Interactive comment on “Algal diversity of temperate biological soil crusts depends on land use intensity and affects phosphorus biogeochemical cycling” by Karin Glaser et al.

Anonymous Referee #1

Received and published: 4 December 2017

General Comments:

The presented paper focuses on algal diversity in biological soil crusts (BSCs) forming in temperate forests. So far little is known about the BSCs in temperate forests and what organisms create them. This makes the topic of this paper very interesting. However, the paper unfortunately does not seem to merge very deep to this topic and gives rather shallow impression with multiple inaccuracies.

As a main problem I see the way how the data for algal diversity were obtained. Even though the authors are aware of the fact that the enrichment cultivation method is not suitable for all groups of algae and cyanobacteria and that it can recover only cultivable taxa, they still decided to use it as the only source for their data. It seems that at least part of the samples (if not all) were also observed directly in the microscope without cultivation. Why the morphological identification was not done also from these direct observations? The combination of culture dependent and independent methods would provide more accurate and detail information about the algae present in the crusts even without using the molecular methods. And the authors would be able to record not only the presence or absence of given taxa, but also their abundance. Most of the conclusions are thus limited only to the cultivable algae and not to the real forest’s crust diversity.

Our results based solely on the identification of cultivable algae. We also observed the algae directly in the crust. But in this case it is impossible to identify the algae correctly for the following reasons: although the crust were rewetted and incubated for a short time, not all algal species are in a reasonable morphological state because of spore formation, presence of extracellular matrix (mucilage etc.), cellular features (accumulation of storage compounds etc.) etc, all of which hamper unambiguous identification based on morphological characteristics. Normally in direct observations, only few cells of one species can be well observed; for correct morphological identification many cells of the same species in different states are necessary. For example, for identification of Chlorococcum-species it is necessary to observe also young cells. In a mixed community like in the soil crusts, it is hard to tell if one algae represents a young status of Chlorococcum, or if it belongs to some Chlamydomonas-like morphotype. This is only possible in a well prepared enrichment culture, where colonies of algae are separated on the agar.

Also most of the detailed morphological descriptions in “Syllabus der Boden-, Luft- und Flechtenalgen” are based on algal cultures. It is known that environmental factors influence the morphology. Therefore, correct identification is only possible with the same or very similar approaches like in algal handbooks; in this case, to use common alga media.

The Referee is right, with direct observation we could have also said something about the abundance and thus about biodiversity. As we can only rely on presence/absence data, we changed the wording throughout the text and rather use “richness” instead of “diversity” to avoid misleading implications. As the same misunderstanding applies for “community composition”, thus, we also changed the wording to presence or absence of individual algal (*for example, p. 4, ls. 24).* As a second parameter, we showed similarity between single plots by presence / absence of individual species, which combines the total number and the identity of the algal species.)

I would appreciate if the Introduction provided more information on the BSCs in forests. Most part of the Introduction introduces BSCs as we know them from the arid regions, including their ecological roles and what threatens them there. But the desert areas and open arid sites in temperate regions are very different from temperate forests, so I think it would be useful if the authors talked a little bit more about whether these facts are true for forests as well. How are the BSCs in forests defined and established? Is "green cover" really equal to BSC? (If "just" green cover was present on a statue or a wall, it would be probably called biofilm, rather than a crust.) Why should they be interesting? Maybe providing more information about the specific sampling sites would help to clarify it as well (did the authors have to remove the litter first to look for the green cover or was the sampling done in open sites in forest, : : :). I know the sampling itself was done as part of different study, but I think this information is worth repeating (maybe as part of Table 1), because it would be important also when looking at the algal diversity and which exact factors influence it.

We understand the doubts of the Referee, because most literature deals indeed with BSCs from arid regions. Thus, we followed the suggestion to enhance the introduction part. We included some pictures from our sampling campaign, which might help to get an impression of BSCs from temperate forest (figure 1).

p. 2, ls. 7 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, for example, from erosion and due to the biological introduction of carbon and nutrients into the soil regrowth of vascular plants is initiated (Seitz et al., 2017). Seed germination of vascular plants strongly benefits from biogeochemical activities of BSCs (Li et al., 2005; Su et al., 2009).

p. 3, ls. 29 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).

p. 10, ls. 8 BSCs are able to coexist in temperate forest ecosystems, because natural and human-induced disturbances, such as wind fall and skid trails, regularly provide free space for crusts to develop.

I am a little confused about the terms silvicultural management intensity, managed forest, and so on. Could the authors please specify more what it means in practice with regard to the BSCs? Do I understand it right that in more managed forests the soil is more often disturbed by heavy machines, traffic, etc? Maybe the authors could provide more detail on how the protected forest differed from the managed forest specifically with regard to the crusts (overall soil cover,

amount of dead biomass on the ground, density of the tree stand,: : :). Also it is not clear which samples were collected from the protected and which from the managed forest. The only indication the readers get is that the SMI is lower for natural forests and higher for pines. But the authors do not specify anywhere above/below what number the SMI needs to be so the forest can be considered protected/managed. Thus, in Table 1 it is not possible to find out which and how many samples were taken from which protected vs. managed type of forest (and I was not able to find it anywhere else in the text as well).

We understand that with more details on the silvicultural management intensity and a careful wording we can avoid confusion about it. We added the requested information if the sampling sites were located in a natural or managed forest in table 1 as well as in the text.

p. 4, ls. 29 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 disturbed due to e.g. usage of skid trails and removal of dead trees as well as tree cut. […] The 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.

p. 8, ls. 28 The richness of algal species as well as the proportion of coccal algae were positively correlated with the silvicultural management index (SMI), which means that we discovered more alga species in BSCs from managed than from natural forest ecosystems.

Even though the title promises information about the phosphorus biogeochemical cycling, the readers do not learn much new information and the data connected with P do not seem to be significant. The previous paper of the authors (Baumann et al., 2017) often referenced in the text seem to provide much detail information.

We understand the arguments of the Referee, which is in accordance with the second Referee. Of course, we don't want to make false promises. Thus, we changed the title to "Algal richness of temperate biological soil crusts depends on management intensity and correlates with inorganic phosphorus".

Specific Comments and Technical Corrections:
I would not mix algae and cyanobacteria under the name algae. Instead of ": : :52 different algae species: : :" I would consider "51 algae and a cyanobacterium" to be more precise as the prokaryotic and eukaryotic organisms are not included together.
Good point which we addressed.

The abbreviations "cf." are in italics in many places in the text, please check.
Thanks for the comment, it was corrected.

Methods: Study site: How many of the pinus and fagus samples originated from protected vs. managed forests?
This information is included now in the text as well as in table 1.

page 2, line 3: e.g., Belnap: : : ! e.g. Belnap (no comma)
p. 2, l. 31: mucilage SHEDS - mucilage SHEATHS maybe?
p. 3, l. 20: What does DFG stand for?
p. 3, l. 27: : : :the upper two millimeters of the crust WERE: : :
p. 4, l. 18: Community composition based only on algae recovered by cultivation on

agar plates does not reflect the real situation.

We corrected the wording to presence or absence of indivdiual species.

p. 5, l. 3: algaL richness

p. 5, l. 19: 26 out or 23 samples: : : confusing statement
p. 6, l. 2: , which IS based on: : :
p. 6, ls. 29-31: To overcome these limitations, researchers proposed to combine (!) molecular and morphological methods, SINCE molecular techniques ALONE sometimes ALSO fail to detect some algae.
p. 7, ls. 7-8: Absence or presence: : : The whole sentence in unclear, please check.
p. 7, l. 17: which HAS filamentous nature and WERE determined: : : unify
p. 8, l. 1: Figure 2 does not show anything about Klebsormidium morphospecies.
p. 10, l. 8: bulk soil (Baumann et al., 2017) - space missing
Table 2 : Pearson CORRELATION...
All very specific comments were followed as suggested.

