrients that are mobilized by microfauna is thought to be related to the stoichiometry of the biomolecules that are used and extracted by the organism (Sternner and Elser 2002). Sugars and simple carbohydrates are high C-containing biomolecules, proteins are rich in N, and nucleic acids are one of the molecules that contain a large proportion of phosphorous. Thus, the biomolecules that microfauna use and synthesize in response to biotic and abiotic stress are biased in their chemical stoichiometry (Elser et al. 2000), and we can use ecological genomics approaches to understand how microfauna are adaptations to environmental stress and how these adaptations will influence the environmental cycling of key nutrients. Fortunately, advances in high-throughput sequencing technologies allow for more advanced genomic analysis of non-model organisms from ecological systems (Ungerer et al. 2008). Ecological genomics approaches can be used to identify the adaptively significant genomic variation that may lead to our understanding of how changes in community composition affect the functioning of biocrust microfauna.

## 8.8 Conclusion

In conclusion, biocrusts serve as unique habitat for a broad range of microfauna, including protozoa, nematodes, tardigrades, rotifers, mites, collembolans, and even larger arthropods and mollusks. These microfauna feed on the bacteria, cyanobacteria, algae, fungi, bryophytes, and plant roots that are found in the biocrusts. Consumer food web as a whole performs several important functions, such as cycling nutrients, dispersing propagules, and moderating their microbial prey populations. Many species of biocrust microfauna tolerate periods of drought in an anhydrobiotic dormant state, so they are typically active only during brief windows of time. Most microfaunal groups tend to be more abundant, species rich, and diverse in mature, late-successional stage biocrusts that are dominated by diverse microflora (such as lichens, bryophytes, fungi, and cyanobacteria) than in early-successional stage biocrusts that are dominated by less diverse microflora (such as cyanobacteria alone). Biocrust microfauna are susceptible to the same surface disturbances that affect biocrust microflora, such as physical trampling or altered temperature and summer precipitation, but the specific ecosystem consequences of altered community composition due to surface disturbances are still largely unknown. To fully understand the ecosystem consequences of biocrust microfauna, we propose that the three main research needs in the future are to: (1) identify specific feeding behaviors of individual species, (2) increase the taxonomic resolution of ecological studies to the level of species, and (3) identify

the ecologically relevant genetic and genomic aspects of microfaunal adaptations to the biocrust habitat.

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# Chapter 9

## Composition and Macrostructure of Biological Soil Crusts

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### 9.1 Introduction

Surface crusting, even at small spatial scales, has a strong impact on many soil properties, which ultimately determine various ecosystem functions (Assouline 2004). Being a physical discontinuity in the soil profile (Coppola et al. 2011), a soil crust changes the soil structure and morphology of the soil surface, therefore changing soil properties such as infiltration, runoff, and erosion. It is crucial to understand and to describe the spatial structure of biological soil crusts (here referred to as “biocrust” because this term has been recently gaining favor as it is short and understandable, although less precise) and to classify different surface structure types in order to understand the influence of biocrust structure on those soil properties. The structure of biocrusts itself is affected by numerous physical, biological, and chemical characteristics, all of which may as well interact with each other, making a classification and general statements challenging.

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## 9.2 Abiotic Crust Structure

Abiotic crusts can be either physical or chemical. Chemical crusts occur wherever mineral-bearing water evaporates, leaving behind precipitating soluble salts, gypsum, carbonates, or silica, or when the soil above an illuvial horizon (enriched in minerals) is eroded. Chemical crusts (also termed duricrust; Woolnough 1927; Khalifa et al. 2009) reduce the hydraulic conductivity of the soil. Physical soil crusts are either formed by raindrop impact that destroys soil aggregates (resulting in soil compaction) or by direct soil compaction provoked by livestock trampling or vehicles, which again causes a reduction of hydraulic conductivity (Assouline 2004). There are three types of physical crusts: (1) structural crusts, formed by rearrangement of soil particles without lateral movement; (2) depositional crusts that develop as a consequence of lateral movement of sediment (Chen et al. 1980); and (3) erosional crusts, which are comprised of only one thin, smooth surface layer that is enriched in fine soil particles and which results from the erosion of a structural crust (Valentin and Bresson 1992). While chemical crusts are restricted to areas with high evaporation, physical crusts can occur in various environments and in almost all textures, except on very coarse sandy soils (Lemos and Lutz 1957).

## 9.3 Biocrust Structure: Biotic Influences

In nature, soils are never sterile, so it is difficult to draw the line between an abiotic and initial biocrust. Here, we define a soil crust as “biotic” when the organisms play any ecological role, such as altering fertility, stability, or soil structure. Soil structure, topography, and morphology, here in the range of millimeters to only a few centimeters, are strongly determined by the size and the shape of the occurring organisms themselves.

Filamentous pro- and eukaryotic algae form the matrix of biocrusts and grow in the uppermost millimeters. There, they are important for initial soil particle aggregation that leads to enhanced soil stability. Pócs (2009) describes two main cyanobacterial crusts: (1) the epiterranean type, having all photosynthesizing components above the soil surface and therefore needing UV-protective pigments, and (2) the subterranean type, which has at least one active, photosynthesizing layer below the soil surface. In the subterranean type the uppermost layer of soil or rock protects the organisms from fast desiccation. The resulting crusts are horizontally structured (Fig. 9.1a), and in sandy soils layering may be observed. With higher cyanobacterial abundance in flat crusts, the physical status of the soil changes, for example, by having finer grain sizes, lower infiltration rates, lower soil moisture contents, and an almost four times higher breaking pressure (Zaady et al. 2014). On the other hand, cracks in cyanobacterial crusts, that either derive from frost or biogenic (Fig. 9.3), can increase infiltration and therefore soil moisture. Cyanobacteria influence soil cohesion and resistance to erosion. The filamentous

Fig. 9.1 Schemes of typical biocrust types. (a) Light or thin cyanobacterial crust. Filamentous cyanobacteria (*Microcoleus* sp.) dominate this crust, which is only a few millimeters thick. Patches of bare soil are visible. (b) Dark or thick cyanobacterial crust. Besides the filamentous species of *Microcoleus*, also coccoid species (*Nostoc* colonies) and other filamentous cyanobacteria (*Phormidium*) form this up to 5 mm thick biocrust. (c) Crustose “rugose” cyanolichen biocrust. Different *Collema* species or other cyanolichens dominate this crust type, but free-living cyanobacteria and green algae occur as well. (d) Rugose moss crust. Moss stems grow mainly embedded within the uppermost centimeters of soil. Only the uppermost leaves or the fruiting bodies rise over the soil surface. (e) Rolling chlorolichen crust. Mainly crustose and squamulose chlorolichens on top of the soil with rhizines penetrating deep into the soil dominate this crust type. Other components like cyanobacteria or green algae are also free living in this biocrust. (f) Rolling “thick” moss crust. Up to 5 cm thick moss carpets and cushions with cyanobacteria and green algae living on top of or in between the stems. (g) Pinnaced crust. Turret-like structures are elevated over the ground surface where organisms prevent soil erosion

Fig. 9.2 Soil crust forming organisms and their structure. (a) Cyanobacterial crust with patches of bare ground visible. (b) Cross section through a green algae (*Zygogonium*)-dominated biocrust; the filaments are smoothly aggregated at the surface but also penetrate into the soil and aggregating soil particles. (c) Dark cyanobacterial crust including green algae. Picture from the wet and humid orobiome in the high Austrian Alps. (d) Dark cyanobacterial crust showing the influence of mechanical disturbance. (e) The effect of oversanding and the layering of cyanocrusts. (f) Chlorolichen thalli growing in close association with moss stems. (g) Crustose cyanolichen crust. Lichens grow closely associated with the soil and form a more or less hard layer. (h) Burial by sand of several layers of biocrusts, Tengger Desert, China. (i) Pinnacled soil crust. Turret-like structures are elevated over the ground surface, where organisms prevent soil erosion. (j)

microorganisms trap sand particles and finer particles stick on the filament surfaces (Fig. 9.2b). Soil porosity is also increased by the microbial cover, with additional pores delineated by filaments on the surfaces of crusts and porous organic bodies derived from microbial remains at depth (Malam Issa et al. 1999). Biocrusts consisting of green algae are equivalent to cyanocrusts in being horizontally structured (Lan et al. 2012). Initial algal crusts show an inorganic surface layer with no or few algae from 0 to 0.02 mm, followed by a dense algal layer at a depth of 0.02 to 1 mm and a sparse algal layer underneath that at a depth of 1 to 5 mm (Lan et al. 2012). In the temperate zone, these crusts cover the soil surface more or less completely forming a smooth green carpet that can be easily removed from the soil surface when dry (Belnap et al. 2003).

