We would like to thank the reviewers for their helpful comments, which helped to improve our manuscript greatly. The revised manuscript includes all the points raised by the reviewers. While the reviewers' comments are shown in grey text, our responses are formatted as standard text. Line indications refer to the revised manuscript without marked changes.

Response to referee's letter:

Referee #1, Thomas Fischer

The particular value of the study is the comparison of the eco-physiological performance between a cyanobacterial and a green-algal biocrust from temperate habitats, which are somewhat underrepresented in the biocrust related literature. I recommend publication of the manuscript after minor revision.

Minor remarks

Remark #1: Figure 4: I guess the upper line in each graph is under light, and the lower line in the dark? What was the PPFD?

We have edited figure itself and the figure caption to clarify which line represents which physiological process.
Also, we have added information about the light intensity (PPFD) applied during the measurements.
P21; Line 1-4.

Remark #2: p. 7 l. 26 and Fig. 5: Water contents are given in mm here, but as normalized water content in the rest of the manuscript. I think the paper would benefit from providing some information on how many mm were 100% for each BSC type. For soils, water content expressed as mm links with volumetric water content (or water potential) through soil texture, depth and humus content, which are essential to relate to each other optimum moisture ranges for BSC_all, BSC_dom and BSC_soil. While, for example, the optimal ranges for G-BSC_dom and C-BSC_dom are similar, the difference between G-BSC_dom and G-BSC_soil is larger than the respective difference for the cyanobacterial crust: This could mean that the amount of fine particles, or sampling depth, or soil C, or all together, were greater for the Zygogonium crust. The authors are aware of that point (p. 9 l. 12-13): "A general difference between BSC_all and BSC_dom concerning optimal water content is likely owed to the different water holding capacities of the soil."

Remark #3: p. 8 l. 19-20: High abiotic CO2-release may point to carbonates being present in the soil solution and to high pH. The authors discuss that issue on p. 10 l. 20 ff.

Remarks #2 and #3 let me recommend to provide some information on soil texture class, pH, organic C content and sampling depth for each site in the M&M section.

According to this suggestion we have included information about soil texture, organic carbon content, pH, sampling depth and also water holding capacity of the soil. The results underline the reviewers suggestions that especially the fine particle size is responsible for the higher water holding capacity of the soil in the *Zygogonium* crust:
P.4, L. 13 - 15
P.4, L. 21 - 23
P.4, L. 26
We would like to thank the reviewer for the suggestion to provide information about the maximum water holding capacities, as this helps to understand and interpret the gained data and makes the values available for comparison with literature. According to the suggestion the maximum water holding capacities of both BSCs were added, to make the optimum water content comparable to maximum saturation situations. The values were calculated as follows: maximum water holding capacity of BSC_{soil} added to maximum water holding capacity of BSC_{org}.
P. 8, L. 13-14

Remark #4: p. 10 l. 1-2: The authors state a higher water holding capacity (WHC) of the Nostoc crust than the Zygogonium crust and attribute this to exopolysaccharides (EPS), which is in full agreement with the literature. However, apart from its lower NP performance, the Zygogonium crust had higher amounts of chlorophyll (Table 1), which traditionally is interpreted as a biomass equivalent. Is it possible that high Zygogonium biomass compensates for high WHC of the EPS of Nostoc? I think that the statement of higher WHC of the Nostoc crust could be substantiated by some experimental data, or, for example, from presenting some close-up photographs of the crusts to get a visual impression of crust development.

The referee is correct in saying that it would be only logical for *Z. ericetorum* to hold more water than *N. commune*, as the green algal crust has a higher chlorophyll concentration and therefore more biomass per area than the cyanobacterial crust. However, it is difficult to compare chlorophyll content between cyanobacteria and green algae. As we explain in our discussion (P. 11 L. 25-29), chlorophyll doesn't seem to be a suitable reference value to compare NP rates between green algae and cyanobacteria, because the current calculations exclude the phycobilisomes of cyanobacteria. Therefore, the photosynthetic active pigments in cyanobacteria are underestimated and their biomass as well, as this value is traditionally interpreted as biomass.

Additionally, the factor EPS masks the effect of more biomass generally being able to hold more water: *Nostoc commune* does possess very thick EPS layers, that are able to hold up to 20 – 30 times their dry weight, while *Z.* ericetorum can't take up as much water (SATOH, Kazuhiko, et al. Recovery of photosynthetic systems during rewetting is quite rapid in a terrestrial cyanobacterium, Nostoc commune. Plant and cell physiology, 2002, 43. Jg., Nr. 2, S. 170-176. SHAW, Eric, et al. Unusual water flux in the extracellular polysaccharide of the cyanobacterium Nostoc commune. Applied and environmental microbiology, 2003, 69. Jg., Nr. 9, S. 5679-5684.). In percent the cyanobacterial crust from Fig. 4 could hold up to 4562% H_2O compared to its dry weight while having 88% of its maximum NP rate. The green algal crust could only hold 435% H_2O compared to its dry weight while having 18% of its maximum NP rate. This is also now stated in the manuscript on page 8, lines 13-15.

Referee #2

Early successional stages of biocrusts are not only important due to the fact of being pioneer colonizers of barren habitats, but also because climatic predictions point to them as possible dominant organisms in areas under strong hydric stress, where later successional stages would not succeed. Up to the authors to use this concept in the introduction in order to remark even more the importance of their study.

We agree with the reviewer that climate change might increase the difficulty of later developmental stages of BSC to establish in habitats with less available water and increased temperatures. It might therefore be possible that a climax community dominated by cyanobacteria and green algae will be established. Nonetheless, it still needs to be mentioned, that there are in fact studies of hot and dry habitats, where e.g. lichens or bryophytes are present as the climax community (e.g. Zedda, L., Gröngröft, A., Schultz, M., Petersen, A., Mills, A., & Rambold, G. (2011). Distribution patterns of soil lichens across the principal biomes of southern Africa. Journal of Arid Environments, 75(2), 215-220. Or Weber, B., Graf, T., & Bass, M. (2012). Ecophysiological analysis of moss-dominated biological soil crusts and their separate components from the Succulent Karoo, South Africa. Planta, 236(1), 129-139.)

Nonetheless, we found the comment really helpful and are glad that this point has been brought to our attention. We will include it in our introduction as it strengthens the need for more studies similar to ours. However, it is important to mention that the BSCs investigated in this study are from temperate regions in which climate change will most probably not reduce rainfall as much as that later successional stages of BSC will disappear completely, although a change in community composition is expected. We will include a remark that explains that studies taken in habitats that are more sensitive to changes in rainfall should be investigated. It is discussed now on page 2, lines 18-23.

INTRODUCTION

Page 4 lines 4-5: Please clarify this sentence. I think that authors want to say here that depending of the treatment made to the sample (sample with soil, without it, or bare soil) a different response will be found in the gas exchange experiments. But I do not understand the sentence: "We expect that the position and arrangement of the sample inside the measurement system, here a cuvette, will influence the photosynthetic values".

Are the authors analyzing, at some point, how the position of the sample inside the cuvette is influencing gas exchange measurements?

I think that the sentence is confusing and is not a good choice to close a, on the other hand, well developed introduction

The referee is correct in pointing out, that we did in fact, not alter the position of the sample inside the cuvette. We have removed this sentence from the introduction and discuss the topic in greater detail in the discussion (Page 11, line 9-30).

MATERIAL AND METHODS

P5, L13: Could authors provide some info about why was this set of temperatures chosen for the experiment?

The chosen temperatures are in accordance with other eco-physiological studies on BSCs (e.g. Weber, B., Graf, T., & Bass, M. (2012). Ecophysiological analysis of moss-dominated biological soil crusts and their separate components from the Succulent Karoo, South Africa. Planta, 236(1), 129-139. Or Lange, O. L., Belnap, J., Reichenberger, H., & Meyer, A. (1997). Photosynthesis of green algal soil crust lichens from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO 2 exchange. Flora, 192(1), 1-15. Or Lange, O. L. (1980). Moisture content and CO 2 exchange of lichens. Oecologia, 45(1), 82-87.)

Additionally, they represent the average temperature range of temperate Europe (see e.g. site Homburg in Raggio, J., Green, T. A., Sancho, L. G., Pintado, A., Colesie, C., Weber, B., & Büdel, B. (2017). Metabolic activity duration can be effectively predicted from macroclimatic data for biological soil crust habitats across Europe. Geoderma, 306, 10-17.) which the study organisms face most often during a year. We wanted to investigate a broad but realistic range of temperatures to create a very detailed response of the organisms to different climatic conditions.

We have added the appropriate information on page 6, lines 2 – 4.

P6, L9: I do not see clear how a one-way ANOVA can be, at the same time, a multifactorial ANOVA. To my understanding, the authors are using a one way ANOVA with type of crust being the factor (meaning that only on efactor is being analyzed), and each of the dependent variables analyzed at each moment (NP, DR, WC…..being the variable. Is this correct? Probably just a matter of terminology but I see it a bit confussing as written now

We have corrected this sentence. We used a multifactorial ANOVA where we used NP, DR, optimum water content range and WCP as the response variables. The explaining variables were temperature and organization form (BSC_{all}, BSC_{org} and BSC_{soil}), or an interaction of the two variables. For light compensation and light saturation only a grouped t-test has been performed.

This is now clarified on page 6, lines 16 – 19.

P6, L15: A space is needed in “bystatistically”. Besides, which methodology was used to compare these limits?

Space was added. Also, the statistical method was added and described in detail (page 6, line 24-27). Here a multifactorial ANOVA was used, where the explaining variables were organization form and crust dominating species (green algae or cyanobacteria) and the response variable was optimal water content.

RESULTS

P7 L23-25. After having a look to Fig. 4 I agree with what is written here, but I think that is falling in contradiction with what is written in the abstract about the issue: “and low or no depression in carbon uptake at water suprasaturation” (abstract L18). I think that the text in the abstract regarding this issue should be changed to fit more accurately what is written in results

The sentence in the abstract was rephrased. Also, we rephrased “low” to “minor depression” to emphasize that we mean a depression where the NP is only inhibited slightly (Page 1, line 18-19)

P7 L27-28: I think that what authors want to underline here is that C-BSC and G-BSC water content values are close between them both situations, “all” samples and “dom” samples. But as it is written now it seems that, for example, for C-BSC “all” and “dom” values are similar between them, which does not seem to be correct. Just a small correction would solve the possible confusion.

This sentenced was rephrased (P: 8, L. 10-12).

FIGURES

Fig. 2. I think that both sub-graphs should be scaled equally at the Y axis in order to compare gas exchange rates between C and G crust types easily

The Y axis has been changed according to the suggested amendments.

Fig. 4. Please indicate in the figure legend the amount of light used for the experiment

Added the PPFD under which the water curve was measured according to suggestion of both referees.

