Response to reviewer comments on manuscript bg-2017-99: “Bryophyte-dominated biological soil crusts mitigate soil erosion in an early successional Chinese subtropical forest”

We would like to thank the reviewers for their helpful comments, which greatly improved our manuscript. We have prepared a revised manuscript where we account for all points raised by the reviewers, as described below. We show the reviewers’ comments in grey text, while our responses are formatted as standard text. Line indications refer to the revised manuscript without marked changes.

Anonymous referee #1:

Thank you very much for taking the time to revise this manuscript and for giving this positive evaluation with constructive comments.

Compared with lots of reports regarding biocrusts from drylands, little topics were discussed in humid region. This paper selected a novel issue and conducted a scientific experiment, and whereby some clear but not unexpected results were concluded. My suggestions are as follows to improve the manuscript:

1. while authors analyzed the influence of vegetation, soil, and terrain on biocrusts cover, they should emphasized the interactive impact of different factors, but not only single factor’s influence;

    - This work benefits from the large dataset of the BEF China project and we tried to include a high number of single influences. Nevertheless, we agree with you that interactions of different factors are of high importance and more explanations regarding interactions are needed in the manuscript. We already tried to address this issue by using linear mixed effects models, which account for a combination of fixed and random effects (lines 182-187, 188-196, 223-226, Table 3, 233-238, Table 4). We now widened the discussion part of the manuscript in this regard and tried to better explain combined effects of single factors, such as vegetation (crown cover and LAI) or terrain (e.g. northness) (lines 286-290, 299-310, 311-318).

2. the authors must quatitatively describe the effects of biocrusts on sediment and runoff, and also in the discussion section, they should compared their results with other researchers’ conclusions;

    - Thank you very much for this legitimate comment. We widened the description of our results, demonstrating the effects of biocrusts on soil erosion, by presenting measured values of runoff and sediment delivery (see lines 231-233). We also widened the discussion section of the manuscript by including additional comparisons with other studies (lines 320-324, 339-343, 344-348).
    Nevertheless, as correctly stated by all reviewers, these comparisons have to remain incomplete, as there are only very few studies on biocrust development in forests under mesic conditions and their impact on soil erosion.

3. generally, this manuscript present too much emphasis on qualitative description instead of quatitative analysis;
    - We considered this aspect in the revised version of the manuscript and indeed put a larger emphasis on our quantitative results and widened the discussion (see above).

4. the experiment was conducted in PR China, however, there is none of authors or affiliation from Chinese territory, which is not logical or even not permitted by China government
    - The BEF China project is a joint Sino-German research project with a high level of close cooperation between Chinese and German universities. Thus, our authors' team already included a Chinese national, who was originally based at the Institute of Soil Science, CAS, Nanjing. Nevertheless, we agree that affiliations were not sufficiently presented and our Chinese cooperation partner and supervisor of fieldworks in China Prof. Xuezheng Shi from the Institute of Soil Science in Nanjing agreed to join the authors' team and contributed to the revision of the manuscript (see affiliations).

Anonymous referee #2:

Many thanks for your critical and constructive review. We considered your comments and reworked the manuscript as suggested. Please find more detailed responses to your remarks below.

1.) I have received your manuscript "Bryophyte-dominated biological soil crusts mitigate soil erosion in an early successional Chinese subtropical forest" for review. There are elements to like about this paper, especially the fact that this is one of the rare studies that addresses the influence and role of biological soil crusts on in early secondary succession after severe human impact. Before the manuscript can be considered for publication in Biogeosciences, the authors should nevertheless consider some general comments and rework parts of the manuscript. There is a general question as to how the soil crust in this studied can be referred to. In the introduction (first sentence) the authors refer to the importance of biocrusts in many ecosystems. By checking the reference and also other major biocrust research and literature it becomes obvious that the biocrust in this study is very special because it occurs in a forest. Such ecosystems are dominated by trees are their sheer occurrence indicates a high water availability. So, here it comes to a contradiction to the definition of a biocrust, which were recently defined to occur "in regions where water availability limits vascular plant cover" (Weber et al. 2016 - same reference as used by the authors). Almost every other biocrust study is taking place in drylands or at least areas where an arid element occurs. In the most recent review about biocrust distribution patterns by Bowker et al. 2016, the presence of biocrust is discussed as a function of effective precipitation within semiarid, arid and hyperarid ecosystems, certainly not in the humid forest with a mean precipitation of 1635 mm as in this case. This makes this study very special and requires that the authors explain very precisely why they discuss the topic in the biocrust background.

- We would like to thank the reviewer for this overall positive review and especially for the comment above. It indeed is right that the biocrust described in this manuscript is a special one, as it occurs within a forest. Biological soil crusts are defined to occur in arid environments and in places where arid (microclimatic) conditions are met. Thus, biocrusts are mostly described for dryland regions, where they form a key and enduring ecosystem component. In addition to this main habitat, however, biocrusts have also been described as a transient feature in mesic environments, where annual rainfall amounts are larger, but where biocrusts may form after major singular or repeated disturbance events. Examples for such transient biocrusts are e.g. these of dry grasslands ("Mainfränkische Trockenrasen", Germany) and biocrusts occurring on Öland, Sweden (Büdel et al., 2014), but also biocrusts in former mining areas (Fischer et al., 2014). In all these habitats, biocrusts developed due to severe disturbance caused by trampling and driving, continuous grazing, soil removal and biomass removal. Once these regular disturbance events stop, a dense layer of vascular vegetation would develop and replace the biocrusts.

  In the current study, an existing forest has been clear-cut and trees have been replanted. After this severe disturbance, transient biocrusts developed, which could grow on the bare ground under fairly sunny conditions. However, we already observed an alteration in species inventory and expect, that eventually these biocrusts will disappear again, being replaced by vascular vegetation (in light forests) or buried under persisting leaf litter (under darker conditions) (lines 269-276).

  In the revised version, we sharpened the discussion and conclusion about biocrusts in mesic environments and explained the relationship between biocrust occurrence and vegetation disturbances (lines 64-67, 69-76, 81-83, 249-252, 269-276, 361-364).

2.) It should be stated in the manuscript that biocrusts only contribute a minor ecological role in this ecosystem, certainly because of their low biomass and soil penetration depth, compared with trees and it should be taken into account that the trees are the major driver of this ecosystem. The presence of the mosses and algae may certainly have an effect as shown in this paper, but this should be seen in the bigger context and appropriately assigned.

- We fully agree with the comment, that biomass of biocrusts within this habitat is nearly negligible. Nevertheless, we observed that biocrusts play a key role within this early-successional system. By minimizing erosion and stabilizing the soil surface, they effectively preserve soil fertility within this disturbed forest habitat. Thus, despite their low biomass, we consider biocrusts to fulfil key ecosystem services within this habitat. Nevertheless, we agree that the bigger context should be better assigned and we added further information on that issue to the discussion (lines 324-326, 341-343).

3.) In the ongoing introduction, the authors explicitly describe the role of biocrusts in early succession, while the study site cannot be referred to as in early succession because of the existence of trees, that indicate quite a late successional stage. Nevertheless, the study site is special, because the trees were artificially planted, so the soil itself remains at an early successional stage (straight after disturbance) while the occurring vascular vegetation is at a later stage, due to human impact (at least the trees. What other vegetation occurs?). A more detailed explanation of the hypothetical background should be taken into consideration.

- We agree that the special circumstances of the study site indeed need to be described in more detail in the paper. From a forestry perspective, the study site was referred to as an early successional tree plantation in 2013 (see Bruelheide et al. 2014). To establish the experiment and help the tree saplings (~5-15 cm height) grow in their first two years, shrubs and coppices have been weeded from 2010 to 2012. Thus, it is an artificial setup, but following common practice in forestry and tree plantations of this area. Understory growth was generally low, with smaller patches of e.g. *Miscanthus* at southward slopes and only little leaf abscission from trees in the first years. We gave a more detailed explanation in the revised manuscript (lines 131-137, 146-147).

4.) Additionally, it should be clearly defined which ecological process is in the focus of this study. From the study background, the most reasonable is secondary succession after human disturbance. Within this, the biocrust may occur as one of the initial players, thus it will provide the basis for other plants but also disappear with ongoing succession. This should be stated.

- We agree and thank you again for this very helpful comment. Some further statements were added (line 110 f). We do expect that biocrusts are an initial player (lines 247-249, 253-255, 255-258) and they will disappear with ongoing succession (line 269-270, 273-276). Actually, we were surprised that their extent was still increasing after five years of tree growth, when some trees were already up to a height of 7 m.