Unlike soil cyanobacteria and algae, lichens and bryophytes with their complex thalli have almost all of their photosynthetic tissue on or above the soil surface. The above-surface thalli create roughness of the biocrusts' surface. In addition, capping of the soil surface provides protection from raindrop erosion (Fig. 9.2i). The size and type of biotic structures (i.e., organism morphology) can control the amount of dust captured, which ultimately defines the resulting sedimentary features. For example, the leaf structure of mosses controls the size of trapped grains (Fig. 9.2n), and the high shrink–swell potential of gelatinous lichens and incremental dust accretion cause the formation of sharp surface topographies (Fig. 9.2g). Thallus parts below the surface, such as rhizines of lichens or rhizoids and protonemata of bryophytes, create soil aggregates and extend the stabilized soil structure deeper into the soil (Figs. 9.1c–e and 9.2f, k). In contrast to the filamentous pro- and eukaryotic algae, these thalloid organisms add a vertically growing component to the biocrust and allow three-dimensional expansion (Fig. 9.2 l). Lan et al. (2012) describe lichen crusts as showing a thallus layer up to 1 mm above the soil surface, a rhizoid layer from 0.1 to 3 mm, and a sub-rhizoid layer from 3 to 7 mm depth. Depending on the lichen species, the above-ground layer thickness (as a proxy for surface roughness) can be even higher (Fig. 9.2j, l). For example, a crustose lichen-dominated biocrust from Antarctica was found to be 4.5 mm thick (Colesie et al. 2014a), whereas for fruticose or foliose lichen-dominated biocrusts, this may be in the range of several centimeters (Fig. 9.1e). Lan et al. (2012) describe typical moss-dominated biocrusts characterized by a stem–leaf layer, which stands 2 mm above the soil surface, a rhizoid layer from 0.2 to 6 mm depth, and a sub-rhizoid layer at depths of 6–15 mm from Chinese deserts. Generally, in dry habitats thin moss crusts with the stems being deeply embedded into the soil

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 Fig. 9.2 (continued) Chlorolichen crust. *Psora decipiens* growing crustose on the soil surface (Photo by L. Williams). (k) Chlorolichen thallus and cyanobacterial filaments embedded tightly into the soil in a crustose chlorolichen crust (Photo by M. Cardinale). (l) Natural appearance of chlorolichen-dominated crusts, in this case the Bunte Erdflechten Gesellschaft (colored lichen community). (m) Moss-dominated crust. Individual moss stems are mainly embedded into the soil, and only the upper parts are visible on the surface. View from above. (n) Moss stems in moss-dominated crusts are embedded into the soil. Moss tips catching sand grains. (o) Natural appearance of the thick moss-dominated crust



Fig. 9.3 CT scan of a cross section through a dark cyanobacteria/lichen crust from the Karoo, South Africa. Biogeneous macropore (arrow) besides buried lichen (CT scans by courtesy of Stephan Peth and Rainer Horn, soil sample by courtesy of Bettina Weber)

(Figs. 9.1d and 9.2m) are frequent, but short and tall mosses occur there as well. In wetter habitats the moss layer gets thicker (Figs 9.1f and 9.2o).

## 9.4 Biocrust Structure: Abiotic Influences

### 9.4.1 Macroclimatic Influences

On a continental scale, only a few studies exist that correlate macroclimatic influences to biocrust occurrence and diversity. These studies include Büdel et al. (2009), Green et al. (2011), and Colesie et al. (2014b) and were conducted in southwestern Africa and the ice-free Drylands of Antarctica. They present descriptions of the cryptogamic composition and diversity of biocrusts extending over several degrees of latitude being correlated to the overall macroclimate. Interestingly, the studies show that (1) water availability has the strongest influence on biocrust occurrence and composition (therefore structure), and (2) biocrust occurrence is much more the result of the natural scenery and water availability than of regional macroclimate. In Fig. 9.4 we indicate macroclimatic regions in different colors and include recent findings and descriptions of different biocrust types into the same map (marked as different symbols). It becomes obvious that

Fig. 9.4 Distribution of biocrusts on Earth. Macroclimatic regions are color-coded. Symbols indicate individual locations of diverse crust types dominated by different organism groups (their distribution may be much more extended). Each of the four color-coded macroclimatic regions include all types of different crust types (different symbols), either defined by topography or taxonomic composition. Data based on Büdel (2003), Orlovsky et al. (2004), and personal observations of authors until recently

macroclimate cannot be correlated to biocrust type on a global scale. Each of the four color-coded macroclimatic regions include all types of different crust types (different symbols), either defined by topography or taxonomic composition. This finding can be interpreted in the concept of zonal vs. azonal vegetation that was first applied by Walter in 1985. He distinguishes between zonal vegetation, the vegetation/plant occurring typically in a certain climatic zone, and the azonal vegetation/plant, occurring inside another climatic zone but, due to the local meso-/microclimate, resembling the climate of its origin. Single biocrust communities can be considered as functional types, and besides the zonal biocrust type, other types occur azonal according to the local variation of the meso-/microclimate.

On a regional scale, the general temperature regime of a biocrust habitat can have a formative influence on its structure mainly by controlling the species composition. Also frost heaving, freezing events, and the rainfall regime of an area are relevant for biocrust formation and structure. There are a few general trends for biocrust structure being influenced by regional climate:

- Cyanobacterial biocrusts (smooth, rugose, or pinnacled) mainly occur in geographical regions with an at least temporarily expressed arid element (tropical, subtropical, mediterranean, dry continental but also the arctic-alpine climatic (higher altitudes) zones; Figs. 9.1a, b and 9.2a, c, d).

- Green algal biocrusts (smooth, rugose, or pinnaced) preferentially occur in temperate but also arctic–alpine (lower altitudes) climatic zones (Fig. 9.2b, c).
- Lichens and bryophytes add to the primary crusts (rolling crusts) in habitats with higher water availability (Fig. 9.2l, o).
- The difference between the occurrence of cyanobacterial lichens or green algal lichens as a dominant component of the biocrusts depends on the type of water source. If rainfall is the predominant water source, cyanobacterial lichens become an important element of biocrusts, whereas if dew and/or high air humidity are prevailing, green algal lichens dominate the climax state of local biocrusts.
- Bryophyte presence depends on the total amount of water per annum and the frequency of wet–dry cycles (e.g., Hoppert et al. 2004; Büdel et al. 2009; Reed et al. 2012).

