Dear Bettina Weber,

Thanks for your detailed remarks. We asked for help and corrected punctuation and other language issues throughout the manuscript.

I hope, our manuscript fulfills the standards of the journal now.

Kind regards,

Karin Glaser

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

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Abstract

Biological soil crusts (BSCs) form the most productive microbial biomass in manyare highly important communities in drylands and disturbed areas worldwide, where the higher vegetation is sparse, with a diverse microalgal community as key component. They conductperform important ecological functions, such as stabilization of soil and nutrient enrichment of nutrients.. In temperate regions, BSCs are also common, but generally less studied. Changes in land use and itsland use intensity strongly influence biodiversity per se and its role for ecosystem processes, as can be seen particularly in regions which are densely populated regions like Europe. AnyhowHowever, systematic studies on the effect of land use (gradients, i.e. forest management intensity) gradients in temperate forests, on BSCs are missing up to now. To close this gap of knowledge gap 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., key primary producers of these communities (eukaryotic microalgae and cyanobacteria) were studied. Phototrophic microorganisms were identified morphologically based on enrichment cultivation and categorized as either coccal taxa, which occur 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 could be observed.. The most abundant crust-initiating filamentous algae were three species of *Klebsormidium* (Streptophyta), a ubiquitous genus often associated with regularly occurring in BSCs worldwide because of their generallyits broad ecophysiological tolerances such as to low pH.tolerance. Increasing management intensity in the forests resulted in higher numbersnumber of algal species, especially the number of coccal taxa roseincreased. 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 in the BSC.

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 highervascular plant vegetation or disturbed areas in open sites (e.g. former mining sites) typically inheritpromote the development of BSCs (Fischer et al., 2010b; Langhans et al., 2009; Lukešová, 2001; Schulz et al., 2016; Szyja et al., 2018).

Although BSCs received raisingEven though there is a rising interest in the past years, for example,BCSs as global playerplayers 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 and thus, which strongly limit their development is often limited. Especially in. In forests, thelight limitation of light and the occurrence of litter restrictsadditionally restrict the development of BSCs on the crust development. But disturbances forest ground. Therefore, any disturbance of the higher vegetation layer change thischanges the competitive situation and allow, allowing the development of BSCs. Such disturbancesDisturbances occur frequently in temperate forests, for example, natural tree fall, pits of wild boars,. They include litter free spots at hill slopes, tree falls, pits of wild boars and molehill-like humps, oras well as human-induced disturbances such as skid trails and clear-cut areas. EspeciallyAn increase in tree--falls after storm events is a risinggrowing problem in Europe due to increasing, especially with raise in number and strengthsstrength of storms, probably because as potentially caused by the global climate change (Schwierz et al., 2010). In places where a consequence of global change (www.dwd.de). At such spots,substantial disturbance of intact forest ecosystems had occured BSCs typically serve asrepresent pioneer vegetation for the 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 tobare the soil. BSC organisms initiate the biological introduction of carbon and nutrients into the soilsoil, promoting the regrowth of vascular plants (Seitz et al., 2017). and erosion protection after heavy disturbance and destruction of intact forest ecosystems.

DisturbanceDestruction of BSCs due toBSC cover caused by land use has been reported to have strongnumerous negative effects on BSC cover, which resultedsuch as an increase in higher soil erosion, changes in water regime and C and N losses from the top soiltopsoil (Barger et al., 2006; Belnap, 2003). Studies ondealing with the effect of land use on BSCs were mainly conducted in arid and semiarid regions. These studies reported, for example, a showed strong negative influenceeffects of intensive livestock grazing on BSC cover due to trampling with aand 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 BSCsBSC cover dramatically (Daryanto et al., 2013). In contrast,, to reports from arid areas there are no reports studies on the effect of land use effects in temperate regions or aspects, nor on the effect of land use activities other than grazing or human activities on BSCs. Also missing are Further, reports on the benefits for BSCs in terms of coverage due to how disturbances in continuous vegetation like forestsmight promote the development of BSCs are missing.