5.) The hypotheses should come with explanations or at least theoretical background. In Hyp 1 is the parameter tree growth or canopy cover or light intensity? Hyp 2, what is the exact expectation here? This sound very vague. Please be precise.

- We adapted the introduction to give more theoretical background (lines 57ff) and sharpened the hypotheses (116-121). Regarding Hyp 2, we tried to focus on the humid forest environment and to keep it somewhat more general, as we will not be able to explain all influences based on our data set. The pH for example, influences crust components (lichens, algae etc.) differently and e.g. different bryophyte species show variable responses on pH changes.

6.) In general, the introduction could benefit from more precise statements and direct explanations. In the moment, many sections ready like overall summaries rather than leading to explicit research questions for the study.

- Thank you for this comment. We adapted the introduction and tried to be more precise and to better link the introductory part to the statement of hypotheses. We also included assumptions to each paragraph, leading to the hypothesis generation (lines 81-83, 88-91, 107-109).

7.)

Material and Methods 135: which were the determinants for the crust types

- Biocrusts were described in the field based on appearance, functional groups and species composition and biocrust types determined based on the dominating autotrophic component. Further details were added to the manuscript (lines 140-142).

Results 210: Please explain why the existence of vascular plants indicates any developmental stage of biocrust? Is this climax or are the plants taking over and the crust will disappear? If this is the case you should refer to the developmental stage of the vegetation in general and the crusts occur only for a little while.

- The existence of vascular plants does not indicate a developmental stage of biocrusts; the expression was somewhat misleading. Instead, we believe that vascular plants like *Selaginella* and *Poaceae* will take over and biocrust cover will decline, even without a continuous leaf litter layer (see above). We changed the phrasing accordingly (lines 215 - 216)

Discussion Overall the discussion could clearly benefit from more explicit arguments of the given results rather than summarising literature. Sections read like reviews and summaries of recent literature. Could you please discuss your own data and indicate what information these add to the existing knowledge? Here I strongly agree with the first reviewer how also stated that the discussion needs improvement. Please explain more detailed what your own findings mean and implement.

- We agree with you and reviewer #1 (see comment above) and sharpened the discussion and strengthened the focus on our own data. Major parts of the discussion have been rearranged and widened (e.g. lines 249-251, 253-255, 256-258, 269-272, 274-276, 277-278, 290-294, 302-304, 309-310, 311-313, 316-318, 321-324, 324-326, 335-339, 341-343, 350-351).

Additionally, you might want to consider reading more about bryophytes and their growth in forest understories. Surely the discussion could benefit from some comparisons for growth rates and microenvironments. For the implication of the story, the authors should clearly underline, that this is a case study in a single, very special subtropical forest ecosystem and therefore findings cannot easily be extrapolated to other systems.

- We agree with you that findings cannot be extrapolated to other ecosystems and it is not our objective to do so. We clarified this point in the revised conclusion (lines 361-363). Nevertheless, we believe that they could be compared to other forest plantations in subtropical China and it would be very interesting to evaluate the biocrust occurrence in other forest ecosystems after clear-cut and replantation of trees.
  Furthermore, we added more literature about biocrust recovery (Read et al 2011, Read et al 2016, Eldridge 1998) and bryophyte development in forests (Fenton and Frego 2005, Goffinet and Shaw 2009, Spitale 2017, Tinya and Odor 2016, Gilliam 2007). We fully agree that this study could benefit from comparisons of growth rates, for example. Nevertheless, there are not so many other studies on biocrust recovery in those subtropical climates and to our knowledge, generally studies in forest environments are rare (except work done by Read et al. and Eldridge from Australian semi-arid woodlands, see above).

In the first section of the discussion, statements are made, that do not refer to the presented data. 243: biocrusts were highly competitive 244: biocrusts prepared the upper soil layer 246: tree growth provides shade and protection from the wind, which then leads to advancement in biocrust development (Please explain that you use crown cover as a proxy for shading. Are there data about the wind?). Other 260: Replace competitive by coexisting. 261-265: The authors provide a very nice list of moss species for this study and assume here that species composition changes with decreasing light availability. It would be excellent to underline this finding by data. Can you provide data that show this shift of species? The statement could significantly gain importance if the change in species could be correlated to the decreasing light. As it stands now, it reads like an assumption.

- We changed the discussion according to your suggestions (lines 246-263). Crown cover is a proxy for shading and there is no detailed data about wind speed or direction.
  Furthermore, we agree that adding more data about single species from e.g. 2011 and 2015 would be very useful and beneficial. Unfortunately, we do not have any further detailed species lists as it was not possible to sample biocrusts but in 2013. Classifications of biocrust types in other years were done by visual judgement in the field. Thus, we cannot substantiate the species shift with further data, but would like to do so in further studies.

279-280: Irrelevant for the study. Can be deleted.

- Deleted.

Additional minor comments:

Some of the writing does not seem to be appropriate. Please reconsider

34: "Our“ experimental forest ecosystem

36: Biocrust “covers” were still increasing

42: quickly colonise gaps in” higher vegetation layers” – what do you mean with layers? Which gaps are closed?

207: “traces of lichens”

210: organisms were found in minor numbers – is this fewer species, individuals or coverage?

243: early stage of the ecosystem

283: fasten themselves on the soil surface

329: They developed quickly to later-stages

- Thank you for pointing out mistakes and incomprehensibilities in writing. We changed the writing according to your comments and counterchecked the manuscript.
- 42: Higher vegetation layers in this context are the tree or shrub layer and gaps occur by treefall or tree cutting. 220: This is fewer species (then bryophyte species).

Anonymous referee #3:

Thank you very much for your review and the very valuable suggestions to improve the manuscript.

1.) The topic of this paper is likely to have a substantial impact. However, it is very difficult to follow the numbers of sample replicates across the study. Perhaps a table would help where the hierarchy of sampling is broken down and all in one place.

- Thank you for this comment. We agree that sample numbers may appear somewhat confusing, which is due to the fact that the study was initially not designed to investigate biocrust development. Within the BEF China experiment, 34 research plots were used and equipped with five runoff plots each (thus 170 ROPs in total). Measuring four rainfall events in 2013, we came up with an n=334 of valid measurements for the erosion assessment. From 2011 to 2015, a selection of 70 ROPs could be continuously checked for biocrusts. We added further information to the methods section (lines 139-144, 155-162) and table 1 to clarify sample numbers in the revised version of the manuscript.

2.) The authors also put a lot of influence on canopy cover dictating cover of biocrusts but their abiotic variables are likely influencing the canopy cover. These things should be addressed together or the abiotic setting should be controlled for when looking at canopy cover. The disturbance that is mentioned, that is the reason for the development of biocrusts is not described.

- Thank you for this comment. We agree that abiotic variables are influencing the canopy cover just as well. Nevertheless, abiotic factors were mainly used to explain biocrust covers as their influence on the tree layer is investigated by other scientists in separate studies within the BEF China consortium. In our opinion, widening the analysis would lead beyond the scope of this study.
  Nevertheless, we added further information on clear-cutting and pre-disturbance vegetation (lines 131-137). Unfortunately, there is no further data on biocrust species before the setup of the project. The potential natural vegetation of this region is a subtropical broadleaved forest with dominating evergreen species, which was replaced by a commercial forest plantation in the 1980's. This plantation was then clear-cut in 2008 when the BEF-China experiment was established (see methods 2.1, Bruelheide et al. 2014, Yang et al. 2013).

3.) Specific comments: Line 114: The hypotheses could be stated more clearly. (1) "Biocrusts ARE widely developED (2) "The development of biocrust is influenced by BOTH the surrounding vegetation cover AND THE soil and terrain attributes."

- Hypotheses were adapted according to your and reviewer #2's comments (lines 116-121)

Line 173- It is not clear is the analyses met the assumptions of ANOVA.

- The dataset was tested and met the assumptions for ANOVA. We added further information on normality and multi-collinearity to this paragraph (lines 197-198).

Line 185- "Than" should be "then".

- Changed

Line 239- I thought that this paper was primarily about soil erosion and biocrusts but that it not clear from the first paragraph of the discussion.

- The paper is structured along the three hypotheses (1) Biocrust extend under forest, (2) Influence of vegetation, soil and terrain on biocrust development, (3) Impact of biocrusts on soil erosion. Thus, we used the same order in the results and discussion part. The title is pointing more on soil erosion, though, as this was the most important finding in our opinion. Nevertheless, biocrust development and e.g. classified moss species are of high importance, too.

Line 240- It is confusing to state hypotheses by numbers but quickly paraphrasing the hypothesis would make interpretation easier for the reader.

- We agree that paraphrasing the hypotheses in the discussion part enhances the comprehensibility for the reader. Thus, we added short repetitions of the hypotheses at the beginning of each discussion paragraph (lines 247-248, 265-266, 285-286, 320-321).

