Algal richness in BSCs from forest under different management intensity with some implications for P cycling

5   Karin Glaser[1], Karen Baumann[2], Peter Leinweber[2], Tatiana Mikhailyuk[3], Ulf Karsten[1]

[1] Institute for Biological Sciences, Applied Ecology and Phycology, University Rostock, Germany
[2] Faculty for Agricultural and Environmental Sciences, Soil Science, University Rostock, Germany
[3] M.H. Kholodny Institute of Botany, National Academy of Science of Ukraine, Tereschenkivska St. 2, UA-01004 Kyiv, Ukraine

10   *Correspondence to*: Karin Glaser (karin.glaser@uni-rostock.de)

Abstract

Biological soil crusts (BSCs) form the most productive microbial biomass in many drylands and disturbed areas worldwide, where higher vegetation is sparse, with a diverse microalgal community as key component. They conduct important ecological functions, such as stabilization of soil and enrichment of nutrients. In temperate regions, BSCs are also common, but generally
15   less studied. Changes in land use and its intensity strongly influence biodiversity per se and its role for ecosystem processes, particularly in regions which are densely populated like Europe. Anyhow, systematic studies on land use (i.e. management intensity) gradients in temperate forests on BSCs are missing up to now. To close this gap of knowledge and enhance the understanding of management effects on BSCs, eukaryotic microalgae and cyanobacteria as key primary producers of these communities were identified from pine and beech forests under different management regimes. Phototrophic microorganisms
20   were identified morphologically based on enrichment cultivation and categorized as either coccal taxa, which occur typically in high diversity, or filamentous taxa, which have the potential to initiate BSC formation. In total, 51 algal species were recorded, most from the phylum Chlorophyta, followed by Streptophyta and Stramenopiles, and only 1 cyanobacterial taxon could be observed. The most abundant crust-initiating filamentous algae were three species of *Klebsormidium* (Streptophyta), a ubiquitous genus often associated with BSCs worldwide because of their generally broad ecophysiological tolerances such
25   as to low pH. Increasing management intensity in the forests resulted in higher numbers of algal species, especially the number of coccal taxa rose. Furthermore, the proportion of inorganic phosphorus showed tendencies towards a correlation with the number of algal species. Thus, management of forests has an impact on the diversity of phototrophic organisms in BSCs, which might affect biogeochemical P cycling in the BSC.

30   Key words: biological soil crusts, forest, management intensity, phosphorus, algae richness, *Klebsormidium*

Introduction

Biological soil crusts (BSCs) occur as important and often dominant vegetation on all continents on Earth, predominantly in arid and semi-arid habitats, but also in temperate regions (e.g. Belnap et al., 2001; Weber et al., 2016). In semiarid and arid environments, BSCs were studied, for example, in deserts of Israel and USA but also in polar regions (Borchhardt et al., 2017; Flechtner et al., 1998; Kidron et al., 2010). In temperate regions, dunes with sparse higher vegetation or disturbed areas in open sites (e.g. former mining sites) typically inherit BSCs (Fischer et al., 2010b; Langhans et al., 2009; Lukešová, 2001; Schulz et al., 2016; Szyja et al., 2018).

Although BSCs received raising interest in the past years, for example, as global player in terrestrial nitrogen fixation (Elbert et al., 2012), reports on BSCs from forests are very rare (Seitz et al., 2017). Under mesic conditions BSCs have to compete with vascular plants and thus their development is often limited. Especially in forests, the limitation of light and the occurrence of litter restricts the crust development. But disturbances of the higher vegetation layer change this competitive situation and allow the development of BSCs. Such disturbances occur frequently in temperate forests, for example, natural tree fall, pits of wild boars, litter free spots at slopes, molehill-like humps, or human-induced disturbances such as skid trails and clear-cut areas. Especially tree falls after storm events is a rising problem in Europe due to increasing number and strengths of storms, probably because as a consequence of global change (www.dwd.de). At such spots, BSCs typically serve as pioneer vegetation for colonialization of naked soils after heavy disturbance and destruction of intact forest ecosystems. Thus, BSCs can protect disturbed areas, from erosion. Regrowth of vascular plants is initiated due to the biological introduction of carbon and nutrients into the soil (Seitz et al., 2017).

Disturbance of BSCs due to land use has been reported to have strong negative effects on BSC cover, which resulted in higher soil erosion and C and N losses from the top soil (Barger et al., 2006; Belnap, 2003). Studies on the effect of land use on BSCs were mainly conducted in arid and semiarid regions. These studies reported, for example, a strong negative influence of intensive livestock grazing on BSC cover due to trampling with a recovery period of up to 27 years (Concostrina-Zubiri et al., 2014; Gomez et al., 2004; Williams et al., 2008). Also, ploughing in Australian sand plains reduced the BSCs cover dramatically (Daryanto et al., 2013). In contrast, there are no reports on land use effects in temperate regions or aspects of land use other than grazing or human activities on BSCs. Also missing are reports on the benefits for BSCs in terms of coverage due to disturbances in continuous vegetation like forests.

BSCs can be characterized as "ecosystem-engineers" forming water-stable aggregates that have important ecological roles in primary production, nitrogen cycling, mineralization, water retention, and stabilization of soils (Castillo-Monroy et al., 2010; Evans and Johansen, 1999; Lewis, 2007). While the role of BSC in the C- and N-cycle is well documented, less is known about their role in P cycling. However, recent studies indicated that the number of microalgal species in BSCs is related to soil P content (Baumann et al., 2017; Schulz et al., 2016). But still, only little is known about environmental factors that shape BSC communities and how BSCs in turn affect soil characteristics.