BSCs can be characterized as “ecosystem-engineers” formingsince they form water-stable aggregates that, which have an important ecological rolesrole 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, lesslittle is known about their role in P cycling. However, recentRecent studies indicated that the number of microalgal species in BSCs iscan be related to the soil P content (Baumann et al., 2017; Schulz et al., 2016). But still, only little is known aboutNevertheless, the effect of environmental factors that shape BSC communities and how BSCs in turn affect soil characteristics is still unstudied.

Cyanobacteria andTogether with the macroscopic lichens and bryophytes cyanobacteria and eukaryotic 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 anmicroalgae, essential componentcomponents of suchbiocrust communities because of theiras major contributioncontributors to C fixation (Büdel et al., 2016; Szyja et al., 2018)., are still the least studied phototrophs in BSCs. BSC algaemicroalgae can be categorized asdivided into two functional groups.: (I) filamentous algae asand (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 presence/excretion of sticky mucilage. The filamentous forms occurThey usually occur in high biomass but low diversity but produce high biomass. (II) coccoid algae which. Coccoid algae are attached to the soil particles or other algae and typically occur in higherhigh diversity but lowerlow 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. 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 presented hintsindicated that differences ofthe BSC's algal richness in BSCs areis related to P cycling. (Baumann et al., 2017). The data indicatedimplied that BSCs are particularlywere involved in the transformation of inorganic P to organic P compounds, thus playing a key role in the biologically drivenbiological P cycling in temperate soils. In addition, BSCs responded differently to management intensity depending on forest type (beech versus pine). WhileHowever, BSC algal species richness of BSCs was only considered as a sum parameter, detailed information on species occurrence is still missing (Baumann et al., 2017).. Therefore, in the present study we identified focused on the identification of algal species in a temperate forests and investigated for the first time in detail the influenceeffect of silvicultural management intensity on algal species richness in BSCs collected atfrom the same plots as in Baumann et al. (2017), plus some) and additional sampling sites. The correlation of BSC algal richness andwith C, N, and P content, and in particular on the different P fractions of P, was assessedinvestigated in order to uncover the relationlink between biogeochemical cycles in BSCs and the underlyingBSC 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 ExploratoriesExploratories' with natural protected forests and managed forest (age-class forest) (Fischer et al., 2010a). Forest plots were sampledlocated in the Schorfheide-Chorin Biosphere Reserve in Northeast Germany. The, 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 the disturbed areas where BSCs could developdeveloped on the litter--free bare soil (for illustration see Figure 1).

The top millimeters of soil, on whichwhere BSC had been visually detected as a green cover, were collected by pressing a petri dish in the respective crust and removing gently with a a spatula. After transportation to the lab the upper two millimeters of the crust wereBSCwere separated from the adhering soil underneath usingwith a razor blade andbefore stored dry in paper bags before cultivation.. In total, 31 BSCs were collected from 13 pine and 18 beech standsplots, 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 in Petri dishes (9.5 cm diameter).. Several 7–10 mm^2 BSC pieces were cleaned with forceps to remove all roots and leaves, in order 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 after four to six weeks ~~after~~ incubation, using a light microscope (BX51, Olympus) with Nomarski differential interference optics and 1000x magnification. ~~Light micrographs~~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 ~~crust~~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). ~~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 were excluded from the analyses as the mentioned enrichment cultivation ~~is~~was not suitable for this group of microalgae (e.g. Schulz et al., 2016).

Since the enrichment cultivation ~~does~~did not ~~allow a~~provide clear ~~conclusion~~information on the abundance of each identified ~~algal~~ taxon, ~~richness of algae (~~we used the total number of algae and cyanobacteria species per sample~~) was used~~, also known as species richness, as the measure ~~for~~of alpha diversity. As a ~~second parameter for biodiversity~~measure of beta diversity, the similarity between ~~single~~the plots was shown by presence~~ / ~~/absence of individual species, combining the total number and the identity of all algal taxa observed. ~~Further~~Furthermore, the identified algae and cyanobacteria were categorized ~~in~~ based on their life form (filamentous or coccal), since different life ~~form, because both~~forms differ in their ecological function. The proportion of filamentous algae ~~on~~in the 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~~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 ~~due to, for example, usage of skid trails and~~ by tree cuts, removal of dead trees ~~as well as tree cut~~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 ~~age~~density and age, as well as the aboveground living and dead wood biomass~~, i.e. stand density~~ (Schall and Ammer, 2013). ~~Natural forest has~~High stand density is reflected by a high SMI, therefore natural forests have a lower SMI than ~~the~~ managed ~~forest;~~forests, and a pine stand has a higher SMI than a beech stand~~; high stand density is reflected by a high SMI~~ (Schall and Ammer, 2013).

