

# 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.

5 **Anonymous Referee #1**

Received and published: 4 December 2017

General Comments:

10 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.

15 **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.**

25 *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, algae are not in a good state. A lot of assimilates or irregular shape make it very hard to see and identify the 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 mixture like in the soil crusts, it is hard to tell if one*

30 *algae is a young status of Chlorococcum, or if it belongs to some Chlamydomonas-like morphotype. This is possible in a well prepared enrichment culture, where colonies of algae are separated on the agar. Also most of the detailed morphological description 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 the handbooks; in this case, to use common alga media.*

35 *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, we also changed the wording to, presence or absence of individual algal (for example, p. 4, ls. 19 As a second parameter, we showed similarity between single plots by presence / absence of individual species, which combines the total*

40 *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 deal 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, 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 forest the limitation of light and the occurrence of litter restricts the crust development. But disturbances of vegetation layer change this competitive situation and allow the development of biological soil crusts. Such disturbances occur frequently in temperate forests, for example natural tree fall, pits of wild boars, litter free spots at slopes or molehill-like humps, or human-induced disturbances such as skid trails and clear-cut areas. At these spots, biological soil crust can develop and serve as a starting point for colonialization after heavy disturbance and destruction of intact forest ecosystems. Thus, soil crusts can protect disturbed areas from e.g. erosion until the successful regrowth of vascular plants (Seitz et al., 2017) and even enhance the process of regrowth. It has been shown that sperm germination of vascular plants benefit from biological soil crusts (Li et al., 2005; Su et al., 2009).

*p. 3, ls. 26* 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. 2* We observed that BSCs are able to coexist in temperate forest ecosystems, because natural and human-induced disturbances, such as wind fall and skid trails, leave 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 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. 25* In natural forests, no management was conducted, meaning that fallen trees were left in place and no trees were cut.

5 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. 21* 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.

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**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.**

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*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".*

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**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.**

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**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?**

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*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?**

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**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 individual species.*

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**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 is unclear, please check.**

5 **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.*

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# 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.

5 **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  
10 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.

## 15 **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 P217 or P2117 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.**

35 *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, 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.  
40 Especially in forest the limitation of light and the occurrence of litter restricts the crust development. But disturbances of vegetation layer change this competitive situation and allow the development of biological soil crusts. Such disturbances occur frequently in temperate forests, for example natural tree fall, pits of wild boars, litter free spots at slopes or molehill-like humps, or human-induced disturbances such as skid trails and clear-cut areas. At these spots, biological soil crust can develop and

serve as a starting point for colonialization after heavy disturbance and destruction of intact forest ecosystems. Thus, soil crusts can protect disturbed areas from e.g. erosion until the successful regrowth of vascular plants (Seitz et al., 2017) and even enhance the process of regrowth. It has been shown that sperm germination of vascular plants benefit from biological soil crusts (Li et al., 2005; Su et al., 2009).

5 p. 3, ls. 26 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. 2 We observed that BSCs are able to coexist in temperate forest ecosystems, because natural and human-induced disturbances, such as wind fall and skid trails, leave space for crusts to develop.

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## 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 wasn't 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)

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*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). We changed the wording throughout the text to avoid misunderstandings.*

## 3.) Phosphorous biogeochemical cycling

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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.

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*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”.*

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*P10, ls 9. We expected a correlation between the total content of phosphorus, N, and P with the number of algal species or their identity, respectively, because it was described before that BSCs enhance nutrients compared to bulk soil. In contrast, we observed no correlation between the total content of C, N and P and the species richness of algae. Nevertheless, the fraction of inorganic P showed tendencies towards a correlation with the algae in BSCs, especially with the content of filamentous species. Our study gives the first hint of a potential relation between the biogeochemical cycle in BSCs and alga species. This relation should be studied in more detail by e.g. gene expression analyses to understand if and how algae in BSCs influence the cycling of P.*

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#### 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. 25* 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. 21* 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 (<0.1), managed forests a high SMI; the line indicates the best linear fit (slope: 13.6,  $p < 0.001$  (Anova))