Line 241- Is there any pre-disturbance data? It is hard to understand the connection between interspaces and disturbance without some description of the pre-disturbance structure of the vegetation.

- See comment above. Unfortunately, we do not have any data on biocrusts and biocrust development derived before the establishment of the experiment in 2009-2010. The pre-disturbance vegetation was a *Cunninghamia lanceolata* plantation (lines 132-133). The methods section has been adapted accordingly (131-137).

Line 271- Cite Condon and Pyke 2016, who have been able to restore a great deal of moss cover very quickly.

- Thank you for pointing out further literature, which has been added. The work of Condon and Pyke gives very valuable insights on moss development after vegetation disturbance and fits well in our context (line 280).

Line 321- You would have a stronger close if you finished with the sentence that ends here. It's also unclear given your findings if there is much of a need to restore biocrusts since you saw recovery of bryophytes really quickly.

- We completely agree and the last two sentences have been removed from the manuscript. Furthermore, we also believe that the need to restore biocrusts in mesic environments where biocrusts establish quickly is less evident, than in arid environments (lines 281-282). Nevertheless, we assume that biocrusts play an important role in young tree plantations, as high soil losses can already occur in single heavy rainfall events, causing high damage when soil surfaces are not sufficiently covered. Additionally, there is not much literature about biocrust recovery in temperate climates and under forest plantations. The end of the paragraph has been adapted accordingly (lines 276-282).

Line 335- You should remind the reader here of your scale as this likely influenced the effects of soil attributes.

- We added further information about scale and improved the manuscript as suggested by the reviewer (line 366).

The authors need to work on the storyline of the paper as well.

- We generally improve the writing and storyline throughout the manuscript and changed major parts of the introduction and discussion.

Bryophyte-dominated biological soil crusts mitigate soil erosion in an early successional Chinese subtropical forest

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Abstract. This study investigated the development of biological soil crusts (biocrusts) ~~covers~~ in an early successional subtropical forest ~~ecosystem~~ plantation and their impact on soil erosion. Within a biodiversity and ecosystem functioning experiment in Southeast China (BEF China), the effect of these biocrusts on sediment ~~discharge~~ delivery and runoff ~~measurements were conducted~~was assessed within micro-scale runoff plots under natural rainfall and biocrust cover~~s~~ w~~ere~~as surveyed over a five-year period.

Results showed that biocrusts occurred widely in ~~our~~the experimental forest ecosystem and developed from initial light cyanobacteria- and algae-dominated crusts to later-stage bryophyte-dominated crusts within only three years. Biocrust cover~~s~~ w~~ere~~as still increasing after six years of tree growth. Within later stage crusts, 25 bryophyte species were determined. ~~The development of biocrusts was significantly influenced by the s~~Surrounding vegetation cover and terrain attributes significantly influenced the development of biocrusts. Besides high crown cover and leaf area index, the development of biocrusts was favoured by low slope gradients, slope orientations towards the incident sunlight and the altitude of the research plots. ~~Our m~~Measurements showed~~,~~ that bryophyte-dominated biocrusts ~~were importantly decreasing~~strongly decreased soil erosion ~~and~~being more effective ~~in erosion reduction~~ than abiotic soil surface cover~~s~~. Hence, their significant role to mitigate sediment ~~discharge~~ delivery and runoff generation in mesic forest environments and their ability to quickly colonize ~~gaps in higher vegetation layers~~soil surfaces after forest disturbance are of particular interest for soil erosion control in early stage forest plantations. ~~A detailed record of different biocrust species and their functional influence on soil erosion processes as well as a thorough monitoring of biocrust covers under closing tree canopy in subtropical forests is required in further studies.~~

1 Introduction

Biological soil crusts (hereinafter referred to as biocrusts) are a living soil cover, which plays significant functional roles in many environments (Weber et al., 2016). In initial ecosystems, communities of cyanobacteria, algae, fungi, lichens, bryophytes and bacteria in varying combinations are the first to colonize the substrate (Evans and Johansen, 1999). ~~Biocrusts~~They are often dominated by one organism group, with cyanobacterial crusts being indicators for early stage crusts and drier conditions (Malam Issa et al., 1999; Malam Issa et al., 2007) and bryophyte-dominated crusts being indicators for later stage crusts and moister conditions (Colesie et al., 2016; Seppelt et al., 2016). Those highly specialized communities form a biological crust immediately on top or within the first millimetres of the soil surface (Büdel, 2005). Biocrusts ~~generally~~ preferably occur under harsh conditions of temperature or light, ~~and when the cover of~~where vascular vegetation ~~is sparse~~tends to be rare (Allen, 2010). Therefore, biocrusts are generally widespread under dryland conditions (Berkeley et al., 2005; Belnap, 2006; Büdel et al., 2009), whereas under mesic conditions they mostly occur as a successional stage after disturbance or in environments under regularly disturbed regimes (Büdel et al., 2014).

In direct competition~~Biocrusts are generally less capable of competing~~ with phanerogamic plants, biocrusts are generally in an inferior position and thus their ~~crust~~ development is limited ~~when~~ under closed plant canopies or when leaf litter layers ~~come into play~~occur (Belnap et al., 2003a). This limitation is due to the competition for light (Malam Issa et al., 1999) and nutrients (Harper and Belnap, 2001). ~~Nevertheless,~~ Disturbance of the phanerogamic vegetation layers, however, changes this competitive situation. Such disturbances can occur ~~e.g.~~ in forest ecosystems by natural treefall or ~~after~~human-induced clear-cutting (Barnes and Spurr, 1998). ~~The c~~Complete removal of a forest ~~signifies~~causes a harsh ~~cut~~shift in vegetation development and creates a starting point for new vascular plant as well as biocrust communities (Bormann et al., 1968; Keenan and Kimmins, 1993; Beck et al., 2008). Biocrusts are able to quickly colonize ~~gaps in higher vegetation~~natural clearances in tree layers (Belnap et al., 2003a) ~~or~~as well as gaps appearing after human disturbance (Dojani et al., 2011; Chiquoine et al., 2016)~~. Biocrusts are often dominated by one organism group, with cyanobacterial crusts being indicators for early stage crusts and drier conditions (Malam Issa et al., 1999; Malam Issa et al., 2007).~~ Generally, it can be stated that ~~a high number of studies could not clarify~~ current knowledge on the relation between the development of biocrust cover and vascular plant cover leaves room for further research (Kleiner and Harper, 1977; Belnap et al., 2003b; Zhang et al., 2016)~~and some studies even showed a positive correlation (Belnap et al., 2003b)~~. ~~This coherence was explained with enhanced nutrient levels provided for vascular plants growing on crusted compared to non-crusted soil surfaces (Kleiner and Harper, 1977; Belnap, 2002). Therefore, the improvement of soil fertility by biocrusts has been shown to be fundamental for the development of vascular plant communities in some regions (St. Clair and Johansen, 1993; Harper and Belnap, 2001).~~ ~~Biocrusts are able to quickly colonize gaps in higher vegetation layers (~~Belnap et al., 2003a~~) or gaps appearing after disturbance (~~Dojani et al., 2011; Chiquoine et al., 2016)~~. Such disturbances can occur e.g. in forest ecosystems by treefall or after clear-cutting (~~Barnes and Spurr, 1998~~). The complete removal of a forest signifies a harsh cut in vegetation development and creates a starting point for new vascular plant as well as biocrust communities (~~Bormann et al., 1968~~;~~Keenan and Kimmins, 1993~~;~~ Beck et al., 2008~~). Nevertheless~~In particular, the development of biocrusts in early successional forest ecosystems ~~under a closing tree canopy~~ has not been in focus of research so far and thus there are only few studies on this topic (Su et al., 2007; Zhang et al., 2016). Furthermore, ~~evidence for~~descriptions of different biocrust types in mesic vegetation zones and ~~especially from~~investigations in southeast Asia are rare (Büdel, 2003a; Bowker et al., 2016). We assume that biocrusts are also able to coexist in mesic subtropical forest environments shortly after deforestation, but their cover decreases with ongoing tree canopy closure and decreasing light intensity.