### 9.4.2 Mechanical Disturbance

Different kinds of mechanical disturbance, such as human influences (trampling, vehicular traffic), and burial by soil particles (see also Chap. 21 by Zaady et al.) affect biocrust structure. Soil disturbance by humans, livestock, or vehicles flattens the biocrust. Since the structure of biocrust changes greatly with succession (Williams et al. 2012), a mechanical disturbance sets this succession and attendant structure back to an earlier level (Kuske et al. 2011, Fig. 9.2d). Although only very few studies explicitly investigated the impact of disturbance on soil microstructure, it is well known that biocrust disturbance drastically increases the soil susceptibility to both, wind (Belnap and Gillette 1998; Zhang et al. 2006) and water erosion (Eldridge 1998; Herrick et al. 2010), which always results in a depletion of fine soil particles, thus changing the structure to a more coarse-grained one (Belnap et al. 2007). Further, the reduction of soil carbon and nitrogen after disturbance (Kuske et al. 2011) will cause a breakdown of organo-mineral complexes and ultimately decrease aggregate stability of micro- and macroaggregates (Amézketa 1999), resulting in higher compaction and a partial breakdown of the secondary pore system (Horn und Peth 2012).

To our knowledge, the only available study that explicitly investigated the influence of mechanical disturbance on internal biocrust structure was conducted by Menon et al. (2011). Using 3D computed tomography techniques and the Lattice Boltzmann method on a disturbed Kalahari Desert cyanobacterial crust, they detected a significant reduction of the modeled water flow through the crust after disturbance, which they also attribute to the loss of secondary pores and paths of preferential infiltration.

Burial by soil is a special kind of disturbance for two reasons. First, it does not actively destroy the biocrust structure; rather it significantly reduces light and water availability in the microenvironment (Rao et al. 2012). Second it can, to a certain degree, induce or promote a structuring process (Fig. 9.2e, h). A study on the impact

of burial in the Hopq desert, China, found that if the thickness of burial by sand does not exceed a threshold of 1 cm, it can actually promote a structuring process by applying selective stress on the biocrust organisms that favors mobile genera (e.g., *Microcoleus*) (Rao et al. 2012), which can move upward to the new surface, thereby creating new surface layers (Felde et al. 2014). However, if the sand burial height exceeds this threshold, the biocrust is severely damaged (Rao et al. 2012) and may not be able to recover. Here, it should be considered that burial by quartz sand may be tolerated to a larger depth compared to silt or clay, as the former has better light-transmissive qualities (Ciani et al. 2005).

### 9.4.3 Pedogenic Influences

In contrast to many studies that focus on the influence of biocrusts on soil properties, very little is known about the influence of soil properties on biocrust structure. This is an important field of research, as biocrusts may not establish or structure soils equally on different soil types. The main processes of the formation of biocrust structure and topography as described by Williams et al. (2012) for the hot Mojave Desert, USA, are (1) mineral precipitation and stabilization, (2) wetting–drying with resultant expansion–contraction of soil, (3) dust capture, (4) microscale mass-wasting, and (5) biologically mediated vesicular horizon formation. For biocrusts in the Mojave Desert, these processes lead to the formation of two layers at the macroscale, called the bio-rich and bio-poor zone of the crust. At the microscale, they describe nine distinct morphological features: (1) filament sheets, (2) filament knobs, (3) upturned or curled features, (4) rafts, (5) pedestals, (6) towers, (7) micro-hoodoos and sharp protrusions, (8) curved features, and (9) biosediment bridges. The unique characteristics of each of these nine features are tied to associated biota and vary with crust type.

Some other trends for pedogenic influences on biocrust structure are suggested by Belnap (2006). Biocrusts with similar species and biomass are flatter when they occur on clay and silty soils compared to those on adjacent coarser soils. In soils with weak crystalline structures (e.g., soils derived from calcite and gypsum), extracellular polysaccharide materials combine with the dissolved minerals when soils are wet to create very strong microbial sheaths that consist partly of organic and partly of inorganic materials. The internal strength of these soils resists winter frost heaving, and thus they do not form the highly dissected surfaces that may be found in adjacent sandy soils. Cyanobacteria generally dominate soils that are very sandy (>90 %), very salty, or have a high content of shrink–swell clays, regardless of the climatic zone. Lichen cover generally increases with an increase in the amount of carbonate, gypsum, and/or silt in the soil (Belnap et al. 2003). The importance of the silt content for vesicle formation is highlighted by Dietze et al. (2012), who showed that vesicular horizons can be found in a large variety of texture classes under natural conditions, which, however, always have a high silt content. In soils with heavy physical crusting, the surface morphology of biocrusts

is primarily controlled by soil physical and chemical characteristics, and the biological components have only a limited effect. If only cyanobacteria are present under these circumstances, the resultant biocrusts are smooth. If lichens and mosses colonize as well, the slight roughening of the soil surface creates a rugose or rolling crust. Pinnacled crusts seldom form in soils with a high degree of physical crusting.

### 9.5 Classification of Biocrusts

There are multiple ways to classify biocrusts. Classification can be based on species composition, functional groups, or a combination of surface appearance and functional groups (Table 9.1 and Fig. 9.2). All approaches have advantages and disadvantages.

**Composition Approach** This is the most desired but most expensive approach, as it provides information on biocrust morphology as well as species composition. The advantage of an approach based on taxonomic composition is that knowledge on the species composition also comprises information on the ecological roles of that biocrust. The drawbacks are that it is time-consuming, and expertise on field identification of lichens, mosses, and other biocrusts components is needed.

**Functional Group Approach** Eldridge and Rosentreter (1999) first provided a framework to classify biocrusts on the level of morphological groups (see also Chap. 7 by Rosentreter et al.). The advantage of using such an approach is that less expertise is needed to identify organisms on a species level. Büdel et al. (2009) utilized this approach along a 2000 km long transect through South Africa and southern Namibia, using a classification of biocrusts based on the dominating organism group. The authors distinguish seven general crust types: light

Table 9.1 Suggested classification of different biocrust types

Surface texture	Biocrust appearance	Dominant organism group	Thickness	Characteristic localities (examples)
Smooth	Light	Cyanobacteria, green algae	0–2 mm	Negev Desert
	Dark	Cyanobacteria, green algae		Austrian Alps, Alaska, Australia, Central Europe, Karoo, savannas
Rugose		Cyanobacteria	2–4 mm	Sonoran Desert, Tengger Desert, Gobi Desert, Central Europe
Rolling	Thin	Lichens	5–50 mm	Namibia, Greenland, Columbia Plateau, Tabernas badlands, Russian steppe
	Thick	Mosses		Iceland, Columbia Plateau, maritime Antarctica
Pinnacled		Cyanobacteria, lichens, mosses	6–150 mm	Colorado Plateau, NE Australia, Central Europe

cyanobacterial crust, cyanobacterial crust, cyanobacterial crust with cyanolichens, cyanobacterial crust with cyanolichens and/or green algal lichens, crust with bryophytes, hypolithic crust, and the unique Namib Desert lichen fields.

In addition, the functional groups used can be defined relative to the questions of interest. For example, if nitrogen inputs are of interest, then having two categories for lichens, those that fix nitrogen and those that do not, would be necessary. If soil stability is of interest, separating lichen types best at stabilization (e.g., foliose) from those less good (e.g., crustose) can be useful.

**Combined Approaches** There have been two main combined approaches suggested over time. Belnap (2003) developed four categories that combine surface morphology and functional groups: (1) Smooth crusts that consist mostly of endodaphic cyanobacteria, algae, and fungi. The soil surface consists mainly of mineral particles and has a very low surface roughness. We suggest subdividing this category into two subtypes, light smooth crusts (Fig. 9.1a) and dark smooth crusts (Fig. 9.1b). The light subtype is almost exclusively composed of endodaphic cyanobacteria and extremely flat (Fig. 9.2a). The dark subtype may rise a few millimeters upon the surface, has a higher abundance of organisms, and appears like a smooth carpet covering the ground (Fig. 9.2c). Smooth biocrusts represent the initial stage of crust development and are also very common in areas with frequent disturbance. (2) Rugose crusts that are also dominated by cyanobacteria and fungi. They have a low surface roughness (up to approx. 3 cm), originating from scattered lichen and/or moss clumps (Fig. 9.1c, d). (3) Pinnacled crusts that are generally dominated by cyanobacteria but can have up to 40 % lichen/moss cover. They exhibit a micro-topography of up to 15 cm, resulting from frost heaving and subsequent differential water erosion (Figs. 9.1g and 9.2i). (4) Rolling crusts that are dominated by a lichen/moss cover, creating a gently rolling surface (Fig. 9.1e, f). The heavy lichen and moss cover restricts pinnacle formation during frost heaving to a height of approx. 5 cm, due to the strong cohesion of the lichens and mosses.