Interactive comment on “Algal diversity of temperate biological soil crusts depends on land use intensity and affects phosphorus biogeochemical cycling” by Karin Glaser et al.

Anonymous Referee #2

Received and published: 14 December 2017

The goal of the presented study was to describe and characterize a biological soil crust that occurs in a temperate forest in Germany (p3. L 3). This was done by assessing the species composition and evaluating the effects of the crust on the soil chemistry (C;N;P). In a second step effects of land use on the number of algal species of this crust was examined. The study is well written and might represent a new and interesting contribution. Nevertheless, there are some major drawbacks, which should be considered before publication.

1.) Definition of BSC in forests

This is a critical topic in this manuscript because the authors do not provide enough explanations here. In the classic BSC literature, a BSC is found in “ regions where water availability limits vascular plant cover” (Belnap, Weber, Büdel 2016) or “in arid and semiarid lands throughout the world, where the cover of vegetation is sparse or absent” (Belnap and Lange 2003). Both definitions are taken from the exactly cited works as given in the introduction. In the present study, the authors examine a crust from a temperate forest which contradicts this definition. A temperate forest is a habitat with a dense vegetation cover and a biome characterized by a mean precipitation between 750 and 1500 mm. This sets the presented study into a critical position for two reasons. First, because the authors do not indicate this strong discrepancy between the classical BSC definition and their own approach and explain why they still aim to refer to a BSC in this context. Secondly, because there is a vast number of publications handling effects of land use on forest understory vegetation as well as microflora and –fauna that is not considered in the discussion. It is a recent trend in BSC literature that more and more BSC are found and described in humid and forest ecosystems and I would, therefore, like to encourage to authors to critically discuss this point here, especially because this publication is part of a special issue about BSC. This study provides a chance to introduce BSC in this ecosystem if the authors try to catch up on this point and explain carefully. Statements, like given in P2l7 or P2l17 about the lack of information regarding temperate forest BSC, might just be a result from a limited literature search that focused only on BSC and not on studies regarding understory community assemblies in temperate forests. Nevertheless, as it stands now I cannot see the difference between the studies on understory forest vegetation and the presented study. In this context, the study would clearly benefit from pictures showing this crust type and how it is assembled.

We enlarged the introduction section for a clearer explanation of biological soil crusts in temperate forests and the differences to crusts from arid regions, where BSCs are the dominating life form. We included some pictures from our sampling campaign, which might help to get an impression of BSCs from temperate forest (figure 1).

p. 2, ls. 7 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, for example, from erosion and due to the biological introduction of carbon and nutrients into the soil regrowth of vascular plants is initiated (Seitz et al., 2017). Seed germination of vascular plants strongly benefits from biogeochemical activities of BSCs (Li et al., 2005; Su et al., 2009).

p. 3, ls. 29 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).

p. 10, ls. 8 BSCs are able to coexist in temperate forest ecosystems, because natural and human-induced disturbances, such as wind fall and skid trails, regularly provide free space for crusts to develop.

2.) Diversity

According to the title, algal diversity was evaluated in this study but I wonder why this terminology was used here. Species diversity consists of three components: species richness, taxonomic or phylogenetic diversity and species evenness. With these parameters, diversity or diversity indices can be calculated. In the given study the authors provide species richness and frequency data and I think it would be more precise to refer to these (or species composition) throughout the text, rather than to diversity or even biodiversity, which wasn0t studied here. The terminology should be consistent throughout the text. (examples of the used terminology in the manuscript: diversity, biodiversity, alga richness, algal richness, community composition of alga, richness of alga, algal species richness, algal biodiversity, biodiversity of microalgae and cyanobacteria)

The Referee is right, we estimated only the richness of cultivable algae. The drawbacks of our method is described well in the MS (p. 6. ls. 25). As we can only rely on presence/absence data, we changed the wording throughout the text and rather use "richness" instead of "diversity" to avoid misleading implications. As the same misunderstanding applies for "community composition", thus, we also changed the wording to presence or absence of individual algal (*for example, p. 4, ls. 14).* As a second parameter, we showed similarity between single plots by presence / absence of individual species, which combines the total number and the identity of the algal species.)

3.) Phosphrous biogeochemical cycling

The title promises information about phosphorus biogeochemical cycling and in the introduction, the authors state that "the effect of BSC algal biodiversity on C, N, and P content, in particular on the different fractions of P was assessed". Nonetheless, different P proportions are not shown but taken from a previous study from the authors, that is cited very often throughout the article. The only data given here are C, N, and P contents for n=19 samples which seems to be a little database for the conclusions drawn. I also wonder about the statistical test that was chosen to interpret the results, because correlation does not imply causation and the authors should be careful with interpreting their results in such a broad way.

*We understand the arguments of the Referee, which is in accordance with the first Referee. Of course, we don't want to make false promises. Thus, we changed the title to "*Algal richness of temperate biological soil crusts depends on management intensity and correlates with inorganic phosphorus*".*

p. 10, ls. 14 Increasing algal richness in BSCs was supposed to enhance biogeochemical cycling of nutrients, as documented for P compared to bare soils, 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.

4.) Land use intensity

Land use intensity was approximated by applying the silvicultural management index. This was determined for each study site. In table 3 it is given that SMI affects algal richness with 30,5% and the proportion of filamentous algae with 37.7%. It is stated in p 6 L 13 that higher SMI resulted in higher species richness given in Figure 2. Figure 2 represents a pie chart with mean phylum numbers of all plots. So I assume Figure 4 should show this. This graph is difficult to understand. The caption needs to be improved and explain what the symbols show. I assume these are the different forest stands and the correlation was pooled stand independently? (So why include this information?). What was the correlation index? Where is the information about coccal algae that is given in the text? What does "richness of algae" mean? From the discussion it becomes clear that SMI basically effects the BSC composition via tree density, thus shading and light availability. Therefore, it is critical to refer to land use in this context. The authors need to define how they expect SMI to affect the BSC directly or explain the SMI was used as a proxy for tree stand density.

We understand that with more details on the silvicultural management intensity and a careful wording we can avoid confusion about it.

p. 4, ls. 29 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 disturbed due to e.g. usage of skid trails and removal of dead trees as well as tree cut. […] The 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.

p. 8, ls. 28 The richness of algal species as well as the proportion of coccal algae were positively correlated with the silvicultural management index (SMI), which means that we discovered more alga species in BSCs from managed than from natural forest ecosystems.

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))

Additional comments: - P1l10: What do you mean with disturbed areas -
p1., ls.11 disturbed areas worldwide, where higher vegetation is sparse,

P1l20: This study only examined samples from one specific area, though it's tough to generalise this finding to all temperate forests –
misleading statement deleted

P1l24: Please explain what mechanisms you expect to drive this relationship. Why would a higher algal species richness lead to a more closed P cycle? –
statement deleted

P2l2: Please give exact citations on the distributions/occurrences of BSC in temperate habitats –
p. 2, ls. 5 In temperate regions these habitats include dunes with sparse higher vegetation or disturbed areas in open sites (e.g. former mining sites) (Fischer et al., 2010b; Langhans et al., 2009; Lukešová, 2001; Schulz et al., 2016).

P2l11: richness of BSC organisms? –

p. 2, l. 30 the number of microalgae species in BSCs
P2l22: Elbert et al. 2012 does not distinguish between different crust components and instead pools information from all photoautotrophs in cryptogamic covers. Please find an adequate citation for your statement. –
p. 2, l. 31 (Belnap et al., 2001)
P2l24: please provide a precise citation for this statement.
changed to Büdel et al., 2016
- P3l6: this information is irrelevant here -
deleted
P3l13: which plots were these? – P3l16: what is a microecosystem? –
last sentence was deleted
P4l2-8: I wonder whether this cultivation technique does not influence the species assembly because some species might be excluded and others overestimated. –
p. 6, ls. 29 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 typically covers mainly 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).