Cyanobacteria and microalgae represent the most important phototrophic components of BSCs along with macroscopic lichens and bryophytes (Belnap et al., 2001). Eukaryotic algae are probably the least studied phototrophs in BSCs, although these organisms are an essential component of such communities because of their major contribution to C fixation (Büdel et al., 2016; Szyja et al., 2018). BSC algae can be categorized as two functional groups. (I) filamentous algae as major BSC forming taxa that stabilize soil particles by gluing them together due to the presence/excretion of sticky mucilage. The filamentous forms occur usually in low diversity but produce high biomass. (II) coccoid algae which are attached to the soil particles or other algae and typically occur in higher diversity but lower biomass (Büdel et al., 2016).

Filamentous cyanobacteria, especially of the genus *Microcoleus*, are often the dominant phototrophic organisms in most BSCs of drylands and in dunes from temperate regions (Garcia-Pichel et al., 2001; Schulz et al., 2016). They are described as important for BSC formation due to their ability to produce mucilage sheaths and extracellular polymeric substances forming a sticky network between soil particles (Gundlapally and Garcia-Pichel, 2006). In temperate regions, this key function is often taken over by filamentous eukaryotic algae, like *Klebsormidium*, *Xanthonema* or *Zygogonium* (Fischer and Subbotina, 2014; Lukešová, 2001; Pluis, 1994).

The aim of the present study was to characterize for the first time the algal community in BSCs collected from disturbed sites in temperate forests of different silvicultural management intensities. In a previous study, we presented hints that differences of algal richness in BSCs are related to P cycling. The data indicated BSCs are particularly involved in the transformation of inorganic P to organic P compounds, thus playing a key role in the biologically driven P cycling in temperate soils. In addition, BSCs responded differently to management intensity depending on forest type (beech versus pine). While algal species richness of BSCs was considered as sum parameter, detailed information on species occurrence is still missing (Baumann et al., 2017). Therefore, in the present study we identified algal species in a temperate forests and investigated for the first time in detail the influence of silvicultural management intensity on algal richness in BSCs collected at the same plots as in Baumann et al. (2017), plus some additional sampling sites. The correlation of BSC algal richness and C, N and P content, in particular on the different fractions of P, was assessed in order to uncover the relation between biogeochemical cycles in BSCs and the underlying alga species.

Material and Methods

Study site

BSC samples were collected in June 2014 and 2015 from plots of the German Biodiversity Exploratories (Fischer et al., 2010a). Forest plots were sampled in the Schorfheide-Chorin Biosphere Reserve in Northeast Germany. The plots differed in the dominant tree species: Scots pine (*Pinus sylvestris* L.) or European beech (*Fagus sylvatica* L.). Samples were taken from natural, protected forests and from managed forest (age-class forest) on disturbed areas where BSCs could develop on litter free bare soil (for illustration see Figure 1).

The top millimeters of soil, on which BSC had been visually detected as green cover, were collected by pressing a petri dish in the respective crust and removing gently with a spatula. After transportation to the lab the upper two millimeters of the crust were separated from the adhering soil underneath using a razor blade and stored dry in paper bags before cultivation. In total, 31 BSCs were collected from 13 pine and 18 beech stands, of which 23 were managed and 8 were natural forest plots (Table 1).

Culturing, identification and richness of algae

Solid 3N-Bolds Basal Medium (1.5% agar) with vitamins (Starr and Zeikus, 1993) was used for enrichment cultures in Petri dishes (9.5 cm diameter). Several 7–10 mm^2 BSC pieces were cleaned with forceps to remove all roots and leaves to avoid the additional growth of fungi and bacteria, and were placed on the surface of an agar plate under sterile conditions. Plates were incubated at 20°C, 30–35 μmol photons m^{-2} s^{-1} (Osram Lumilux Cool White lamps L36W/840) under a light/dark cycle of 16:8 h L:D. The plates were regularly inspected and colonies were identified four to six weeks after incubation using a light microscope (BX51, Olympus) with Nomarski differential interference optics and 1000x magnification. Light micrographs were taken with an Olympus UC30 camera attached to the microscope and processed with the software cellSens Entry (Olympus). For direct observation of BSC samples, pieces of crust were rewetted with tap water, put on slide and analyzed with the above mentioned microscope at 400x magnification.

Morphological identification of algae/cyanobacteria was based on the standard Syllabus (Ettl and Gärtner, 1995), and more recent taxonomic publications on certain algal groups (Darienko et al., 2010; Kostikov et al., 2002; Mikhailyuk et al., 2015). Mucilage of algae was stained with an aqueous solution of methylene blue. Phototrophic microorganisms were identified as Cyanobacteria, Chlorophyta, Streptophyta and some Stramenopiles (Eustigmatophyceae). Diatoms were regularly found in direct observations, but excluded from the analyses as the mentioned enrichment cultivation is not suitable for this group of microalgae (e.g. Schulz et al., 2016).

Since enrichment cultivation does not allow a clear conclusion on the abundance of each identified algal taxon, richness of algae (total number of algae and cyanobacteria species per sample) was used as measure for diversity. As a second parameter for biodiversity the similarity between single plots was shown by presence / absence of individual species, combining the total number and the identity of all algal taxa observed. Further, the identified algae were categorized in filamentous or coccal life form, because both differ in their ecological function. The proportion of filamentous algae on total number of algae was used for statistical analyses. Filamentous algae, in contrast to coccal algae, have the potential to initiate crust-formation and stabilize soil particles by gluing them together.