The second type of a combined approach utilizes the overall appearance or dominant genera of the biocrust. Belnap et al. (2008) suggested a classification using surface coloration, roughness, and presence of different biocrust components as an indicator for the level of development (LOD) of biocrusts. For the SE Utah crusts that were studied by the authors, they developed six categories with the lightest type of cyanobacterially dominated biocrusts designated as LOD Class 1, and the darkest type dominated by cyanobacteria, but also containing mosses and lichens designated as LOD Class 6. The authors noted that this index could be extended to higher numbers for biocrusts dominated by lichens and mosses. This approach has the advantage of a quick and easy classification for experts and nonexperts alike and allows an easy classification of biocrust types, facilitating a worldwide comparison of biocrusts. The disadvantage is a highly generalized scheme of crusts and complications with a categorization of lichen- and moss-dominated crusts.

## 9.6 Conclusions

Classification of biocrusts can be based on macroscopic structures, taxonomic composition, and overall appearance (including color) or combined by overall morphology and taxonomic composition. However, a universal classification system in more detail than given here is disputable. First, the composing organisms and the various proportions of them have significant influence on the macrostructure of a biocrust. Second, physical parameters such as climate and physical and chemical soil properties impact biocrust macrostructure, to various extents.

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# Chapter 10

## Controls on Distribution Patterns of Biological Soil Crusts at Micro- to Global Scales

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### 10.1 Introduction

Like all biological phenomena, biological soil crusts (biocrusts) are spatially variable. Considerable research has been devoted to determining what drivers generate this heterogeneity. The earliest investigations, to our knowledge, are

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those of Rod Rogers in Australia in the early 1970s (Rogers 1972, 1973). He developed a continental scale conceptual model depicting biocrust type and abundance as a function of amount and seasonality of rainfall (Rogers 1973). In the 1990s, additional work in Australia further delineated the types of biocrusts occupying a system of landscape types (Eldridge and Tozer 1997). In the early 2000s, Belnap and Lange (2003) synthesized in several chapters what was known about the composition and characteristics of biocrusts within different continents and regions, and two chapters addressed the specific drivers of biocrust distribution at multiple scales and their quantitative relationships with biocrusts or particular biocrust components (Garcia-Pichel and Belnap 2003; Ullmann and Büdel 2003). At the time the latter two chapters were written, the amount of literature to be reviewed was sparse, and the collective knowledge was that there were a few key soil properties (alkalinity, calcareousness, gypsum concentration, texture) and climate-related factors (continentality, annual precipitation, thermal regime) known to commonly influence biocrust abundance or composition (Eldridge and Tozer 1997; Rogers 1972). Also in Belnap and Lange (2003), Büdel (2003) provided the first global study of the biogeography of biocrust genera. As our science has progressed, literature on this topic has accumulated, and the geographic scope of our regional knowledge of biocrust distributions has expanded in North America (e.g., Bowker et al. 2005; Ponzetti and McCune 2001; Rivera-Aguilar et al. 2006; Root et al. 2011), Asia (e.g., Rosentreter et al. 2014; Tirkey and Adhikary 2005; Zhang et al. 2007; Zhang et al. 2011), Africa (e.g., Büdel et al. 2009; Lalley et al. 2006; Zedda et al. 2011), the Middle East (e.g., Abed et al. 2010, 2013), and Europe (e.g., Concostrina-Zubiri et al. 2013; Martínez et al. 2006). Our synthesis presented here does not encompass the distribution of hypoliths (see Chap. 11 by Pointing).

### 10.1.1 Nomenclature for Scale

Because biocrust distribution patterns may differ based on the spatial scale of observation (Bowker et al. 2006a; Concostrina-Zubiri et al. 2013), we adopt the following nomenclature to denote scale. Microscopic and submillimeter scales (Garcia-Pichel and Belnap 2003) are discussed in another chapter (see Chap. 13 by Garcia-Pichel et al.) and are thus omitted here.

Global scale—Pertaining to variability across all habitats in the world (e.g., Büdel 2003)

Intracontinental scale—Pertaining to variability across a continent or major land mass [e.g., Australia (Eldridge 2003), North America (Rivera-Aguilar et al. 2006)]

Ecoregional scale—Pertaining to variability across an ecologically defined (based on environmental conditions, major vegetation associations, etc.) portion of a major land mass [e.g., Gurbantunggut Desert (Zhang et al. 2007)]

Local scale—Pertaining to variability within a collection of nearby sites [e.g., a local altitudinal-climatic gradient (Hernandez and Knudsen 2012) or a comparison among soil types (Bowker et al. 2006a)]

Intra-site scale—Pertaining to variability within a “typical” (as defined by most literature) sample unit which may range from multiple 10s of m<sup>2</sup> to 1 ha (Bowker et al. 2005, 2006b; Büdel et al. 2009; Concostrina-Zubiri et al. 2013; Eldridge and Tozer 1997), such as distance gradients from shrub canopies (Thomas and Dougill 2007) or small-scale soil gradients (Martínez et al. 2006)

Microscale—Pertaining to variability within a few square meters or less [e.g., soil chemistry or texture gradients within interspaces (Bowker et al. 2006a) or micro-aspect effects (George et al. 2000)]

## 10.2 Determinants of Biocrust Distribution at Different Spatial Scales

The forces underlying the distribution of biocrusts in space can be described as biogeographic, climatic, edaphic, topographic, and biotic (Fig. 10.1). These forces are distinct but partially dependent upon one another. The influence of these forces abruptly shifts from primarily biogeographic at the largest scales, to primarily climatic at intermediate scales, to primarily edaphic, topographic, and biotic at smaller scales. Biogeographic influences are those that act on the dispersal capabilities of the biocrust organisms themselves. For example, distance or degree of isolation is a barrier for biocrust propagule (e.g., spores, cells, thalli) dispersal over long distances (Marshall and Chalmers 1997). We may hypothesize that land masses that are isolated from one another by large distances or lacking connection via major wind patterns will tend to support less similar biocrusts; the temporal duration of this isolation will also act to promote distinction.

Biocrust variation within the dryland biome is primarily climatic. Climatic forces change among geographic areas, with latitude and altitude shaping thermal regimes and rain shadows and continentality further shaping the amount, type, and timing of precipitation received. For example, several different, yet contiguous, dryland regions are present in western North America and are distinguished by climate (e.g., Chihuahuan desert, hot/arid to semiarid, dominated by summer rainfall; Great Basin, cool/semiarid, dominated by winter rain/snow).

At ecoregional and smaller scales, biocrust variation is dictated increasingly by edaphic, topographic, and biotic forces. The physical and chemical properties of soils are determined by the parent materials and the degree of weathering that these parent materials have undergone. Most ecoregions are a mosaic of different soils, and substantial heterogeneity exists within a given soil, even at the very smallest scales. At smaller scales, topographic influences generate deviations from larger-scale climate patterns. The erosional-depositional setting generates geomorphological features that can be important across ecoregional to microscales. Biotic forces,

Fig. 10.1 Scale dependency of forces underlying biocrust distribution

especially the type and arrangement of vascular plants, are additional modifiers by providing shade and capturing or redirecting the flow of resources (e.g., water, nutrients, litter, and/or soil) at local or smaller scales.