P4l16-18: how were the frequency data gained? How were the 'proportion' data generated? –
p. 4, ls. 25 Further, the identified algae were categorized in filamentous or coccal life form, because both differ in their ecological function. Filamentous algae, in contrast to coccal algae, have the potential to initiate crust-formation and stabilize soil particles by gluing them together.

P4l25: is richness here the total species number? - P5l3: alga richness? Did you exclude the Cyanobacteria? –
p. 4, ls. 22 richness of algae (total number of algae and cyanobacteria species per sample)
P4l7: specify community composition of algae –
p.4, ls. 23 As a second parameter for biodiversity the similarity between single plots is shown as reflected in the presence / absence of individual species which combines the total number and the identity of all algal taxa observed.
P10l4: This statement about the moss protonema is surprising because this was not studied here and just occurred as a side note in the discussion. Why is this included in the conclusion? –
as suggested, deleted from the conclusion
P10l8: A citation of a different study in the conclusion seems misplaced. Consider summarising the data presented here.
We rewrote this paragraph accordingly.

Table 1: this can be provided in the supplement.

We decided to keep table 1 in the main text but added two information: managed or unmanaged site; proportion of inorganic P

Algal richness of temperate biological soil crusts in forests depends on management intensity and correlates with inorganic phosphorus

~~Algal diversity of temperate biological soil crusts depends on land use intensity and affects phosphorus biogeochemical cycling~~

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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. In temperate regions, BSCs are also common, but generally less studied, and they conduct important ecological functions, ~~like~~ such as stabilization of soil and enrichment of nutrients. Changes in land use and its intensity strongly influence biodiversity per se and it~~’~~s role for ecosystem processes, particularly in regions which are densely populated like Europe. But 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, ~~Cyanobacteria and~~ eukaryotic microalgae and cyanobacteria as key primary producers of these communities were identified from pine and beech forests under different management regimes. ~~Algae~~ Phototrophic microorganisms were identified morphologically based on enrichment cultivation and categorized ~~in~~ as either coccal taxa, which occur typically in high diversity, or filamentous taxa, which have the potential to initiate BSC formation. In total, 51~~2~~ algal species were recorded, most from the phylum Chlorophyta, followed by Streptophyta and Stramenopiles, and only 1~~;~~ ~~C~~cyanobacterial taxon could be observed. ~~were much less abundant in temperate forest BSCs~~. The most abundant crust-initiating filamentous algae were three species of *Klebsormidium* (Streptophyta), a ubiquitous genus often associated with BSCs worldwide ~~and~~ ~~with~~because of ~~a their~~their generally broad ecophysiological tolerances such as ~~a high tolerance~~ to low pH. Increasing management intensity in the forests resulted in ~~a~~ higher ~~richness~~ numbers of alga~~e~~l species, especially the ~~proportion~~ number of coccal ~~algae~~ taxa rose. Furthermore, the proportion of inorganic phosphorus ~~was~~ showed tendencies towards a positive~~ly~~ correlat~~ed~~ion with the number of algal ~~richness~~species~~, indicating that higher diversity of algae results in a more closed P cycle~~. Thus, management of forests has an impact on the diversity of phototrophic organisms in BSCs, which ~~in~~ might ~~turn~~ affect~~s~~ biogeochemical P cycling in the BSC.

~~key~~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 ~~or~~ but also in polar regions (Borchhardt et al., 2017; Flechtner et al., 1998; Kidron et al., 2010). In temperate regions these habitats include dunes with sparse higher vegetation or disturbed areas in open sites (~~like~~ e.g. former mining sites) (Fischer et al., 2010b; Langhans et al., 2009; Lukešová, 2001; Schulz et al., 2016).

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 ~~the~~ BSCs have to compete with vascular plants and thus their development is often limited. Especially in forests the limitation ~~for~~of light and the occurrence of litter restricts the crust development. But disturbances of the higher vegetation layer change this competitive situation and allow~~s~~ the development of ~~biological soil crusts~~BSCs. Such disturbances occur frequently in temperate forests, for ~~exampl~~example,e natural tree fall, pits of wild boars, litter free spots at slopes, ~~or~~ molehill-like humps, or ~~are~~ human-induced disturbances such as~~like~~ 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 ~~these~~such ~~-~~spots, ~~biological soil crust~~BSCs ~~can develop and~~typically serve as pioneer vegetation ~~a starting point of~~for colonialization of naked soils after heavy disturbance and destruction of intact forest ecosystems. Thus, ~~soil crusts~~BSCs can protect disturbed areas, for example, from ~~e.g.~~ erosion and due to the biological introduction of carbon and nutrients into the soil ~~until the successful~~ regrowth of vascular plants is initiated (Seitz et al., 2017)~~ and even enhance the process of regrowth~~. ~~It has been shown that sperm~~Seed germination of vascular plants strongly benefits from ~~biological soil crusts~~biogeochemical activities of BSCs (Li et al., 2005; Su et al., 2009).

~~Although BSCs received raising interest in the past years, reports on BSCs from temperate forests are still missing up to now.~~Disturbance of BSCs due to land use has been reported to have strong negative effects on BSC~~s~~ cover, which resulted in higher soil erosion and C and N losses from ~~in~~ 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 on BSCs, ~~like~~such as, for example, fertilization of grass or arable land and silvicultural management.

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~~amount~~ of microalgale species in BSCs is related to soil P content (Baumann et al., 2017; Schulz et al., 2016). ~~Also, soil texture and carbon content seem to affect the BSC community .~~ But still, only little is known about environmental factors that shape BSC communities and how BSCs in turn affect soil characteristics.

~~Disturbance of BSCs due to land use has been reported to have strong negative effect on BSCs cover, which resulted in higher soil erosion and C and N loss in the top soil (Barger et al., 2006; Belnap, 2003). Studies on the effect of land use on BSCs were up to now exclusively conducted in arid regions. These studies reported, for example, a strong negative influence of intensive livestock grazing due to trampling on BSC cover 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 on BSCs, like, for example, fertilization of grassland or arable land and silvicultural management.~~

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 ~~BSCs~~ such communities because of their major contribution to C fixation (Büdel et al., 2016). BSC algae can be categorized ~~in~~ as two functional groups. ~~First,~~(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. ~~And second,~~(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 shea~~d~~ths 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 in temperate forests of different silvicultural management intensities. In a previous study we presented hints that differences of algal richness in

BSCs contributing to P cycling ~~were~~are detectable~~ed~~, and that the data indicated ~~that~~ BSCs as~~re~~ particularly involved in the transformation of inorganic P to organic P compounds, ~~and~~ thus playing a key role in the biologically driven P cycling in temperate soils~~provided a very detailed picture on the distribution of P content, P pools and P species in temperate BSCs and adhering soil~~ (Baumann et al., 2017).~~ Differences of algal richness in BSCs contributing to P cycling were detected, and the data indicated that BSCs are particularly involved in the transformation of inorganic P to organic P compounds and thus play 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 ~~the biodiversity~~ species occurrence~~s~~ 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 ~~biodiversity~~ richness ~~and species identification~~ in BSCs collected at the same plots as in Baumann et al. (2017), plus some additional sampling sites. The correlation of BSC algal ~~biodiversity~~ richness and C, N and P content, in particular on the different fractions of P, was assessed in order to uncover (disentangle?) the relation between biogeochemical cycles in ~~biological soil crusts~~BSCs and the ~~BSC-associated~~underlying alga species.