Environmental variables

The natural and managed forest plots were characterized by differences in the silvicultural management intensity. In natural forests, no management was conducted, meaning that fallen trees were left in place and no trees were cut. In managed age-class forests, the stands were regularly disturbed due to, for example, usage of skid trails and removal of dead trees as well as

tree cut. To evaluate the effect of management, the silvicultural management index (SMI) was used. This index takes into account the tree species, stand age and aboveground living and dead wood biomass, i.e. stand density (Schall and Ammer, 2013). Natural forest has a lower SMI than the managed forest; a pine stand has a higher SMI than a beech stand; high stand density is reflected by a high SMI (Schall and Ammer, 2013).

5 To assess potential linkages between BSC organisms and environmental parameters, the richness, presence or absence of individual algal species and proportion of filamentous algae was linked to the following environmental parameters: main tree species (pine or beech), silvicultural management intensity (SMI), water content and pH of the bulk soil for all 31 plots (water content and pH kindly provided by I. Schöning, Table 1) and, further, for a subset of the samples (n=19), total C, N and P content, organic and inorganic P proportions, both for labile, moderately labile and stable P. Data on latter are not shown here

10 but were already presented in detail by Baumann et al. (2017).

Statistical analyses

All statistical analyses were done using the statistical software R version 3.3.0 (R Development Core Team, 2009). Analysis of Variance (ANOVA) was conducted to reveal the effect of environmental parameters on algal and cyanobacteria richness and proportion of filamentous species; their best predictors were selected by backward elimination stepwise regression analysis

15 based on the BIC (Bayesian information criterion) using 'step' command in R. The correlation between environmental parameters were checked by Pearson correlation ('cor' and 'cor.test' commands in R).

To reveal correlations of single environmental parameters with the presence or absence of individual algal species, PerManova (with adonis function in R (Anderson, 2001)) was applied using the Bray–Curtis dissimilarity index (Bray and Curtis, 1957), including permutation test with 1000 permutations. The function 'adonis' allows applying non-Euclidean distance metrics and

20 handles both categorical and continuous predictors. For analysis of co-correlation of environmental factors Pearson correlation was used. To test significant differences of environmental factors between tree species, unpaired, two-tailed t-test was performed. Differences with a p-value below or equal to 0.05 were taken as significant.

Results

25 **Algae identification**

In total 51 different algae species and one Cyanobacterium were detected in enrichment cultures of all 31 BSC samples. *Stichococcus bacillaris* was the most ubiquitous taxon, observed in 27 out of 31 samples; followed by *Coccomyxa simplex* and *Klebsormidium* cf. *subtile* in 26 out of 23 samples, respectively. All other algal species were detected in less than 50% of the plots; 22 algal species were observed exclusively at one plot (Figure 2). The richness of algae, i.e. the total species number, at

30 each plot ranged from three to 14 species, with a mean of eight and a standard deviation of 2.6 (complete species list is provided in the supplemental Table S1).

The phylum Chlorophyta made up 81% of all detected algal species, followed by Streptophyta (11%) and Stramenopiles (6%). Cyanobacteria were rare in these BSCs, just one species, *Microcoleus vaginatus*, was observed in only one sample.

The identified algal species were differentiated according to their organization form (Figure 3). Five species with strong filaments (*Klebsormidium* cf. *flaccidum, K.* cf. *subtile, K.* cf. *nitens, Xanthonema* cf. *exile, Microcoleus vaginatus*) were found and two genera with short or easily disintegrated filaments (*Interfilum paradoxum, Stichococcus bacillaris*). In each BSC at least two different filamentous taxa were detected indicating their importance for BSC formation. Especially the genus *Klebsormidium* seemed to be highly important for BSCs in forest: in each BSC at least one of in total three observed morphospecies was found (Supp. Table S1).

Correlation of algae richness with plot characteristics and nutrient content

The silvicultural management intensity was measured by applying the silvicultural management index (SMI), which is based on stand density, tree species and stand age. The correlation analyses between environmental factors were conducted to understand the interrelation between the factors, which might be a driver for algae in BSCs. The gravimetric water content of the bulk soil was correlated with the SMI; the pH was independent of the water content, SMI and the main tree species (Table 2). The N content correlated with the C content and both were independent of the SMI and pH. Total P and the proportion of inorganic P were independent of the C and N content, as well as from pH and SMI (Table 2).

The richness of algal species and the proportion of filamentous algae in BSCs only correlated with SMI, water content and proportion of inorganic P (Table 3). All other tested parameters (C and N content, total P, proportion of organic P, pH, main tree species, and soil horizon) were excluded by stepwise model simplification based on the BIC. Thus, these factors had no measurable effect on the algal species richness nor on the proportion of filamentous algae. A higher SMI resulted in a higher species richness (Figure 2), especially the proportion of coccal algae was enhanced. BSCs with higher algal richness tended to a lower proportion of inorganic P.

The presence or absence of individual algal species in BSCs significantly correlated with the main tree species (15% explained variance) and with the water content (10% explained variance). The SMI and proportion of inorganic P explained each 5% of the variance, but this was not significant (Table 3). This implies an effect of the main tree species and the water content on the community composition of algae in BSCs.