**Additional comments: - P1110: What do you mean with disturbed areas -**

*P1, ls.13* disturbed areas, where higher vegetation is sparse,

**P1120: This study only examined samples from one specific area, though it's tough to generalise this finding to all temperate forests –**

*misleading statement deleted*

**P1124: 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*

**P212: 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).

**P2111: richness of BSC organisms? –**

*p. 2, l. 27* the number of microalgae species in BSCs

**P2122: 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)

**P2124: please provide a precise citation for this statement.**

*changed to Büdel et al., 2016*

**- P316: this information is irrelevant here -**

*deleted*

**P3113: which plots were these? – P3116: what is a microecosystem? –**

*last sentence was deleted*

**P412-8: I wonder whether this cultivation technique does not influence the species assembly because some species might be excluded and others overestimated. –**

5 *p. 6, ls. 25 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 only cultivable algae, which represent only a small part of all algae in the BSCs (Langhans et al., 2009). A recent paper comparing metagenomic data with morphological data based on estimated a match of about 10% (Rippin et al., 2018). Furthermore, it is not always possible to distinguish dormant from currently active microalgae. However, direct observation of a BSC sample*  
10 *under the microscope gave at least a hint for the dominant active organisms. Using this approach we could prove that all filamentous algae were abundant and always alive in the BSC samples. The morphological identification of algae has known challenges: 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, since molecular techniques alone sometimes also fail to detect some algae (Büdel et al., 2009; Garcia-Pichel et al., 2001).*

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**P4116-18: how were the frequency data gained? How were the ‘proportion’ data generated? –**

*p. 4, ls. 22 Further, we categorized the identified algae 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 particles by gluing them together.*

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**P4125: is richness here the total species number? - P513: alga richness? Did you exclude the Cyanobacteria? –**

*p. 4, ls. 18 richness of algae (total number of algae and cyanobacteria species in a sample)*

**P417: specify community composition of algae –**

*p.4, ls. 19 ... we showed similarity between single plots by presence / absence of individual species, which combines the total number and the identity of the algal species...*

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**P1014: 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*

**P1018: A citation of a different study in the conclusion seems misplaced. Consider summarising the data presented here.**

*We rewrote this paragraph accordingly.*

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**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*

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# Algal richness of temperate biological soil crusts 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, ~~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 its 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 as key primary producers of these communities were identified from pine and beech forests under different management regimes. Algae 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, 52 algal species were recorded, most from the phylum Chlorophyta, followed by Streptophyta and Stramenopiles; Cyanobacteria 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~~ a high tolerance to low pH. Increasing management intensity resulted in ~~a~~ higher ~~richness numbers~~ of algal species, especially the ~~proportion number~~ of coccal algae rose. Furthermore, the proportion of inorganic phosphorus ~~was showed tendencies towards a~~ positively correlated ~~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~~ affects P cycling in the BSC.

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

## Introduction

Biological soil crusts (BSCs) occur 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 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, 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 forest the limitation for of light and the occurrence of litter restricts the crust development. But disturbances of vegetation layer change this competitive situation and allows the development of biological soil crusts. Such disturbances occur frequently in temperate forests, for example 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. At these spots, biological soil crust can develop and serve as a starting point for colonialization after heavy disturbance and destruction of intact forest ecosystems. Thus, soil crusts can protect disturbed areas from e.g. erosion until the successful regrowth of vascular plants (Seitz et al., 2017) and even enhance the process of regrowth. It has been shown that sperm germination of vascular plants benefit from biological soil crusts (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 BSCs 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 microalgae 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 algae represent the most important phototrophic components of BSCs along with macroscopic lichens and bryophytes (Elbert et al., 2012). Eukaryotic algae are probably the least studied phototrophs in BSCs, although these organisms are an essential component of BSCs because of their major contribution to C fixation (Büdel et al., 2016). BSC algae can be categorized ~~in~~ as two functional groups. First, filamentous algae as major BSC forming taxa that stabilize soil particles by gluing them together due to the presence/excretion of mucilage. The filamentous forms occur usually in low diversity but produce high biomass. And second, coccoid algae which are attached to the soil particles or other algae and typically occur in higher diversity but lower biomass (Büdel et al., 2016).