Fig. 6. This figure is hard to follow for me. I think that the variable “effect size” is a ratio between C and G crust types calculated for “dom” and “all” samples and based on area of each sample and chlorophyll content, but I do not understand why such ratio is called “effect size”. Could authors please provide more explanations about this graph? I do not understand either that bump of the effect size at 25 C for chlorophyll based net photosynthesis. I have read in different parts of the text that authors consider that net photosynthesis has not a statically significant drift with temperature on an area basis, at least for the green algae crust. Does this graph mean that temperature has a significant effect over photosynthesis on a chlorophyll basis but not on area basis? Besides, the figure is supposed to show differences in the effect size for both N. commune crusts and Z. ericetorum, but I do not see clearly which is which in the graph.

Paragraph in results (P. 8, L 23- P.9 L 4) has been rephrased. We would like to provide some more information here and explain the name “effect size” on the chart. We saw that *Z. ericetorum* crusts always had much lower NP rates then *N. commune* crusts and separated organism, even though we would expect the exact opposite, as the green algal crust had up to 181 times higher chlorophyll rates per area, which would enable the crust to assimilate much more CO_2 than the cyanobacterial crust. We were therefore interested if this higher NP rates of *N. commune* were caused by the eco-physiological features, like a CCM or caused by methodological mistakes. Therefore, we compared the NP rates of both organisms for both reference values, chlorophyll and area. If we could detect the same pattern of much higher NP rates in *N. commune* in both reference values, we would prove that eco-physiology was the driving factor. What we did was: We calculated NP for *N. commune* and for *Z. ericetorum* based on area and on chlorophyll each. Then divided the NP/Chlorophyll rates of *N. commune* with the NP/chlorophyll rates of *Z. ericetorum*. Next, we did the same division for the NP rates based on area. If the resulting ratios would have the same size, reference values would have no effect on the higher NP rates, therefore only eco-physiological differences would explain the much higher NP rates in the cyanobacterial crust. Our results showed the opposite: there was an obvious effect on reference values, showing in the always higher bars in chlorophyll based NP rates. We suppose therefore, that chlorophyll calculations as they are used at the moment, are not suitable to calculate NP rates in cyanobacteria, as they exclude phycobilisomes that also are responsible for NP rates. This will result in an overestimation of NP rates in cyanobacteria: In BSC 25 °C we can see that NP based on area supports that *N. commune* does have a seven times higher NP rate than *Z. ericetorum*. But NP based on chlorophyll describes a difference of 42 times higher NP rates for the cyanobacterial crust, resulting in an overestimation of NP rates in cyanobacteria up to six times compared to NP rates based on area.

We did not only do this calculation for the separated organism but for the intact BSC systems, too. The much higher value of 42 times higher NP rates if they are based on chlorophyll instead of area is also owed to a temperature dependency of *Z. ericetorum* that we could not detect in *N. commune*, increasing the effect at 25 °C. The graph does not show that there is a temperature dependency visible if the NP values are based on chlorophyll but not on area basis. It only shows that the effect of temperature is stronger on chlorophyll than on area basis, but an effect is visible for both reference values. The shape of the response is only different, because the reference values are of different suitability.

The name effect size is originating from the effect that the reference value has on the NP rate, but as this will confuse readers we changed it to “Ratio of NP of C-BSC/ G-BSC”.

DISCUSSION

P9 L13-22: Authors discuss in this paragraph about the differences in depression of net photosynthesis at high water content between C ”dom” crusts and G ”domÂ´l crusts, explaining ecologically why makes sense the fact of not finding this depression in Nostoc (C) and finding it in Zygogonium (G). After having a look at figure 4, it seems to me that there are more measured points at high water content (over 80% of maximum water content) in Zygogonium than in Nostoc (I mean, for CBSC dom it seems that there is a gap between 80% and 100% of water content). Any explanation for this? Could this affect the ecological interpretation of the depression of net photosynthesis at high water contents or authors are using other indicators to analyze this issue?

The displayed data represent normalized water contents, as the absolute water content was different between both crust types and comparison therefore difficult. In the completely oversaturated *N. commune* crust, the amount of water brought into the measuring system was too much for the system to produce reliable measurement values. This is because of the high cross-sensitivity of the sensor between water and CO_2 molecules. Very high water contents result in unreliable data, as water molecules might mistakenly be detected as CO_2 molecules. Due to the mentioned system limitations it was impossible to measure higher H_2O contents in *N. commune*.

This is clarified on page 8, lines 4 – 7.

P9 L23-27: I have gone to the supplement figure S2 in order to try to follow the detection of the CCM mechanism and its relationship with depression of photosynthesis at high water contents. This is something quite interesting physiologically under my pointy of view that deserves more research efforts in the literature. I have seen that authors propose (correct me if I am wrong) that the fast changes in differential CO2 response in the gas analyzer after light changes supports the existence of the CCM in Nostoc, and that this was not found in Zygogonium. Do you mean that the response of Zygogonium after light changes was different or somehow slower that in Nostoc? Is there any support in the literature for this pattern? (I mean presence or absence of CCMs in cyanobacterias Vs green algae)

We are glad to provide some in depth explanation on the carbon concentrating mechanism and how it was detected in *N. commune* but not in *Z. ericetorum*.

In general, it is known from literature that most green algae as well as all cyanobacteria do possess an inorganic CCM (Raven, J.A., Cockell, C.S., De La Rocha, C. I. The evolution of inorganic carbon concentration mechanisms in photosynthesis. In: Phil. Trans. Soc. B. (2008)). Although the mechanisms have multiple evolutionary origins, the function is the same: CCMs accumulate CO_2 around rubisco. While the mechanisms behind the accumulation might be different, the photosynthetic response is the same, which can be seen in supplement figure S2 (a): There is a strong peak in carbon uptake as soon as the light is turned on, which flattens itself after a few minutes into a straight line. Usually the uptake of CO_2 during photosynthesis looks like a sudden drop of the CO_2 concentration in the measurement system gas. Afterwards the assimilation curve stays on the same level. This can be seen in S2 (b), in the downward curve just before the black arrow marks the peak in the upwards curve. If a CCM is present, this pattern is changed. As soon as the light is turned on more CO_2 is accumulated than would normally be the case under continuous conditions of water content, light and temperature. This is because the reservoir around rubisco is filled up, which can be seen as a sudden peak in the picture S2 (a; marked by a black arrow). As soon as the light is turned off again, CO_2 that has not been used during photosynthesis is released again, which is shown with a sudden increase of CO_2 in the measurement system gas. Here the same applies: More gas is released than normally would. After a few minutes this peak drops again, under light and in dark conditions and a continuous respiration or assimilation can be detected.

We were unable to detect the same pattern in the green algae BSC, even under heavy manipulation of the measurement conditions, which included different temperatures, water contents, PPFDs and time intervals of measurement. Therefore, we conclude that no CCM can be detected in Z. ericetorum. As this was the first study to test this for this species, we provide a first insight in how this green alga photosynthesizes.

This has been clarified in the caption of Table S2.

P10 L1-2: I have been following with interest the lack of optimum temperature for net photosynthesis in the green algal crusts because it was something initially unexpected to me. What I see in relation to this in Fig. 3 regarding C and G "dom" subgraphs, is that Nostoc follows a pattern of raised net photosynthesis with temperature through all the temperature range and that Zygogonium shows a raise up to 17 C and a decrease at 22 C (but 22 showed highest photosynthesis compared with 12 C). I know that authors are supporting their idea of lack of temperature optima in the stats, which I think that is right and interesting, but after looking the graphs it seems to me that it could be perfectly said that Nostoc dom has a temperature optima at 25 C and Zygogonium at 20 C.

If Zygogonium is less adapted to long activity periods than Nostoc, I would expect a concentration of metabolic activity during softer environmental conditions, and this should shift temperature optimals to lower values rather that erase the concept of optimum temperature for net photosynthesis. On the other hand, author0s statement of lack of temperature optima in the green algae is supported with the graph 3b for GBSC all, where the link between net photosynthesis and

temperature is clearly erratic and defined by a lack of pattern. I just would like to know author0s opinion about this, because their approach to T optima concept based in stats is absolutely right to me.

The reviewer has mentioned an interesting point here. It is absolutely possible and likely that *Z. ericetorum* might show an optimum temperature point somewhere between 17 °C and 25 °C, although we can only assume a trend here. As this interval with 8°C is quite broad it would be very interesting to include this temperature. A lower optimum temperature for *Z. ericetorum* compared to *N. commune* would still be in accordance with our theory, that *N. commune* is wet and active at higher temperatures then the green alga. Additionally, it points towards the algae being able to photosynthesize at high temperatures (for Europe; see climatic data in e.g. site Homburg in Raggio, J., Green, T. A., Sancho, L. G., Pintado, A., Colesie, C., Weber, B., & Büdel, B. (2017). Metabolic activity duration can be effectively predicted from macroclimatic data for biological soil crust habitats across Europe. Geoderma, 306, 10-17.). As temperature curves of green algal dominated BSCs are quite rare, this should be done in future studies.

And this is a different issue, but it is surprising to me the lack of statistical differences in Nostoc between C-BSCall and C-BSCsoil net photosynthesis. It means that the photosynthetic cyanobacteria layer of the soil is not creating any relevant C input compared with bare soil. Interpretations for this behaviour?

The p-value responsible for this similarity is not very far from a statistical difference (p= 0.089400). We suppose that the high natural variation that has been shown in the high standard deviations of NP is responsible for this similarity. Increasing the sampling size would most likely result in a statistical difference between net photosynthesis input in C-BSC_{all} and C-BSC_{soil}. As for now, as we cannot detect differences, we have to assume that 1) the low biomass of this very young and not diverse BSC is responsible for this low NP, or 2) that only under optimum conditions a difference can be detected, or 3) that area might not be a suitable reference value to calculate NP rates, although chlorophyll would still not be the better choice here, as it would overestimate NP rates of cyanobacteria and result in a difference that is not real.

Referee #3

Comments to the Authors

The paper of Szyja et al. aims to characterize ecophysiologically early successional biological soil crusts in heavily human impacted areas. For achieving this they choose two locations with a different type of BSC: one dominated by a cyanobacteria and the other by a green alga. Overall, I found the paper representing an interesting contribution to scientific knowledge of BSC ecophysiology because: 1- there are at present not many data available about ecophysiology performance of these type of BSCs and 2- The comparison of the response between bare soil, intact BSC and isolated compo- nent is novel and very interesting. Nevertheless, I found some important problems as how the work is presented. The main problems are in the methodology where the experimental design (mainly number of replicates in each experiment) is not clear and in the results, where some of the figures are quite confusing. The question about whether the NP rates should be expressed on a chlorophyll or surface basis is not relevant here and, obviously, will differ if comparisons are made between cyanobacteria and green algae. In my opinion the number of references (85) exceeds the needs of the paper.

Beside some minor/typographic errors (i.e. check subscript in CO2 throughout the text), in general, the paper is well structured, the discussion is good and conclusions clear but it needs to show results in a way that they appear more conclusive.

In conclusion, I find the paper interesting and scientifically sound but taking into account the amount of data and how they are presented I don't think it reach the standards of BG. I have some comments and suggestions that I think will improve the paper.

Major and minor comments

TITLE

I suggest removing the second part of the title (implications for conservation and succession) as it does not reflect the content of the paper.

Second part of the title has been removed. We agree with the referee that it has no connection to the contents of the paper.