### 10.2.1 Biogeographic Factors

Since the first description in the late eighteenth century by Pallas (1776), the presence of biocrusts has been reported in hot and cold deserts around the world, as well as having some presence in other biomes. However, little is known about the main determinants of their composition, distribution, and abundance at the biogeographic scale (Steven et al. 2013). Despite this situation, some intracontinental studies suggest biogeographic patterning of biocrusts. In a 2000 km transect in southern Africa, the six different dryland ecosystems surveyed had distinct biocrusts (Büdel et al. 2009). Similarly, arid to subhumid regions supporting biocrusts differ strongly in community composition within North America (Rivera-Aguilar et al. 2006).

Table 10.1 Number of species in biocrusts reported for different organism groups on different continents worldwide

	Europe	N. America	Greenland	S. America	Africa	Australia	Asia	Antarctica	Global
Cyanobacteria	98	53		40	83	58	82	66	320
Eukaryotic algae	137	86		1	76	3	179	44	353
Mosses	90	45		22	22	131	28	14	320
Lichens	212	226		4	77	72	126	42	551
Total	537	410		67	258	264	415	166	1544

Compiled from: Büdel et al. (2009), Dojani et al. (2014), Haarmeyer et al. (2010), Zhao et al. (2008), Belnap and Lange (2003), Pichtrova et al. (2013), Eldridge and Tozer (1997), Rogers (2006), McCune and Rosentreter (2007), De los Rios et al. (2011), Nagy et al. (2005), Pushkareva and Elster (2013), Pócs (2009), Frey et al. (1990), Fritsch (1916), Hu et al. (2003), Eldridge (1996), Eldridge and Koen (1998), Pointing et al. (2009), Stewart et al. (2011), Dettweiler-Robinson et al. (2013b), Tirkey and Adhikary (2005), Phillipson (1935), Flechtner et al. (2008), Flechtner et al. (1998), Flechtner (2007), Hawkes and Flechtner (2002), Lewis and Flechtner (2002), Montoya et al. (1998), Novichkova-Ivanova (1972), Novichkova-Ivanova (1980), Azia-Bustos et al. (2009), Azia-Bustos et al. (2011), Forest and Weston (1966), Williams and Büdel (2012)

A meta-analysis of species composition and richness of biocrusts compiled from the literature revealed a total of 1544 cyanobacteria, algae, bryophyte, and lichen species worldwide. When compared on a biogeographic scale, lichen species numerically dominate the European and North American floras, whereas bryophyte and liverwort species prevail in Australian biocrusts (Table 10.1). Europe and Asia stand out as having the highest species numbers of cyanobacteria and eukaryotic algae (Table 10.1). These patterns may indicate a geographic imbalance of biocrust species diversity data and/or possibly of taxonomic expertise.

We conducted a floristic similarity analysis using the Sørensen coefficient (Qs) that weights matches in taxon composition of biocrusts between two samples. As a consequence of the uneven species richness data from continents and sub-continents, this analysis can only be regarded as a first approach to the real conditions.

Cyanobacteria are the most ancient group of biocrust organisms, appearing up to 2.6 billion years ago on land, and as might be expected, they are also the most homogenous when compared among land masses. Even for the most isolated continent, Antarctica, the similarity with all other continents is >10 % (Fig. 10.2a). This pattern may reflect either a common community prior to the breakup of Pangaea or possibly a very effective intercontinental dispersal via the atmosphere. With the exception of South America, lichens are quite well investigated in terms of diversity. The high similarity coefficient between Europe and North America (Fig. 10.2c) might be explained by the long connection between these continents in geological history, but may also be an artifact of more extensive sampling in these regions and therefore a greater degree of detection of the species present. Bryophytes and eukaryotic algae have not been investigated as thoroughly as lichens, and species numbers are much lower, making reliable comparisons possible only for restricted geographic regions (Fig. 10.2b, c). One clear pattern that emerges is the distinctness of the bryophyte flora of Australia from other land masses, possibly reflecting its long-term isolation. While cyanobacteria occur in biocrusts across the globe, eukaryotic algae are more common on continents with a higher proportion of temperate regions (Tables 10.2 and 10.3).

From this preliminary diversity analysis of biocrusts, we can conclude that biocrusts contribute considerably to the biodiversity of the ecosystems to which they belong (also see Chap. 1 by Belnap et al.), despite the species assessment of biocrusts being far from sufficiently known. As most of the data presented here are based on classical determinations and only a few on molecular studies, we would like to emphasize that it is of great importance to relate operational taxonomic units generated by molecular data to described taxa. Only with those analyses can we thoroughly test biogeographic hypotheses.

Fig. 10.2 Sørensen floristic similarity coefficient ( $Q_s$ ) at the species level between continents for (a) cyanobacteria, (b) eukaryotic algae, (c) bryophytes including liverworts, and (d) lichens. Values below a  $Q_s$  of 10 % are not shown; species numbers are given in red numbers at each continent;  $Q_s$  in black numbers at each connecting line between continents; bold lines indicate  $Q_s$  values of 30–39 %; semi-bold lines between 20 and 29 %, and thin lines between 10 and 19 %



Table 10.2 Distribution of algae with a 43 % frequency (three out of seven continents)

	Europe	N-America + Greenland	S- America	Africa	Aus- tralia	Asia	Antarc- tica
<i>Bracteacoccus minor</i> (g)			insuf-				
<i>Pinnularia borealis</i> (d)							
<i>Klebsormidium montanum</i> (g)			ficiently				
<i>Stichococcus bacillaris</i> (g)			investi-				
<i>Hantzschia amphioxys</i> (d)							
<i>Desmococcus olivaceus</i> (g)			gated				
<i>Klebsormidium flaccidum</i> (g)							
<i>Klebsormidium crenulatum</i> (g)							

d ¼ diatom, g ¼ green alga

10.2.2 Moisture Availability

That moisture influences biocrust distribution at multiple scales has been amply demonstrated on multiple continents (Belnap and Lange 2003). In general, where space between plants is large, biocrust abundance and level of development increase with moisture availability (Bowker et al. 2006a; Büdel et al. 2009; Kidron et al. 2010). However, as vascular plant and plant litter cover becomes more continuous, there is less available habitat for biocrusts (Bowker et al. 2005) and less light reaching the soil surface (Belnap et al. 2003). In the most hyperarid regions (Aridity Index < 0.05; Pointing and Belnap 2012; e.g., Atacama, Sahara, Negev, Colorado deserts), biocrusts contain only a low biomass of microbial components (e.g., endedaphic cyanobacteria, bacteria, and fungi). Arid zones often support primarily cyanobacterial biocrusts with subdominant mosses and lichens (Kidron et al. 2010; Pietrasiak et al. 2011a). As aridity further decreases, cyanolichens become more prevalent, followed by chlorolichens (Galun et al. 1982). Mosses and liverworts are generally only found in wetter microhabitats (e.g., under shrubs, on polar exposures), due to their higher moisture requirements than lichens and cyanobacteria. In cooler semiarid deserts and grasslands (e.g., Colorado Plateau, Columbia Basin, and Great Basin, USA; Gurbantunggut Desert, China), soil moisture is much more abundant, and the cover and biomass of biocrusts, especially bryophytes and lichens, increase until they often fully cover soil surfaces (Ponzetti and McCune 2001; Marsh et al. 2006; Zhao et al. 2014).

