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

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Abstract

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

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

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Introduction

Biological soil crusts (BSCs) occur as important 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 vascular plant vegetation or disturbed areas in open sites (e.g. former mining sites) typically promote the development of BSCs (Fischer et al., 2010b; Langhans et al., 2009; Lukešová, 2001; Schulz et al., 2016; Szyja et al., 2018).

Even though there is a rising interest in BCSs as global players 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 highly competitive vascular plants, which strongly limit their development. In forests, light limitation and the occurrence of litter additionally restrict the development of BSCs on the forest ground. Therefore, any disturbance of the higher vegetation changes the competitive situation, allowing the development of BSCs. Disturbances occur frequently in temperate forests. They include litter free spots at hill slopes, tree falls, pits of wild boars and molehill-like humps, as well as human-induced disturbances such as skid trails and clear-cut areas. An increase in tree-falls after storm events is a growing problem in Europe, especially with raise in number and strength of storms potentially caused by the global climate change (Schwierz et al., 2010). In places where a substantial disturbance of intact forest ecosystems had occured BSCs typically represent pioneer vegetation for the colonialization of bare the soil. BSC organisms initiate the biological introduction of carbon and nutrients into soil, promoting the regrowth of vascular plants (Seitz et al., 2017) and erosion protection after heavy disturbance and destruction of intact forest ecosystems.

Destruction of BSC cover caused by land use has numerous negative effects such as an increase in soil erosion, changes in water regime and C and N losses from the topsoil (Barger et al., 2006; Belnap, 2003). Studies dealing with the effect of land use on BSCs were mainly conducted in arid and semiarid regions. These studies showed strong negative effects of intensive livestock grazing on BSC cover due to trampling and reported a subsequent BSC 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 BSC cover dramatically (Daryanto et al., 2013). In contrast to reports from arid areas there are no studies on the effect of land use in temperate regions, nor on the effect of land use activities other than grazing or human activities on BSCs. Further, reports on how disturbances in continuous vegetation might promote the development of BSCs are missing.

BSCs can be characterized as "ecosystem-engineers" since they form water-stable aggregates, which have an important ecological role 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, little is known about their role in P cycling. Recent studies indicated that the number of microalgal species in BSCs can be related to the soil P content (Baumann et al., 2017; Schulz et al., 2016). Nevertheless, the effect of environmental factors that shape BSC communities and in turn affect soil characteristics is still unstudied.

Together with the macroscopic lichens and bryophytes cyanobacteria and eukaryotic microalgae represent the most important phototrophic components of BSCs (Belnap et al., 2001). Eukaryotic microalgae, essential components of biocrust communities as major contributors to C fixation (Büdel et al., 2016; Szyja et al., 2018), are still the least studied phototrophs in BSCs. BSC microalgae can be divided into two functional groups: (I) filamentous and (II) single celled i.e. coccoid. Filamentous green algae are major BSC forming taxa that stabilize soil particles by gluing them together due to the excretion of sticky mucilage. They usually occur in high biomass but low diversity. Coccoid algae are attached to the soil particles or other algae and typically occur in high diversity but low biomass (Büdel et al., 2016).

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

In a previous study, we indicated that the BSC's algal richness is related to P cycling (Baumann et al., 2017). The data implied that BSCs were involved in the transformation of inorganic P to organic P compounds, thus playing a key role in the biological P cycling in temperate soils. However, BSC algal species richness was only considered as a sum parameter, detailed information on species occurrence is still missing. Therefore, in the present study we focused on the identification of algal species and the effect of silvicultural management intensity on algal species richness in BSCs collected from the same plots as Baumann et al. (2017) and additional sampling sites. The correlation of BSC algal richness with C, N, and P content, and in particular different P fractions, was investigated in order to uncover the link between biogeochemical cycles and BSC alga species. The aim of the present study was to characterize for the first time algal community in the BSCs from disturbed sites in temperate forests of different silvicultural management intensities.

Material and Methods

Study site

BSC samples were collected in June 2014 and 2015 from the plots of the Project 'German Biodiversity Exploratories' with natural protected forests and managed forest (age-class forest) (Fischer et al., 2010a). Forest plots were located 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 the disturbed areas where BSCs developed on the litter-free bare soil (for illustration see Figure 1). The top millimeters of soil, where BSC had been visually detected as a green cover, were collected a spatula. After transportation to the lab the upper two millimeters of BSCwere separated from

the adhering soil underneath with a razor blade before stored dry in paper bags. In total, 31 BSCs were collected from 13 pine and 18 beech plots, 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 the establishment of
enrichment cultures. Several 7–10 mm^2 BSC pieces were cleaned with forceps to remove all roots and leaves, in order to avoid
the 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 after four to six weeks incubation, using a light microscope
(BX51, Olympus) with Nomarski differential interference optics and 1000x magnification. Photomicrographs 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 BSC were rewetted with tap water, put on a glass slide and analyzed with the above
mentioned microscope at 400x magnification. Mucilage of algae was stained with an aqueous solution of methylene blue.