ABSTRACT

There is no reference in the abstract to one of the main points in the work that is the differences found between response of intact BSCs and of it isolated dominant components.

We agree with the referee that this topic was not getting enough attention in the abstract. We have included information regarding this topic in the actual version and also moved this section to end of the abstract to underline its significance for the interpretation of the data (, page 1; lines: 21-23).

Page 1. Line 20. I suggest to remove the sentence beginning "Nevertheless, a major. . ." See comment above.

This is a response to the general remark throughout the referee's comment about removing the part of the study where we investigated differences in NP rates if the used reference value is either the chlorophyll content or the sample surface area.

We consider this partial aspect of the study worth mentioning, even though these coherences are well known for eco-physiology experts. Nevertheless, by being a potential contribution to the special issue on biocrusts in Biogeosciences, a major benefit of this manuscript is to reach a broad biocrust readership and also non-physiological experts. We see this as an opportunity to introduce and explain this topic to a new audience, especially because the choice of reference value is variable, depending on the investigated organisms and research question.

Basing NP rates on chlorophyll content will result in an overestimation of NP rates of cyanobacteria dominated BSC compared to other crust organisms or biocrust types. We agree with the reviewer, that a comparison of gas exchange rates between different publications was, of course, not the main goal of this study. Nonetheless, we want to provide a suggestion on how to avoid discrepancies in interpretations of gas exchange data.

In the actual version of the manuscript we have taken great care to clarify this point and give explanations as to how our findings may influence study design and data evaluations of similar studies in the future (Page 11-12, Lines: 32-13).

INTRODUCTION

Page 1. Line 29. Please rewrite the sentence "Investigations. . ." As it is now is contradictory. Are there abundant or few investigations in cyanobacteria?

Sentence has been rephrased so that it is easier to understand now (P 1 – 2; Lines 25-2).

Page 2. Lines 5 to 20. In my opinion the concept of arrested succession should be introduced at the beginning so it is clearer for the reader.

We have restructured and reorganized the paragraph. The concept of arrested succession is now presented in a clearer way (P 2. L -17:)

Page 3. Line 9. Reference Reisser et al. 2007 is not in the list.

The reference Reisser et al. 2007 has been corrected to Reisser, 2007.

Line 23. I suggest to change "or" for "and a"

Redrafted.

Lines 25-26. Were these "in situ" measurements carried out? I think it would be better say "would allow"

Was corrected.

Line 32. Colesie et al. 2014b not in the list. "Higher" than what?

Colesie et al. 2014b was corrected to Colesie et al. 2014 (without b). Sentence has been rephrased to provide a comparison: P. 3 L. 30-31

Page 4. Line 4. The sentence is confusing and I think is not relevant here. I assume that when authors refers to system they refer to BSC and not to the measurement systems. The treatment or position in the cuvette is another question. Of course there will be variability between samples, but here the comparison is between isolated individuals (green algae or cyanobacteria), soil biocrust and soil. I suggest removing this sentence.

As suggested by referee #2 and #3 this sentence has been removed and the topic is now discussed in the discussion section (P. 11; L. 9 – 31).

MATERIAL AND METHODS

Page 5. Line 2. Check reference Honegger 2008. Is 2003 and also it refers to green algae photobiont but not to cyanobacteria.

Reference Honegger has been removed. Reference for *N. commune* (Tamaru et al., 2005) and green algae (Seckbach, 2007) have been included (P. 5, L. 2).

Line 11. n=6. It is not clear to me how the sampling or subsampling was made. From each 6 of C-BSC and 4 of G-BSC you take 3 subsamples?

We agree with the reviewer that this section in the methods was not written clearly. We have rearranged the whole section and tried to clarify terminology as well as the description of the different measurement series and units (P.5, L. 15 – P- 6; L. 6).

Line 12. First, you need to indicate how the saturation light was determined.

We rearranged the methods part and put the determination of saturation light before the determination of water dependent photosynthetic response (P.5, L. 16-30).

Line 16. Delete “from the”

Deleted.

Line 19. Should not be a new paragraph.

Deleted.

Line 21. I understand that the weighing was during the dehydration cycle to have the full response, but not between them. Please explain this.

Because of the sample being located in a closed, gastight cuvette “during” the CO2 exchange measurement, it can only be weighted once this reading is taken and the cuvette is open. For detailed description please see: Photosynthesis and Water Relations of Lichen Soil Crusts: Field Measurements in the Coastal Fog Zone of the Namib Desert; O. L. Lange, A. Meyer, H. Zellner and U. Heber; Functional Ecology; Vol. 8, No. 2 (Apr., 1994), pp. 253-264. We have tried to clarify this in the completely rewritten methods section (P 5 – 6; L. 31-6).

Line 23. I suggest new paragraph. “To obtain the net response to light. . .” n=3. Are the samples BSC or species individuals? It is not clear from the text and in Fig. 2 they appear as individual species measurements.

In agreement with the previous comments we have rearranged this whole section for more clarity and transparency in the used methods (P.5; L. 15-29).

Figure description was also changed. N=3 represents BSC samples, not species individuals.

Line 25. How the optimal temperature was obtain? Are there any regressions done for this? Data is not show. Please explain.

Prior to the light dependent gas exchange experiments the operation temperature was checked by testing if the light saturation point was independent of temperature, by testing if a difference was visible between 17 °C or 25 °C, with n=3 replicates each.

As no difference for the light saturation point could be detected (grouped t-test; p-value for $C\text{-}BSC_{all}$: 0,095; p-value for $G\text{-}BSC_{all}$: 0,597), the operation light for the water dependent gas exchange experiments was therefore set to 985 µmol photons m^{-2} s^{-1} for C-BSC and 1260 µmol photons m^{-2} s^{-1} for G-BSC, which represent the results from the 25 °C measurement. This has been clarified (P. 5, L. 17-23; P. 5 – 6; L. 31-2).

Line 29. Should not be a new paragraph.

Deleted.

Page 6. Line 10. Include “of the two types of BSC” after “levels”. The analysis as it is explained is confusing as there were different number of samples and subsamples for the different experiments. For the drying curves there were 6 C-BSC and 4 G-BSC and from each of these all, dom and soil. But in the light curves there are only 3 CBSC and 3 G-BSC without distinction of components. So, I understand that BSCall, BSCdom and BSCsoil cannot always be the explanatory variables.

The reviewer is absolutely correct in pointing out that the statistical data analysis is written in a confusing way. We acknowledge showing us were we have described it poorly. We included the suggestion of the reviewer and rewrote the paragraph about the light curves, where we only did a grouped t-test, as correctly pointed out, we could not have organization level as a dependent variable (P. 6, L. 16).

RESULTS

The adjustments of the curves in Fig. 2 doesn’t look very good, especially that of Z. ericetorum, showing an increase in the response and no saturation following the points and not the line. Please check this. Also, how where the light parameters (compensation and saturation) calculated, from individual adjusted curves or from one curve? It should be explain in material and methods. There are no supplementary tables or graphs showing values of these parameters.

According to suggestion of the referee we have included the necessary information in the material and methods section (P. 5, L. 27-30) but would like to give further information for the reviewer to follow our argumentation: The mathematical formula used to fit the curve is the so-called Smith function. It is the standard curve to fit light curves of BSC organisms as it : “makes it possible to calculate apparent maximum quantum yield of CO2 fixation (Φ, initial linear slope of light response curve), NPmax (the theoretical maximal rate of NP at saturating PPFD), $PPFD_{sat}$ (the light intensity allowing 90% of NPmax which represents a realistic estimate for light saturation […], and $PPFD_{comp}$ (the light compensation point of CO2 exchange)” (from Lange, O. L., Belnap, J., & Reichenberger, H. (1998). Photosynthesis of the cyanobacterial soil-crust lichen Collema tenax from arid lands in southern Utah, USA: Role of water content on light and temperature responses of CO2 exchange. *Functional Ecology*, *12*(2), 195-202.)

The calculation for the compensation and saturation point were as follows: The original data from the GFS 3000 work sheet were put into the graphics program Sigma Plot. These data only had the following light intensities with corresponding NP rates: 0, 25, 50, 100, 300, 500, 1000, 1500, 1750, 2000 photons m^{-2} s^{-1}. Calculating light saturation and compensation points from this data set is not very accurate, therefore a curve fitting is being done with the smith function. The smith function provides 259 points for our curves interpolated between the actual measured points. Light compensation is calculated by creating a linear regression line from the last negative to the first positive point, that is created by the smith function. With the obtained formula for the slope the intersection with the x-axis can be calculated, which represents the light compensation point, where respiration equals assimilation. Light saturation is done by calculating 90% of NP and looking in the fitted curve for the NP value closest to the $NP_{90\%}$. The corresponding, calculated light value is then considered the light saturation. Each light curve measurement produces one light saturation and one light compensation point. The given values (P. 7 L. 4-11) were means of three measurements each.

To simply say that the Smith function is the standard tool to use for BSC light curves is not sufficient, so we would like to provide the R^2 values of the single curves, to proof that the formula is fitting for the data:

C-BSC: 0.98; 0.98; 0.98; G-BSC: 0.95; 0.97; 0.97.

Page 6. Line 4. From Figs 4a and b they don't contribute to NP response.

That is correct and exactly what we wanted to proof. We wanted to remove the soil crust organisms and only measure the organisms and soil separate. With not having many photosynthetic active cells in the soil we also did not expect a contribution to NP response.

Line 22. Here it is said G-BSCall and C-BSCall but not in Fig. 2. Please clarify. Im suggest changing "almost twice as much" for "higher"

Rephrased. See comment above, description of light curve was clarified, description of Fig. 2 has been clarified also.

Line 24. Why organisms? Is it not BSC? It is not reasonable that the difference in compensation point was twice as much but then there were no significant. As comment above please explain how this analysis was done.

Corrected to BSC. Analysis was explained more in detail in material and methods as suggested by the reviewer. We want to emphasize that one of the main conclusions of the study is that these BSCs (and mainly the separated dominant organisms) show a very broad range of responses to different environmental parameters, also to light. In this case it means that the standard deviations are so big that even though the values for G-BSC are higher than for C-BSC, there is no statistical difference between the means.

Line 26. The same discussion will apply for the saturation points. From Fig. 2 we can understand that there is no saturation at 2000 µmol (just a few lines before it is said that maximum NP rates were reached at 2000 µmol).

Sentence was rephrased, and the following information added: The GFS3000 cannot increase the PAR above 2000 µmol photons m^{-2} s^{-1}. (P. 7, L. 5). Therefore, we need to conclude that the highest NP rates we can measure are at 2000 µmol photons m^{-2} s^{-1}. Additionally, the saturation point is calculated as 90% of NP (see P. 5 L. 27-28) and is not reflected by the slope of the curve.

Page 7. Line 2. Include “dominated BSC” after “commune”. Refer here to Supplementary tables.

Line 6. Include “dominated BSC” after “ericetorum”. Refer here to Supplementary tables.

Included both. We refrained from putting the sentence in P. 7 L. 22 at the end of each paragraph and left it at the end of the segment.