Function~~s~~al roles of biocrusts have been investigated for decades, but less attention has been paid to their spatial distribution and characteristics (Allen, 2010). Biocrust cover varies across ~~different~~ spatial scales (from centimetres to kilometres) and it could be shown that it depends not only on the surrounding vascular vegetation cover, but also on soils, geomorphology and (micro-)topography or terrain (Evans and Johansen, 1999; Ullmann and Büdel, 2003; Kidron et al., 2009; Bowker et al., 2016) in arid, semi-arid, temperate and boreal environments. Different biocrust distributions ~~could~~have be~~en~~ related to elevation and terrain-influenced microclimatic gradients (Kutiel et al., 1998), different geomorphic zones (Eldridge, 1999), varying aspects (George et al., 2000) and~~or~~ soil types (Bu et al., 2016). We assume that this is also true for mesic subtropical forest environments. To our knowledge, investigations on the influence of small-scale (centimetres to metres) topographic variations on biocrust development are rare and further studies will ~~assist in the understanding of their abundance and distribution~~help to understand the role of these small-scale factors (Garcia-Pichel and Belnap, 2003; Bu et al., 2016; Bowker et al., 2016). Furthermore, as the development of biocrusts is characterized by a high complexity and spatial heterogeneity with many micro-climatic and micro-environmental factors, it is of great significance to conduct comparative studies on the spatial distribution of biocrusts (Bu et al., 2013b). This is particularly true for initial forest ecosystems (Weber et al., 2016).

~~Moreover, b~~Biocrusts ~~have been~~were recognized ~~as~~to ~~having~~have a major influence~~s~~ on terrestrial ecosystems (Buscot and Varma, 2005; Belnap, 2006) as they protect soil surfaces against erosive forces by both wind and water (Bowker et al., 2008; Zhao et al., 2014)~~, enhance soil stability (Malam Issa et al., 2001; Warren, 2003) and influence the hydrological cycle (Belnap, 2006)~~. ~~Nevertheless,~~ They can absorb the kinetic energy of rain drops (splash effect), decrease shear forces and stabilize soil particles with protonemal mats and fine rhizoids ~~impacts of biocrusts on~~and thus decrease particle detachment and enhance soil stability (Malam Issa et al., 2001; Warren, 2003; Belnap and Lange, 2003~~) and soil hydrology~~. Those effects~~may~~ differ with regard to soil texture, surface roughness, water repellency and finally different crust species and developmental stages (Warren, 2003; Belnap and Büdel, 2016). ~~Furthermore~~However, studies that directly relate different types of biocrust cover to rates of soil erosion are few (Allen, 2010). Furthermore, ~~and~~ the influence of biocrusts on sediment ~~discharge~~ delivery and runoff has mostly been investigated in arid and semi-arid climates and ~~in~~ humid climates ha~~s~~ve been largely disregarded (Belnap and Lange, 2003; Weber et al., 2016). We assume that biocrusts are effectively counteracting soil losses in early successional subtropical forest plantations and thus may play a major functional role in soil erosion control in mesic areas under anthropogenic influence.

This study aims to investigate the development of biocrust cover in an early successional subtropical forest ecosystem after human disturbance and the impact of those biocrusts on soil erosion. Therefore, interrill erosion was measured with runoff plots and the occurrence, distribution and development of biocrusts was recorded. The study was conducted in an experimental forest plantation (BEF China), which aims to study biodiversity and ecosystem functioning relationships in southeast China (Yang et al., 2013; Bruelheide et al., 2014). During the study, ~~T~~the following hypotheses were addressed:

(1) Biocrusts ~~widely develop~~are able to ~~in~~coexist in mesic early successional subtropical forest ecosystems, but crust cover decreases with ongoing ~~tree growth~~canopy closure and decreasing light intensity.

(2) The development of biocrusts in mesic subtropical forests is not only influenced by the surrounding vegetation cover, but also by soil attributes which influence biocrust growth and terrain attributes which affect microclimatic conditions.

(3) Biocrusts mitigate interrill soil erosion in early successional subtropical forest ~~ecosystems~~plantations.

2 Material and methods

2.1 Study site and experimental design

The study was carried out within the BEF China experiment (Bruelheide et al., 2014) in Xingangshan, Jiangxi Province, PR China (29°06.450′ N and 117°55.450′ E). The experimental area is located in a mountainous landscape at an elevation of 100 m a.s.l. to 265 m a.s.l. with slopes from 15° to 41° (Scholten et al., 2017). The bedrock is non-calcareous slates weathered to saprolite and predominant soil types are Cambisols with Anthrosols in downslope positions and Gleysols in valleys (Scholten et al., 2017). The mean annual temperature is 17.4 °C and the annual precipitation is 1635 mm with about 50 % falling during May to August (Goebes et al., 2015). The climate is typical for summer monsoon subtropical regions. The potential natural vegetation of this region is a subtropical broadleaved forest with dominating evergreen species. It has been widely replaced by tree plantations of mostly *Cunninghamia lanceolata* for the purpose of commercial forestry in the 1980's (Bruelheide et al., 2014). The experimental area (approx. 38 ha) is structured in 566 research plots (25.8 m × 25.8 m each) at two sites (A and B) and was clear-cut and replanted with 400 tree saplings per plot in different tree species mixtures in 2009 and 2010 (Yang et al., 2013). A selection of 34 research plots ~~(VIPs, Very Intensively studied Plots)~~ was used for this study (Seitz et al., 2016). ~~which were clear-cut and replanted with 400 tree saplings per plot in 2009 and 2010, respectively (Yang et al., 2013).~~ Shrubs and coppices were weeded once a year from 2010 to 2012 to help the tree saplings grow, following common practice in forest plantations of this area. ~~A selection of 34 research plots (VIPs, Very Intensively studied Plots) was used for this study.~~

2.2 Field methods

Biocrust cover was determined photogrammetrically in 70 selected micro-scale runoff plots (ROPs, 0.4 m × 0.4 m; Seitz et al., 2015) at five timesteps (November 2011, May 2012, May 2013, May 2014 and May 2015). ~~and general biocrust types~~Biocrusts were described in the field based on appearance, functional groups and species composition and biocrust types determined based on the dominating autotrophic component. During the rainy season in summer 2013, an extended survey linked to soil erosion measurements (see below) was conducted in five ROPs on 34 research plots each ~~in (~~(170 ROPs in total, ~~(see below and~~ Table 1). At each ROP, perpendicular images were taken with a single lens reflex camera system (Canon 350D, Tokio, Japan) and processed with the grid quadrat method in GIMP 2.8 using a digital grid overlay with 100 subdivisions (cf. Belnap et al., 2001). Stone cover and biocrust cover were separated by hue distinction. A continuous leaf litter cover, which may impede analyses, was not present during measurements. Biocrusts were collected in 2013 and samples were dried at 40 °C (Dörrex drying unit, Netstal, Switzerland). The identification of species was carried out by morphological characteristics using a stereomicroscope (Leitz TS, Wetzlar, Germany), a transmitted-light microscope (Leitz Laborlux S, Wetzlar, Germany) and ultraviolet light. Bryophytes (dominating taxa in 2013) were determined to the species level, wherever possible and separated into mosses (Bischler-Causse, 1989; Moos flora of China: Gao et al., 1999; 2001; 2002; 2003; 2005; 2007; 2008; 2011) and liverworts (Zhu, 2006; Söderström et al., 2016 and Alfons Schäfer-Verwimp, personal communication). Comparisons were conducted with specimen hosted in the herbarium of the State Museum of Natural History in Stuttgart, Germany (Herbarium STU).

Sediment ~~discharge~~ delivery and surface runoff were measured ~~within 34 research plots on five micro-scale ROPs each~~ within 170 ROPs in summer 2013 (see above and ~~n=170,~~ Table 1). After four timesteps, 334 valid ROP measurements entered the analysis (for detailed information see Seitz et al., 2016). Sediment ~~discharge~~ delivery was sampled, dried at 40 °C and weighed, whereas surface runoff and rainfall amount were measured in situ. At every ROP, crown cover and leaf area index (LAI) were measured with a fish-eye camera system (Nikon D100 with Nikon AF G DX 180°, Tokio, Japan) and calculated with HemiView V.8 (Delta-T devices, Cambridge, UK). Measurements of tree height and crown width were provided by Li et al. (2014) at research plot scale (n=34). Tree species richness and tree composition resulted from the experimental setup of BEF China (Bruelheide et al., 2014).

Soil attributes (Table 1) were determined for every research plot (n=34) using pooled samples from nine point measurements each. Soil pH was measured in KCl (WTW pH-meter with Sentix electrodes, Weilheim, Germany), bulk soil density was determined by the mass-per-volume method and total organic carbon (TOC) was measured using heat combustion (Elementar Vario EL III, Hanau, Germany). Soil organic matter (SOM) was calculated by multiplying TOC with the factor 2 (Pribyl, 2010).