Morphological identification of algae and 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).
Phototrophic microorganisms were identified as Cyanobacteria, Chlorophyta, Streptophyta and some Stramenopiles
(Eustigmatophyceae). Diatoms were regularly found in direct observations but were excluded from the analyses as the
mentioned enrichment cultivation was not suitable for this group of microalgae (e.g. Schulz et al., 2016).

Since the enrichment cultivation did not provide clear information on the abundance of each identified taxon, we used the total
number of algae and cyanobacteria species per sample, also known as species richness, as the measure of alpha diversity. As
a measure of beta diversity, the similarity between the plots was shown by presence/absence of individual species, combining
the total number and the identity of all algal taxa observed. Furthermore, the identified algae and cyanobacteria were
categorized based on their life form (filamentous or coccal), since different life forms differ in their ecological function. The
proportion of filamentous algae in the total number of algae was used for statistical analyses.

Environmental variables

The natural and managed forest plots were characterized by different 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 forest stands were regularly disturbed by tree cuts, removal of dead trees and usage of skid trails. To evaluate the effect of
management, the silvicultural management index (SMI) was used. This index takes into account the tree species, forest stand
density and age, as well as the aboveground living and dead wood biomass (Schall and Ammer, 2013). High stand density is
reflected by a high SMI, therefore natural forests have a lower SMI than managed forests, and a pine stand has a higher SMI
than a beech stand (Schall and Ammer, 2013).

To assess potential links between BSC organisms and environmental parameters, the species' richness, presence / absence of individual algal species, and proportion of filamentous algae was related to the following environmental parameters: dominant tree species (pine or beech), silvicultural management intensity (SMI), pH and water content of the bulk soil (Table 1; for all 31 samples). Additionally, for a subset of 19 BSC samples data on total C, N and P content, organic and inorganic P compounds, for labile, moderately labile and stable P were included. Element data were presented in detail by Baumann et al. (2017), thus not presented in this paper.

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; the best predictors for their varaince were selected by backward elimination stepwise regression analysis based on the BIC (Bayesian information criterion) using 'step' command in R. The correlation between environmental parameters was determined 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 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

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 and 23 out of 31 samples, respectively. All other algal species were detected in less than 50% of the BSC samples; 22 algal species were observed exclusively in one sample (Figure 2). The richness of algae (total species number) at each plot ranged from three to 14 species with a mean of 8 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, only one species, *Microcoleus vaginatus*, was observed in only one sample.

The identified algal species were differentiated according to their life form (Figure 3). Five species with strong filaments (*Klebsormidium* cf. *flaccidum, K.* cf. *subtile, K.* cf. *nitens, Xanthonema* cf. *exile*, *Microcoleus vaginatus*) and two species with

short or easily disintegrating filaments (*Interfilum paradoxum*, *Stichococcus bacillaris*) were found. In each BSC at least two different filamentous taxa were detected, indicating their importance for the BSC formation. Genus *Klebsormidium* seemed to be highly important for BSCs in forest since it was registered in every BSC sample (Supp. Table S1)

Correlation of algae richness with plot characteristics and nutrient content

5   The gravimetric water content of the bulk soil was negatively correlated with the SMI; the pH was neither correlated with the water content, nor with the SMI nor with the dominant tree species (Table 2). The N content was positively correlated with the C content, and N as well as C content 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 of 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

10   proportion of inorganic P (Table 3). The remaining tested parameters (C and N content, total P, proportion of organic P, pH, dominant tree species, and soil horizon) were excluded by stepwise model simplification based on the BIC. This means that these factors had no measurable effect on the algal species richness or on the proportion of filamentous algae. The SMI was positively correlated with the species richness, meaning that a higher SMI resulted in a higher species richness (Figure 2), especially the proportion of coccal algae was increased. BSCs with higher algal richness tended to have lower proportions of

15   inorganic P.