Line 8. Delete “an” Water dependent photosynthetic response. In my opinion better than exemplifying graphs, average data of all replicates should be represented. Differences between just two samples are not relevant. Also, curves shown in Figures 4 are very difficult to understand as it is not normal the fluctuation around 80% water content. It must be an artifact that could be masked using averages. Also the water depression is not clear.

Using exemplifying graphs for presenting water dependent photosynthesis data is a common and well-accepted style in BSC, lichen and bryophyte physiology literature. Many studies on BSC, as well as lichens make use of this, because it allows a better understanding of the processes and clearer graphical design. One complication that comes with mean values plotted in these graphs, is that they vary not only along the y- but also along the x-axis, which would require a demonstration of standard deviations in two directions, which is clearly complicating the graph and the message that should be transported with it. Rather than “masking” effects, as suggested by the reviewer, by using mean values this is an option to precisely describe and demonstrate processes that are otherwise easily overseen. Plotting the response curves against a standardized water content scale (%) allows comparisons between samples with highly divergent water contents and is a tool used in review articles and book chapters.

As an example to show that even overlaying single curves will not produce a clear picture, we plotted 5 NP curves of C-BSC (all, dom and soil; 25°C) on normalized water content. In this graph we used normalized NP rates instead of total NP rates, as we have strong variations between samples. It is obvious that all the curves for C-BSC_{dom} are very similar, but the ones in C-BSC_{all} vary so much that a clear pattern cannot be shown with this kind of graph. This is because of the strong variations in the soil (shown in C-BSC_{soil}).

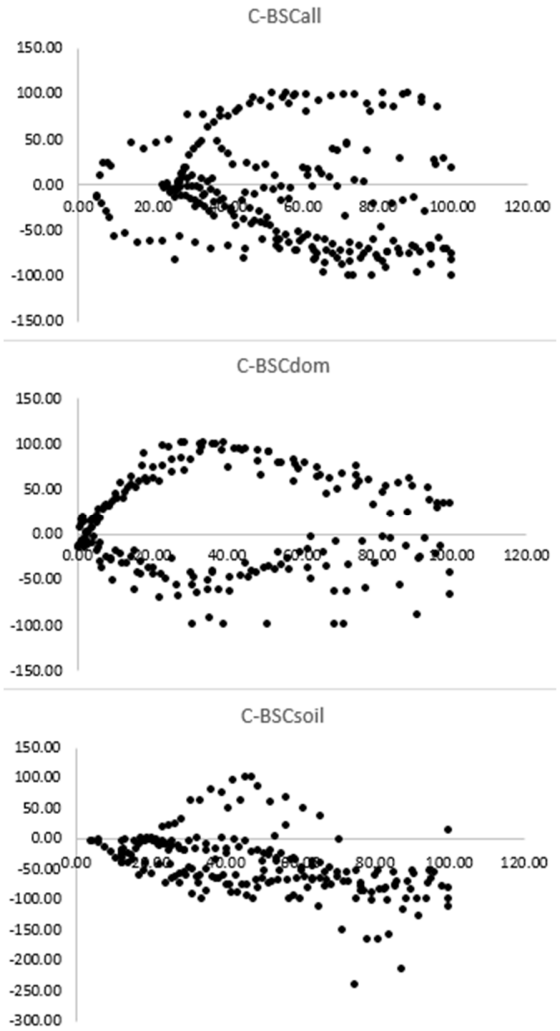

Fig. 1: Normalized NP rates plotted against normalized water content for 5 samples of C-BSC at 25 °C.

In order to clarify which water contents were optimal (90% NPmax) we have included highlights in the graph and provided a table with the mean water contents after which NP is slightly inhibited (below 75%).

Selected literature regarding this topic and showing the same type of graphs:

Lange, O. L., Belnap, J., & Reichenberger, H. (1998). Photosynthesis of the cyanobacterial soil-crust lichen Collema tenax from arid lands in southern Utah, USA: Role of water content on light and temperature responses of CO2 exchange. *Functional Ecology*, *12*(2), 195-202.

Lange, O. L., Büdel, B., Heber, U., Meyer, A., Zellner, H., & Green, T. G. A. (1993). Temperate rainforest lichens in New Zealand: high thallus water content can severely limit photosynthetic CO 2 exchange. Oecologia, 95(3), 303-313.

Lange, O. L., Green, T. A., & Heber, U. (2001). Hydration-dependent photosynthetic production of lichens: what do laboratory studies tell us about field performance?. Journal of Experimental Botany, 52(363), 2033-2042.

Green, T. G. A., Nash III, T. H., & Lange, O. L. (2008). Physiological ecology of carbon dioxide exchange. Lichen biology. Cambridge University Press, Cambridge, 152-181.

Lange, O. L. (2001). Photosynthesis of soil-crust biota as dependent on environmental factors. Biological soil crusts: structure, function, and management, 217-240.

Green, T. A., & Proctor, M. C. (2016). Physiology of photosynthetic organisms within biological soil crusts: their adaptation, flexibility, and plasticity. In Biological Soil Crusts: An Organizing Principle in Drylands (pp. 347-381). Springer International Publishing.

Line 16. Change Table for Tables.

Changed.

Lines 26-28. Data shown in the text of ranges of optimal WC seem different from the ones in Fig. 5 (i.e. upper limit never coincident). Please check.

The referee is absolutely correct. We accidentally used the wrong values in the text, although discussing the correct ones and also doing the statistical analysis with the correct values. We corrected the text passage (P. 8, L. 9-14).

Page 8. Line 5. I would rather delete this subsection as discussed above.

We would like to include this topic, as explained in the comment above.

Line 20. Table S6

Changed.

DISCUSSION

Line 25. BSCs photosynthetic organisms

Changed.

Page 9. Line 5. Delete “none” and better G-BSCall and C-BSCall. What does it means physiological flexibility to water gain?

We have clarified the interpretation of this result and explain now that: “both organism groups take the same functional role in the BSC consortium and can operate at near optimal conditions over a variety of different water contents, as it would also be expected for highly stress tolerant crust pioneer species” (P. 9, L. 21-24).

Line 18. I suggest delete sentence beginning “A depression. . .” as it has already said before.

Deleted.

Line 23. I don't see the detection of a CCM from Fig.S2.

Referee #2 also asked about an explanation as to how we were able to detect that *N. commune* had a CCM and *Z. ericetorum* did not show one. We will copy part of the answer here, as it also describes how a CCM can be seen in gas exchange data:

In general, it is known from literature that most green algae as well as all cyanobacteria do possess an inorganic CCM (Raven, J.A., Cockell, C.S., De La Rocha, C. I. The evolution of inorganic carbon concentration mechanisms in photosynthesis. In: Phil. Trans. Soc. B. (2008)). Although the mechanisms have multiple evolutionary origins, the function is the same: CCMs accumulate CO_2 around rubisco. While the mechanisms behind the accumulation might be different, the photosynthetic response is the same, which can be seen in supplement figure S2 (a): There is a strong peak in carbon uptake as soon as the light is turned on, which flattens itself after a few minutes into a straight line. Usually the uptake of CO_2 during photosynthesis looks like a sudden drop of the CO_2 concentration in the measurement system gas. Afterwards the assimilation curve stays on the same level. This can be seen in S2 (b), in the downward curve just before the black arrow marks the peak in the upwards curve. If a CCM is present, this pattern is changed. As soon as the light is turned on more CO_2 is accumulated than would normally be the case under continuous conditions of water content, light and temperature. This is because the reservoir around rubisco is filled up, which can be seen as a sudden peak in the picture S2 (a; marked by a black arrow). As soon as the light is turned off again, CO_2 that has not been used during photosynthesis is released again, which is shown with a sudden increase of CO_2 in the measurement system gas. Here the same applies: More gas is released than normally would. After a few minutes this peak drops again, under light and in dark conditions and a continuous respiration or assimilation can be detected.

We were unable to detect the same pattern in the green algae BSC, even under heavy manipulation of the measurement conditions, which included different temperatures, water contents, PPFDs and time intervals of measurement. Therefore, we conclude that no CCM can be detected in *Z. ericetorum*. As this was the first study to test this for this species, we provide a first insight in how this green alga photosynthesizes.

Additionally, we want to provide the publication where the method of detection was used for the first time: Badger, M. R., Pfanz, H., Büdel, B., Heber, U., & Lange, O. L. (1993). Evidence for the functioning of photosynthetic CO2-concentrating mechanisms in lichens containing green algal and cyanobacterial photobionts. *Planta*, *191*(1), 57-70

We have clarified this topic in the text of the supplement material in order to make the phenomenon understandable for a broad readership (Figure description of S2).

Page 11. Lines 2 and 7. Species name in italics.

Changed.

Lines 16-26. In my opinion this question is not relevant as it is obvious.

We would like to refer to our comment at the beginning of this letter, that we consider discussing the differences between these two options is an important information and of interest for a broad BSC readership.

CONCLUSIONS

Page 12. Line 3. The authors conclude that there is a relative temperature independence of NP but the results show significant differences in the response of NP to temperature.

Here we disagree with the referee, according to the statistical tests, there is no significant difference in the response of NP to temperature, except for the one mentioned by us (25°C for C-BSC_{dom} C-BSC_{all} and C-BSC_{Soil}).

Line 5. In general, the question about physiological plasticity should be avoid because there are no experiments proving this.

We agree with the reviewer that plasticity was not measured in the presented study and rephrased the sentence for clarity and a more precise ecological interpretation (P. 9, L. 24; L. 10; P.12; L. 17-19).

Line 6. To incorporate the results into global scale carbon cycle models, the work should better provide numerical data sets (i.e. tables).

Part of the publication process for BGS is to upload the original data to an online database, so that it can be accessed easily, therefore the numerical data of this publication will hopefully be made available.

REFERENCES

There are too many for the paper. As mentioned above some cited literature in the text is not in the list. Please check references through the list.

Checked and corrected the literature to fit the text.

Some literature has been removed, as single cited publications behind some statements should be enough. Still, the number of publications did not decline a lot, also because we needed to include some sources because of added comments from the other referees.

Table 1. Following my suggestion about Chlorophyll question then this should not be included.

We would like to include this part of the publication, but we put it in the supplemental material as Table S10. See comment at the beginning.

Figure 2. Legend.The second sentence is not necessary, just n=3.

Removed.

Figure 3. Legend. What do you mean by . . .of one of the group only? Please indicate what vertical bars represent.

“Of one group only” has been corrected to “organization levels”, to make it clear that one BSC_{all}, BSC_{soil} or BSC_{dom} was being compared. Also, vertical bars were described as being standard deviations.

Figure 4. See comment above. Indicate PAR

This has been changed.

Figure 5. This graph is very difficult to understand. See comments above. What does the letters mean? Why n=24 here?

The letters on the graph represent statistical differences between each lower limits (letters a-c) and between all upper limits (d-g). As described in p. 6 L. 24 -27: the optimum water content was compared by statistically testing if the upper and lower limits between the both BSCs and their components differed. This means we compared if the lower limits differed from one another, then we compared if the upper limits differed.

We have now included a clear definition of optimum water content (water content at which 90% of NP is reached to water content at which it decreases below 90% again) (P. 6; L. 4-6).