Discussion

Species composition and abundance

In total 51 microalgal species and one cyanobacterium were identified in all sampled BSCs (Figure 2), which is a similar or slightly lower richness compared to other reports on BSCs from temperate regions at open sites (Langhans et al., 2009; Schulz et al., 2016), but similar or higher compared to previous reports on algae from forest bulk soil (Khaybullina et al., 2010;

Novakovskaya and Patova, 2008; Starks et al., 1981). Nevertheless, the given number is most probably an underestimation of the real algal richness because our results are based on enrichment cultivation followed by morphological assignment. Enrichment cultivation covers only cultivable algae, which represent only a small part of all phototrophic microorganisms in BSCs (Langhans et al., 2009). A recent paper comparing metagenomic data with morphological data based on enrichment cultivation estimated a match of about 10% of all microalgae in a polar BSC (Rippin et al., 2018). Furthermore, it is not always possible to distinguish dormant from currently active microalgae. However, direct observation of a BSC sample under the microscope gives at least a first hint for the dominant active organisms. Using this approach, we could prove that all filamentous algae were abundant and always vital in the BSC samples. The morphological identification of algae has known challenges, for example, sibling species have similar characteristics but are genetically distant (Potter et al., 1997). To overcome these limitations, researchers proposed to combine molecular and morphological methods, since molecular techniques alone sometimes also fail to detect some taxa based on problems with DNA extraction, appropriate primers etc. (Büdel et al., 2009; Garcia-Pichel et al., 2001).

All observed algal species are known as terrestrial taxa, most of them were also reported in other BSCs (Büdel et al., 2016 and references therein; Ettl and Gärtner, 1995). Chlorophyceae were the most abundant phylum, which is typical for temperate regions (Büdel et al., 2016). Especially most of the unicellular taxa belong to the Chlorophyta, and hence a high richness (genera such as *Chlamydomonas*, *Chloromonas*, *Chlorococcum*, and *Tetracystis*) is characteristic for humid habitats and typical for forest soils (Hoffmann 1989).

Cyanobacteria were represented by only one single species. Cyanobacteria are often reported as predominant species in BSCs in arid regions such as Israel and drylands of the USA (Garcia-Pichel et al., 2001; Kidron et al., 2010). Nevertheless, Cyanobacteria are less abundant in temperate regions (Gypser et al., 2016; Langhans et al., 2009; Pluis, 1994) and even rare in acidic soils, as in the forest plots of our study site Schorfheide-Chorin (Hoffmann et al., 2007; Lukešová, 2001; Lukešová and Hoffmann, 1996). It seems that Cyanobacteria play only a minor role in forest ecosystems with consequences for the ecological traits that some taxa occupy. For example, the ability for nitrogen fixation in phototrophic organisms was only reported from Cyanobacteria and never observed in eukaryotic algae. In forest ecosystems litter and other decomposable biomass provides probably sufficient mineral nitrogen compounds, which might lead to the absence of nitrogen-fixing organisms in these systems in contrast to nitrogen-poor habitats such as dunes or deserts (Langhans et al., 2009; Schulz et al., 2016).

The filamentous alga *Klebsormidium* was found in nearly all BSCs of our study, whereas species with similar strong filaments (*Microcoleus* and *Xanthonema*) were only found occasionally. Filamentous algae can be regarded as key players in such communities, because of their potential as BSC-initiating organisms by building tight networks among soil particles (Büdel et al., 2016). In some investigated forest BSCs also moss protonema can exert a similar function, due to their filamentous nature and hence were determined as crust-forming organisms (Weber et al. 2016). However, *Klebsormidium* seems to be the most important crust-initiating alga in forest ecosystems of Schorfheide-Chorin. This genus can tolerate a wide range of environmental factors and, thus, has a cosmopolitan distribution in numerous terrestrial habitats (Karsten et al., 2016; Rindi et

al., 2011 and references therein). Its presence in other terrestrial habitats such as natural rocks in plain and mountainous areas (Mikhailyuk et al., 2008), caves (Vinogradova and Mikhailyuk, 2009), sand dunes (Schulz et al., 2016), tree barks (Freystein et al., 2008), acidic post-mining sites (Lukešová, 2001), bases of urban walls (Rindi and Guiry, 2004) and building facades (Barberousse et al., 2006) is well documented. As many other terrestrial algae, *Klebsormidium* is tolerant to light exposure during dehydration (Gray et al., 2007). This is a typical situation, which BSC algae have to cope with, because increase of light in the morning is often associated with dehydration (Raanan et al., 2016). A recent study in Central Europe, however, observed that *Klebsormidium* is sensitive to increasing light during cellular water loss (Pierangelini et al., 2017). The distribution of *Klebsormidium* in nearly all samples from Schorfheide-Chorin forest plots may be explained by a lower radiation and also lower evaporation of water in the forest ecosystem compared to open habitats (such as inland dunes), where besides *Klebsormidium* other filamentous algae were dominant (Langhans et al., 2009; Pluis, 1994). Also the forest soil pH is rather acidic (min: 3.23; max: 3.86, Table 1) which supports a dominance of *Klebsormidium* (Škaloud et al., 2014). Thus, the low light availability, low water evaporation and the acidic soil conditions plausibly explain the presence and dominance of *Klebsormidium* as a potential BSC-initiating algal taxon in nearly all BSCs from Schorfheide-Chorin forest plots.