Filamentous cyanobacteria, especially of the genus *Microcoleus*, are often the dominant phototrophic organisms in most BSCs of drylands and in dunes from temperate regions (Garcia-Pichel et al., 2001; Schulz et al., 2016). They are described as important for BSC formation due to their ability to produce mucilage sheaths and extracellular polymeric substances forming a 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 *Zygonium* (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 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 ~~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 occurrences is still missing. Therefore, in the present study we identified algal species in a temperate

[forest 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 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 the relation between biogeochemical cycles in [biological soil crusts](#) BSCs and the BSC-associated alga species.

## Material and Methods

### Study site

BSC samples were collected in June 2014 and 2015 ~~from plots of the a 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 \(for illustration see Figure 1\)](#).

The top millimeters of soil, on which BSC had been visually detected as green cover, were collected by pressing a petri dish in the 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 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  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (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 400x magnification.

Morphological identification of algae was based on Syllabus (Ettl and Gärtner, 1995) and, more recent publications on certain algae groups (Dariencko et al., 2010; Kostikov et al., 2002; Mikhailyuk et al., 2015). Mucilage of algae was stained with an aqueous solution of methylene blue. Algae were identified that belong to Cyanobacteria, Chlorophyta, Streptophyta and some

Stramenopiles (Eustigmatophyceae). Diatoms were regularly observed in direct observation, but excluded from the analyses as the mentioned enrichment cultivation is not suitable for estimation-identification of diatom ~~diversity~~.

Since enrichment cultivation does not allow a clear conclusion on the abundance of each species, the richness of algae, i.e. the (-total number of algae species in each a sample), was used as measurement 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, we included showed similarity between the single plots in terms of by presence or/ absence of individual species which combines in order to include not only the total number but also and the identity of the algal 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, we categorized the identified algae 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 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 disturbed due to 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 natural 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.

To assess interactions between BSC biodiversity parameters 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 stable P. Latter Data on latter are not shown here but were 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)) 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 521 different algae species and one Cyanobacterium were detected in enrichment cultures of all 31 BSC samples. *Stichococcus bacillaris* was the most ubiquitous taxon, observed in 27 out of 31 samples; followed by *Coccomyxa simplex* and *Klebsormidium* cf. *subtile* in 26 out of ~~or~~ 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 algae 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 algae species were differentiated according to their organization form (Figure 3). We found five species with strong filaments (*Klebsormidium* cf. *flaccidum*, *K.* cf. *subtile*, *K.* cf. *nitens*, *Xanthonema* cf. *exile*, *Microcoleus vaginatus*) and two genera with short or easily disintegrated filaments (*Interfilum paradoxum*, *Stichococcus bacillaris*). In each BSC at least two different filamentous species 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 (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 significantly~~ 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 52 algal species were identified in all sampled BSCs (Figure 2), which is a similar or 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 cultivable algae, which represent only a small part of all algae 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% (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 at least a hint for the dominant active organisms. Using this approach we could prove that all filamentous algae were abundant and always alive in the BSC samples. The morphological identification of algae has known challenges: 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 (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 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 belong to Chlorophyta; a high richness of this soil algae (genera 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 (Hollerbach & 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 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 because of their potential as BSC-initiating organisms by building tight networks among particles (Büdel et al., 2016). Some investigated forest BSC were formed as well by moss protonema, which has filamentous nature and ~~were was~~ determined as crust-forming organism (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 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 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 three morpho-species of the genus *Klebsormidium* in our samples (Figure\_22). All three morpho-species were reported from aeroterrestrial habitats in Central Europe (Glaser et al., 2017; Mikhailyuk et al., 2015). *Klebsormidium* has morphological features which can be easily recognized, but the identification down to species level is difficult due to



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 (Glaser et al., 2017; Mikhailyuk et al., 2015). In this study, we also observed in BSCs from forests 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 combining potential factors, such as light regimes, desiccation frequency and duration and pH, might in future explain this habitat preferences of *Klebsormidium* clades.