2.3 Digital terrain analysis

Terrain attributes (Table 1) were derived from a digital elevation model (DEM, Scholten et al., 2017) at research plot scale (n=34). Attributes were the terrain ruggedness index (TRI, Riley et al., 1999) to describe the heterogeneity of the terrain, the Monte-Carlo based flow accumulation (MCCA, Behrens et al., 2008) to diagnose terrain driven water availability, altitude above sea level to address elevation effects and the eastness and the northness (Roberts, 1986) to describe plant related climatic conditions. Those terrain attributes cover major landscape features of the experimental area and were not correlated. Slope was additionally measured with an inclinometer at every ROP (n=170, see Seitz et al., 2016).

[Table 1]

2.4 Statistical methods

The temporal development of biocrust cover~~s~~ (1) from 2011 to 2015 was assessed at five timesteps within 70 ROPs (see above) by an analysis of variance (ANOVA) and Tukey's Honestly Significant Difference (HSD) test (n=350).

The influences of vegetation, soil and topographic attributes on biocrust cover (2) in 170 ROPs (see above) were assessed by linear mixed effects (LME) models (n=334). Crown cover, bulk soil density, SOM, pH, altitude, slope, MCCA, TRI, eastness, northness and tree species richness were fitted as fixed effects and biocrust cover as response variable. The attributes were tested with Pearson's correlation coefficient before fitting. LAI was fitted individually in exchange to crown cover due to multi-collinearity. Experimental site and research plot were fitted as random effects and hypotheses were tested with an ANOVA type 1 with Satterthwaite approximation for degrees of freedom.

The influences on soil erosion (3) were assessed by LME models with restricted maximum likelihood (n=334) and sediment ~~discharge~~ delivery and surface runoff as response variables, respectively. Crown cover, slope, surface cover, SOM, rainfall amount and tree species richness were fitted as fixed effects. Surface cover was th~~a~~en split into surface cover by biocrusts and by stones, which entered the analysis as fixed conjoined factors. Precipitation events nested in plot, tree species composition, experimental site and ROP nested in plot were fitted as random effects. Attributes were not correlated. The hypothesis was tested with an ANOVA type 1 with Satterthwaite approximation for degrees of freedom. Moreover, the Wilcoxon rank sum test was applied to test for differences between biocrust cover and stone cover on sediment ~~discharge~~ delivery and surface runoff. Therefore, the dataset was split into data points where biocrust cover exceeds stone cover (n=281) and data points where stone cover exceeds biocrust cover (n=53).

All response variables were log-transformed before modelling. ~~and~~ The dataset was tested for multi-collinearity and met all prerequisites to carry out ANOVAs. All analyses were performed with R 3.1.2 (R Core Team, 2014). LME modelling was conducted with "lmerTest" (Kuznetsova et al., 2014) and rank sum tests with "exactRankTests" (Hothorn and Hornik, 2015). Figures were designed with "ggplot2" (Wickham, 2009).

3 Results

3.1 Temporal development of biocrust cover

Biocrusts ~~were detected~~occurred in 94 % of all ROPs and their cover within ROPs ranged between 1 % and 88 % over ~~all~~ the course of five years. The mean biocrust cover of all ROPs more than tripled from their installation in 2011 to the last measurement in 2015 (Fig. 1). Th~~is~~e increases w~~as~~ere significant from 2011 to 2015 and from 2012 to 2013, 2013 to 2014 and 2014 to 2015 (p<0.001).

[Figure 1]

Whereas a clear bryophyte-dominance of biocrusts was evident at the time of sampling in 2013, different successional stages were identified in the field and on ROP photos from 2011 to 2015 (Fig. 2). In 2011, a smooth, light cyanobacteria- and algae-dominated crust with ~~traces of~~few lichens and ~~few~~ bryophytes indicated an earlier ~~pioneer~~ stage of biocrust development (~~cf.~~ Colesie et al., 2016). In 2013, 25 moss and liverwort species were classified (Table 2) and formed a bryophyte-dominated crust with some cyanobacteria, algae, lichens and micro-fungi still observed ~~in minor numbers~~ within ROPs. The same was true in 2015, but first evidence of vascular plants (*Selaginella* and *Poaceae*) indicated a further ~~advanced biocrust stage~~change in the vegetation cover of the soil surface.

[Figure 2]

[Table 2]

3.2 The influence of vegetation, soil and terrain on biocrust cover

The development of biocrust cover in 2013 was positively influenced by crown cover and LAI as attributes of the surrounding vegetation (Table 3). Furthermore, it was negatively affected by slope and northness and slightly positively affected by the altitude of the research plots as terrain attributes (Table 3). Further ~~soil or~~ terrain attributes or any soil attributes did not affect the development of biocrust cover.

[Table 3]

3.3 The impact of biocrust cover on soil erosion

The results indicate that biocrusts strongly affect soil erosion. ROPs with biocrust cover below 10 % showed a mean sediment delivery of 302 g m^{-2} and a mean runoff volume of 39 L m^{-2}, whereas ROPs with biocrust cover above 50 % showed a mean sediment delivery of 74 g m^{-2} and a mean runoff volume of 29 L m^{-2}. Both biocrust and stone cover, as well as total soil surface cover (comprising both biocrust and stone cover, p<0.001) negatively affected sediment discharge delivery (p<0.001, Table 4). In addition, soil surface cover negatively affected surface runoff (p=0.003). However, only biocrust but not stone cover mediated the effect of runoff. Furthermore, crown cover, SOM and rainfall amount affected sediment dischargedelivery, whereas runoff was affected by crown cover and rainfall amount. ROPs primarily influencedwith increased by stone cover showed higher sediment discharge delivery and surface runoff thancompared to those primarily influenced bywith increased biocrust cover (Fig. 3).

[Table 4]

[Figure 3]

4 Discussion

4.1 Temporal development of biocrust cover

Biocrusts were detected widely within the experiment and occupied a considerable area in the interspaces of the growing tree community. Thus, the first part of hypothesis 1, stating that biocrusts are able to coexist in mesic early successional subtropical forests, can be confirmed, as biocruststhey successfully colonized the newly created habitats originating from the disturbance by forest clear-cutting and weeding (Bruelheide et al., 2014). Although biocrusts have been mainly defined to occur in dryland regions (Weber et al., 2016), they can also appear as a transient feature in mesic environments after major singular or repeated disturbance events (Büdel et al., 2014, Fischer et al., 2014). In the current study,The deforestation provided a local arid micro-environment, which initiated early biocrust development (Büdel, 2003b). At this earlyyoung stage of the forest developmentecosystem, biocrusts were highlyable to competitivecoexist with upcoming tree saplings and formed a pioneer vegetation on the soil surface (Langhans et al., 2009), which then prepared the upper soil layer for furtherprovides the basis for the growth of vascular other plants by the input of carbon and nitrogen (West, 1990; Evans and Johansen, 1999). Biocrusts generally are known to facilitate the succession of vascular plants to more advanced stages (Bowker, 2007), but. Accordingly, tree growth and thus crown cover provide shade and protection from wind, which thencan also leads to an advancement in biocrust development, e.g. due to the protection from direct sunlight (Zhao et al., 2010; Tinya and Ódor, 2016). The bryophyte-dominance of biocrusts in 2013 documented this development into a later and somewhat moister successional stage (Williams and Büdel, 2012). Biocrusts are often dominated by one organism group, with cyanobacterial crusts being indicators for early stage crusts and drier conditions (Malam Issa et al., 1999; Malam Issa et al., 2007). The successional development of biocrusts within the BEF China experiment seemed to be faster than e.g. reported by Zhao et al. (2010) for the Chinese Loess Plateau, who claimed biocrusts from a 3-year old site as early successional dominated by cyanobacteria. Later-stage Bbryophytes in biocrusts have received comparatively little attention in forest understorey (Gilliam, 2007) and biocrust studies (Weber et al., 2016) and in Asia only 23 different species have been reported within biocrusts up to now (Seppelt et al., 2016). Thus, this study with 25 recorded moss and liverwort species, most of them being new records within Asian biocrusts (Burkhard Büdel, personal communication) substantially increases the knowledge on biocrusts of this region.