To assess potential ~~linkages~~links between BSC organisms and environmental parameters, the species' richness, presence ~~or~~/ absence of individual algal species, and proportion of filamentous algae was ~~linked~~related to the following environmental parameters: ~~main~~dominant tree species (pine or beech), silvicultural management intensity (SMI), pH and water content ~~and pH~~ of the bulk soil (Table 1; for all 31 ~~plots (water content and pH kindly provided by I. Schöning, Table 1) and, further~~samples). Additionally, for a subset of ~~the samples (n~~=19~~),~~ BSC samples data on total C, N and P content, organic and inorganic P ~~proportions, both~~compounds, for labile, moderately labile and stable P~~. Data on latter are not shown here but~~ were ~~already~~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; ~~their~~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 ~~were checked~~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~~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 ~~23~~31 samples, respectively. All other algal species were detected in less than 50% of the ~~plots~~BSC samples; 22 algal species were observed exclusively ~~at~~in one ~~plot~~sample (Figure 2). The richness of algae~~, i.e. the~~ (total species number~~,~~) at each plot ranged from three to 14 species~~,~~ with a mean of ~~eight~~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, ~~just~~only one species, *Microcoleus vaginatus*, was observed in only one sample.

The identified algal species were differentiated according to their ~~organization~~life 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~~species with short or easily ~~disintegrated~~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. ~~Especially the genus~~Genus *Klebsormidium* seemed to be highly important for BSCs in forest~~:~~ since it was registered in ~~each~~every BSC ~~at least one of in total three observed morphospecies was found~~sample (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 negatively correlated with the SMI; the pH was ~~independent of~~neither correlated with the water content, ~~SMI and~~nor with the ~~main~~SMI nor with the dominant tree species (Table 2). The N content was positively correlated with the C content, and ~~both~~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 ~~from~~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 proportion of inorganic P (Table 3). ~~All other~~The remaining tested parameters (C and N content, total P, proportion of organic P, pH, ~~main~~dominant tree species, and soil horizon) were excluded by stepwise model simplification based on the BIC. ~~Thus,~~This means that these factors had no measurable effect on the algal species richness ~~nor~~or on the proportion of filamentous algae. ~~A~~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 ~~enhanced~~increased. BSCs with higher algal richness tended to ~~a~~have lower ~~proportion~~proportions of inorganic P.

The presence~~ or ~~/absence of individual algal species in BSCs significantly correlated with the ~~main~~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). ~~This implies an effect of~~Therefore, we concluded that the ~~main~~dominant tree species and the soil water content ~~on~~affect the ~~community~~ composition of ~~algae~~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., 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 ~~is~~ most probably ~~an underestimation of~~ underestimates the real algal richness~~ because~~, since our results are based on the enrichment cultivation followed by morphological ~~assignment.~~identification. Enrichment cultivation ~~covers~~ promotes the growth of only

~~cultivable~~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 with ~~morphological~~ data based on enrichment cultivation ~~estimated a match of~~ and morphological identification of the algae, showed that only about 10% of ~~all microalgae in a polar BSC~~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 ~~for~~of the dominant active organisms. ~~Using~~With this approach~~,~~ we could ~~prove~~confirm 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 of identification, since molecular techniques alone ~~sometimes~~can also fail to detect some taxa~~ based on problems with~~, as a result of unsuccessful DNA extraction, ~~appropriate~~inappropriate primers etc. (Büdel et al., 2009; Garcia-Pichel et al., 2001).