Three morphospecies of the genus *Klebsormidium* were identified in the samples investigated (Figure 2). All three morphospecies were reported from other aeroterrestrial habitats in Central Europe (Glaser et al., 2017; Mikhailyuk et al., 2015). *Klebsormidium* exhibits morphological features, which can be easily recognized. However, the identification down to species level is difficult due to high morphological plasticity (Lokhorst, 1996). And still, in times of molecular identification, the debate on species definition in the genus *Klebsormidium* is ongoing (Mikhailyuk et al., 2015; Rindi et al., 2017). Therefore, the definition of clades within *Klebsormidium* was and still is a helpful tool to differentiate between morpho- or genotypes on a species-like level (Rindi et al., 2011). Studies comparing clades at different localities on the one hand observed a global ubiquity, and local endemism on the other hand (Ryšánek et al., 2014). Especially the clade composition seems to differ depending on the habitat. In detail, *Klebsormidium* cf. *flaccidum* (B/C clade) was abundant in closed as well as in open habitats, whereas *K.* cf. *nitens* and *K.* cf. *subtile* (E clade) were predominantly distributed in forest BSCs (Glaser et al., 2017; Mikhailyuk et al., 2015). In this study, however, BSCs from forests contained more often *Klebsormidium* cf. *subtile* and *K.* cf. *nitens* than *K.* cf. *flaccidum*. Nevertheless, in desiccation experiments the recovery rates of these clades were similar (Donner et al., 2017a, 2017b). It is still an open question, which environmental factors caused the slight habitat preferences of the different clades. Additional ecophysiological experiments along with transcriptomic approaches combining potential environmental factors, such as light regimes, desiccation frequency and duration as well as soil parameters such as pH, might in future explain these conspicuous habitat preferences of *Klebsormidium* clades.

Correlation with SMI

The silvicultural management index (SMI) was used to estimate the management intensity. It takes into account the tree species, stand age and aboveground living and stand density. However, intensive managed forest did not necessarily inherit more disturbed sites suitable for BSC development. In contrast, BSC development is limited in forests with high stand density

(typical for intensively managed stands). However, managed forests have a higher risk for complete stand loss: either because of regular clear-cut or strong storms; it is more likely to lose huge areas in pine stands with high density compared to natural beech forest.

The richness of algal species as well as the proportion of coccal algae was positively correlated with the silvicultural management index (SMI). This means that more algal species were discovered in BSCs from managed than from natural forest ecosystems. This finding corresponds with conclusions about high algal richness on disturbed or cultivated soils (Hollerbakh & Shtina, 1969; Hoffmann, 1989). The SMI reflects the main tree species and the stand density as a result of management practice. Most studies in the Biodiversity Exploratories on soil microorganisms in forests observed rather an effect of the main tree species on the community than of the SMI (Goldmann et al., 2015; Kaiser et al., 2016; Purahong et al., 2014); only one study on litter decaying fungi and bacteria indicated a significant difference between natural and managed beech forests (Purahong et al., 2015). Kaiser et al. (2016) discussed that the different tree species influence soil bacteria by shifting the pH in soil, and hence as the main predictor for bacterial community composition. However, the differences in the bulk soil pH between beech and pine forest were not significant in Schorfheide-Chorin (Table 1) and thus the algae in BSCs were not affected by this abiotic parameter. Therefore, we rejected an effect of the SMI via the pH on the BSC algal species richness in Schorfheide-Chorin.

However, SMI combines other potential factors which might affect BSC microalgae, namely water and light availability due to stand density and tree species. The sampled forest plots in the exploratory Schorfheide-Chorin were dominated by either beech or pine trees, both differing in their light regime: in beech forests the canopy shade changes during spring and therefore radiation on the ground is usually higher in winter and spring than in pine forests. Also, the stand density, another parameter of the SMI, could affect the light regime on the ground: higher density would result in less photosynthetic active radiation for photosynthetic active soil microorganisms. The radiation is often coupled with evaporation of soil moisture (Raanan et al., 2016) and, hence, the stand density could have an indirect effect on the BSC organisms via an altered water regime. Thus, the SMI was expected to affect the algal richness in BSCs via lower light availability and lower evaporation rates. This assumption is well supported by the two-way analysis of water content and SMI, both of which are described as highly important for algal species richness. Nevertheless, it should be noted that the water content was measured in the bulk soil which might differ from that of BSCs. For future studies on microalgae in BSCs it would be important to examine also the incident light on the ground and the BSC water content.

Although the SMI positively affected the algal richness, the presence or absence of individual algal taxa was not correlated with the SMI, but with the main tree species. Broadleaf litter has a higher quality in terms of a more favorable C:N and C:P ratio compared to coniferous litter (Cleveland and Liptzin, 2007; McGroddy et al., 2004). It might be that the community in pine forest is shifted towards algal species, which can cope better with a suboptimal C:N:P ratio. But as mentioned above also light regime and water availability differ between both forest types and could thus have contributed to the observed differences in the occurrence of algal species.

Correlation with C, N, and P

BSCs have different important ecological functions, such as, for example, the enhancement of the nutrient content in the top soil layer (Baumann et al., 2017; Evans and Johansen, 1999). To assess the relationship between BSC community and biogeochemical cycling in BSCs, the content of total C, N and P and additionally the different P fractions (organic, inorganic, labile and stable fractions) were correlated with algal richness. Although a correlation between the richness of algae and the total C, N and P content was not observed, the presence of BSCs clearly led to an enhanced content of total C, N and P and in particular a higher proportion of organic P (Baumann et al., 2017). Hence, it is assumed that algal species are functional redundant and a low species richness in BSCs can still conduct the functional role of enhancing C, N and P content. A more detailed analysis of the P fractions gave a slightly different picture: the proportion of inorganic P was correlated with the proportion of filamentous algae and showed a tendency to correlate with the richness of BSC algae. Soluble inorganic phosphate originates either from P-mineral weathering, desorption of mineral-bound phosphates or from mineralization of organic matter (Mackey and Paytan, 2009) and can be assimilated by organisms. Thus, a low amount of inorganic P could indicate a high take-up rate of BSC organisms and, thus, a more closed P cycle due to higher algal richness (Baumann et al., 2017).