The presence/absence of individual algal species in BSCs significantly correlated with the dominant tree species (15% explained variance) and with the soil 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). Therefore, we concluded that the dominant tree species and the soil water content affect the composition of algal species 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 species richness compared to the other reports on BSCs from temperate regions at open sites (Langhans et al.,

25   2009; Schulz et al., 2016), but similar or higher compared to the previous reports on algae from forest bulk soil (Khaybullina et al., 2010; Novakovskaya and Patova, 2008; Starks et al., 1981). Nevertheless, the given number most probably underestimates the real algal richness, since our results are based on the enrichment cultivation followed by morphological identification. Enrichment cultivation promotes the growth of only culturable algae, which represent only a small part of all phototrophic microorganisms in BSCs (Langhans et al., 2009). A recent paper, comparing metagenomic data of a polar BSC

30   with data based on enrichment cultivation and morphological identification of the algae, showed that only about 10% of the metagenomic data could be confirmed by morphological identification (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 of the dominant active organisms. With this approach we could confirm that all filamentous algae were abundant and 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 of identification, since molecular techniques alone can also fail to detect some taxa, as a result of unsuccessful DNA extraction, inappropriate primers etc. (Büdel et al., 2009; Garcia-Pichel et al., 2001).

All observed algal species are known to be terrestrial taxa, most of them were already reported from 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 (genera such as *Chlamydomonas*, *Chloromonas*, *Chlorococcum*, and *Tetracystis*). A high richness of Chlorophyta is characteristic for humid habitats and typical for forest soils (Hoffmann 1989).

Cyanobacteria were represented by only one species. While they are often reported as predominant species in BSCs of arid regions such as Israel and drylands of the USA (Garcia-Pichel et al., 2001; Kidron et al., 2010), cyanobacteria are less abundant in temperate regions (Gypser et al., 2016; Langhans et al., 2009; Pluis, 1994) and even rare in acidic soils, which corresponds to 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 taxa´s ecological traits. For example, the ability for nitrogen fixation in phototrophic organisms was only reported for cyanobacteria and never observed in eukaryotic algae. In forest ecosystems, litter and other decomposable biomass might have provide sufficient mineral nitrogen compounds, which could have lead to the absence of nitrogen-fixing organisms in these systems in contrast to nitrogen-poor habitats such as dunes or deserts where cyanobacteria are dominant (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 BSC communities, because of their BSC-initiating potential by building tight networks among soil particles (Büdel et al., 2016). In some forest BSCs, moss protonema can exert a similar function, due to their filamentous nature (Weber et al. 2016). However, in the forest ecosystems of Schorfheide-Chorin the green algae *Klebsormidium* seems to be the most important BSC-initiating alga. This genus can tolerate a wide range of environmental factors and 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 lowlands 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), 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, since the increase of light intensity 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 BSC samples from Schorfheide-Chorin forest may be explained by a lower solar radiation and lower evaporation rates in forest ecosystems compared with the open habitats (e.g. inland dunes) where besides *Klebsormidium* other filamentous algae are dominant (Langhans et al., 2009; Pluis, 1994). Also, the forest soil is rather acidic (pH min: 3.23; pH 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 the 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 investigated samples (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 the 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 (Rindi et al., 2011). Studies comparing these *Klebsormidium* clades from different localities observed global ubiquity on one hand, and local endemism on the other (Ryšánek et al., 2014). Clade composition seems to differ depending on the habitat: *Klebsormidium* cf. *flaccidum* (B/C clade) was abundant in both closed and 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 our study, however, BSCs from forests contained more often *Klebsormidium* cf. *subtile* and *K.* cf. *nitens* than *K.* cf. *flaccidum*. In desiccation experiments the recovery rates of these clades were similar (Donner et al., 2017a, 2017b). It is still open which of the environmental factors cause the observed habitat preferences of the different clades. Additional ecophysiological experiments including potential environmental factors, such as light regimes, desiccation frequency and duration, as well as soil parameters such as pH, in combination with transcriptomic approaches might explain these conspicuous habitat preferences of *Klebsormidium* clades.

Correlation with SMI

The silvicultural management index (SMI) was used to estimate the forest management intensity. It takes into account the tree species, forest stand age and density. However, intensively managed forest did not necessarily inherit more disturbed sites suitable for the BSC development. In contrast, BSC development is limited in forests with high density (typical for intensively managed forest 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 large part of 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 agrees with conclusions of high algal richness on disturbed or cultivated soils (Hollerbakh & Shtina,

1969; Hoffmann, 1989). The SMI reflects the effect of management practice on the dominant tree species and the stand density. Most Biodiversity Exploratories studies on forest-soil microorganisms observed a stronger effect of the dominant tree species than of the SMI on the microbial community (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

5   (Purahong et al., 2015). Kaiser et al. (2016) discussed that the different tree species influence soil bacteria by shifting the pH in soil, hence, tree species was designated as the main predictor for bacterial community composition. However, the bulk soil pH did not differ significantly between beech and pine forest in Schorfheide-Chorin (Table 1), hence, 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.