All observed algal species are known ~~as~~to be terrestrial taxa, most of them were ~~also~~already reported ~~in~~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~~, and hence a high richness~~ (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 ~~single~~ species. ~~Cyanobacteria~~While they are often reported as predominant species in BSCs ~~in~~of arid regions such as Israel and drylands of the USA (Garcia-Pichel et al., 2001; Kidron et al., 2010)~~. Nevertheless, Cyanobacteria~~, 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~~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~~cyanobacteria play only a minor role in forest ecosystems with consequences for the taxa´s ecological traits~~ that some taxa occupy.~~. For example, the ability for nitrogen fixation in phototrophic organisms was only reported ~~from Cyanobacteria~~for cyanobacteria and never observed in eukaryotic algae. In forest ecosystems, litter and other decomposable biomass ~~provides probably~~might have provide sufficient mineral nitrogen compounds, which ~~might~~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 ~~such~~BSC communities, because of their ~~potential as~~ BSC-initiating ~~organisms~~potential 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, in the forest ecosystems of Schorfheide-Chorin the green algae *Klebsormidium* seems to be the most important ~~crust~~BSC-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~~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),~~ 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~~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 ~~plots~~ may be explained by a lower solar radiation and ~~also~~ lower evaporation ~~of water~~rates in ~~the~~ forest ~~ecosystem~~ecosystems compared ~~to~~with the open habitats (~~such as~~e.g. inland dunes~~),~~) where besides *Klebsormidium* other filamentous algae ~~were~~are dominant (Langhans et al., 2009; Pluis, 1994). Also, the forest soil ~~pH~~ 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 ~~samples~~ 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 ~~on a species-like level~~ (Rindi et al., 2011). Studies comparing these *Klebsormidium* clades ~~at~~from different localities ~~on the one hand~~ observed ~~a~~ global ubiquity on one hand, and local endemism on the other~~ hand~~ (Ryšánek et al., 2014). ~~Especially the clade~~Clade composition seems to differ depending on the habitat~~. In detail,~~: *Klebsormidium* cf. *flaccidum* (B/C clade) was abundant in both closed ~~as well as in~~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 ~~this~~our study, however, BSCs from forests contained more often *Klebsormidium* cf. *subtile* and *K.* cf. *nitens* than *K.* cf. *flaccidum*. ~~Nevertheless, in~~In desiccation experiments the recovery rates of these clades were similar (Donner et al., 2017a, 2017b). It is still ~~an~~ open ~~question,~~ which of the environmental factors ~~caused~~cause the ~~slight~~observed habitat preferences of the different clades. Additional ecophysiological experiments ~~along with transcriptomic approaches combining~~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~~ in future~~ 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 ~~aboveground living and stand~~ density. However, ~~intensive~~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 ~~stand~~ 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 ~~huge areas in~~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 ~~corresponds~~agrees with conclusions ~~about~~of high algal richness on disturbed or cultivated soils (Hollerbakh & Shtina, 1969; Hoffmann, 1989). The SMI reflects the ~~main~~effect of management practice on the dominant tree species and the stand density~~ as a result of management practice.~~. Most ~~studies in the~~ Biodiversity Exploratories studies on forest-soil microorganisms ~~in forests~~ observed ~~rather an~~a stronger effect of the ~~main~~dominant tree species ~~on the community~~ 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 (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, tree species was designated as the main predictor for bacterial community composition. However, the ~~differences in the~~ bulk soil pH did not differ significantly between beech and pine forest ~~were not significant~~ in Schorfheide-Chorin (Table 1~~) and thus~~), 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.

However, the SMI combines other potential factors which ~~might affect BSC microalgae, namely water~~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. ~~The sampled forest~~ Forest plots in ~~the exploratory~~ Schorfheide-Chorin were dominated by either beech or pine trees, ~~both differing in their~~which affect the light regime differently: in beech forests the canopy shade changes ~~during spring and therefore~~over the year, with usually higher solar radiation on the ground ~~is usually higher~~ in winter and spring than in summer, while in pine forests no such light fluctuations occur. 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~~the one of BSCs. For future studies on microalgae in BSCs it would be important to examine also the incident light on the ground ~~and~~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 ~~be~~have been that the community in the pine forest ~~is shifted towards~~promoted algal species~~,~~ which ~~can~~could cope ~~better~~ with a suboptimal C:N:P ratio. But as mentioned above ~~also~~both, light regime and water availability, differ between ~~both~~the two forest types and could ~~thus~~also 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~~increased content of total C, N and P and in particular a higher proportion of organic P (Baumann et al., 2017). ~~Hence, it is assumed~~These results indicate that algal species are ~~functional~~functionally redundant, and ~~a~~that a BSC community with low species richness ~~in BSCs can~~ still ~~conduct the~~has a functional role ~~of enhancing~~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 ~~correlate~~a negative correlation with the richness of BSC algae. Soluble inorganic phosphate can be assimilated by organisms, and it originates either from ~~P-mineral~~the weathering of P containingminerals, desorption of mineral-bound phosphates or from the 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~~uptake rate of BSC organisms~~ and~~, thus~~,~~ a more closed P cycle due to the higher algal richness (Baumann et al., 2017).