Conclusion

BSCs are able to coexist with continuos forests, because natural and human-induced disturbances regularly provide free space for crusts to develop, such as tree fall and skid trails. For the first time, algal richness in BSCs from such disturbed sites in temperate forests under different management intensity were described. The rather acidic forest soil supported a clear dominance of streptophycean *Klebsormidium*-morphotypes as the main crust-initiating filamentous algae, while Cyanobacteria play a negligible role. Higher forest management intensity resulted in a higher richness of algae, especially the proportion of coccal taxa increased. It is reasonable to assume that the silvicultural management intensity in forests affect the algal richness due to higher stand density in managed forests, which changes the light and water regime. Increasing algal richness in BSCs was supposed to enhance biogeochemical cycling of nutrients, but this hypothesis could not be proven. Nevertheless, the fraction of inorganic P showed tendencies towards a correlation with BSC algae, especially with filamentous species. Consequently, the present study gives the first hint of a potential relation between the biogeochemical cycles in BSCs and algal species. This relation should be studied in more detail, for example, by gene expression analyses to understand if and how algae in BSCs influence the cycling of P. Also, forthcoming studies should include other crust-associated organisms, like fungi and bacteria, to identify key players on the ecological role of BSCs in the P cycle.

Competing interests. The authors declare that they have no conflict of interest.

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Table 1. General information on study sites: sample location, main tree species, management status, silvicultural management index (SMI), water content and pH from bulk soil analyses, and proportion of inorganic P as % of total P; n.d. = not determined, * taken from Baumann et al. (2017)

Plot	latitude	longitude	main tree species	managed	SMI	Water content	pH	proportion of inorganic P (%)*
SW_01	52.900847	13.846367	pine	yes	0.351	12.08	3.64	20.8
SW_02	52.951729	13.778028	pine	yes	0.329	14.36	3.60	n.d.
SW_03	52.920707	13.643002	pine	yes	0.334	11.69	3.47	n.d.
SW_04	52.917347	13.847311	pine	yes	0.136	13.89	3.50	n.d.
SW_05	53.057034	13.885366	beech	yes	0.211	13.89	3.42	22.8
SW_06	53.057034	13.885366	beech	yes	0.211	13.89	3.42	18.6
SW_07	52.907443	13.841688	beech	yes	0.319	17.85	3.67	17.0
SW_08	52.907443	13.841688	beech	yes	0.319	17.85	3.67	14.9
SW_09	53.107348	13.694419	beech	no	0.082	18.61	3.73	20.3
SW_10	53.107348	13.694419	beech	no	0.082	18.61	3.73	18.5
SW_11	53.191797	13.930338	beech	no	0.059	20.67	3.38	13.7
SW_12	53.191797	13.930338	beech	no	0.059	20.67	3.38	n.d.
SW_13	53.044587	13.810103	beech	no	0.017	16.43	3.56	17.2
SW_14	53.044587	13.810103	beech	no	0.017	16.43	3.56	35.0
SW_15	53.091096	13.637843	pine	yes	0.381	9.91	3.70	9.2
SW_16	53.090294	13.633704	pine	yes	0.281	12.38	3.66	7.5
SW_17	52.917914	13.752174	pine	yes	0.276	15.81	3.38	16.7
SW_18	52.914542	13.737553	pine	yes	0.330	6.06	3.72	9.4
SW_19	53.076583	13.863986	pine	yes	0.335	8.40	3.57	n.d.
SW_20	53.088606	13.635384	pine	yes	0.357	8.99	3.66	12.8
SW_21	52.915588	13.740451	pine	yes	0.218	13.02	3.44	12.3
SW_22	52.895826	13.852147	pine	yes	0.217	13.30	3.47	n.d.
SW_23	52.895826	13.852147	pine	yes	0.217	13.30	3.47	n.d.
SW_24	52.940022	13.782612	beech	yes	0.161	16.82	3.62	n.d.
SW_25	52.940022	13.782612	beech	yes	0.161	16.82	3.62	n.d.
SW_26	52.914769	13.862365	beech	yes	0.250	15.66	3.68	25.2
SW_27	52.914769	13.862365	beech	yes	0.250	15.66	3.68	33.3
SW_28	52.900977	13.928326	beech	yes	0.229	18.85	3.72	14.8
SW_29	52.900977	13.928326	beech	yes	0.229	18.85	3.72	n.d.
SW_30	53.051266	13.844995	beech	no	0.070	14.08	3.71	n.d.
SW_31	53.051266	13.844995	beech	no	0.070	14.08	3.71	n.d.

Table 2. Significant Pearson correlation coefficients to reveal correlations between environmental factors, which might affect or be affected by the richness of algae. This co-correlation analysis should support the correct interpretation of potential important factors for the alga community. SMI-silvicultural management index; n.s. – not significant

	main tree species	SMI	water content	pH	C_t content	N_t content	P_t content
SMI	-0.6						
water content	0.77	-0.59					
pH	n.s.	n.s.	n.s.				
C_t content	n.s.	n.s.	n.s.	n.s.			
N_t content	n.s.	n.s.	n.s.	n.s.	0.94		
P_t content	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
proportion of inorganic P	n.s.	n.s.	n.s.	n.s.	n.s.	-0.78	0.6