Material and Methods

Study site

BSC samples were collected in June 2014 and 2015 from plots of the~~as part of the DFG~~ German ~~-priority program 1374~~ 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 ~~f~~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 ~~was~~ were separated from the adhering soil underneath using a razor blade and stored dry in paper bags ~~prior~~ before cultivation. In total, 31 BSCs were collected from 13 pine and 18 beech stands, of which ~~from~~ 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 ~~with a maximum~~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~~e~~ 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. ~~Algae~~ Phototrophic microorganisms were identified ~~that belong to~~as Cyanobacteria, Chlorophyta, Streptophyta and some Stramenopiles (Eustigmatophyceae). Diatoms were regularly ~~observed~~ found in direct observations, but excluded from the analyses as the mentioned enrichment cultivation is not suitable for ~~estimation identification of diatom diversitys~~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~~species~~, ~~The~~ richness of algae ~~,~~ ~~i.e. the~~(total number of algae species and cyanobacteria per~~in each a~~ sample)~~,~~ was used as measure~~ment~~ for diversity ~~rather than diversity indices like evenness, because enrichment cultivation does not allow a clear conclusion about the abundance of each species~~. As a second parameter for biodiversity~~, we included showed~~ the similarity between ~~the~~ single plots is shown ~~in terms of~~~~by~~as reflected in the presence ~~or~~/ absence of individual species which combines ~~in order to include not only~~ the total number ~~but also~~and the identity of all~~the~~ algal taxa observed.~~observed species.~~ ~~Additionally, the community composition of the algae as reflected by the presence or absence of individual species was used as a second parameter for diversity estimation.Further~~. Further, ~~we categorized~~ the identified algae were categorized in filamentous or coccal life form, because both differ in their ecological function. Filamentous algae, in contrast to coccal algae, have the potential to initiate crust-formation and stabilize ~~the~~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 ~~-clear-cut after some years. During the growth phase regular human-induced disturbances occurred~~regularly disturbed due to, for example, ~~e.g.~~ 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). ~~The~~ N~~n~~atural forest has a lower SMI than the ~~used~~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).

To assess interactions between BSC biodiversity ~~parameters~~indicators and environmental parameters, the richness, presence or absence of individual algal ~~community composition of algae and~~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 stab~~i~~le P. ~~Latter ~~Data on latter are not shown here 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 ~~algae~~species; their best predictors 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 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~~community composition of algae~~, ~~we applied ~~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~~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 5~~2~~1 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 o~~r~~f 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~~ total species~~ richness of algae, i.e. the total species number, at each plot ranged from three to 14 species, with the 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~~e~~ 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~~e~~ species were differentiated according to their organization form (Figure 3). ~~We found ~~F~~f~~ive 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*, ~~*Stichoccous*~~*Stichococcus* *bacillaris*). In each BSC at least two different filamentous ~~species ~~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 ~~diversity~~ 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 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 ~~phosphorus~~ 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 and thus had no measurable effect on the algal species richness or proportion of filamentous algae. A higher SMI resulted in a higher species richness (Figure 2), especially the proportion of coccal algae was enhanced.

The presence or absence of individual algal species in BSCs ~~community composition of the algae significatly~~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).

Discussion

Species composition and abundance

In total 51~~2~~ 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 ~~biodiversity~~ richness because our results are based on enrichment cultivation followed by morphological assignment. Enrichment cultivation typically covers ~~only~~ mainly cultivable algae, which represent only a small part of all ~~algae~~ phototrophic microorganisms in ~~the~~ 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 ~~microalge~~microalgae in a polar BSC (Rippin et al., 2018). Furthermore, it is not always possible to distinguish dormant from currently active microalgae. ~~Nevertheless~~However, direct observation of a BSC sample under the microscope ~~gave~~ 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 ~~alive~~ vital in the BSC samples. The morphological identification of algae has known challenges, for example,~~:~~ ~~e.g.~~ 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, ~~but also~~since molecular techniques alone sometimes also fail to detect some ~~algae~~ 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 algae belong to Chlorophyta; a high richness of this soil algae (genera Chlamydomonas, Chloromonas, Chlorococcum, Tetracystis) is characteristic for humid habitats and typical for forest soils~~ Especially most of the unicellular ~~algae~~taxa belong to the Chlorophyta, and hence~~;~~ a high richness ~~of this soil algae~~ (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). ~~Absence or presence in small amount in forest soil is concerning with low pH of soil extract which unfavorable for cyanobacteria (Hollerbakh & Shtina, 1969; Hoffmann, 1989).~~ It seems that Cyanobacteria play only a minor role in forest ecosystems with consequences for the ecological traits that some ~~Cyanobacteria species~~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 ~~BSCs~~ such communities because of their potential as BSC-initiating organisms by building tight networks among soil particles (Büdel et al., 2016). In s~~S~~ome investigated forest BSCs ~~were formed as well by~~also moss protonema can exert a similar function, ~~which has~~due to their filamentous nature and ~~were~~ hence w~~as~~ere 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 ~~and freshwater~~ 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 ~~reaction~~ 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.

~~We identified~~ T~~t~~hree morpho-species of the genus *Klebsormidium* were identified in the~~our~~ samples investigated (Figure~~ 2~~2). All three morpho-species were reported from other aeroterrestrial habitats in Central Europe (Glaser et al., 2017; Mikhailyuk et al., 2015). *Klebsormidium* ~~has~~ exhibits morphological features which can be easily recognized, but 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, ~~we also observed in~~ 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~~and~~ soil parameters such as pH, might in future explain these~~is~~ conspicuous habitat preferences of *Klebsormidium* clades.

Correlation with SMI

The richness of algal species as well as the proportion of coccal algae ~~were~~was positively correlated with the silvicultural management index (SMI), which means that ~~we discovered~~ more algal species were discovered in ~~biological soil crusts~~BSCs from managed than from natural forest ecosystems. ~~t~~Th~~at~~is finding corresponds~~ed~~ with conclusions about high algal ~~biodiversity~~ 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); ~~just~~ only one study on litter decaying fungi and bacteria ~~observed~~ 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 ~~the community of~~ soil bacteria by shifting the pH in soil, and hence ~~; the pH was described in this the mentioned study~~ 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 ~~soil pH~~this abiotic parameter. We therefore 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 ~~may~~ might affect BSC microalgae, namely water ~~regime~~ 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 ~~can be~~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 ~~pore water~~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, ~~we expect that~~ the SMI was expected to affect~~ed~~ the ~~algae~~ algal ~~diversity~~ 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~~is~~ 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 ~~algal biodiversity~~microalgae in BSCs it would be important to examine also ~~available~~ the incident light on the ground and the BSC water content ~~in the BSC~~.

Although the SMI positively affected the algal richness, the presence or absence of individual algal ~~the community composition was~~~~species~~taxa was correlated with the main tree species but not with the SMI. 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 ~~low nutrient availability~~~~the~~ a suboptimal C:N:P ratio. But as mentioned above also ~~other, above mentioned factors (~~light regime and water ~~evaporation)~~availability differ between both forest types and could thus have contributed to~~cause~~ the observed differences in ~~the~~ the occurrence of algal ~~community composition~~species~~intentification~~.

Correlation with C,~~/~~ N, and ~~/~~P

BSCs have different important ecological functions, such as, for example, ~~BSCs~~ the enhancement of the nutrient content in the top soil layer (Baumann et al., 2017; Evans and Johansen, 1999). To assess the relationship between ~~biodiversity~~ 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 ~~diversity~~richness. ~~Baumann et al. (2017) reported that the presence of BSCs leads to the enhanced content of total C, N and P and in particular the proportion of organic P. The present study shows that thereby~~~~We did not observe~~Although a correlation between the richness of algae ~~was independent~~

~~of~~and the total C, N and P content was not observed, ~~although~~ the presence of BSCs clearly le~~a~~d~~s~~ to ~~the~~an enhanced content of total C, N and P and in particular ~~the~~a higher proportion of organic P (Baumann et al., 2017). Hence~~Thus~~, ~~we~~ 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~~ in BSCs~~. 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~~s~~ a tendency to ~~a correlation~~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~~e~~ richness (Baumann et al., 2017).