~~Nevertheless, t~~The extent of biocrusts was strongly increasing since 2012 i.e. three years after tree replantation and still gaining coverage in the sixth year after ~~our~~the experimental setup. Thus, the second part of hypothesis 1, stating that crust cover decreases with ongoing canopy closure, has to be rejected. Even if single trees were already up to 7.4 m high (Li et al., 2014) and LAI was up to 5.35 in 2013, biocrusts still remained ~~competitive~~ coexisting within the early stage forest ecosystem. ~~Moreover~~Furthermore, increasing crown cover and LAI seemed to foster the development of bryophyte-dominated biocrusts at this ecological stage. By the end of this study, there were indications that biocrust cover may start to be pushed back, as first vascular plants appeared in between. This is in line with existing literature, demonstrating that~~It is assumed that with~~ continuing tree growth will cause~~the~~ biocrust communities ~~will~~to adapt ~~and the~~with an altered composition of moss and liverwort species ~~will further change~~ (Eldridge and Tozer, 1997; Fenton and Frego, 2005; Goffinet and Shaw, 2009). ~~Thus~~It has been shown, that bryophytes ~~will likely~~ switch from species favouring sunny habitats to more shade-tolerant species (Zhao et al., 2010; Müller et al., 2016). In addition, there might also be a reduction in bryophyte diversity due to shady conditions, where only a smaller number of species could prevail. ~~Nevertheless, adapting biocrusts seem to be able to coexist widely with vascular plants under a nearly closed tree canopy, even if i~~In~~t~~ later stages ~~is assumed that~~ biocrust cover will be replaced by vascular vegetation (in light forests) or buried under persisting leaf litter (under darker conditions). ~~decrease in later years with an increasing leaf litter layer (Belnap and Lange, 2003).~~ In this context, the ecological roles of biocrusts in succession models and plant restoration are of interest (Hawkes, 2004; Bowker, 2007). In particular, biocrust succession in temperate climates has received limited scientific attention (Read et al., 2016). ~~Restoration of biocrusts in disturbed ecosystems could be a practical approach to improve and accelerate plant community rehabilitation after disturbance and~~ Furthermore, there are several projects under way to establish successful restoration techniques in arid and semi-arid environments (Rosentreter et al., 2003; Bowker, 2007; Chiquoine et al., 2016; Condon and Pyke, 2016), which could be adapted to mesic environments. Nevertheless, it has to be stated here that biocrust restoration might be dispensable in some mesic systems, as natural reestablishment appeared to be very fast in this study.

4.2 The influence of vegetation, soil and terrain on biocrust cover

In the current study, ~~T~~the development of biocrusts was influenced by vegetation and terrain ~~attributes~~, but not by soil attributes. Thus, hypothesis 2, stating that the biocrust development is not only influenced by surrounding vegetation, but also by soil and terrain, can only~~be~~ partly be confirmed for this ecosystem. As ~~already shown before~~demonstrated above, high crown cover and LAI positively affected the development of biocrust cover in 2013. This increase in biocrust cover is likely caused by~~finding is due to the~~ successional alteration of biocrusts towards bryophyte-dominance. Mosses and liverworts profit from humid conditions and a higher protection from light compared to cyanobacteria- or lichen-dominated crusts (Ponzetti and McCune, 2001; Marsh et al., 2006; Williams et al., 2013).

The successional development of biocrusts within the BEF China experiment was faster than reported by Zhao et al. (2010) for Chinese grasslands (Loess Plateau), who claimed biocrusts from a 3-year old site as early successional and dominated by cyanobacteria. The recovery rate was also faster than described by Eldridge (1998) and Read et al. (2011) for semi-arid Australia, each one of the very few studies on biocrust recovery under woodland. In the study presented here, the rapid change in biocrust community composition is mainly linked to the growth rates of surrounding trees in this subtropical forest. As functions of biocrusts, such as erosion reduction, are species-dependent, the rapid change in species composition might also lead to considerable variations in functional responses. Further studies are required to investigate species changeover times in different environments and particularly in disturbed mesic ecosystems. ~~Environmental factors such as water content, light intensity and temperature influence e.g. photosynthesis and respiration (Zhao et al., 2010; Weber et al., 2012).~~

Furthermore, several terrain attributes affected biocrust cover. Slope was the most prominent of those factors, causing a considerable decline in biocrust cover with increasing slope.~~,~~ This finding was ~~being~~ explained by their decreasing ability to f~~asten~~ix themselves on the soil surface at high slope angles and thus their tendency to erode from the soil surface, ~~especially~~ when large surface water flows occur~~red~~ during rainfall events (Chamizo et al., 2013; Bu et al., 2016). Thus, the surface-protecting effect of biocrusts decreases at steep plantation sites and during heavy monsoon rainfall events, which frequently occur in the broader research area in Jiangxi Province, China (Yang et al., 2013; Goebes et al., 2015). Moreover, microclimatic factors played a role in the development of biocrusts. Northness showed a positive impact on biocrust cover~~s~~ and indicated that slope orientations towards the incident sunlight directly influence the biocrust development. This was also observed in other studies in arid and semi-arid areas (Bowker et al., 2002; Zaady et al., 2007). Furthermore, biocrust development depended on the altitude, which is probably also by affecting microclimatic conditions (Kutiel et al., 1998; Chamizo et al., 2016; Bu et al., 2016). Those microclimatic factors are additionally altered by the growing tree vegetation itself.

Interestingly, SOM and pH did not affect biocrust cover in this study~~.~~, whereas generally, underlying substrates are a main factor for bryophyte development (Spitale, 2017) and soil attributes are known to strongly influence biocrust cover (Bowker et al., 2016). At the experimental area, ~~I~~increased organic matter contents and acidic conditions have been determined~~, as they were found at the experimental area~~ (Scholten et al., 2017), which ~~generally~~ favour the development of bryophyte-dominated biocrusts (Eldridge and Tozer, 1997; Seppelt et al., 2016). Nevertheless, ~~discrepancies~~the variation between the research plots w~~ere~~as small and apparently not large enough to cause prominent differences in biocrust development. Comparisons between forest plantations on different substrates would help to clarify the influence of soil attributes on biocrust development in those environments and to assess their effect in a broader environmental context (Spitale, 2017).

4.3 The impact of biocrust cover on soil erosion

Biocrust cover clearly mitigated interrill soil erosion in this early stage ecosystem and thus hypothesis 3 was confirmed. Sediment delivery was strongly reduced with increasing biocrust cover. For arid environments, e.g. Cantón et al. (2011) and Maestre et al. (2011) showed that sediment delivery from soil surfaces covered with biocrusts decreases compared to bare soil surfaces with physical crusting (from 20 g m^{-2} to <1 g m^{-2} and 40 g m^{-2} to <5 g m^{-2}, respectively), both studies using micro-scale runoff plots (0.25 m^{2}). The study presented here shows, that biocrusts fulfil this key ecosystem service also within a particular mesic habitat, even if their biomass and soil penetration depth is low compared to trees. This functional role is due to the fact that ~~B~~biocrusts attenuate the impact of raindrops on the soil surface and greatly improve its resistance against~~ soil erosion~~ sediment detachment (Eldridge and Greene, 1994; Goebes et al., 2014; Zhao et al., 2014). Moreover, they have the ability to glue loose soil particles by polysaccharides extruded by ~~cyanaobacteria~~cyanobacteria and green algae (Buscot and Varma, 2005). In the current study, protonemata and rhizoids of mosses and liverworts were observed to be most effective by weaving and thus fixing the first millimetres of the top soil, as also described by ~~(~~Bowker et al., 2008~~)~~ Bowker et al. (2008). *Pogonatum inflexum* and *Atrichum subserratum* are well known to have a positive effect on erosion control due to their sustained protonema system (Martin Nebel, personal observation). Furthermore, bryophytes increase the formation of humus, which in turn assists to bind primary particles into aggregates (Scheffer et al., 2010; Zhang et al., 2016). ~~Thus, biocrusts contribute to the aggregation of soil particles and stabilize the upper soil surface.~~