### Correlation with SMI

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 biological soil crusts BSCs from managed than from natural forest ecosystems. †This finding corresponded with conclusions about high algal biodiversity-richness on disturbed or cultivated soils (Hollerbach & 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 on study on litter decaying fungi and bacteria observed 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; 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 the algae in BSCs were not affected by soil pH. We therefore rejected an effect of the SMI via the pH on the algal species richness in Schorfheide-Chorin.

However, SMI combines other potential factors which may 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 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 organisms. The radiation is often coupled with evaporation of pore water (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 affected the algae diversity-richness in BSC via lower light availability and lower evaporation rates. This is supported

by the two-way analysis of water content and SMI, both of which 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 BSC. For future studies on algal biodiversity/microalgae in BSCs it would be important to examine also available light on the ground and the water content in the BSC.

5 Although the SMI positively affected the algal richness, the presence or absence of individual algal the community composition was species 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 suboptimal C:N:P ratio. But also other, above mentioned factors (light regime and water evaporation) differ between both  
10 forest types and could thus have contributed to cause the observed differences in the algal community compositions/species identification.

### **Correlation with C, N, and P**

BSCs have different important ecological functions, for example BSCs enhance 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  
15 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 therebyWe did not observe a correlation between the richness of algae was independent of and the total C, N and P content, although the presence of BSCs leads to the an enhanced content of total C, N and P and in particular the proportion of organic  
20 P (Baumann et al., 2017). Hence/Thus, we assume that algal species are functional redundant and a low species richness in BSCs can 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 shows a tendency to a correlation 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  
25 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 algae 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 space for crusts to develop.

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~~This studies reports f~~For the first time we report on the algae biodiversity richness in BSCs from temperate forests with under different management intensity. The rather acidic forest soil supports a clear dominance of *Klebsormidium*-morphotypes as the main crust-initiating filamentous algae, while Cyanobacteria 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 management intensity resulted in a higher richness of algae, especially the proportion of coccal taxa increased. We expect that the land usesilvicultural management intensity in forests affect the algae biodiversity richness via higher stand density in managed forest, which changes in the light regime ~~(less light in high stand density and in pine forests)~~, and thus also the which is positively coupled with water evaporation.

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 P nutrients 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 phosphorusP showed tendencies towards a correlation with the algae in biological soil crustsBSCs, especially with the content of filamentous species. Our study gives the first hint of a potential relation between the biogeochemical cycle in BSCs and alga species. In our opinion, it is worth to study t~~This relation should~~ eshould be studied in more detail by e.g. gene expression analyses to understand if and how algae in BSCs influence the cycling of phosphorusP. 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.~~ Forthcoming studies should include other crust-associated organisms, like fungi and bacteria, to identify key players on the ecological role of BSCs in the P cycle.

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

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Table 1. ~~General information on study sites: Sample location, main tree species, 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 correlation 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 <sub>i</sub> content | N <sub>i</sub> content | P <sub>i</sub> content |
|---------------------------|-------------------|-------|---------------|------|------------------------|------------------------|------------------------|
| SMI                       | -0.6              |       |               |      |                        |                        |                        |
| water content             | 0.77              | -0.59 |               |      |                        |                        |                        |
| pH                        | n.s.              | n.s.  | n.s.          |      |                        |                        |                        |
| C <sub>i</sub> content    | n.s.              | n.s.  | n.s.          | n.s. |                        |                        |                        |
| N <sub>i</sub> content    | n.s.              | n.s.  | n.s.          | n.s. | 0.94                   |                        |                        |
| P <sub>i</sub> 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                    |

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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

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|                        | algae richness | proportion of filamentous algae | <u>presence or absence of individual algal species</u><br><del>community composition</del> |
|------------------------|----------------|---------------------------------|--|
| 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.