Conclusion

~~We observed that biological soil crusts~~BSCs are able to coexist in temperate forest ecosystems, because natural and human-induced disturbances, ~~like~~such as wind fall and skid trails, ~~leave~~regularly provide free space for crusts to develop. ~~This studies reports f~~For the first time ~~we report on the~~ algal~~e~~ ~~biodiversity~~ richness in BSCs from temperate forests are described~~with~~ under different management intensity. The rather acidic forest soil supports a clear dominance of streptophycean *Klebsormidium*-morphotypes as the main crust-initiating filamentous algae, while Cyanobacteria always play a negligible role. ~~in~~ ~~at temperate forests~~our study site. ~~Moss protonema is registered as crust-forming agent in forest ecosystems as well.~~ Higher forest management intensity resulted in a higher richness of algae, especially the proportion of coccal taxa increased. ~~We~~ It is ~~expect~~ reasonable to assume that the ~~land-use~~silvicultural management intensity in forests affect the algal~~e~~ ~~biodiversity~~ richness ~~via~~ due to, for example, higher stand density in managed forests, which changes ~~in~~ the light and water ~~regime~~. ~~(less light in high stand density and in pine forests),~~ and thus,also the ~~which is positively coupled with water evaporation.~~ ~~Increasing~~regime. Increasing algal richness in BSCs was supposed to enhance biogeochemical cycling of nutrients, as documented for P compared to bare soils, but this hypothesis could not be proven.

~~We expected a correlation between the total content of carbon, nitrogen and phosphorusphosphorus, N, and P with the number of algal species or their identity, respectively, because it was~~

~~As described before, that BSCs enhance the content of C, N and Pnutrients compared to bulk soil(Baumann et al., 2017). In contrast , we observed no correlation between the total content of C, N and P and the species richness of algae and Cyanobacteria~~. Nevertheless, the fraction of inorganic ~~phosphorus~~P showed tendencies towards a correlation with ~~the~~ BSC algae~~ in biological soil crustsBSCs~~, especially with ~~the content of~~ filamentous species. ~~Our~~ Consequently, the present study gives the first hint of a potential relation between the biogeochemical cycles in BSCs and algal species. ~~In our opinion, it is worth to study t~~This relation ~~should be~~should be studied in more detail, for example, by ~~e.g.~~ gene expression analyses to understand if and how algae in BSCs influence the cycling of ~~phosphorus~~P. Also, ~~In this study, we observed a relation between~~

~~the proportion of inorganic P with the biodiversity of algae, especially a positive correlation with the proportion of filamentous algae. Thus, the BSC does not only enhance the total amount of P but its algal biodiversity affects the proportion of the inorganic P. F~~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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References

Anderson, M. J.: A new method for non-parametric multivariate analysis of variance, Austral Ecol., 26(1), 32–46, doi:10.1111/j.1442-9993.2001.01070.pp.x, 2001.

Barberousse, H., Tell, G., Yéprémian, C. and Couté, A.: Diversity of algae and cyanobacteria growing on building facades in France, Algol. Stud., 120(1), 81–105, 2006.

Barger, N. N., Herrick, J. E., Van Zee, J. and Belnap, J.: Impacts of Biological Soil Crust Disturbance and Composition on C and N Loss from Water Erosion, Biogeochemistry, 77(2), 247–263, doi:10.1007/s10533-005-1424-7, 2006.

Baumann, K., Glaser, K., Mutz, J.-E., Karsten, U., MacLennan, A., Hu, Y., Michalik, D., Kruse, J., Eckhardt, K.-U., Schall, P. and Leinweber, P.: Biological soil crusts of temperate forests: Their role in P cycling, Soil Biol. Biochem., 109, 156–166, doi:10.1016/j.soilbio.2017.02.011, 2017.

Belnap, J.: The world at your feet: desert biological soil crusts, Front. Ecol. Environ., 1(4), 181–189, 2003.

Belnap, J., Büdel, B. and Lange, O. L.: Biological soil crusts: characteristics and distribution, in Biological soil crusts: structure, function, and management, vol. 1, edited by J. Belnap and O. L. Lange, pp. 3–30, Springer-Verlag, Berlin, Heidelberg., 2001.

Borchhardt, N., Schiefelbein, U., Abarca, N., Boy, J., Mikhailyuk, T., Sipman, H. J. M. and Karsten, U.: Diversity of algae and lichens in biological soil crusts of Ardley and King George islands, Antarctica, Antarct. Sci., 1–9, doi:10.1017/S0954102016000638, 2017.

Bray, J. R. and Curtis, J. T.: An ordination of the upland forest communities of southern Wisconsin, Ecol. Monogr., 27(4), 325–349, doi:10.2307/1942268, 1957.

Büdel, B., Darienko, T., Deutschewitz, K., Dojani, S., Friedl, T., Mohr, K. I., Salisch, M., Reisser, W. and Weber, B.: Southern african biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency, Microb. Ecol., 57(2), 229–247, doi:10.1007/s00248-008-9449-9, 2009.

Büdel, B., Dulić, T., Darienko, T., Rybalka, N. and Friedl, T.: Cyanobacteria and Algae of Biological Soil Crusts, in Biological Soil Crusts: An Organizing Principle in Drylands, edited by B. Weber, B. Büdel, and J. Belnap, pp. 55–80, Springer International Publishing, Cham., 2016.

Castillo-Monroy, A., Maestre, F., Delgado-Baquerizo, M. and Gallardo, A.: Biological soil crusts modulate nitrogen availability in semi-arid ecosystems: insights from a Mediterranean grassland, Plant Soil, 333(1–2), 21–34, doi:10.1007/s11104-009-0276-7, 2010.

Cleveland, C. C. and Liptzin, D.: C:N:P stoichiometry in soil: is there a “Redfield ratio” for the microbial biomass?, Biogeochemistry, 85(3), 235–252, doi:10.1007/s10533-007-9132-0, 2007.

Concostrina-Zubiri, L., Huber-Sannwald, E., Martínez, I., Flores, J. L., Reyes-Agüero, J. A., Escudero, A. and Belnap, J.: Biological soil crusts across disturbance–recovery scenarios: effect of grazing regime on community dynamics, Ecol. Appl., 24(7), 1863–1877, 2014.

Darienko, T., Gustavs, L., Mudimu, O., Menendez, C. R., Schumann, R., Karsten, U., Friedl, T. and Pröschold, T.: *Chloroidium* , a common terrestrial coccoid green alga previously assigned to *Chlorella* (Trebouxiophyceae, Chlorophyta), Eur. J. Phycol., 45(1), 79–95, doi:10.1080/09670260903362820, 2010.

Daryanto, S., Eldridge, D. J. and Wang, L.: Ploughing and grazing alter the spatial patterning of surface soils in a shrub-encroached woodland, Geoderma, 200–201, 67–76, doi:10.1016/j.geoderma.2013.02.006, 2013.

Donner, A., Glaser, K., Borchhardt, N. and Karsten, U.: Ecophysiological Response on Dehydration and Temperature in Terrestrial Klebsormidium (Streptophyta) Isolated from Biological Soil Crusts in Central European Grasslands and Forests, Microb. Ecol., 73(4), 850–864, doi:10.1007/s00248-016-0917-3, 2017a.

Donner, A., Ryšánek, D., Mikhailyuk, T. and Karsten, U.: Ecophysiological traits of various genotypes of a green key alga in biological soil crusts from the semi-arid Colorado Plateau, USA, J. Appl. Phycol., doi:10.1007/s10811-017-1158-7, 2017b.

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M. O. and Pöschl, U.: Contribution of cryptogamic covers to the global cycles of carbon and nitrogen, Nat. Geosci., 5(7), 459–462, doi:10.1038/ngeo1486, 2012.

Ettl, H. and Gärtner, G.: Syllabus der Boden-, Luft- und Flechtenalgen, Spektrum Akademischer Verlag., 1995.