Conclusion

BSCs are able to coexist with ~~continuos~~continuous forests, because natural and human-induced disturbances regularly provide free space ~~for crusts to develop, such as~~(e.g. tree fall~~ and~~, 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 ~~crust~~BSC-initiating filamentous algae, while ~~Cyanobacteria play~~cyanobacteria played a negligible role. Higher forest management intensity resulted in a higher richness of algae, especially ~~the~~in a hihger proportion of coccal taxa~~ increased~~. 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 ~~potential~~ relation between the biogeochemical cycles in BSCs and algal species. This relation should be studied in more detail, ~~for example,~~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 ~~crust~~BSC-associated organisms, ~~like~~such as fungi and bacteria, to identify key players ~~on~~and the ecological role of BSCs in the P cycle.

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

Special issue statement. This article is part of the special issue “Biological soil crusts and their role in biogeochemical processes and cycling”

Acknowledgements. The authors would like to thank Nadine Borchhardt for her help during BSC sampling. Water content and pH data were provided by Ingo Schöning, Theresa Klötzing and Marion Schrumpf (May Planck Institute for Biogeochemistry, Jena, Germany). Special thanks go to Elena Samolov for her contribution to English corrections.
We thank the managers of the three Exploratories, Martin Gorke and all former managers for their work in maintaining the plot and project infrastructure; Christiane Fischer for giving support through the central office, Michael Owonibi for managing the central data base, and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser and the late Elisabeth Kalkofor their role in setting up the Biodiversity Exploratories project. The work has been funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (subproject Crustfunction - KA899/28-1 and LE903/12-1). Fieldwork permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG). TM thanks the Alexander von Humboldt Foundation for financial support.

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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)