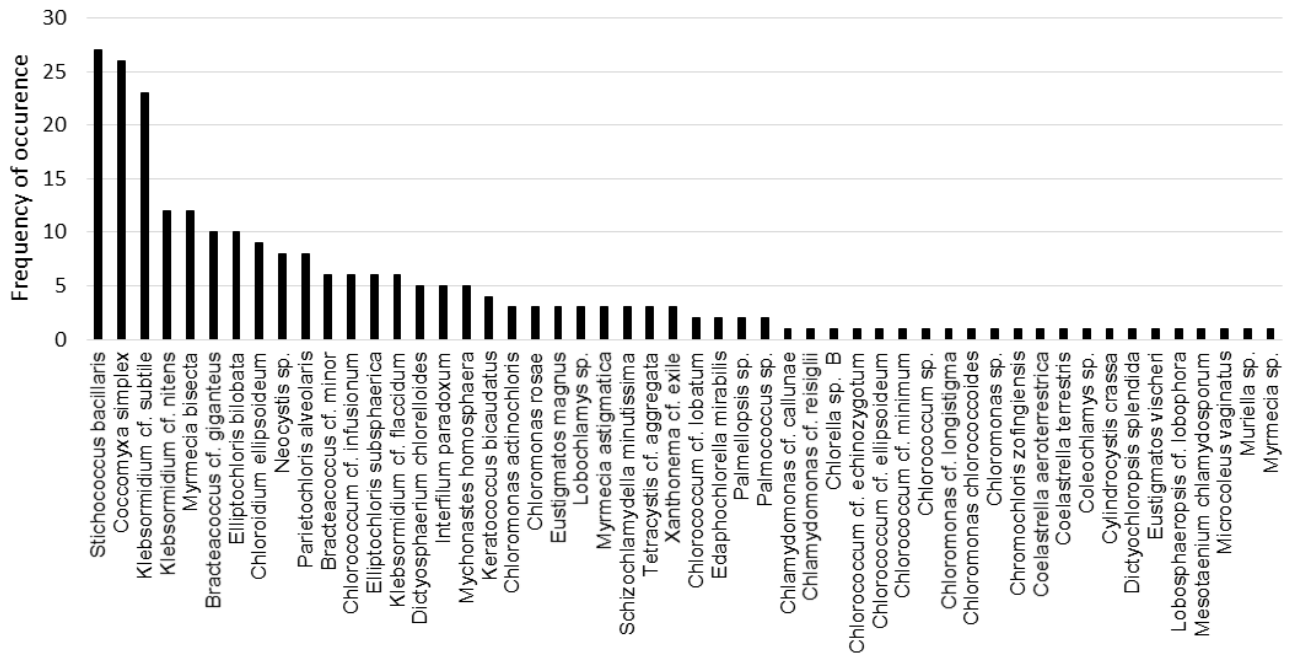


Figure 2. Frequency of occurrence of each algae species in biological soil crust from forest sites (n=31).