Table 10.3 Most frequent species

	Aus- tralia	Africa	S- America	Antarc- tica	Asia	N- America + Greenland	Europe
<i>Nostoc commune</i> (c)							
<i>Microcoleus vaginatus</i> (c)							
<i>Coleofasciculus chthonoplastes</i> (c)							
<i>Trichocoleus sociatus</i> (c)							
<i>Chlorella vulgaris</i> (g)							
<i>Bryum argenteum</i> (b)							
<i>Schizothrix calcicola</i> (c)							
<i>Nostoc microscopicum</i> (c)							
<i>Diploschistes diacapsis</i> (l)							
<i>Diploschistes muscorum</i> (l)							
<i>Heppia despreauxii</i> (l)							
<i>Placidium lacinulatum</i> (l)							
<i>Placidium squamulosum</i> (l)							
<i>Psora decipiens</i> (l)							
<i>Toninia sedifolia</i> (l)							
<i>Fulgensia fulgens</i> (l)							
<i>Tolypothrix byssoidea</i> (c)							
<i>Collema tenax</i> (l)							
<i>Klebsormidium flaccidum</i> (g)							
<i>Peltula patellata</i> (l)							
<i>Collema coccophorum</i> (l)							
<i>Heppia lutosa</i> (l)							
<i>Bryum caespitium</i> (b)							
<i>Placidium pilosellum</i> (l)							
<i>Microcoleus paludosus</i> (c)							
<i>Nostoc muscorum</i> (c)							
<i>Ceratodon purpureus</i> (b)							
<i>Calothrix parietina</i> (c)							
<i>Nostoc punctiforme</i> (c)							
<i>Aphanothece saxicola</i> (c)							
<i>Stigonema ocellatum</i> (c)							
<i>Chroococcidiopsis</i> spp. (c)							

c ¼ cyanobacterium, g ¼ eukaryotic alga, b ¼ bryophyte or liverwort, l ¼ lichen, black ¼ in all areas (100 %), dark gray ¼ 6 of 7 continents/subcontinents (86 %), gray ¼ 5 of 7 continents/subcontinents (71 %), light gray ¼ 4 of 7 continents/subcontinents (57 %)

### 10.2.3 Moisture Mode, Seasonality, and Temperature Effects

In addition to the total amount of precipitation received, the timing, frequency, and size of precipitation events are critical in determining the species composition of biocrusts. Summer monsoonal events can be large but are often short and intense, with little water infiltrating into the soils. Soil temperatures after summer events can rise quickly, and rapid evaporation rates result in short activity times for biocrusts. Small rain events, especially combined with the high temperatures of summer, also



Fig. 10.3 Conceptual model depicting the general interplay of amount and timing of precipitation and its influence on community composition in biocrusts. The model applies to cool to hot semiarid and drier zones, excluding polar and alpine regions, fog deserts, and unique or unusual edaphic environments such as gypsiferous soil

result in short activity times. When wetted, all biocrust organisms respire carbon, but the replacement rate of this carbon is species specific; thus, only some species are able to handle short wetting times (e.g., Lange 2003). Other species will die: experimentally repeated frequent small rain events resulted in moss mortality within only a few months on the Colorado Plateau, USA (Reed et al. 2012). Garcia-Pichel et al. (2013) recently showed that the cyanobacterium *Microcoleus vaginatus* dominates cool desert soils dominated by winter precipitation, whereas *Microcoleus steenstrupii* dominates hot arid to semiarid deserts with summer precipitation. Thus frequency of rain events may also influence biocrust composition at a given locality.

The lichen composition of biocrusts has been observed to also vary where rainfall timing is different (i.e., winter versus summer dominated) in North America (Rosentreter and Belnap 2003), Africa (Büdel et al. 2009), Australia (Eldridge 2003), and Asia (Mongolia to Uzbekistan; Belnap pers obs). Figure 10.3 illustrates in a general sense how amount and seasonality of precipitation codetermine absolute and relative abundance of different groups of biocrust species in these drylands.

The type of precipitation is also important in determining the composition of biocrusts. Cyanobacteria, and therefore also cyanolichens, require liquid water for photosynthesis, whereas green algae and chlorolichens can also utilize water vapor (Lange 2003). Thus, in deserts where most moisture is derived from fog and dew (e.g., Namib, Atacama, central Negev), the lichen flora is dominated by chlorolichens, and cyanolichens are generally absent. In addition, fog and dew are more effectively captured by species with a three-dimensional growth form (e.g., foliose lichens) compared to those appressed (e.g., crustose lichens) to the surface.

### 10.2.4 Soil Properties

Biocrust cover, richness, and composition are strongly influenced by differences in soil properties at ecoregional to micro-scales. The extent to which the biocrusts themselves have an effect on underlying soil properties by forming a stable, nutrient-rich, near-surface layer is described elsewhere (see Chap. 1 by Belnap et al., Chap. 13 by Garcia-Pichel et al., and Chap. 23 by Weber et al.).

At ecoregional and local scales, parent material influences substrate quality and degree of weathering, directly affecting soil water-holding capacity (Noy-Meir 1973) and thus indirectly controlling the distribution and composition of biocrusts. Biocrust organisms have been shown to vary in abundance and richness among soils derived from different parent material (e.g., sandstone and shale bedrock-derived soils on the Colorado Plateau in the western USA, Bowker et al. 2006a; on igneous, sedimentary, and metamorphic bedrock-derived soils in the Mojave Desert, Belnap et al. 2014) or in soils subjected to different levels of weathering (e.g., fluvisols, regosols, and calcisols in the Tehuacan Desert, Mexico; Rivera-Aguilar et al. 2006). For example, filamentous cyanobacteria can flourish in sandy, poorly aggregated soils, which are less likely to support highly developed lichen and moss communities (Root and McCune 2012), whereas mosses and lichens are more likely to reach their strongest development on calcareous or gypsiferous soils (Bowker et al. 2006b; Bowker and Belnap 2008; Martínez et al. 2006).

Globally, the most significant soil properties influencing the ecoregional-scale cover and richness of biocrusts in dryland environments are soil texture, pH, and to a lesser extent, soil calcareousness (e.g., Rogers 1972; Eldridge and Tozer 1997; Ponzetti and McCune 2001; Eldridge 1996; Lalley et al. 2006; Lobel et al. 2006; Bowker and Belnap 2008; Root et al. 2011; Ochoa-Hueso et al. 2011). At smaller local, intra-site, or micro-scales, however, biocrust distribution and cover are tightly coupled to a relatively narrow range of soil physical and chemical properties, often in idiosyncratic ways. Biocrusts are likely to respond to small gradients in nutrients, such that small-scale changes in microrelief, temperature, and/or soil characteristics such as texture, salinity, structure, porosity, and oxidation can potentially play an important part in determining patterns of fine-scale distribution (Bowker et al. 2006a).

The concentrations of macro- (C, N, P, Ca, K, Mg) and micro- (Cu, Fe, Mn, Zn) nutrients are also important in influencing biocrust distribution and composition. Lichens are often associated with high levels of soil N, C, and P (e.g., Read et al. 2008) or K (Martínez et al. 2006), but the extent to which these nutrients are the drivers or the result of a well-developed crust is unknown. Lichen and moss biocrusts have been shown to be positively correlated with Mn, Zn, K, and Mg, but can also be negatively correlated with P across a range of spatial scales (Bowker et al. 2005; Bowker et al. 2006a). Similarly, Fe, Mg, and Ca have been shown to be positively associated with lichen cover, while Mn and sometimes Zn have been negatively associated with lichen diversity (Ochoa-Hueso et al. 2011). Other minerals such as Cd, Li, Cu, Mo, and Sr are known to negatively affect either

abundance or diversity of algae (Starks and Shubert 1979). Read et al. (2011) identified the Th/K ratio as a chemical signature that can be a remotely sensed proxy for soil texture and thus predict biocrust distribution (see Chap. 12 by Weber and Hill).