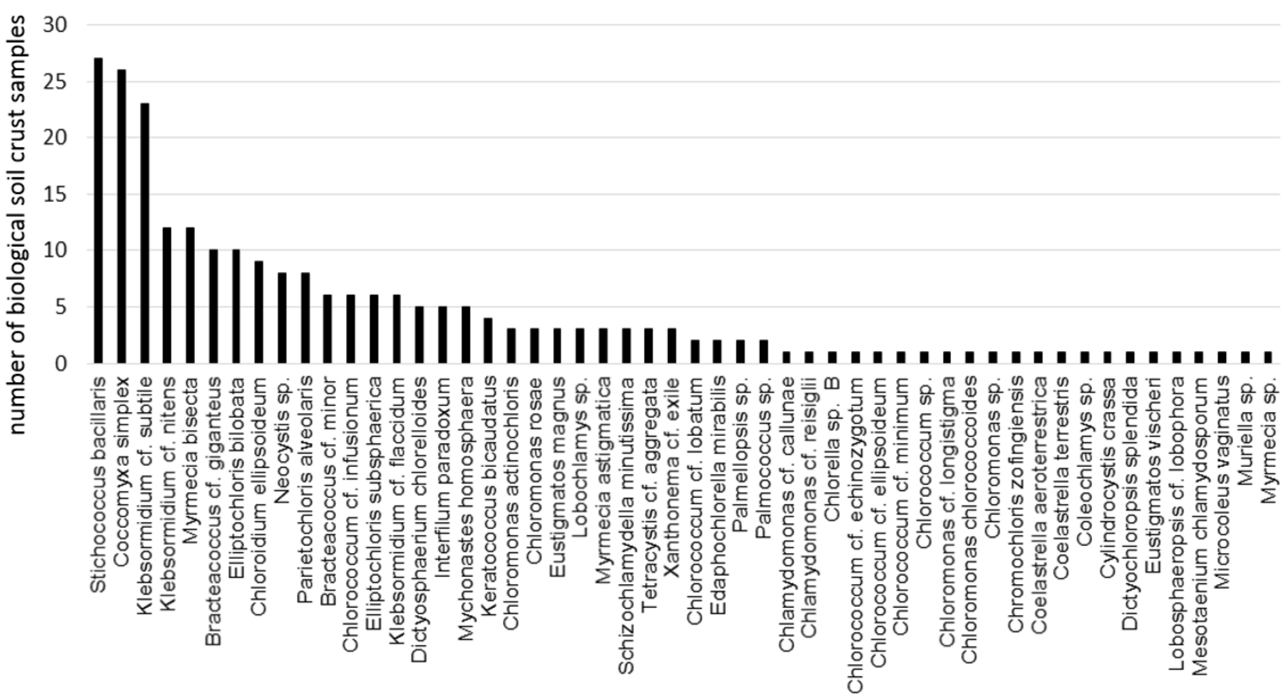

Figure 2. Occurrence of each algal species in biological soil crusts from forest sites (n=31).