Evans, R. D. and Johansen, J. R.: Microbiotic crusts and ecosystem processes, Crit. Rev. Plant Sci., 18(2), 183–225, doi:10.1080/07352689991309199, 1999.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E. K. V., Linsenmair, K. E., Schulze, E.-D. and Weisser, W. W.: Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories, Basic Appl. Ecol., 11(6), 473–485, doi:10.1016/j.baae.2010.07.009, 2010a.

Fischer, T. and Subbotina, M.: Climatic and soil texture threshold values for cryptogamic cover development: a meta analysis, Biologia (Bratisl.), 69(11), doi:10.2478/s11756-014-0464-7, 2014.

Fischer, T., Veste, M., Wiehe, W. and Lange, P.: Water repellency and pore clogging at early successional stages of microbiotic crusts on inland dunes, Brandenburg, NE Germany, CATENA, 80(1), 47–52, doi:10.1016/j.catena.2009.08.009, 2010b.

Flechtner, V. R., Johansen, J. R. and William, H. C.: Algal composition of microbiotic crusts from the central desert of Baja California, Mexico, Gt. Basin Nat., 58(4), 295–311, 1998.

Freystein, K., Salisch, M. and Reisser, W.: Algal biofilms on tree bark to monitor airborne pollutants, Biologia (Bratisl.), 63(6), doi:10.2478/s11756-008-0114-z, 2008.

Garcia-Pichel, F., Lopez-Cortes, A. and Nubel, U.: Phylogenetic and Morphological Diversity of Cyanobacteria in Soil Desert Crusts from the Colorado Plateau, Appl. Environ. Microbiol., 67(4), 1902–1910, doi:10.1128/AEM.67.4.1902-1910.2001, 2001.

Glaser, K., Donner, A., Albrecht, M., Mikhailyuk, T. and Karsten, U.: Habitat-specific composition of morphotypes with low genetic diversity in the green algal genus *Klebsormidium* (Streptophyta) isolated from biological soil crusts in Central European grasslands and forests, Eur. J. Phycol., 52(2), 188–199, doi:10.1080/09670262.2016.1235730, 2017.

Goldmann, K., Schöning, I., Buscot, F. and Wubet, T.: Forest Management Type Influences Diversity and Community Composition of Soil Fungi across Temperate Forest Ecosystems, Front. Microbiol., 6, doi:10.3389/fmicb.2015.01300, 2015.

Gómez, D. A., Aranibar, J. N., Tabeni, S., Villagra, P. E., Garibotti, I. A. and Atencio, A.: Biological soil crust recovery after long-term grazing exclusion in the Monte Desert (Argentina). Changes in coverage, spatial distribution, and soil nitrogen, Acta Oecologica, 38, 33–40, doi:10.1016/j.actao.2011.09.001, 2012.

Gomez, E. D., Garland, J. L. and Roberts, M. S.: Microbial structural diversity estimated by dilution-extinction of phenotypic traits and T-RFLP analysis along a land-use intensification gradient, Fems Microbiol. Ecol., 49(2), 253–259, 2004.

Gray, D. W., Lewis, L. A. and Cardon, Z. G.: Photosynthetic recovery following desiccation of desert green algae (Chlorophyta) and their aquatic relatives, Plant Cell Environ., 30(10), 1240–1255, doi:10.1111/j.1365-3040.2007.01704.x, 2007.

Gundlapally, S. R. and Garcia-Pichel, F.: The Community and Phylogenetic Diversity of Biological Soil Crusts in the Colorado Plateau Studied by Molecular Fingerprinting and Intensive Cultivation, Microb. Ecol., 52(2), 345–357, doi:10.1007/s00248-006-9011-6, 2006.

Gypser, S., Herppich, W. B., Fischer, T., Lange, P. and Veste, M.: Photosynthetic characteristics and their spatial variance on biological soil crusts covering initial soils of post-mining sites in Lower Lusatia, NE Germany, Flora - Morphol. Distrib. Funct. Ecol. Plants, 220, 103–116, doi:10.1016/j.flora.2016.02.012, 2016.

Hoffmann, L., Ector, L. and Kostikov, I.: Algal Flora from Limed and Unlimed Forest Soils in the Ardenne (Belgium), Syst. Geogr. Plants, 77(1), 15–90, 2007.

Kaiser, K., Wemheuer, B., Korolkow, V., Wemheuer, F., Nacke, H., Schöning, I., Schrumpf, M. and Daniel, R.: Driving forces of soil bacterial community structure, diversity, and function in temperate grasslands and forests, Sci. Rep., 6(1), doi:10.1038/srep33696, 2016.

Karsten, U., Herburger, K. and Holzinger, A.: Living in biological soil crust communities of African deserts—Physiological traits of green algal *Klebsormidium* species (Streptophyta) to cope with desiccation, light and temperature gradients, J. Plant Physiol., 194, 2–12, doi:10.1016/j.jplph.2015.09.002, 2016.

Khaybullina, L. S., Gaysina, L. A., Johansen, J. R. and Krautová, M.: Examination of the terrestrial algae of the Great Smoky Moutains National Park, USA, Fottea, 10(2), 201–215, 2010.

Kidron, G. J., Vonshak, A., Dor, I., Barinova, S. and Abeliovich, A.: Properties and spatial distribution of microbiotic crusts in the Negev Desert, Israel, CATENA, 82(2), 92–101, doi:10.1016/j.catena.2010.05.006, 2010.

Kostikov, I., Darienko, T., Lukešova, A. and Hoffmann, L.: Revision of the classification system of Radiococcaceae Fott ex Komárek (except the Subfamily Dictyochlorelloideae) (Chlorophyta)., Algol. Stud., 104(142), 23–58, 2002.

Langhans, T. M., Storm, C. and Schwabe, A.: Community Assembly of Biological Soil Crusts of Different Successional Stages in a Temperate Sand Ecosystem, as Assessed by Direct Determination and Enrichment Techniques, Microb. Ecol., 58(2), 394–407, doi:10.1007/s00248-009-9532-x, 2009.

Lewis, L. A.: Chlorophyta on land: independent lineages of green eukaryotes from arid lands, in Algae and Cyanobacteria in Extreme Environments, edited by J. Seckbach, Springer Netherlands, Dordrecht., 2007.

Li, X.-R., Jia, X.-H., Long, L.-Q. and Zerbe, S.: Effects of Biological Soil Crusts on Seed Bank, Germination and Establishment of Two Annual Plant Species in the Tengger Desert (N China), Plant Soil, 277(1–2), 375–385, doi:10.1007/s11104-005-8162-4, 2005.

Lokhorst, G. M.: Comparative Taxonomic Studies on the Genus *Klebsormidium* (Charophyceae) in Europe, Gustav Fischer, Stuttgart., 1996.

Lukešová, A.: Soil algae in brown coal and lignite post-mining areas in Central Europe (Czech Republic and Germany), Restor. Ecol., 9(4), 341–350, doi:10.1046/j.1526-100X.2001.94002.x, 2001.

Lukešová, A. and Hoffmann, L.: Soil algae from acid rain impacted forest areas of the Krušné hory Mts. 1. Algal communities, Vegetatio, 125(2), 123–136, 1996.

Mackey, K. R. M. and Paytan, A.: Phosphorus cycle, in Encyclopedia of Microbiology, vol. 3, edited by M. Schaechter, pp. 322–334., 2009.

McGroddy, M. E., Daufresne, T. and Hedin, L. O.: Scaling of C: N: P stoichiometry in forests worldwide: Implications of terrestrial redfield-type ratios, Ecology, 85(9), 2390–2401, 2004.

Mikhailyuk, T., Sluiman, H. J., Massalski, A., Mudimu, O., Demchenko, E. M., Kondratyuk, S. Y. and Friedl, T.: New streptophyte green algae from terrestrial habitats and an assessment of the genus *Interfilum* (Klebsormidiophyceae, Streptophyta), J. Phycol., 44(6), 1586–1603, doi:10.1111/j.1529-8817.2008.00606.x, 2008.