Table 3. Effect of environmental factors on algae richness, filamentous algae proportion (both estimated by ANOVA) and presence or absence of individual algal species (estimated by PerMANOVA) quantified by the percentage of explained variance. The significance level is indicated by: ***-$p<0.001$, **-$p<0.01$, *-$p<0.05$, °-$p<0.1$, ns- not significant; (+) indicates positive correlation, (-) negative correltaion

	algae richness	proportion of filamentous algae	presence or absence of individual algal species
SMI	30.5 % ** (+)	37.7 % *** (-)	5.6 % n.s.
water content	15.7 % * (-)	14.0 % ** (+)	9.6 % *
proportion inorganic P	11.0 % ° (-)	29.1 % *** (+)	5.8 % n.s.
main tree species	0.9 % n.s.	0.3 % n.s.	14.7 % ***

Figure 1. general overview of managed pine forest (a) and natural beech forest (c) and close-up of the respective biological soil crusts (BSC): BSC on bare soil in a managed pine forest (b); BSC on a root plate of a fallen tree in a natural beech forest (d)
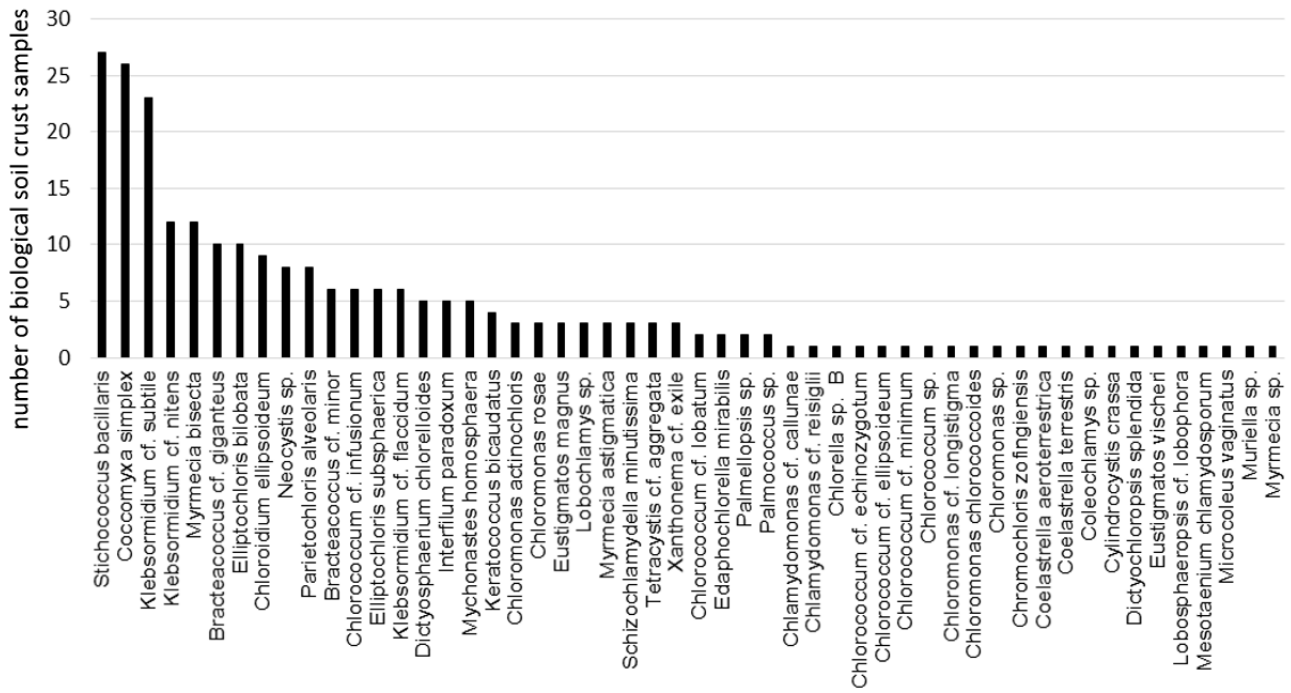
Figure 2. Occurrence of each algal species in biological soil crusts from forest sites (n=31).
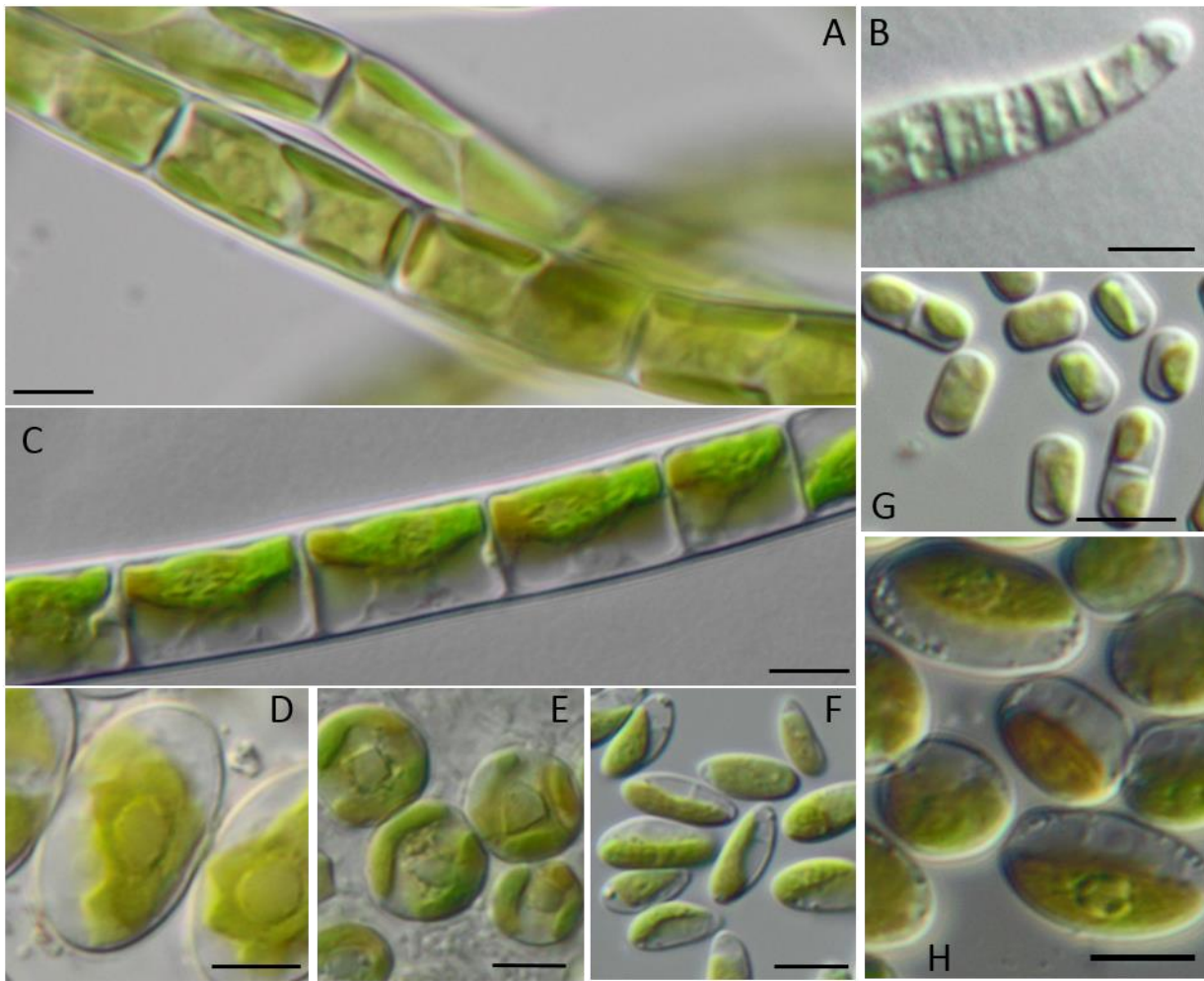
Figure 3. Filamentous and examples of coccal algae from forest BSCs: algae with strong filaments: A-*Xanthonema* cf. *exile,* B-*Microcoleus vaginatus,* C-*Klebsormidium* cf. *flaccidum;* coccal algae: D-*Chloroidium ellipsoideum,* E-*Eustigmatos magnus,* F-*Coccomyxa simplex;* algae with short or easily disintegrated filaments*:* G-*Stichococcus bacillaris,* H-*Interfilum paradoxum*; scale bar = 5µm
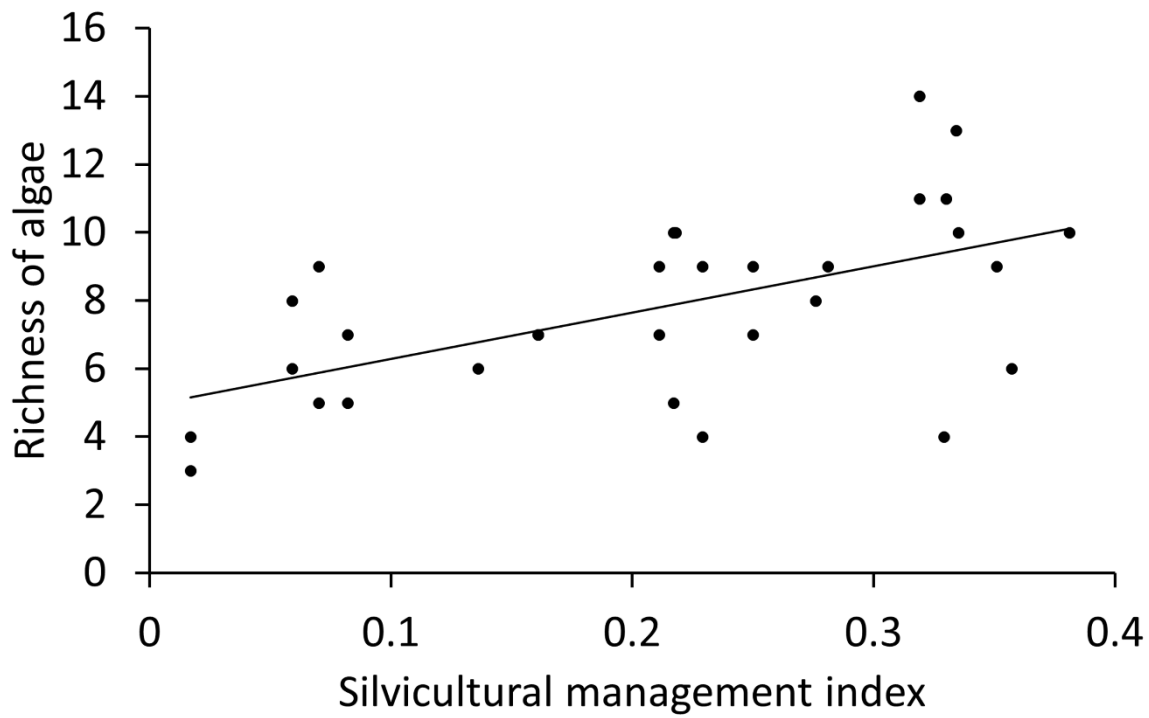
Figure 4. Plot of algae richness in BSCs from forests over the silvicultural management index (SMI), natural forest has a low SMI, managed forests a high SMI; the line indicates the best linear fit (slope: 13.6, p<0.001(Anova))