### 10.2.5 Solar Radiation Load

Most biocrust organisms exhibit the photosynthetic characteristics of “sun” plants (reviewed in Lange 2003). Despite this, the production, abundance, and diversity of biocrusts are often negatively correlated with high radiation at local and smaller scales. This is because high-light habitats are also drier due to shorter residence time of moisture and receive detrimental ultraviolet radiation loads. Polar-facing aspects receive lower radiation loads, resulting in greater biocrust abundance at the local or subhectare scale, on both hillslopes (Nash et al. 1977) and dune slopes (Veste et al. 2001), although not all authors have observed this effect (Dettweiler-Robinson et al. 2013b). Radiation load may also be reduced by shade-providing vascular plant canopies or rocks, favoring greater biocrust abundance at intra-site scales (Bowker et al. 2006a; Li et al. 2010; Maestre 2003), although in the case of plant canopies, burial by litter or dew interception by the plant canopy may counterbalance this positive effect (Hernstadt and Kidron 2005; Thompson et al. 2005). Protruding rocks provide favorable microhabitats and the capture of resources (e.g., nutrient-rich dust and water, spores, biocrust fragments) which, in turn, facilitates biocrust development, especially moss and lichen propagation (Pietrasiak et al. 2011b, 2014; Williams et al. 2012, 2013). Even at microscales, different faces of 10 cm biocrust pinnacles (Bowker et al. 2006a; George et al. 2000) or depressions such as hoof prints (Csotonyi and Addicott 2004) may generate different micro-aspects supporting differing levels of biocrust cover or different communities.

### 10.2.6 Vegetation Cover and Spatial Patterns

At intra-site- and microscales, biocrust communities often differ among habitats when comparing beneath plant canopies and plant interspaces. The influence of plant canopies on soil stability, fertility, and moisture is complex. Plants create shade, increase or decrease dew and moisture inputs to soils depending on their architecture, and collect wind- and waterborne sediments and plant materials at their base, increasing soil fertility. Furthermore, plants facilitate or discourage animal digging and trampling. Often, biocrust absolute cover and richness are greater in microsites with a sparse cover of vascular plants (e.g., Eldridge et al. 2002, 2005; Pintado et al. 2005; Langhans et al. 2010; Zaady et al. 2013) and litter (e.g., Briggs and Morgan 2008; Serpe et al. 2013; Zhang et al. 2013).

However, enhanced biocrust cover and/or richness in habitats nearby or under plant canopies is also reported (Maestre 2003; Bowker et al. 2005; Li et al. 2010) because vascular plants buffer environmental stress by generating distinct microhabitats. Different effects of plants on biocrusts can be mediated by differences in soil type (Eldridge et al. 2005), vegetation community type, plant successional stage (Dettweiler-Robinson et al. 2013a), or intensity of grazing (Root and McCune 2012). For example, when erosion or grazing impacts are high, biocrusts may refuge near shrubs (Zhao et al. 2010, 2011). Effects of plants will also vary according to the distributional pattern of vascular plants (Maestre and Cortina 2002) or the composition of the biocrust community. For example, positive plant-biocrust correlations in space are common for bryophytes, but not necessarily for other biocrust organisms (Pharo and Beattie 1997).

Banded and other patterned landscapes have distinctive distributional patterns of plants and biocrusts. Banded landscapes are usually found on gentle uniform slopes in arid and semiarid climate around the world (Malam Issa et al 1999). Biocrusts play a substantial role in the flow of water, seed, and sediment to the downslope run-on zones that are usually dominated by perennial vegetation (Tongway and Ludwig 1994; Malam Issa et al 1999; Belnap et al. 2005). These source-sink relationships, which operate across at mostly local and intra-site scales, arise largely through the redistribution of water, which exerts tight controls on landscape function, productivity, and diversity (Ludwig et al. 1997). Sources and sinks may sometimes support fundamentally different biocrust communities. For example, sinks tend to be dominated by biocrust morphological types that trap resources (e.g., tall mosses, fruticose lichens), while those in the runoff zones tend to be resource-shedding types (e.g., squamulose and crustose lichens or cyanobacteria; Dunkerley and Brown 1995).

### 10.2.7 Geomorphological Features

The distribution of dryland biocrusts is shaped by both eolian (Li et al. 2010; Veste et al. 2001) and alluvial geomorphologies (Briggs and Morgan 2008) at ecoregional, local, and intra-site scales. For example, the distribution of biocrusts on the dune fields of the Negev Desert in Israel has been described in detail by several authors [reviewed in Veste et al. (2001)]. Dune crests lack biocrusts, while lower slopes are stabilized by biocrusts and interdune spaces are characterized by higher vegetative cover and biocrusts. Aspect effects may be expressed on dune slopes with mosses becoming more common on north slopes. Zhang et al. (2007) and Li et al. (2010) describe a similar segregation of different organisms on dune crests, hollows, leeward, and windward slopes in the deserts of China. At ecoregional or local scales, different depositional-erosional processes can lead to distinct alluvial geomorphological surfaces, such as outwash slopes, sand plains, or riverine plains, which support distinctive vegetation and biocrust communities (Briggs and Morgan 2008; Eldridge 1996). Similar effects can be observed at

intra-site scales. For example, in the badland clay domes of Tuscany, Italy, biocrust cover increases from the eroded slope to the edge of the eroding surface, but eventually decreases in portions of domes with greater plant cover (Loppi et al. 2004). More recently, a detailed understanding of the ecoregional influence of alluvial geomorphology on biocrusts has been developed for the Mojave Desert (Sect. 10.3).

### 10.3 The Emerging Understanding of Ecoregional Biocrust Distribution in Three Case Studies

Studies of the controls on biocrust distribution at the ecoregional scale are becoming less descriptive, more predictive, and more often being expressed in the form of maps or conceptual models than in the past. Three case studies including the Sahel region of Africa and both the Colorado Plateau and Mojave Deserts of North America allow some generalizations to be made. First, they support the generalization in Fig. 10.1 that, at ecoregional scales, biocrust distribution is controlled by climatic gradients and edaphic gradients, both of which may be dictated by geomorphological gradients. Second, the specific climatic, edaphic, or geomorphic driver that is most informative differs by ecoregion. Third, heterogeneity in biocrust distribution patterns is largely driven by the degree of edaphic heterogeneity. In an area with a low degree of edaphic complexity (e.g., the Sahel Region), biocrust distribution will be primarily based on (usually) gradual climate gradients. In an edaphically complex region with young soils (e.g., the Colorado Plateau), distinctions among parent materials may be among the best predictors of biocrust distribution. Finally, in edaphically complex regions with older, more weathered soils and complex ancient and modern alluvial features (e.g., the Mojave Desert), geomorphological age may emerge as the most informative parameter.

#### 10.3.1 Case Study: Ecoregional Patterns in the Sahel (Africa)

The Sahel is normally defined as the north to south zone that corresponds to the 200–600 mm mean annual precipitation gradient. It is located between the Sahara in the North and the Sudanian zone in the south and between the Atlantic Ocean in the west and the Red Sea in the east. Previous studies demonstrated that biocrusts (mostly cyanobacterial) are present over a large proportion of the Sahel, mostly in the form of filamentous cyanobacteria (Malam Issa et al. 1999; Valentin et al. 2004). Later, a north-south transect to document biocrusts along a latitudinal rainfall gradient concluded that biocrust fractional soil cover was strongly positively correlated with average annual rainfall, with very little biocrust cover where



Fig. 10.4 Upscaling of biocrust spatial distribution maps from local scale to ecoregional (central Sahel) based on satellite-derived variables, the ESA GlobCover dataset, and a logistic regression predictive model

precipitation was  $< 350$  mm (Malam Issa et al. 2010). A geomorphological gradient was also quite important because it dictated both human use and edaphic properties. Soil cover of biocrusts was observed in the two main representative geomorphological units: ferricrete-capped (erosion-resistant sediment layer cemented by iron oxides) plateau soils with tiger bush vegetation and vegetated sand dune deposits that have lain fallow for up to 10 years.

More extensive data from western Niger and Burkina Faso were used to produce a map of the spatial extent and distribution of biocrusts over the central portion of the Sahel region, based on a logistic regression model that combined annual average rainfall, land use, vegetation cover, and soil types with field data on biocrust fractional soil cover and satellite imagery (Beaugendre et al. 2012; Fig. 10.4). The model was later upscaled for the entire central Sahel (Bontemps et al. 2013). As the region is characterized by two main types of geomorphic surface, a large proportion of the variability in the region is explained by a simple total precipitation gradient.