10   However, the SMI combines other potential factors which could explain its positive correlation with the richness of algal species as well as the proportion of coccal algae. Water and light availability might have affected BSC microalgae due to forest stand density and tree species. Forest plots in Schorfheide-Chorin were dominated by either beech or pine trees, which affect the light regime differently: in beech forests the canopy shade changes over the year, with usually higher solar radiation on the ground in winter and spring than in summer, while in pine forests no such light fluctuations occur. Also, the stand

15   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) 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. Nevertheless, it should

20   be noted that the water content was measured in the bulk soil, which might differ from the one of BSCs. For future studies on microalgae in BSCs it would be important to examine also the incident light on the ground as well as 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 have been that the

25   community in the pine forest promoted algal species which could cope with a suboptimal C:N:P ratio. But as mentioned above both, light regime and water availability, differ between the two forest types and could also have contributed to the observed differences in the occurrence of algal species.

Correlation with C, N, and P

30   BSCs have different important ecological functions, such as 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 increased content of total C, N and P and in particular a higher proportion of organic P (Baumann et al., 2017). These results indicate that algal species are functionally redundant, and that a BSC community with low species richness still has a functional role in increasing C, N and P content. A more detailed analysis of the P fractions gave a slightly different picture: the proportion of inorganic P was positively correlated with the proportion of filamentous algae and showed a tendency to a negative correlation with the richness of BSC algae. Soluble inorganic phosphate can be assimilated by organisms, and it originates either from the weathering of P containingminerals, desorption of mineral-bound phosphates or from the mineralization of organic matter (Mackey and Paytan, 2009). Thus, a low amount of inorganic P could indicate a high uptake rate of BSC organisms, thus a more closed P cycle due to the higher algal richness (Baumann et al., 2017).

Conclusion

BSCs are able to coexist with continuous forests, because natural and human-induced disturbances regularly provide free space (e.g. tree fall, skid trails) for BSCs to develop. 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 BSC-initiating filamentous algae, while cyanobacteria played a negligible role. Higher forest management intensity resulted in a higher richness of algae, especially in a hihger proportion of coccal taxa. It is reasonable to assume that the silvicultural management intensity in forests affect the algal richness due to the higher forest 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 negative correlation with BSC algae, especially with filamentous species. Consequently, the present study gives the first hint of a relation between the biogeochemical cycles in BSCs and algal species. This relation should be studied in more detail, e.g. by gene expression analyses to understand if and how algae in BSCs influence the cycling of P. Also, forthcoming studies should include other BSC-associated organisms, such as fungi and bacteria, to identify key players and 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