Whereas a partial stone cover d~~oes~~id not decrease surface runoff in this study, bryophyte-dominated biocrusts positively influenced the hydrological processes in the top soil layer regarding erosion control. Thus, they actively mitigated initial soil erosion compared to abiotic components such as stones and pebbles. ~~Furthermore, b~~Biocrusts ~~are known~~have been frequently shown to influence hydrological processes such as surface runoff and infiltration rates (Belnap, 2006~~;~~ Cantón et al., 2011; Chamizo et al., 2012; Rodríguez-Caballero et al., 2013). ~~Just r~~Recently, Chamizo et al. (2016) showed that ~~runoff and infiltration also depend on the investigation scale. Whereas point based measurements showed both increasing and decreasing runoff through biocrusts depending on the study site, studies of larger scale (>2 m^{2}) revealed that~~ biocrusts decrease runoff generation at larger scale (>2 m^{2}~~(~~Chamizo et al., 2016), but converse behaviour has also been found (Cantón et al., 2002; Maestre et al., 2011). ~~Whereas a partial stone cover does not enhance infiltration, bryophyte-dominated biocrusts positively influence the hydrological processes in the top soil layer regarding erosion control. Thus, they actively mitigate initial soil erosion compared to abiotic components such as stones.~~ ~~Moreover, r~~Reducing effects on runoff are related to ~~the~~ biocrusts species composition (Belnap and Lange, 2003) and later developmental biocrust stages with higher biomass levels provide more resistance to soil loss (Belnap and Büdel, 2016). Especially bryophyte-dominated crusts ~~appear~~ have shown to enhance infiltration and reduce runoff due to their rhizome system, ~~while~~causing soil erosion rates to stay low (Warren, 2003; Yair et al., 2011). Also other ~~F~~field studies ~~in Utah, USA,~~ revealed that later stage biocrusts, containing both lichens and ~~mosses~~bryophytes, offer more protection against soil erosion than cyanobacterial crusts (Belnap and Gillette, 1997)~~.~~, as ~~T~~they provide higher infiltration potential ~~than biocrusts dominated by cyanobacteria~~ (Kidron, 1995)~~ and decrease the aggradation of soil pores by reducing the kinetic energy of raindrops (~~Eldridge and Greene, 1994~~)~~. Moreover, biocrusts dominated by bryophytes increase surface roughness and thus slow down runoff (Kidron et al., 1999; Rodríguez-Caballero et al., 2012). F~~urthermore~~inally, they also absorb water and provide ~~a certain~~comparably high water storage capacity (Warren, 2003; Belnap, 2006)~~. Especially~~ For example, *Leucobryum juniperoideum*, which has been widely found in this study,~~ –~~ is known for its water absorbing capacity (Martin Nebel, personal observation). Thus, the observed rapid change in biocrust composition from cyanobacteria to bryophyte dominance improved soil erosion control in this forest environment. Whereas a partial stone cover does not enhance infiltration, bryophyte-dominated biocrusts positively influence the hydrological processes in the top soil layer regarding erosion control. Thus, they actively mitigate initial soil erosion compared to abiotic components such as stones. This study showed, that biocrust covers play an important role in the avoidance of severe soil erosion in early successional forest plantations. This effect should be considered for the replantation of forests in regions endangered by soil erosion. Furthermore, the artificial cultivation of mosses in such initial forest ecosystems could improve erosion control (Bu et al., 2013a; Zhao et al., 2016). At this point, the importance of biocrusts in the rehabilitation of disturbed ecosystems comes into focus again (Bowker, 2007).

5 Conclusion

This study investigated the development and distribution of biocrusts in an early stage subtropical forest ecosystem plantation as well as their impact on interrill soil erosion after human disturbance. The following conclusions were obtained:

(1) Biocrusts occurred widely in this mesic early successional forest ecosystem in subtropical China. They developed quickly to later-stages in this mesic environment and were already dominated by bryophytes after three years of tree growth (25 bryophyte species classified). After six years of continuing canopy closure, biocrust cover was still increasing. Further monitoring under closing tree canopy is of importance to detect changes in biocrust cover and species composition in subtropical environments. As this study discusses a very particular subtropical forest environment, where trees were replanted after clearcutting, results have to be viewed with this particular setup in mind. Further studies on biocrust development in different disturbed forest ecosystems appear to be of high interest.

(2) The surrounding vegetation and underlying terrain affected biocrust development, whereas soil attributes did not have an effect at this small experimental scale. Besides high crown cover and LAI, the development of biocrusts was favoured by low slope gradients, slope orientations towards the incident sunlight and altitude. Further research appears to be necessary to explain effects of terrain attributes such as aspect or elevation and effects of underlying soils and substrates.

(3) Soil surface cover of biocrusts largely affected soil erosion control in this early stage of the forest ecosystemplantation. Bryophyte-dominated crusts had showed erosion-reducing characteristics regarding both with regard to sediment discharge delivery and surface runoff. Furthermore, they were more effectively decreasing to decrease soil losses compared tothan abiotic soil surface covers. Thesee functional propertieserosion-reducing influence of bryophytes-dominated biocrusts and their rapid development from cyanobacteria-dominated crusts with regard to soil erosion need should to be considered forin management practices in early stage forest plantations. Further research is required on functional mechanisms of different biocrust and bryophyte species and their impact on soil erosion processes.

Data availability

Data are publicly accessible and archived at the BEF China data portal (http://china.befdata.biow.uni-leipzig.de).

Author contribution

Steffen Seitz and Thomas Scholten designed the experiment and Steffen Seitz, Zhengshan Song, Kathrin Käppeler and Carla L. Webber carried it out. Martin Nebel and Kathrin Käppeler classified biocrust types and determined bryophyte species. Steffen Seitz, Philipp Goebes and Karsten Schmidt performed the statistical models. Steffen Seitz, Xuezheng Shi and Bettina Weber prepared the manuscript with contributions from all co-authors. The authors declare that they have no conflict of interest.

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Tables

Table 1: Erosion, soil, soil cover, vegetation and terrain attributes in 170 runoff plots (ROPs~~, n=170~~) and on 34 research plots (~~n=34~~with five ROPs each) in Xingangshan, Jiangxi Province, PR China in 2013.

	Min	*Mean*	*Max*
Runoff plots (ROPs, four measured rainfall events, n=~~170~~334)			
Sediment ~~discharge~~ delivery [g]	21.6	195.5	989.0
Surface runoff [ml]	3.1	40.3	111.8
Rainfall amount [ml]	25	94	178
Runoff plots (ROPs in use, n=170)			
Slope [°]	5	29	60
Soil cover [%]	0	19	62
- Biological soil crust cover [%]	0	24	62
- Stone cover [%]	0	4	42
Crown cover [%]	0.00	0.32	1.00
Leaf area index (LAI)	0.00	0.73	5.35
Research plots (n=34)			
Bulk soil density [g cm^{-2}]	0.83	0.98	1.12
Soil organic matter [%]	4.2	6.5	9.7
pH (KCl)	3.24	3.66	4.00
Altitude [m]	119	167	244
MCCA	0.98	2.07	3.81
TRI	0.72	2.39	3.86
Eastness	-0.86	0.09	0.99
Northness	-0.87	0.23	0.99

Tree height [m]	1.0	2.2	7.4
Crown width [m]	0.4	1.2	3.0

Soil cover: proportion of soil surface area covered by biocrusts or stones, crown cover: proportion of soil surface area covered by crowns of live trees, leaf area index: one-sided green leaf area per unit soil surface area, MCCA: Monte-Carlo based flow accumulation (Behrens), TRI: terrain ruggedness index (Riley), Eastness and Northness: state of being east or north (Roberts), tree height: distance from stem base to apical meristem, crown width: length of longest spread from edge to edge across the crown

Table 2: Liverwort and moss species sampled in the BEF China experiment in Xingangshan, Jiangxi Province, PR China in 2013.

Family	**Species**		**Author**
Liverworts			
Calypogeiaceae	*Calypogeia*	*fissa*	(L.) Raddi
Conocephalaceaes	*Conocephallum*	*salebrosum*	Szweyk., Buczk. et Odrzyk.
Lophocoleaceae	*Heteroscyphus*	*zollingeri*	(Gottsche) Schiffn.
Marchantiacea	*Marchantia*	*emarginata*	Reinw., Blume et Nees
Acrobolbaceae	*Notoscyphus*	*lutescens*	(Lehm. et Lindenb.) Mitt.
Mosses			
Polytrichaceae	*Atrichum*	*subserratum*	(Harv. et Hook. f.) Mitt.
Pottiaceae	*Barbula*	*unguiculata*	Hedw.
Bryaceae	*Bryum*	*argenteum*	Hedw.
Leucobryaceae	*Campylopus*	*atrovirens*	De Not.
Dicranellaceae	*Dicranella*	*heteromalla*	(Hedw.) Schimp.
Pottiaceae	*Didymodon*	*constrictus*	(Mitt.) K. Saito
Pottiaceae	*Didymodon*	*ditrichoides*	(Broth.) X.J. Li et S. He
Ditrichaceae	*Ditrichum*	*pallidum*	(Hedw.) Hampe
Entodontaceae	*Entodon*	spec.	sterile
Hypnacaea	*Hypnum*	*cupressiforme*	Hedw.
Hypnacaea	*Hypnum*	*macrogynum*	Besch.
Leucobryaceae	*Leucobryum*	*juniperoideum*	(Brid.) Müll. Hal.
Bartramiaceae	*Philonotis*	*marchica*	(Hedw.) Brid.
Bartramiaceae	*Philonotis*	*mollis*	(Dozy et Molk.) Mitt.
Bartramiaceae	*Philonotis*	*roylei*	(Hook. f.) Mitt.
Mniaceae	*Plagiomnium*	*acutum*	(Lindb.) T.J. Kop.
Polytrichaceae	*Pogonatum*	*inflexum*	(Lindb.) Sande Lac.
Thuidiaceae	*Thuidium*	*glaucinoides*	Broth.
Mniaceae	*Trachycystis*	*microphylla*	(Dozy et Molk.) Lindb.
Pottiaceae	*Trichostomum*	*crispulum*	Bruch