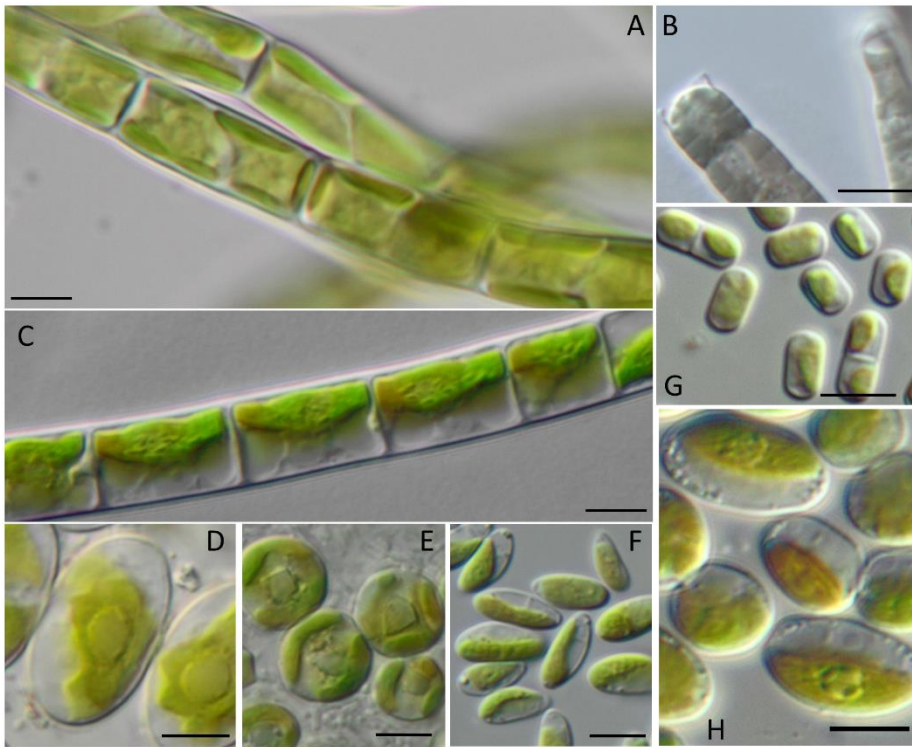


Figure 3. Filamentous and some examples of coccal algae from forest BSCs: algae with strong filaments: A-*Xanthonema* cf. *exile*, B-*Microcoleus vaginatus*, C-*Klebsormidium* cf. *flaccidum*; coccal algae: D-*Chloroidium ellipsoideum*, E-*Eustigmatos magnus*, F-*Coccomyxa simplex*; algae with short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

5

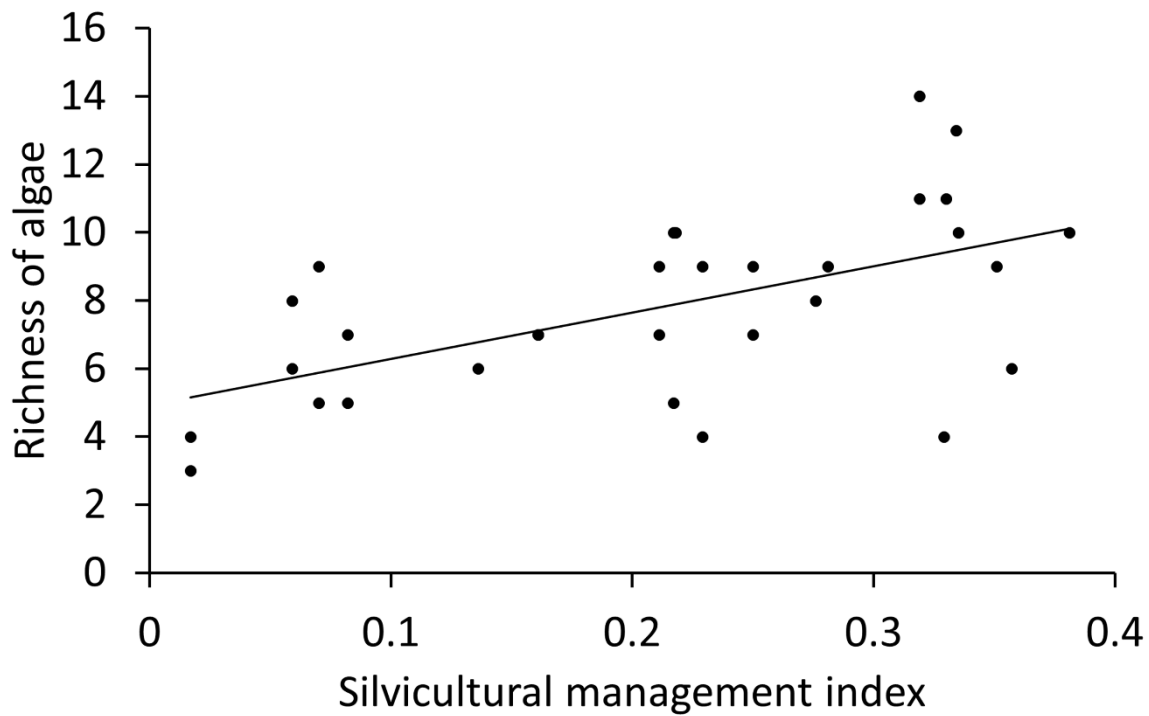


Figure 4. Plot of algae richness in biological soil crust BSCs from forests over the silvicultural management index (SMI), natural forest has a low SMI, managed forests a high SMI; the line indicates the best linear fit (slope: 13.6,  $p < 0.001$  (Anova))