The optimum water content is calculated independent of temperature, as it is not influenced by temperature. Therefore, we have pooled all readings (6 samples times 4 temperatures) for C-BSC. The sampling size for G-BSC was missing, which is 16 (4 samples times 4 temperatures). We clarified this in the figure description.

Figure 6. As suggested above I would not include this graph.

We would like to include this part of the publication. See comment at the beginning.

Eco-physiological characterization of early successional biological soil crusts in heavily human impacted areas ~~– Implications for conservation and succession~~

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Abstract. Eco-physiological characterizations of photoautotrophic communities ~~is~~ are not only necessary to identify the response of carbon fixation related to different climatic factors, but also to evaluate risks connected to changing environments. In biological soil crusts (BSCs), the description of eco-physiological features is difficult, due to the high variability in taxonomic composition and variable methodologies applied. Especially for BSCs in early successional stages, the available datasets are rare or focused on individual constituents, although these crusts may represent the only photoautotrophic component in many heavily disturbed ruderal areas, like parking lots or building areas with increasing surface area worldwide. We analyzed the response of photosynthesis and respiration to changing BSC water contents, temperature and light in two early successional BSCs. We investigated if the response of these parameters was different between intact BSC and the isolated dominating components. ~~One~~ BSC ~~was~~ dominated by the cyanobacterium *Nostoc commune* and dominated ~~, the other~~ by the green alga *Zygogonium ericetorum* were examined. A major divergence between the two BSCs was their absolute carbon fixation rate on a chlorophyll basis, which was significantly higher for the cyanobacterial crust. Nevertheless, ~~I~~independent of species composition, both crust types and their isolated organisms had convergent features like high light acclimatization and ~~low~~ a minor and ~~or no~~ very late occurring depression in carbon uptake at water suprasaturation. This particular setup of eco-physiological features may enable these communities to cope with a high variety of climatic stresses, and may therefore be a reason for their success in heavily disturbed areas with ongoing human impact. However, the shape of the response was different for intact BSC compared to separated organisms, especially in absolute net photosynthesis rates. ~~Nevertheless, a major divergence between the two BSCs was their absolute carbon fixation rate on a chlorophyll basis, which was significantly higher for the cyanobacterial crust.~~ This ~~study~~ emphasizes the importance of measuring intact BSCs under natural conditions for collecting reliable data for meaningful analysis of BSC ecosystem services.

1 Introduction

In drylands, the eco-physiological characteriz~~s~~ation of biological soil crusts (BSCs) is a useful instrument for the evaluation and prediction of ecosystem functioning under recent climate change scenarios (Maestre et al., 2011). Biological soil crusts ~~(BSCs)~~ are small scale communities, composed of bryophytes, lichens, cyanobacteria, green algae, heterotrophic bacteria and microfungi, within or on top of the uppermost millimeter~~re~~s of soil surfaces (Belnap et al., 2016), that are often used as model systems to characterize the biodiversity–ecosystem function relationship in soils (Bowker et al., 2010). ~~Investigations describing eco-physiological characterizations of the poikilohydric soil crust organisms, i.e. lichens, bryophytes and terrestrial cyanobacteria are relatively abundant, whereas studies on terrestrial green algae in general and cyanobacteria in temperate habitats are not.~~ While there is sound documentation regarding eco-physiological characteriz~~z~~ations for BSC organisms from hot and cold deserts as well drylands (Hawes et al., 1992; Lange et al., 1992; Housman, 2006; Novis et al., 2007), studies from temperature regions are rare. In temperate regions, BSCs are not a typical 'steady state' vegetation type. They are either restricted to continuously disturbed habitats, are an initial stage of succession after heavy disturbances or present in areas held in arrested succession. In such early successional stages, BSCs are mainly composed of cyanobacteria and/or green algae (Fischer et al., 2010)~~, which~~. Although the ~~in most climax BSC communities~~ physiological capacity ~~of cyanobacteria and green algae~~ of these organisms may be negligible ~~due to their little biomass~~ in relation to lichen~~s~~ and bryophyte~~s~~ ~~(Belnap et al., 2001)~~ dominated BSCs (Belnap et al., 2001), they are crucial study organisms for understanding BSC function in temperate regions. ~~, in early BSCs (Fischer et al., 2010) and BSCs in arrested succession their eco-physiological efficiency might be a key driver for ecosystem functioning. Additionally, habitats where cyanobacteria-dominated BSCs in a climax community have been found, e.g. in high altitudes as Hochtor in Austria or in high latitudinal areas as in Ny-Ålesund in Svalbard (Williams et al., 2016).~~

~~In temperate regions, BSCs are not a typical 'steady state' vegetation type. There they are either restricted to continuously disturbed habitats or are an initial stage of succession after heavy disturbances. Biological soil crusts are a typical element of at least temporarily arid ecosystems (Büdel, 2001) and in ecosystems with extremes in hot or cold periods and with long-lasting snow (Büdel et al., 2014).~~ In temperate regions a~~A~~nthropogenic disturbances like forestry, traffic lanes or trampling (Webb and Wilshire, 1983) create new land surfaces (Walker and Willig, 1999) where microclimatic conditions can favor BSC ~~occurrence~~development ~~even within temperate habitats~~. This is due to the fact that BSCs in general are initial colonizers of open surfaces (Fischer et al., 2010; Veste et al., 2011) where cyanobacteria and green algae appear as pioneers (Belnap, 2006)~~.~~ . Ongoing disturbance prevents proceeding recovery; thus, the species richness remains at a low level, a phenomenon also referred to as arrested succession (Webb and Wilshire, ~~1983~~2012). ~~While I~~in the natural BSC succession, lichens and bryophytes would broaden the initial colonization (~~Cameron et al., 1970;~~ Belnap and Eldrigde, 2001; Belnap, 2006), however, in areas of arrested succession cyanobacteria and green algae are more resistant to the disturbance and thus remain the dominant BSC organisms (Kuske et al., 2011). ~~ongoing disturbance prevents proceeding recovery, thus remaining at a low level species richness (Webb and Wilshire, 1983). Cyanobacteria and green algae are more resistant to disturbance than bryophytes and~~

~~lichens, subsequently frequent disturbance can maintain a BSC at an early successional stage (Kuske et al., 2011), a phenomenon also referred to as arrested succession.~~ Areas where vegetation remains in a~~n~~ state of arrested succession are appearing more frequently due to a growing need for space by humans (Housman, 2006)~~.~~ and ~~n~~N~~n~~ew habitats derived from accelerating human activities are fairly understudied (Rindi, 2007~~); Belnap et al., 2016)~~. Aside from ongoing human disturbance, areas affected negatively by climate change might experience shifts in species composition towards cyanobacteria and green algae as the dominant BSC contributors ~~(Zelikova et al., 2012; Reed et al., 2012; Escolar et al., 2012)~~, due to warming and a lower water availability (Zelikova et al., 2012; Reed et al., 2012; Escolar et al., 2012). These areas will increase in space until the end of the 21st century (Solomon et al., 2007), which strengthens the need for eco-physiological investigations on cyanobacteria and green algae in the BSC context. Nonetheless, climax communities with mosses or lichens being present exist also in dry areas with high temperatures (e.g. Zedda et al., 2011 or Weber et al., 2012), so it is not possible to generalize this pattern.

Organisms of ruderal habitats often ~~expose~~ possess specific physiological adaptations, for example high physiological plasticity (~~Belnap & Lange, 2001;~~ Grime & Pierce, 2012). C~~Both, c~~yanobacteria and green algae are key ~~the main~~ constituents and only the primary producers during a) early succession, b) regeneration processes of habitats under constant anthropogenic pressure, and c) in BSCs ~~in~~ of demanding habitats, e.g. hot (Büdel, 1999~~; Karsten et al., 2010~~) and cold deserts (~~Büdel et al., 2008;~~ Büdel et al., 2016; Karsten et al., 2010a). Typical taxa of green algae and cyanobacteria found in early successional BSCs of the temperate zone are, for example: *Zygogonium ericetorum* (Pluis, 1994; Büdel, 2001a), *Klebsormidium* spp. (Pluis, 1994), *Microcoleus* spp. (~~Ashley and Rushforth, 1984; Belnap, 1996;~~ Belnap et al., 2001) and *Nostoc* spp. (Pandey et al., 2005).

Comparing eco-physiological literature of cyanobacteria and green algae reveals that cyanobacteria are in general a well-studied group of organisms. In the absence of other photoautotrophic organisms in BSCs, they provide the most important ecosystem services (Makhalanyane et al., 2015 and sources therein). Terrestrial cyanobacteria are important in many ecosystems, due to their ability to fix atmospheric nitrogen and sequester carbon (Dojani et al., 2011; Büdel et al., 2016) and play important roles in global biogeochemical cycles (Raven, 2012). Most studies on the ecophysiology of single cyanobacteria species or cyanobacterial dominated BSCs were carried out in desert or polar environments (Hawes et al., 1991; Lange et al., 1992; Housman, 2006; Novis et al., 2007)~~, rarely in temperate regions~~. In contrast to cyanobacteria, reliable records of eukaryotic algal groups appear to be restricted to studies in soils of temperate and alpine regions (Karsten et al., 2010b). Although green algal dominated BSCs occur rarely in temperate regions, where they do, they have high soil surface coverage (Büdel et al., 2016). Green algae serve as key organisms in BSC formation in all ecosystems, especially in temperate, arctic and high alpine regions (Büdel et al., 2016). A lack of information on green algae in general and especially on temperate, ruderal areas seems surprising because green algae occur in virtually all terrestrial habitats and on manmade surfaces (Gaylarde and Morton, 1999; Tomaselli et al., 2000; Büdel, 2011). The ecosystem services provided by green algae include stabilization of soil surfaces, improvement of soil structure, soil fertility and the influencing of hydrological processes (Bailey et al., 1973; Hu et al., 2002; Reisser, 2007). ~~Reisser et al., (2007) described the~~ The current status of eco-physiology of terrestrial green

algae has ~~being~~ been described as being ~~rather~~ based on assumptions and deductions rather than on experimental data (Reisser, 2007). Additionally, most green algal focused studies have investigated organisms after a prolonged period of cultivation (e.g. Karsten et al., 2010a, ~~2010~~b~~, Karsten, 2013~~), which could have changed their eco-physiological responses over time, as these organisms are well known to have a high acclimatization potential to differing environmental factors (~~Dietz et al., 2000; Nash, 2008;~~ Colesie et al., 2012; Belnap et al., 2016).

One application for detailed eco-physiological descriptions is modelling on a global scale. Post millennial interest in carbon gain of BSCs has increased (Lange and Belnap, 2016) and their CO_2 exchange rates are now considered relevant even on a global scale (Elbert et al., 2012; Porada et al., 2013, 2014). Unfortunately, modern process based models as used by Porada et al. (2013; 2014) are still based on few available datasets, that cover few different BSC types, organisms, geographical regions, and climatic situations which~~;~~ even exclud~~cing~~ cyanobacteria and green algal dominated BSCs. Problematic is also the focus on isolated organisms rather than studying the whole BSC system (see Colesie et al., 2016 or sources in Elbert et al., 2012). One organism studied out of several BSC organisms does not represent the ecological response of a complete BSC (Weber et al., 2012).