10   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)
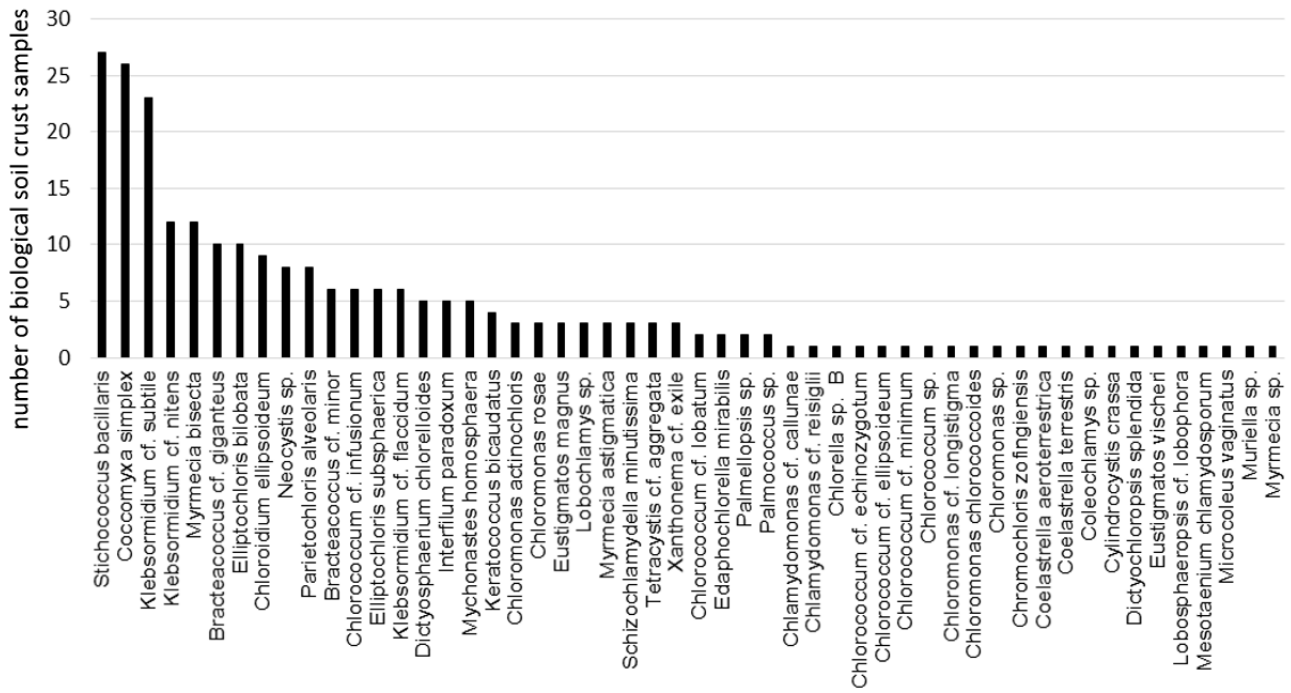
Figure 2. Occurrence of each algal species in biological soil crusts from forest sites (n=31).
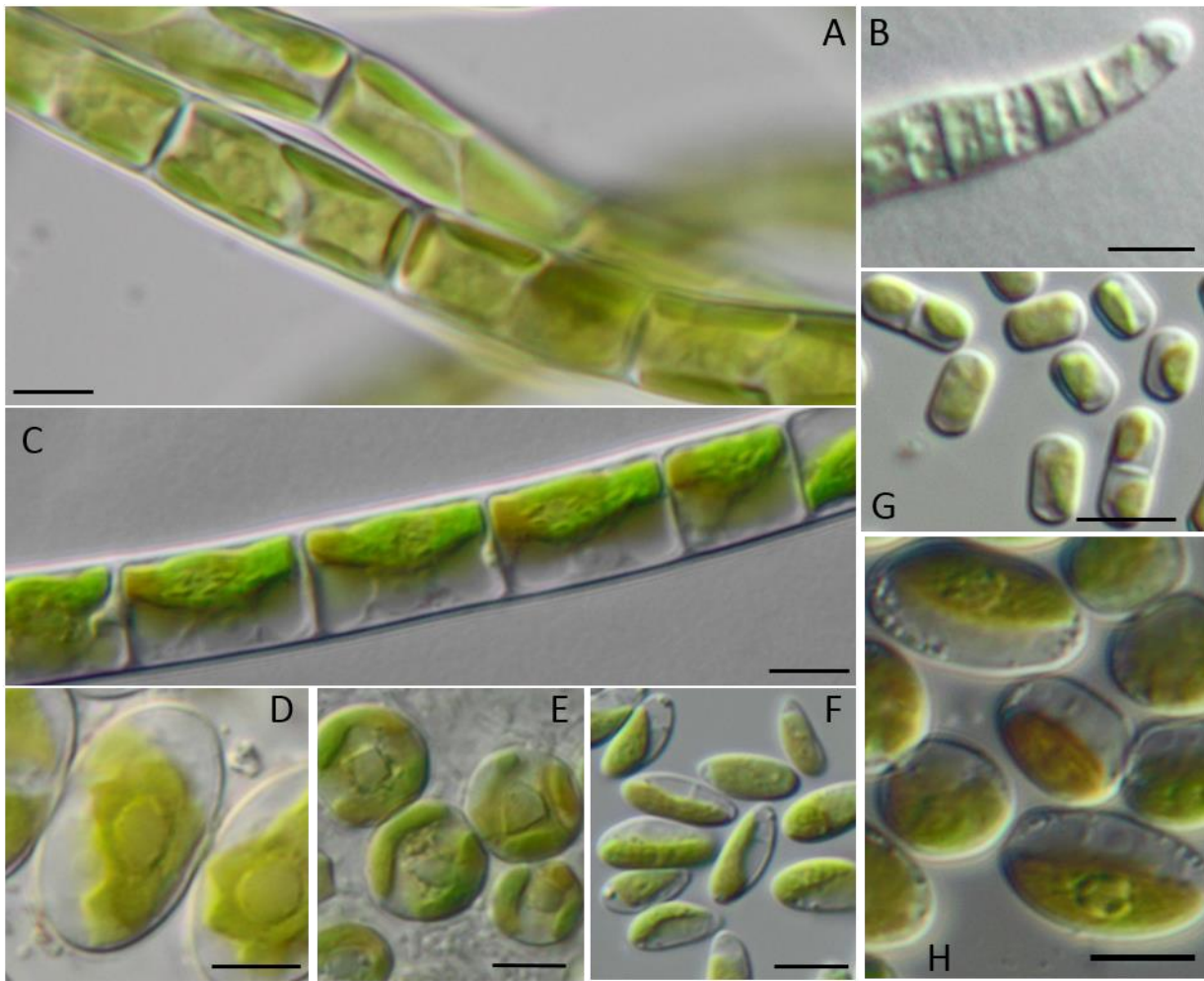
Figure 3. Filamentous and examples of coccal algae from forest BSCs: algae with strong filaments: A-*Xanthonema* cf. *exile,* B-*Microcoleus vaginatus,* C-*Klebsormidium* cf. *flaccidum;* coccal algae: D-*Chloroidium