### 10.3.2 Case Study: Ecoregional Patterns on the Colorado Plateau (USA)

In contrast to the Sahel, other ecoregions are made up of widely different parent materials and can be expected to exhibit very heterogeneous mosaics of higher and lower quality biocrust habitat. The Colorado Plateau ecoregion is one such area. It is typified by many young soil types and much exposed parent material that ranges from marine limestones and shales to eolian sandstones. A recent ecoregional-scale modeling effort produced a map and statistical model of potential biocrust distribution of the Colorado Plateau (Bryce et al. 2012). The model was based upon an integrated dataset of 593 samples from around the Colorado Plateau and its Northern, Southern, and Eastern ecotones assembled from several sources (summarized in Bryce et al. 2012). All sites were in low-disturbance condition at the time of sampling, and biocrust cover was assumed to be at or near its potential. The models used 16 predictors aimed at capturing key climatic (based on longer-term 1971–2000 averages), edaphic, and topographic influences.

At the ecoregional scale, out of all 16 predictors, the proportional summer precipitation was the single most informative predictor (Fig. 10.5). A threshold was identified, whereby if greater than ~one third of rainfall was received in summer, late successional biocrust cover was only about 2 %, whereas sites receiving a lower proportion of precipitation in summer had anywhere from 6 to 44 % cover, depending on other predictors. The low cover of late successional elements is believed to result from the inability of lichens and mosses to withstand the frequent short wetting events associated with summer precipitation (see discussion above in Sect. 10.2.3; Reed et al. 2012). This result indicates that the seasonality of precipitation can be as influential, or more so, than total precipitation where

Fig. 10.5 Potential biocrust distribution in the Colorado Plateau ecoregion. (a) A regression tree model indicates that the most informative predictor of late successional biocrust cover is proportional summer precipitation. (b) A map of potential late successional biocrust abundance based on an ensemble of regression tree models. The palest yellow shades particularly common in the southeastern part of the extent receive mostly summer precipitation and thus have low biocrust potential

these gradients exist. The next two most informative predictors, percent gypsum and parent material, indicate the tremendous influence that different soil types can have on biocrusts. As the distribution of parent materials on the Colorado Plateau is highly heterogeneous, the map of biocrust abundance and development is a patchwork of biocrust types, with abrupt transitions from very high to very low cover. These characteristics contrast strongly with the more gradual transitions within the Sahel.

### 10.3.3 Case Study: Ecoregional Patterns in the Mojave Desert (USA)

The Mojave Desert displays typical intermontane basin geomorphology based on a long history of alluvial processes (Peterson 1981). Episodes of erosion, sediment movement, and deposition alternated with periods of stability throughout the Holocene (up to 11,700 years old) and Pleistocene (11,700–2,500,000 years old) eras, creating a mosaic of differently aged soil surfaces that we see today (Miller et al. 2009). It is a more complex geomorphological system than the Sahel, has a greater mixing of soil parent materials than the Colorado Plateau, and is a system where age of surfaces is expected to dictate soil properties and habitat quality.

These geomorphic surfaces are associated with suites of unique environmental factors important to biocrust establishment and propagation, such as surface stability, topography, rock cover, soil texture, and hydrological dynamics. Biocrust cover is greatest on moderately young to intermediate aged (20–7000 years old) surfaces, whereas coverage is negligible on very young (<20 year; e.g., active washes, recent sediment deposits) and very old surfaces covered with well-developed desert pavements (i.e., surfaces of interlocking rock fragments that are at least thousands of years old; Pietrasiak et al. 2014; Williams et al. 2013; Belnap et al. 2014).

Moreover, diversity and dominance of biocrust community types varies with geomorphology. Cyanobacterial crusts are most abundant on moderately active sand sheets of Holocene age, suggesting that motile filamentous cyanobacteria can withstand some sand deposition and burial (Williams et al. 2013; Fig. 10.6). In contrast, moss and lichen biocrusts are more prevalent on stable surfaces and are associated with fine-grained substrates that occur between embedded surface rocks (Pietrasiak et al. 2014; Williams et al. 2013; Belnap et al. 2014; Fig. 10.5). These conditions are commonly met in soils of early to late Holocene age, with the highest diversity of biocrust types found on moderately young (0.5–1 kyr) surfaces (Pietrasiak et al. 2014). Though perhaps less influential than surface age, parent material also influences biocrust type in the Mojave. Soils derived from grussy granites and those containing mixed rock and fine sand show the highest biocrust cover, with cover then decreasing from igneous to limestone to metamorphic-derived soils (Pietrasiak et al. 2011a; Belnap et al. 2014; Williams et al. 2013).

Fig. 10.6 Geomorphic surface type and age predicts interspace cover by biocrusts and desert pavements; reproduced with permission from Williams et al. (2013), courtesy of Elsevier. Fine sand sources include sand sheets, active channels, and alluvial flats or playas (not shown)

## 10.4 Conclusions: Gaps in Our Knowledge and the Way Forward

Although knowledge has accumulated significantly in the past decade on the distribution patterns of biocrusts and factors controlling the distribution of specific taxa, the state of our collective knowledge is heterogeneous at best. Our missing knowledge can be categorized as geographic gaps and taxonomic gaps.

Most studies on biocrusts have occurred in Australia, China, Europe, Israel, and North America. It has only been in the last few years that surveys have included major portions of Africa and the Indian subcontinent (Büdel et al. 2009; Rosentreter et al. 2014). There remain significant geographic gaps, where few, if any, surveys have been conducted. The biggest gaps currently include central Asia, South America, and the Middle East/Arabian Peninsula (excluding Israel). Data on species composition of biocrusts in South America are especially rare and would benefit from a major research effort in the future. Even within relatively well-studied land masses, there are areas that have received little attention. This is likely a result of uneven distribution of research funding, infrastructure, and the availability of researchers.

Taxonomic gaps arise primarily because few researchers are simultaneously competent in the taxonomy, identification, or molecular characterization of all of the diverse groups of biota encompassing biocrusts and thus do not report on all of them in detail sufficient to build an understanding of their distribution patterns. We

may, for example, have a detailed understanding of lichen distribution, but know little about cyanobacterial distribution, within a given region. A related problem is taxonomic inconsistency, which restrains our ability to compare results from one place to another. In addition, molecular tools are not available to all researchers, making identification of the microbial components of the biocrusts difficult to impossible.

How can we move beyond some of these gaps? The most effective way to fill our information gaps is with more scientific effort. As most of the taxonomists that work on biocrusts are reaching retirement age, this will require training of young scientists in the taxonomy of the different biocrust organisms. To accomplish this, we urge universities to maintain strong programs in taxonomy of these organisms. Also, we should continue to make easily used identification resources such as field guides available to and targeted to the public (rather than taxonomic specialists; e.g., Rosentreter et al. 2007) and transition into web-based resources and smartphone apps.

With additional survey efforts, we can begin filling our data gaps. This information would then allow for intra- and intercontinental comparisons, giving us the ability for truly global-scale studies. The effort required for a global study is clearly too great for any single research group. A promising development has been networked studies, which are becoming increasingly common in a variety of fields. Within the biocrust research community, one such network completed a variety of similarly designed research in multiple arid regions of Africa (Büdel et al. 2009), and another network (Soil Crust InterNational) is currently maintaining a linked set of sites in Europe (Büdel et al. 2014). We envision a multidisciplinary network of international researchers simultaneously sampling biocrusts along key environmental gradients in multiple deserts of the world. The important gradients will differ among ecoregions, but a set of common sampling methods, pooled taxonomic expertise, and pooled analytical capabilities (e.g., soil measurements, GIS, and statistical analysis) will facilitate comparisons among regions.

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