The goal of this study is to present a detailed description of the eco-physiological performance of a cyanobacterial ~~or~~ and a green algal dominated BSC regarding their photosynthetic response to different water, light and temperature conditions of temperate habitats. This ~~allows~~ will~~ould~~ allow an overview of in situ gas exchange rates correlated to local climate and therefore produce a suitable database for potential global scale models. The study also provides an eco-physiological dataset for BSCs in habitats with ongoing human disturbance. Additionally, it demonstrates the value of measuring BSCs as a system instead of as single components.

Two major research questions were ~~raised are~~: 1) What is the ~~gas exchange rate~~eco-physiological performance of an intact cyanobacterial or green algal BSC? ~~We expect a lower gross and net photosynthesis of both crusts compared to BSCs of later successional phases as their photosynthetic performance should be lower due to less biomass or lower development stage (Belnap and Lange, 2001; Colesie et al., 2014b). At the same time, a~~ A higher physiological ~~plasticity~~ flexibility is predicted for cyanobacteria and green algae compared to bryophytes and lichens. ~~which~~ This would enable the ~~both organism~~ groups to cope with a wide~~r~~ range of abiotic stresses.

2) To what extent can the photosynthetic rate of the BSC be delineated from single organism measurements? We expect differences between measurements of complete BSCs (with attached soil and soil organisms), of the isolated organisms, and bare soil alone. In theory, a mathematical addition of "separated organisms" plus "bare soil" should equal the complete system reading. ~~We expect that the position and arrangement of the sample inside the measurement system, here a cuvette, will influence the photosynthetic values, as treatment of samples will always shape their response.~~

2 Material and methods

2.1 Study site and organisms

Two anthropogenically impacted sites with constant disturbance were selected. Both sites were located in south western Germany (Fig. 1a) and were dominated by either green algae or cyanobacteria. The sites were 50 km ~~apart~~ from each other, which excludes any macroclimatic differences. Mean annual air temperature is 9.9 °C and mean annual precipitation 741.3 mm (Weather station of the Agrarmeteorologie Rhineland–Palatinate Morlautern).

Site 1 – Mehlinger heath. The Mehlinger heathland (MH, Fig. 1b) is a former military training ground (Ruby 1979) close to the city of Kaiserslautern (49°48' N, 7°83' E). Once the military use was abandoned, a BSC dominated by green algae developed between dense heather stands, which formed as a part of the natural successional process. With 150 ha, the site is the largest heathland system of southern Germany. It is situated 320 to 340 m a.s.l. and soils are acidic (pH = 5.28, Felde, personal communication), mostly due to their origin from red sandstone of the early Triassic (Landesamt für Geologie und Bergbau, Rhineland–Palatinate), with a loamy soil texture, very low organic carbon content (<1%) and a water holding capacity of 40%. Since 2001 it has been a natural reserve with an ongoing human management regime to preserve the heathland system. Vascular plant vegetation is dominated by *Calluna vulgaris*. In general, the cryptogamic diversity concerning cyanobacteria and green algae in this habitat is poor (Stanula, 2011), with only five and one species described, respectively. The sampling site is close to a look-out point, where trampling is unpreventable. The dominant organism in the occurring BSC is the green algae *Zygogonium ericetorum* (Fig. 1c).

Site 2 – Parking lot. Cyanobacteria dominated BSC samples were collected from a parking lot (PL) at an equestrian farm (Fig. 1d) near the city of Zweibrücken (49°19' N, 7°25' E), 369 m a.s.l. The bedrock is composed of base rich (pH = 6.81; Felde, personal communication) limestone that originates from early Triassic with a coarse gravel overlay, with a loamy sand soil texture, 6% organic carbon and a water holding capacity of 30%. Daily use by cars and trampling prevent the development of higher vegetation. Some bryophyte species occur: *Hypnum cupressiforme* and *Tortula muralis*. The cyanobacterium *Nostoc commune* Vaucher ex Bornet & Falhault (Fig. 1e) is the dominant organism in these BSCs and is clearly visible with the naked eye. Sampling depth at both sides was between 0.8 to 1 cm.

2.2 Sample collection

Sample collection was conducted in spring 2016 at both study sites. Samples were selected according to the dominant occurrence of *N. commune* or *Z. ericetorum*. A green algal or cyanobacterial dominated BSC was defined as covering at least 50% of the soil surface in a 20 cm diameter petri dish. Once collected, the samples were first allowed to dry at room temperature and then were kept frozen at -20 °C until ~~used for~~ measurements. Frozen storage is described as being suitable for long term storage of BSC components for experimental studies (~~Honegger, 2008~~ Tamaru et al., 2005; Seckbach, 2007).

2.3 CO_2 exchange

CO_2 exchange measurements were ~~done~~ completed according to Colesie et al. (2014). Before measurements, the intact BSC samples underwent a reactivation proces~~sdure~~ which consisted of two days exposure to~~at~~ 4 °C in the dark. Afterwards they were fixed in the gas exchange cuvette and sprayed with sterile, filtered water to activate their metabolism 24 hours prior to measurement. Ahead of the measurements, full water saturation was achieved by submerging the samples in water for ten minutes. Excessive water and droplets were carefully shaken from the sample before measurements.

Within each crust type (cyanobacterial and green algal) three separate series of measurements were conducted. First the intact crust (named $BSC_{all;}$ defined as the entire non-manipulated BSC including attached soil with an unknown amount of heterotrophic organisms), was used for the measurements. Once these were ~~finished~~completed we separated the dominant organisms from the crust and measured the separated organism (named BSC_{dom}; the dominant organism of the crust, isolated from the soil, washed and dissected thoroughly) and the underlying soil (named BSC_{soil}; the underlying soil and all other microscopic organisms, except for the dominant one) separately. The following terminology will henceforth be used for the cyanocrust: C-BSC_{all}; C-BSC_{dom} and C-BSC_{soil}; for the green algal crust: G-BSC_{all}; G-BSC_{dom} and G-BSC_{soil}.

The CO_2 gas exchange measurements were conducted under controlled laboratory conditions using a minicuvette system (GFS 3000, Walz Company, Effeltrich, Germany). To obtain full eco-physiological response to changing light conditions and water contents fully hydrated samples (n=3 each sampling site) were exposed to stepwise increasing light from 0 to 2000 µmol photons m^{-2} s^{-1} (0, 25, 50, 100, 300, 500, 1000, 1500, 1750, 2000 photons m^{-2} s^{-1}) at two temperatures (17 °C and 25 °C) and ambient CO_2 concentrations to test for light levels required to saturate the photosynthesis and the operation temperature for this experiment. The lack of difference between the light saturation points at these two temperatures (grouped t-test; C-BSC_{all}: t-value=-0,971, FG=3, p=0.403; G-BSC_{all}: t-value=-1,271, FG=4, p=0.273) demonstrated ~~-~~that light saturation does not vary with temperature~~s~~ and ~~can~~could therefore be he~~o~~ld stable during the following experiments. The light cycles (about 40 min duration) were repeated until the samples were completely dry (after 6 – 7 h) and samples were weighted after each light cycle in order to determine the water content. WC was calculated as mm precipitation equivalent. Sample dry weight was determined after 3 days in a drying oven (Heraeus Instruments T6P, Thermo Fischer Scientific Inc.) at 60 °C. The CO_2 exchange of the samples was related to soil crust surface and chlorophyll content, the latter determined after Ronen and Galun, (1984). The curves for the 25 °C measurements were fitted with the Smith function (e.g. Lange et al., 1998) and light saturation was defined as the photosynthetic photon flux density at 90% of maximum NP according to the fitted curve. Light compensation was the intersection of the curve with the x-axis, calculated from the last negative and first positive point of the fitted curve, which was completed for each sample separately.

Additionally, t~~T~~he response of net photosynthesis (NP) and dark respiration (DR) to water content (WC) at different temperatures was determined ~~for the cyanobacterial crust (n=six) and the green algal crust (n=4).~~ f~~F~~rom c~~C~~omplete desiccation cycles (~~from~~ the water saturated phase to the air-dried status)~~ were measured under~~ at saturating light conditions (the operational light was set to 985 µmol photons m^{-2} s^{-1} for C-BSC and 1260 µmol photons m^{-2} s^{-1} for G-BSC, which represent

the results from the 25 °C light cycle measurement), ambient CO_2 and a set of different temperatures (7, 12, 17, 25 °C) for n=6 C-BSC and n=4 G-BSC. The chosen temperatures are in accordance with other eco-physiological studies on BSCs (e.g. Weber et al., 2012; Lange et al., 1997; Lange, 1980) and represent the average temperature range of temperate Europe/ Germany (see e.g. site Homburg in Raggio et al., 2017). Optimum water content was calculated as the amount of water in mm precipitation equivalent where NP was above 90% of maximal NP, whereas a minor depression because of suprasaturation was defined as NP being constantly below 75% of maximum NP of the sample.

~~Within each crust type three sampling units were subject to measurements, which are referred to as organization levels. 1) Intact crust (named BSC_{all}): defined as the entire non-manipulated BSC including attached soil with an unknown amount of heterotrophic organisms. 2) Separated organism (named BSC_{dom}): This sampling unit is the dominant organism of the crust, isolated from the from the soil, washed and dissected thoroughly. 3) Separated soil (named BSC_{soil}): This sampling unit contains the soil and all other microscopic organisms, except for the dominant one which was removed for type 2.~~

~~The following terminology will henceforth be used for the cyanocrust: C-BSC_{all}; C-BSC_{dom} and C-BSC_{soil}; for the green algal crust: G-BSC_{all}; G-BSC_{dom} and G-BSC_{soil}.~~

~~Samples were weighed between each measurement cycle and the WC was then calculated as mm precipitation equivalent. Sample dry weight was determined after 3 days in a drying oven (Heraeus Instruments T6P, Thermo Fischer Scientific Inc.) at 60 °C. To obtain the net photosynthetic response to light, fully hydrated samples (n = three for each site) were exposed to stepwise increasing light from 0 to 2000 µmol photons m^{-2} s^{-1} (0, 25, 50, 100, 300, 500, 1000, 1500, 1750, 2000 photons m^{-2} s^{-1}) at optimal temperature and ambient CO_2 concentrations. The light cycle (about 40 min duration) was repeated until the samples were completely dry (after 6 – 7 h). Light saturation was defined as the photosynthetic photon flux density at 90% of maximum NP. The CO_2 exchange of the samples was related to soil crust surface and chlorophyll content, the latter determined after Ronen and Galun, (1984).~~

To determine a possible effect of abiotic CO_2 release from BSC attached soil, the soil was measured before and after being autoclaved~~ing~~ (see supplemental material Table S6).

2.4 Species identification

N. commune and *Z. ericetorum* were studied using a light microscope (Axiokop, Zeiss, Germany) and identified using Geitler, (1932) and Ettl & Gärtner, (1995). Additionally, other photoautotrophic cells from one gram of soil material were identified and counted, to get an overview of the photosynthetic active organisms that were present in the soil after the most abundant organism of the BSC had been removed.