Mikhailyuk, T., Glaser, K., Holzinger, A. and Karsten, U.: Biodiversity of *Klebsormidium* (Streptophyta) from alpine biological soil crusts (Alps, Tyrol, Austria, and Italy), edited by P. Gabrielson, J. Phycol., 51(4), 750–767, doi:10.1111/jpy.12316, 2015.

Novakovskaya, I. and Patova, E.: Green algae in spruce forests in the north-east of European Russia, Biologia (Bratisl.), 63(6), doi:10.2478/s11756-008-0109-9, 2008.

Pierangelini, M., Ryšánek, D., Lang, I., Adlassnig, W. and Holzinger, A.: Terrestrial adaptation of green algae Klebsormidium and Zygnema (Charophyta) involves diversity in photosynthetic traits but not in CO2 acquisition, Planta, doi:10.1007/s00425-017-2741-5, 2017.

Pluis, J. L. A.: Algal crust formation in the inland dune area, Laarder Wasmeer, the Netherlands, Plant Ecol., 113(1), 41–51, 1994.

Potter, D., Lajeunesse, T. C., Saunders, G. W. and Anderson, R. A.: Convergent evolution masks extensive biodiversity among marine coccoid picoplankton, Biodivers. Conserv., 6(1), 99–107, 1997.

Purahong, W., Hoppe, B., Kahl, T., Schloter, M., Schulze, E.-D., Bauhus, J., Buscot, F. and Krüger, D.: Changes within a single land-use category alter microbial diversity and community structure: molecular evidence from wood-inhabiting fungi in forest ecosystems, J. Environ. Manage., 139, 109–119, 2014.

Purahong, W., Kapturska, D., Pecyna, M. J., Jariyavidyanont, K., Kaunzner, J., Juncheed, K., Uengwetwanit, T., Rudloff, R., Schulz, E., Hofrichter, M., Schloter, M., Krüger, D. and Buscot, F.: Effects of Forest Management Practices in Temperate Beech Forests on Bacterial and Fungal Communities Involved in Leaf Litter Degradation, Microb. Ecol., 69(4), 905–913, doi:10.1007/s00248-015-0585-8, 2015.

R Development Core Team: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna Austria [online] Available from: http://www.R-project.org/, 2009.

Raanan, H., Oren, N., Treves, H., Berkowicz, S. M., Hagemann, M., Pade, N., Keren, N. and Kaplan, A.: Simulated soil crust conditions in a chamber system provide new insights on cyanobacterial acclimation to desiccation: Simulation of BSC conditions and acclimation, Environ. Microbiol., 18(2), 414–426, doi:10.1111/1462-2920.12998, 2016.

Rindi, F. and Guiry, M. D.: Composition and spatial variability of terrestrial algal assemblages occurring at the bases of urban walls in Europe, Phycologia, 43(3), 225–235, 2004.

Rindi, F., Mikhailyuk, T. I., Sluiman, H. J., Friedl, T. and López-Bautista, J. M.: Phylogenetic relationships in *Interfilum* and *Klebsormidium* (Klebsormidiophyceae, Streptophyta), Mol. Phylogenet. Evol., 58(2), 218–231, doi:10.1016/j.ympev.2010.11.030, 2011.

Rindi, F., Rysanek, D. and Skaloud, P.: Problems of epitypification in morphologically simple green microalgae: a case study of two widespread species of Klebsormidium (Klebsormidiophyceae, Streptophyta), Fottea, doi:10.5507/fot.2016.017, 2017.

Ryšánek, D., Hrčková, K. and Škaloud, P.: Global ubiquity and local endemism of free-living terrestrial protists: phylogeographic assessment of the streptophyte alga *Klebsormidium*: Global biogeography of a terrestrial protist, Environ. Microbiol., 17(3), 689–698, doi:10.1111/1462-2920.12501, 2014.

Schall, P. and Ammer, C.: How to quantify forest management intensity in Central European forests, Eur. J. For. Res., 132(2), 379–396, doi:10.1007/s10342-013-0681-6, 2013.

Schulz, K., Mikhailyuk, T., Dreßler, M., Leinweber, P. and Karsten, U.: Biological Soil Crusts from coastal dunes at the Baltic Sea: cyanobacterial and algal biodiversity and related soil properties, Microb. Ecol., 71(1), 178–193, doi:10.1007/s00248-015-0691-7, 2016.

Seitz, S., Nebel, M., Goebes, P., Käppeler, K., Schmidt, K., Shi, X., Song, Z., Webber, C. L., Weber, B. and Scholten, T.: Bryophyte-dominated biological soil crusts mitigate soil erosion in an early successional Chinese subtropical forest, Biogeosciences, 14(24), 5775–5788, doi:10.5194/bg-14-5775-2017, 2017.

Škaloud, P., Lukešova, A., Malavasi, V., Ryšánek, D., Hrčková, K. and Rindi, F.: Molecular evidence for the polyphyletic origin of low pH adaptation in the genus *Klebsormidium* (Klebsormidiophyceae, Streptophyta), Plant Ecol. Evol., 147(3), 333–345, doi:10.5091/plecevo.2014.989, 2014.

Starks, T. L., Shubert, L. E. and Trainor, F. R.: Ecology of soil algae: a review, Phycologia, 20(1), 65–80, 1981.

Starr, R. C. and Zeikus, J. A.: UTEX the culture collection of algae at the University of Texas at Austin, J. Phycol., 29 (Suppl.), 1–106, 1993.

Su, Y.-G., Li, X. R., Zheng, J.-G. and Huang, G.: The effect of biological soil crusts of different successional stages and conditions on the germination of seeds of three desert plants, J. Arid Environ., 73(10), 931–936, doi:10.1016/j.jaridenv.2009.04.010, 2009.

Vinogradova, O. N. and Mikhailyuk, T. I.: Algal flora of the caves and grottoes of the National Nature Park “Podilsky Tovtry” (Ukraine), Int. J. Algae, 11(3), 289–304, doi:10.1615/InterJAlgae.v11.i3.80, 2009.

Weber, B., Büdel, B. and Belnap, J.: Biological soil crusts: an organizing principle in drylands, Springer Nature., 2016.

Williams, W. J., Eldridge, D. J. and Alchin, B. M.: Grazing and drought reduce cyanobacterial soil crusts in an Australian Acacia woodland, J. Arid Environ., 72(6), 1064–1075, doi:10.1016/j.jaridenv.2007.11.017, 2008.

Table 1. General infor~~a~~mation on study sites: ~~S~~sample location, main tree species, ~~if the stand is managed or natural forest~~management status, silvicultural management index (SMI), ~~soil horizon material, on which BSC was growing,~~ water content and pH from bulk soil analyses, and proportion of inorganic ~~phosphorus~~ P as % of ~~from~~ total P ~~(water content and pH were kindly provided by Ingo Schöning)~~; 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 correl~~t~~ation coefficients to reveal correlations between environmental factors, which might affect or be affected by the biodiversity of algae. This co-correlation analysis should support the correct interpretation of potential important factors of the biodiversity. 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 ~~community composition of algae~~ (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

	algae richness	proportion of filamentous algae	presence or absence of individual algal species~~community composition~~
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. Top row: overview of the sampling sites; bottom row: close-up of the sampled crusts. Left pictures were taken from an intensively managed pine forest; right pictures from a natural beech forest.