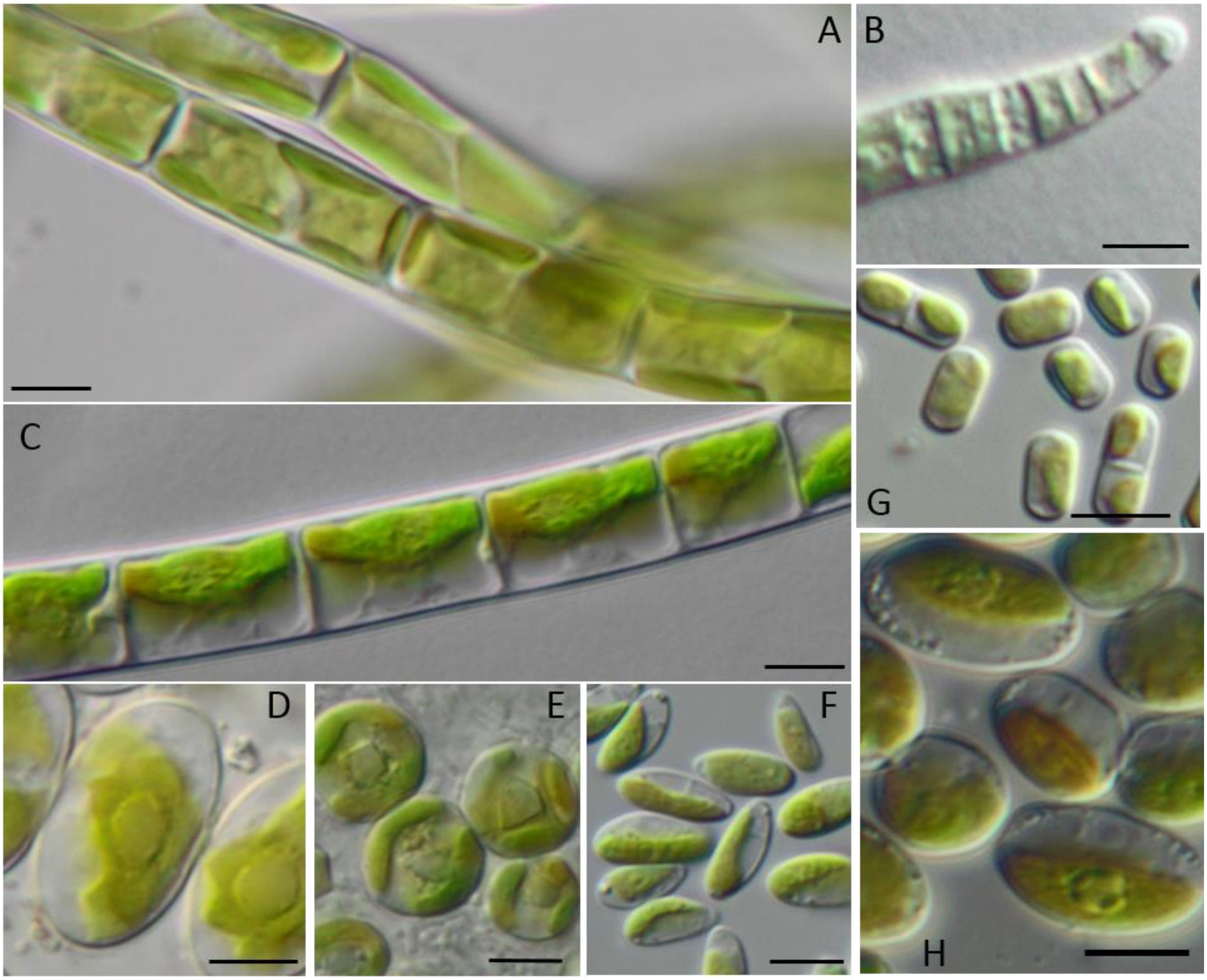

Figure 3. Filamentous and examples of coccal algae from forest BSCs: algae with strong filaments: A-*Xanthonema* cf. *exile*, B-*Microcoleus vaginatus*, C-*Klebsormidium* cf. *flaccidum;* coccal algae: D-*Chloroidium ellipsoideum*, E-*Eustigmatos magnus*, F-*Coccomyxa simplex;* algae with short or easily disintegrated filaments*:* G-*Stichococcus bacillaris*, H-*Interfilum paradoxum*; scale bar = 5µm

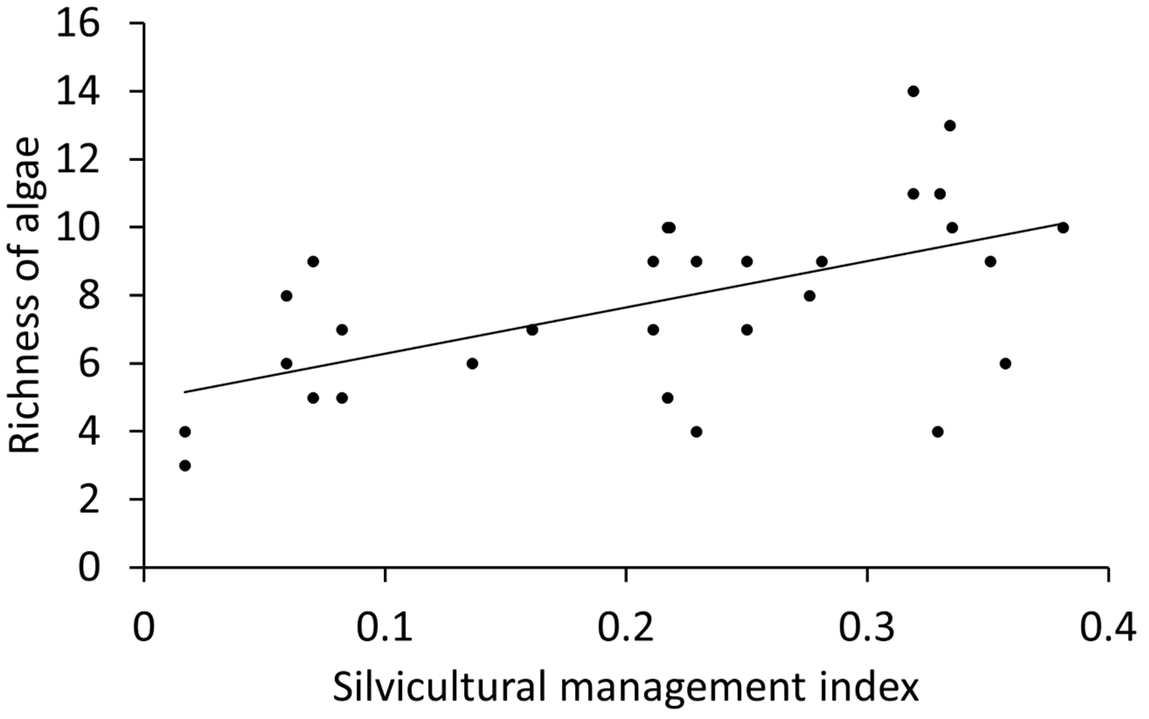

Figure 4. Plot of algae richness in BSCs from forests over the silvicultural management index (SMI), natural forest has a low SMI, managed forests a high SMI; the line indicates the best linear fit (slope: 13.6, $p<0.001$(Anova))