2.5 Data analysis

Light compensation points and light saturation levels of the two types of BSC were compared with a grouped t-test. To test for differences between mean values of cardinal points for photosynthesis (maximum NP and DR at the same temperatures, optimal water content range and water compensation points) for BSC_{all}, BSC_{soil} and BSC_{dom}, ~~complete BSCs, soil alone and~~

~~isolated organism, light compensation points and light saturation levels~~ a multifactorial ~~one-way~~ analysis of variance (Statistica 10, Stat soft), with a Tukey post-hoc test was~~ere~~ applied. ~~.~~ Prior to the analysis, all data were checked for Gaussian distribution and homogeneity of variance and successfully log transformed if they did not fit these criteria. BSC_{all}, BSC_{dom}, ~~and~~ BSC_{soil} (~~named~~referred to as "organization level" from here on) and temperature were always the explanatory variables, while ~~light compensation, light saturation,~~ optimum water content, water compensation point, maximum net photosynthesis and maximum dark respiration were dependent variables. ~~.~~ Paired t-tests were applied to detect differences in total NP rates of BSC_{all} and NP rates of BSC_{dom} and BSC_{soil} taken together. The optimum water content range was compared by statistically testing if the upper and lower limits between the ~~both~~ BSC_{dom}, BSC_{soil} or BSC_{all} differed. ~~Used was a~~A multifactorial ANOVA was applied where organization level and temperature were the explanatory variables while either (a) the upper or (b) the lower limit of the optimum water content range was the dependent variable.

3 Results

3.1 Gas exchange

3.1.1 Light dependent photosynthetic response

Maximum photosynthetic rates per area were reached at 2000 µmol photons m^{-2} s^{-1} for both, C-BSC_{all}~~dom~~ and G-BSC_{all}~~dom~~ (Fig. 2a and 2b), as it was impossible to increase PAR above this value with the GFS 3000 due to instrument limitations. ~~Both~~ Neither organism~~s did not~~ showed photoinhibition even at the highest light intensities applied (2000 µmol photons m^{-2} s^{-1}). The light compensation point of photosynthesis was ~~almost twice as much~~ higher for G-BSC_{all} (254 ± 53 µmol photons m^{-2} s^{-1}) compared to C-BSC_{all} (151 ± 25 µmol photons m^{-2} s^{-1}). However, there was no statistical support for the difference between the ~~organisms~~ BSCs (grouped t-test: t-value=2.58; df=4; p=0.06), mostly owing~~ed~~ to the high standard deviations caused by high sample variation.

Light saturation of NP (90% of maximal) was significantly different for both types and reached 985 ± 31 µmol photons m^{-2} s^{-1} for C-BSC_{all} and 1260 ± 53 µmol photons m^{-2} s^{-1} for G-BSC_{all} (grouped t-test: t-value=7.75; df=4; p=0.002).

3.1.2 Net photosynthesis

For the *N. commune* dominated BSC ~~.~~(Fig. 3a) the organization level had a significant effect on the NP performance (F=38.06; p=0.000). NP was up to 4.3 times higher in C-BSC_{dom} than in C-BSC_{all} (Tukey post-hoc test: p= 0.000), whereas there was no difference between C-BSC_{all} and C-BSC_{soil}. NP at 25 °C was~~is~~ significantly higher than at 7 °C and 12 °C for all, C-BSC_{all}, C-BSC_{dom} and C-BSC_{soil} (F=9.41; p=0.000; Tukey post-hoc test: p 7 °C=0.000; p 12 °C=0.000).

In the *Z. ericetorum* dominated BSC (Fig. 3b) NP also changed with organization level (F=53.61; p=0.000). There was a significant difference between G-BSC_{soil} and G-BSC_{all} (Tukey post-hoc test: p=0.03), and G-BSC_{dom} NP differed from both

(Tukey post-hoc test: p G-BSC_{all}=0.000; p G-BSC_{soil}=0.000). NP of ~~an~~ G-BSC_{dom} was 5.5 times higher than in G-BSC_{all}. There was n~~N~~o temperature dependency of NP ~~is~~ visible for either the G-BSC_{all}, G-BSC_{dom} or G-BSC_{soil}.

~~E~~The effects of organization level and temperature on DR can be seen in Fig. S1 and Tables S7-S9 ~~in supplemental material~~.

3.1.3 Water dependent photosynthetic response

The response to changing water contents in both BSCs and their separate components are shown in two exemplifying graphs (*N. commune* Fig. 4a and *Z. ericetorum* Fig. 4b). Neither the water-response curve of G-BSC_{dom}, nor C-BSC_{dom}, resembled the response of BSC_{all}. The NP in C-BSC_{dom} was three times higher compared to C-BSC_{all}, and doubled in G-BSC_{dom} (for statistical analyses see Table S1-3 ~~supplemental material~~). Respiration in C-BSC_{soil} was strikingly small in a~~n~~ *N. commune* dominated system and did not resemble the respiratory response in C-BSC_{all} or the C-BSC_{dom}, whereas respiration was pronounced in a *Z. ericetorum* dominated G-BSC_{all}. Respiration of G-BSC_{soil}, G-BSC_{all} and G-BSC_{dom} all seemed to follow the same pattern ~~in the green algal-dominated BSC~~, although the values differed slightly between all three, with highest rates in G-BSC_{soil}. A general observable pattern was that NP of BSC_{soil} and BSC_{dom} combined never equalled NP of BSC_{all} in both BSC types (paired t-test; results for *N. commune*-crust: t-value=-6.43; df=23; p=0.000; *Z. ericetorum*-crust: t-value=-5.05; df=15; p=0.000).

C-BSC_{dom} showed a ~~very slight~~ minor depression in net photosynthesis at high water contents (Table 1). An even smaller depression was visible in the C-BSC_{all}. Due to the cross sensitivity of the GFS 3000 analyzer for CO_2 and H_2O molecules, it was impossible to measure such high water contents for the C-BSC_{dom}, as the amount of water brought into the measuring system was too high to produce reliable measurement values. Also in G-BSC_{dom} and in G-BSC_{all} a minor depression was expressed between 63–71% normalized water content.

The optimum water content had a ~~broader~~smaller range for C-BSC_{all} (1.21 to 1.39 mm) compared to C-BSC_{dom} (0.56 to 0.83 mm); f~~F~~or G-BSC_{all} it was between 1.44 and 1.57 mm and for G-BSC_{dom} between 0.58 and 0.79 mm. The values for optimum water content between both BSC_{all} ~~are~~types were close, as well as between both BSC_{dom} which show similar values, independent of species. The maximum water holding capacity was 3.29 ± 0.89 mm for C-BSC_{all} and 4.66 ± 1.38 mm for G-BSC_{all}. In percent dry weight C-BSC_{dom} could hold up to 4562%, while ~~having~~sustaining 88% of its maximum NP rate, ~~when~~but G-BSC_{dom} ~~only~~ could only take up 435% with ~~hile having~~ 18% of its maximum NP rate (see Fig. 4). ~~Also, only a small depression in the C-BSC_{all} was visible. In G-BSC_{dom} and in G-BSC_{all} a clear depression was expressed between 80–100% normalized water content.~~

~~The optimum water content had a broader range for C-BSC_{all} (0.63 to 1.20 mm) compared to C-BSC_{dom} (0.18 to 0.26 mm). For G-BSC_{all} it was between 0.88 and 1.26 and for G-BSC_{dom} between 0.25 and 0.27, so the values between both crust types and their isolated organisms was close.~~ Both BSC_{all} optimum water content ranges were significantly higher than the corresponding BSC_{dom} optimum water content ranges (multifactorial ANOVA *N. commune*: df=2; F=15.24; p=0.000; multifactorial ANOVA *Z. ericetorum*: df=2; F=30.08; p=0.000). The optimal water content differed heavily with organization level and was broadest in BSC_{dom} for both BSC-types (Fig. 5; *N. commune*: F=43.20; p=0.000; *Z. ericetorum*: F=66.28;

p=0.000). This pattern is expected, as extracellular polymeric substances have a different water holding capacity than soil. Nonetheless, both BSC_{all} and their respective BSC_{dom} samples, showed a broad optimum water content range (Fig. 5), compared to soil alone. Both limits of BSC_{dom} ~~are~~ in both types, were not statistically different, which was ~~as~~ also the case for ~~in~~ BSC_{all} (for statistical results see Table S4 & S5 ~~in supplemental material~~)

3.2 Net photosynthesis per area vs. net photosynthesis per chlorophyll content

A significant difference between NP calculated per area and NP per chlorophyll content became obvious after comparing the results: NP/chlorophyll was up to two magnitudes higher in C-BSC than in G-BSC, although G-BSC had an up to 181 times higher chlorophyll content per area (Table S9), which would theoretically enable the G-BSC to assimilate more CO_2 than the C-BSC. To investigate whether the higher NP rate in C-BSC was due to actual eco-physiological differences (like a carbon concentrating mechanism, CCM) or because of the reference value used, we calculated the effect the reference value had on the NP rates between both investigated organisms.

First, NP per area was calculated for C-BSC_{dom} and G-BSC_{dom} at each temperature. Then the ratio of C-BSC_{dom} to G-BSC_{dom} was calculated for NP/area rates. The same ratio of NP/area rates was calculated between C-BSC_{all} and G-BSC_{all}.

Afterwards, NP was calculated on chlorophyll basis for the same samples and each temperature. The ratio of NP/chlorophyll between C-BSC_{dom} and G-BSC_{dom} and then between C-BSC_{all} and G-BSC_{all} was calculated. If both ratios, NP/area and NP/chlorophyll, were of equal size, it would be possible to conclude that only eco-physiological reasons, like a CCM, were responsible for the much higher NP rates in the cyanobacterial dominated crust. However, t~~T~~he NP/chlorophyll ratio was always higher than NP/area ratio (grouped t-test: t-value=-2.167; df=14; p=0.05; Fig. 6) e.g. BSC_{all} at 25 °C: NP/area 6 times higher in C-BSC_{all}; NP/chlorophyll 42 times higher in C-BSC_{all}.

~~A significant difference between NP calculated per area and NP per chlorophyll content became obvious after comparing the results. Besides having an up to 181 times higher chlorophyll content per area (Table. 1), net photosynthesis of G-BSC_{dom} was always up to two magnitudes lower than in C-BSC_{dom}. To investigate whether this difference was due to actual eco-physiological differences or because of the reference value used, an "effect size" was calculated. The ratio between NP at a certain temperature between C-BSC_{dom} and G-BSC_{dom}, based on area was calculated. The same was done for NP rates based on chlorophyll content and besides the single organism also for BSC_{all}. The difference of chlorophyll based NP between C-BSC_{dom} and G-BSC_{dom} and in BSC_{all}, was always higher (up to 42 times in BSC_{all} 25 °C), than the difference in area based NP (grouped t test; t value= 2.167; df=14; p=0.05; Fig. 6), although the ratio should be similar, if both reference values (area and chlorophyll content) were equally suited for gas exchange measurements in terrestrial cyanobacteria and green algae crusts. A difference with temperature might be explained by the dependency of net photosynthetic enzyme activity on temperatures.~~

3.3 Photosynthetic active and heterotrophic organisms in soil

The number of cells of photosynthetic active organisms in soil samples was similar for both study sites (26 ± 3 ~~organisms~~ cells per gram soil for MH and 19 ± 2 for PL). The abiotic gas release, measured after autoclaving the soil, was about 20 % of the gas exchange before autoclaving (Table S6 ~~suppl. Material~~).