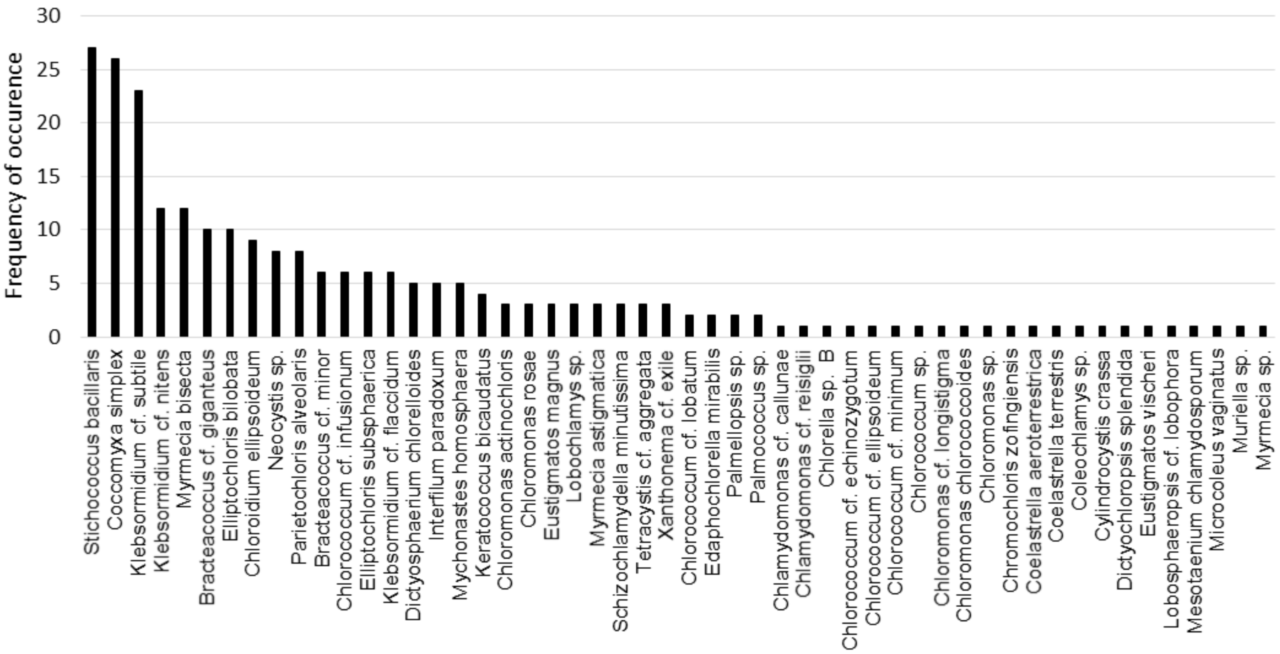

Figure 2. Frequency of occurrence of each algale species in biological soil crusts from forest sites (n=31).

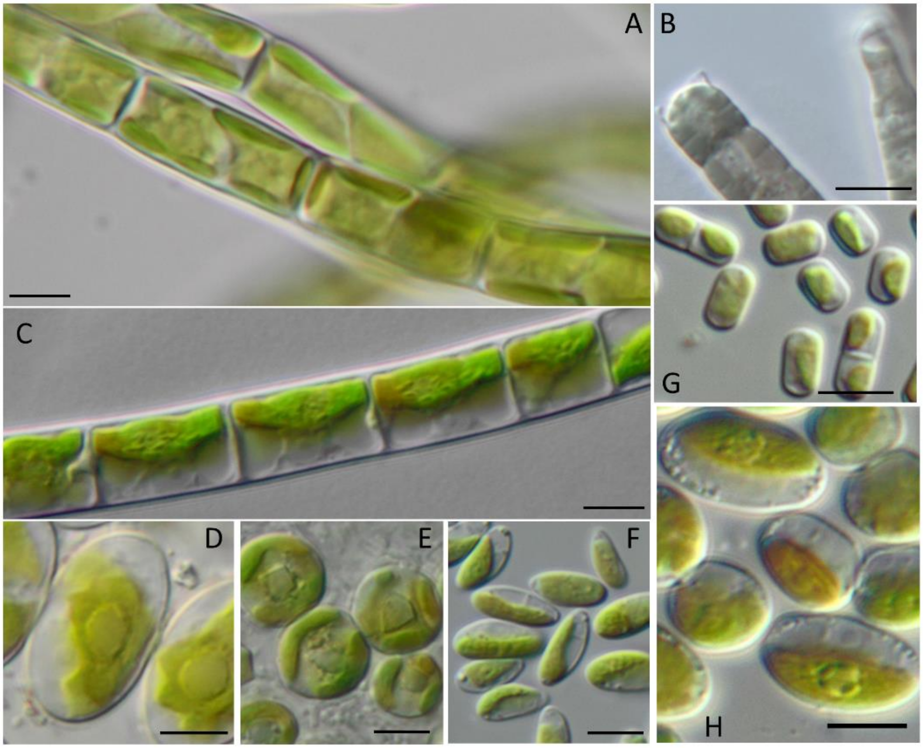

Figure 3. Filamentous and ~~some~~ examples of coccal algae from forest BSCs: algae with strong filaments: A-*Xanthonema* cf. *exile,* B-*Microcoleus vaginatus,* C-*Klebsormidium* cf. *flaccidum;* coccal algae: D-*Chloroidium ellipsoideum*, E-*Eustigmatos magnus*, F-*Coccomyxa simplex;* algae with short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

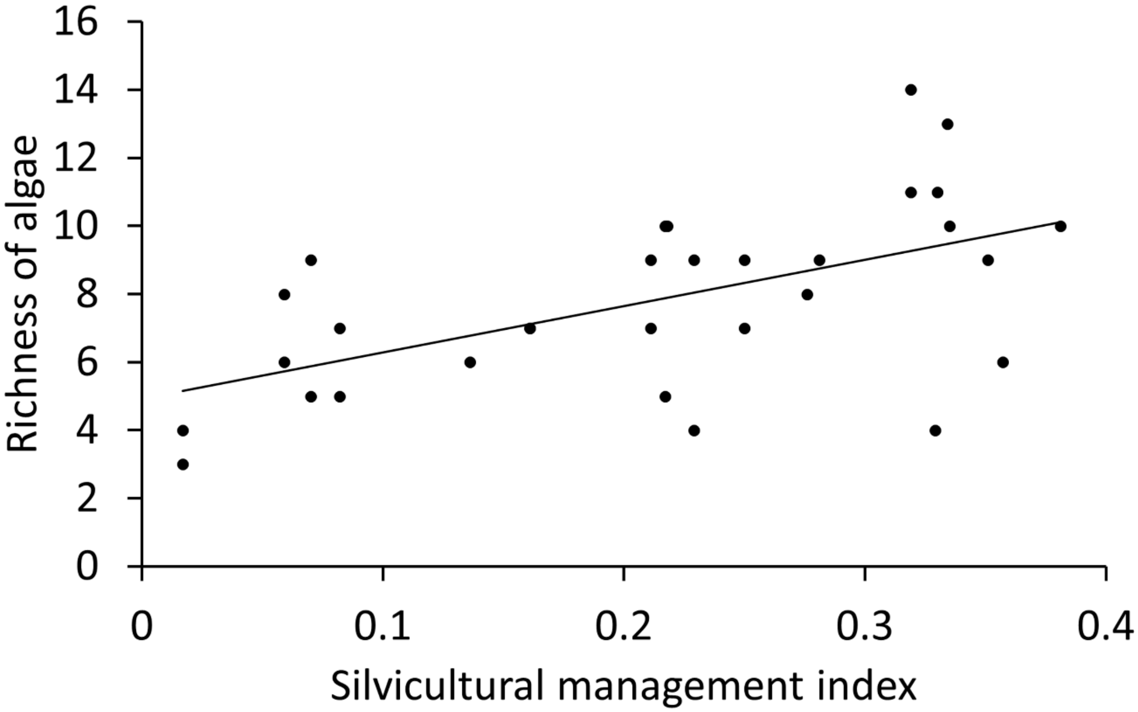

Figure 4. Plot of algae richness in ~~biological soil crust~~BSCs from forests over the silvicultural management index (SMI), natural forest has a low SMI, managed forests a~~n~~ high SMI; the line indicates the best linear fit (slope: 13.6, $p<0.001$(Anova))