Table 3: Results of the final linear mixed effects (LME) model for vegetation, soil and terrain attributes on biological soil crust cover in Xingangshan, Jiangxi Province, PR China in 2013 (*: p < 0:001; **: p < 0:01; *: p < 0:05; .: p < 0:1; ns: not significant; n=215).**

	Biological soil crust cover			
	denDF	F	Pr	estim.
Fixed effects				
Crown cover	136	12.9	***	10.8
Bulk soil density	37	0.03	ns	3.65
SOM	39	1.11	ns	(-)0.95
pH (KCl)	38	2.47	ns	(-)16.7
Altitude	37	3.69	.	0.80
Slope	191	7.53	**	(-)2.72
MCCA	39	0.02	ns	0.33
TRI	38	0.04	ns	(-)0.40
Eastness	37	2.73	ns	(-)4.23
Northness	37	9.14	**	5.99
Tree species richness	38	1.22	ns	(-)0.27
Random effects		*SD*	*Variance*	
Site		<0.01	<0.01	
Plot		<0.01	<0.01	
Vegetation attribute fitted in exchange to crown cover				
Leaf area index	107	42.8	***	5.98

SOM: soil organic matter; MCCA: monte carlo based flow accumulation; TRI: topographic roughness index; denDF: denominator degrees of freedom; F: F value; Pr: significance; estim.: estimates

Table 4: Results of the final linear mixed effects (LME) models for sediment ~~discharge~~ delivery and surface runoff with surface cover split into biological soil crust cover and stone cover in Xingangshan, Jiangxi Province, PR China in 2013 (*: p < 0:001; **: p < 0:01; *: p < 0:05; .: p < 0:1; ns: not significant; n=334).**

	Sediment ~~discharge~~delivery				Surface runoff			
	den DF	F	Pr	estim.	den DF	F	Pr	estim.
Fixed effects								
Crown cover	130	6.53	*	(-)0.15	173	9.11	**	(-)0.14
Slope	151	1.23	ns	0.06	168	2.25	ns	(-)0.06
Surface cover								
- Biocrust	151	50.2	***	(-)0.38	159	8.11	**	(-)0.12
- Stone	136	10.3	**	(-)0.19	188	1.66	ns	(-)0.06
SOM	44	5.71	*	(-)0.08	72	2.43	ns	0.12
Rainfall	95	5.46	*	(-)0.08	302	13.2	***	0.14
Tree species richness	22	0.46	ns	0.05	68	0.11	ns	(-)0.03
Random effects		*SD*	*Variance*			*SD*	*Variance*	
Precip. event : plot		0.199	0.040			0.537	0.288	
Tree composition		0.292	0.085			0.000	0.000	
Site		0.466	0.217			0.443	0.196	
Plot : ROP		0.441	0.195			0.269	0.073	

SOM: soil organic matter; denDF: denominator degrees of freedom; F: F value; Pr: significance; estim.: estimates

Figures

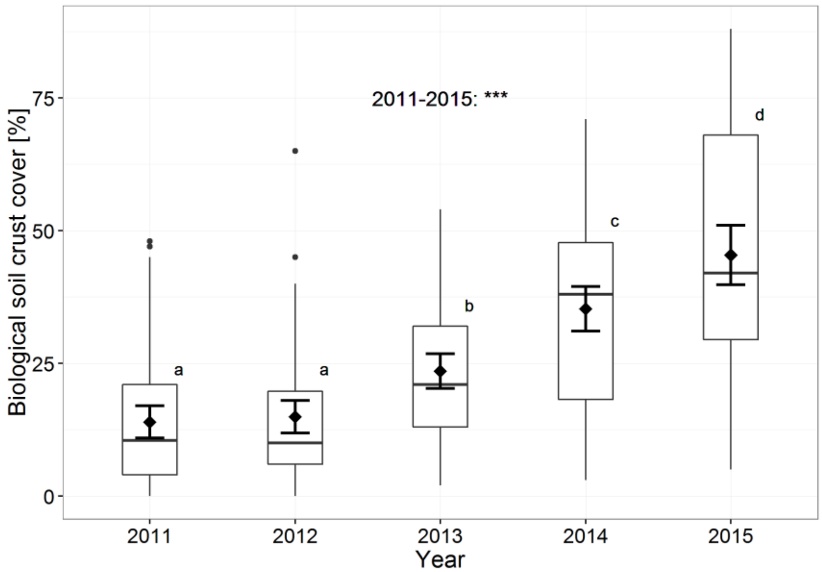
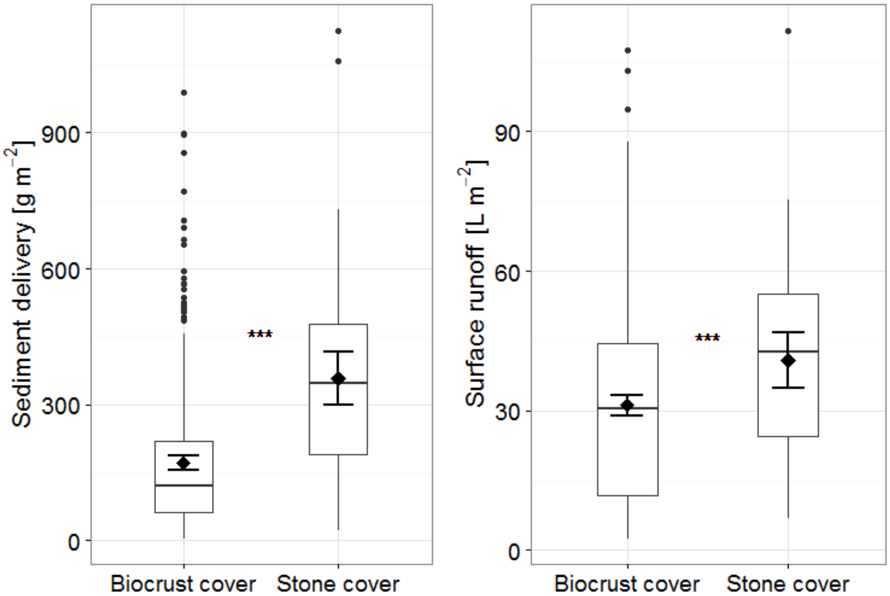


Figure 1: The development of biological soil crust cover in runoff plots of the BEF China experiment from 2011 to 2015 in Xingangshan, Jiangxi Province, PR China (n=350). Horizontal lines within boxplot represent medians and diamonds represent means with standard error bars. Points signify outliers and small letters significant differences (p<0.001).

Figure 2: Successional stages of biological soil crusts in two exemplary runoff plots (top row and bottom row, 0.4 m × 0.4 m each) in 2011, 2013 and 2015 (from left to right) at the BEF China experiment in Xingangshan, Jiangxi Province, PR China.



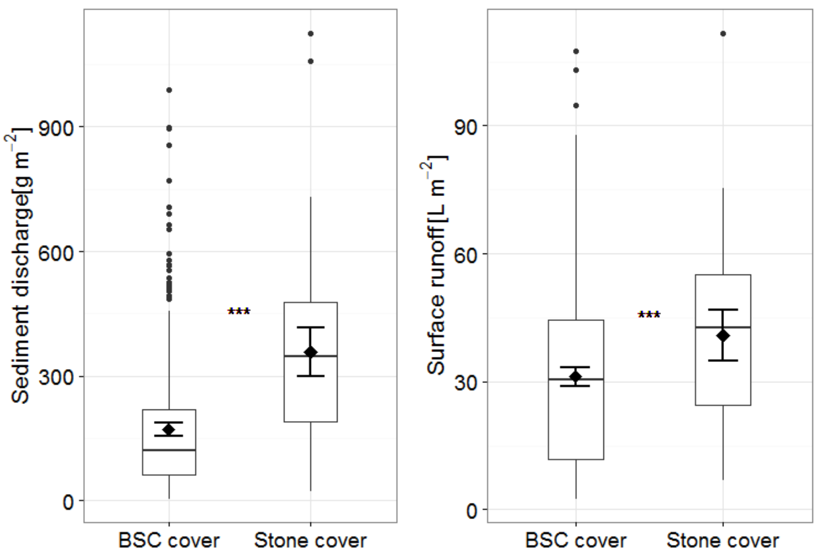


Figure 3: The influence of runoff plots dominated by biological soil crust cover (~~BSC,~~ n=281) and stone cover (n=53) on sediment ~~discharge~~ delivery and surface runoff in Xingangshan, Jiangxi Province, PR China in 2013. Horizontal lines within box plots represent median and diamonds represent mean with standard error bars.