ellipsoideum,* E-*Eustigmatos magnus,* F-*Coccomyxa simplex;* algae with short or easily disintegrated filaments*:* G-*Stichococcus bacillaris,* H-*Interfilum paradoxum*; scale bar = 5µm
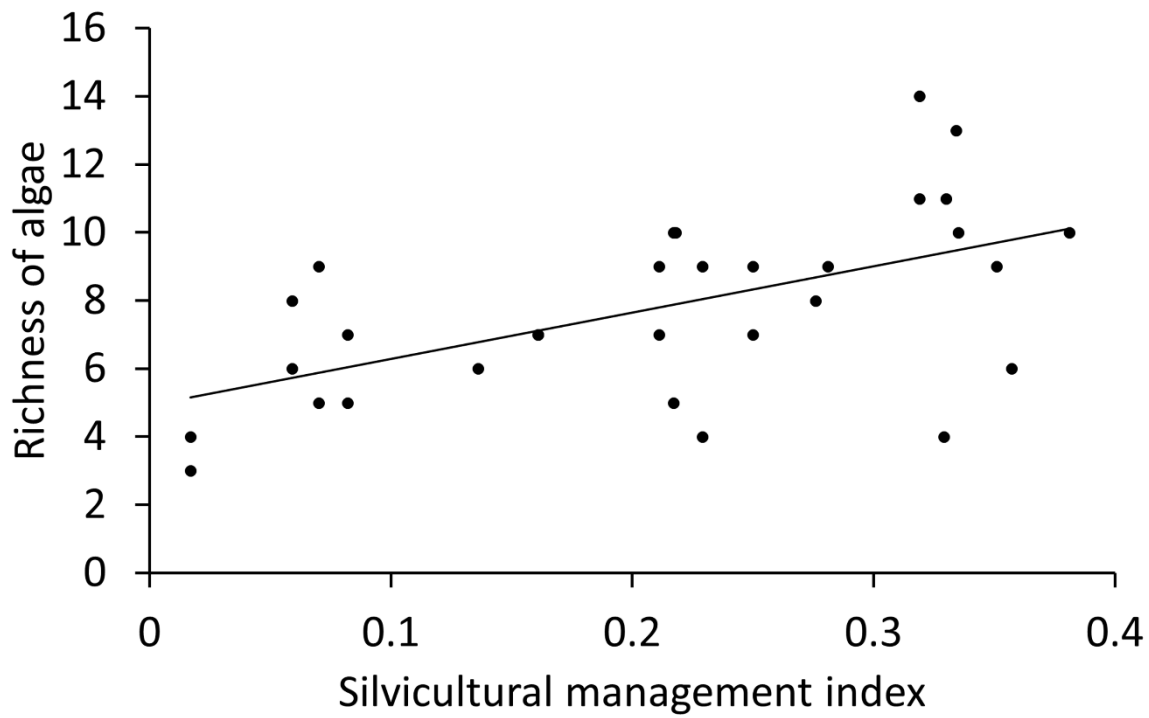
Figure 4. Plot of algae richness in BSCs from forests over the silvicultural management index (SMI), natural forest has a low SMI, managed forests a high SMI; the line indicates the best linear fit (slope: 13.6, p<0.001(Anova))