4 Discussion

In this study, we received profound evidence that early successional BSCs expose a considerable physiological ~~plasticity~~ flexibility which in turn might be responsible for their pronounced stress tolerance and ~~finally~~ their success in heavily disturbed habitats~~. This will be discussed here in detail.~~. As light is one of the major drivers for photosynthetic rates in BSCs, the cardinal points in response to light were examined. For BSCs photosynthetic organisms the light level compensating respiration normally ~~is~~ lies between 60 to 100 photons m-2 s^{-1} (Green & Proctor, 2016), which indicates comparability to classical "sun plant" features. Our results support these findings and the variation within our measurements, indicated by high standard deviations, reflects a very high sampling site internal variation. This may be a result of spatially small-scale shading of, e.g. *Calluna vulgaris* in the Mehlinger heathland, or higher plants at the border of Parking Lot. As high light adapted organisms, light saturation points of BSC organisms are almost always at, or above, 700 µmol photons m^{-2} s^{-1} (Green & Proctor, 2016). This is well supported by our data with LSP consistently being over 900 µmol photons m^{-2} s^{-1} for both, C-BSC_{all} and G-BSC_{all}.

The second major driver for photosynthetic responses in BSCs is water, thus the photosynthetic cardinal points in response to water content were examined. The lack of differences in the optimal water content between C-BSC_{dom} and G-BSC_{dom}, and ~~none~~ between the ~~green algal and cyanobacterial~~ G-BSC_{all} and C-BSC_{all}, indicates ~~a high physiological flexibility of the organisms to water gain.~~ that both organism groups ~~take~~share the same functional role in the BSC consortium and can operate at near optimal conditions over a variety of different water contents, as it would be expected for highly stress tolerant crust pioneer species. Explaining th~~e~~~~is~~ variability in~~of~~ eco-physiological response to water content are the relatively high standard deviations and ~~the~~ broad range of ~~the~~ optimal water contents for the dominant organisms, compared to other species (e.g. 0.25 – 0.35 mm in *Fulgensia fulgens* (Lange et al., 1998)). Optimal water content of a BSC in a temperate habitat (Homburg; 3.32 mm; Europe, Germany; Colesie et al., 2014~~b~~) is 2 mm higher than in our study (1.~~30~~ 21 – 1.~~46~~ 57mm), probably ~~owed~~ due to the low biomass in the investigated early successional habitats in this study. Colesie et al., (2014~~b~~) proposed that biomass is the driving factor shaping the optimal water content within a system, with low biomass needing less water to achieve maximum net photosynthesis. A general difference between BSC_{all} and BSC_{dom} concerning optimal water content is likely ~~owed~~ due to the different water holding capacities of the soil. Even at high water contents, C-BSC_{dom} only showed a slight depression of NP (Fig. 4). Depression in G-BSC_{dom} occurred relatively late (Table 1). Considering that these crusts live in a temperate climate, where precipitation is high enough to support forest vegetation, a depression of NP at high water contents might be a disadvantage, although a depression is common in other BSC organisms (e.g. several lichens; Lange et al., 1997). Additionally,

N. commune can gain up to 20–30 times its dry weight in water (Satho et al., 2002; Shaw et al., 2003), which is stored mostly in exopolymeric substances (EPS) (Tomaselli & Giovannetti, 1993; Kovacik, 2000). A depression of NP at a high water content while simultaneously being exposed to high water contents for a long time period would be disadvantageous. *Z. ericetorum* only shows a slight difference in morphology when dried (Fritsch, 1916; Holzinger et al., 2010), and therefore cannot which means that it does not store as much water as *N. commune*. In addition, *Z. ericeoturm* and is not as often as strongly rarely exposed to high water contents around the cell, and t. Therefore, it might have may show an earlier depression of net photosynthesis at high water contents. AdditionallyFurthermore, a carbon concentrating mechanism (CCM) was detected in *N. commune* (see supplemental material Fig. S2), but not in *Z. ericetorum*. Through this mechanism, the internal CO_2 partial pressure around the carboxylating enzymes is increased, which improves photosynthetic efficiency. Simultaneously, CCMs decrease the CO_2 concentration around the photosynthesizing cells. Through this increasing diffusion gradient for CO_2 transport the adverse effects of suprasaturation with water can be overcome (Lange, 2001).

The third major driver of photosynthesis in BSCs is temperature. Temperature showed different effects on net photosynthesis rates in both organism groups. In C-BSC_{all} NP was only higher at 17 °C and 25 °C compared to lower temperatures (7 °C and 12 °C), whereas in G-BSC_{all} no difference was observable at any temperature. This indicates a high variability in temperature tolerance, which was also noticed by Borstoff et al. (2005), who could not pinpoint an exact temperature optimum for a BSC during field studies in western Mojave Desert. BSC components are not necessarily adapted to high temperatures. Although soil surfaces at which BSCs live can reach up to 50 °C on a normal summer day (Hoppert et al., 2004; Pentecost & Whitton, 2012), the organisms are already dry and inactive when these temperatures are reached (Raggio et al. 2017). Presumably this is the case for G-BSC_{all}, but not likely for the C-BSC_{all} in this study, due to the high water holding capacities of *Nostoc* thalli, therefore activity periods during daytime are prolonged. This may coincide with a temperature increase, as it has been reported for gelatinous, slow drying lichens (e.g. *Collema tenax*; Lange, 2001). In Antarctica, where Novis et al., (2007) conducted a study on the importance of *N. commune* in antaretic Antarctic habitats, it was observed that this organism tends to have its highest NP rates at unusually high temperatures (20.5 °C). However, the results of Novis et al., (2007) should be treated with caution, because it is very likely that organisms corresponding to the description of *N. commune* from polar and temperate regions may be genetically distinct (Novis & Smissen, 2006) and therefore should not be compared so readily. Nevertheless, in general cyanobacteria are better adapted to high temperatures than green algae are (Castenholz & Waterbury, 1989; Lange et al., 1998).

In Ssummaryized, both crust types were largely unaffected by changes in water content and had high light compensation and exceptionally high light saturation points. Net photosynthesis of G-BSC_{all} was unaffected by increasing temperatures, while C-BSC_{all} only had increased NP rates with higher temperatures. Both fit well within known eco-physiological patterns of different BSC components (see Lange & Belnap, 2001), and show a lower net photosynthesis compared to BSC components of later advanced successional stages (see e.g. Lange, 2001). The high physiological variability in photosynthetic cardinal points places *N. commune* and *Z. ericetorum* crusts as similar to other BSC contributors, such as lichens and bryophytes. This characterizes these organisms as stress tolerators within the typical patterns of Grimes CSR-model (Grime & Pierce, 2012).

Life history traits of stress tolerators include slow growth rates, high rates of nutrient retention, low phenotypic plasticity and a response to environmental stresses through physiological variability (Grime & Pierce, 2012).

~~In addition to this eco-physiological description, methodological procedures are discussed for~~ To aid in future investigations on BSCs methodological procedures will now be discussed. First, an unavoidable complication in gas exchange measurements of BSCs is to take abiotic release of CO_2 into account (Inglima et al., 2009; Weber et al., 2012), aside from the biotic respiration of BSC ~~organisms~~, phototrophic and heterotrophic organisms. The CO_2 release of alkaline and saline substrates can even exceed those of organic activity (~~Xie et al., 2009;~~ Shanhun et al., 2012; ~~Ma et al., 2013;~~ Sancho et al., 2016). The abiotic release in this study accounted for only 20 % and 26 % (MH and PL, respectively) of total soil respiration rate, which is close to what Weber et al., (2012) measured in the Succulent Karoo ~~or~~ and Shanhun et al., (2013) with 25% in Antarctica.

Secondly, besides an obvious effect of organization level on NP and DR rates (see Fig. 3, and ~~supplemental material~~ Fig. S1), the water response curves of BSC_{all} and BSC_{dom} alone differed. Although the courses of their curves were similar, net photosynthesis rates ~~never~~ were never equally high for BSC_{all} and BSC_{dom} (Fig. 4a and b). Adding NP rates of BSC_{soil} to BSC_{dom} did not equal the values and NP was always higher in BSC_{dom} compared to BSC_{all} in both crust types. This fact confirms the view of BSCs being ~~as~~ communities or systems rather than random accumulations of organisms and strengthens the need for long term field monitoring studies of an intact BSC. Causes that might have led to the unexpected ~~an altered~~ NP rate could be self-shading or water logging. An organism l~~a~~ying on top of an ~~unaltered~~ intact BSC has a species specific structure (e.g. lobes of *N. commune* over one another or the spherical structure of *Z. ericetorum* algal mats) that will be changed and rearranged while being washed and placed separately in ~~the~~ a cuvette ~~of the GFS 3000~~. Through this thallus manipulation and subsequent exposure ~~not only~~ the internal diffusion resistance is decreased and~~, but also~~ the self-shading protective mechanisms in those organisms damaged ~~are no longer functional.~~ Aeroterrestrial filamentous green algae, such as *Klebsormidium crenulatum* form multilayers mat like structures on top of or interwoven with the upper ~~millimeters~~millimeters of soil (Karsten et al., 2010b), contributing to self-shading of individual filaments inside a population. The same is visible in *Z. ericetorum*. While rearranging the organisms the protective layer of dead or highly melanosed cells on top of the crust is either removed or shifted, resulting in ~~and~~ unprotected but highly active cells being ~~are now~~ subjected to high light intensities. So a~~A~~lthough the high light intensities will cause damage, ~~e.g.~~ through reactive oxygen species production for example, the NP response itself is higher than before. Overlapping lobes in *N. commune* ~~also~~ may also cause reduced NP rates in an intact BSC system. Bowker et al., (2002) hypothesized that sunscreen pigments produced by *Nostoc* protect other, less pigmented taxa, which ~~does not exclude~~includes a self-shading protective mechanism ~~in~~ for lower lobes of the same species. Recent data suggests that shading effects due to such three dimensional spatial arrangements may be more important than previously assumed (Karsten & Rindi, 2010). Another possibility that ~~might~~ could lead to decreased NP in a complete BSC system is water logging between filaments of the organisms (Garcia-Pichel & Belnap, 2001). The diffusion resistance of CO_2 in water is higher than in air (Cowan et al., 1992), and will reduce NP rates. A water suprasaturated system, as it can be found in the closely growing mats of *Z. ericetorum* or *N. commune*, could have a disadvantage against a widely spread organism surface in the cuvette, that is aerated all around.

Thirdly, we propose a methodological consideration concerning reference values of photosynthesis in gas exchange measurements in general. To compare cardinal points of photosynthesis between organisms or samples of the same species it is necessary to base the photosynthetic values on either dry weight, area or chlorophyll content, which are the most common reference values in literature. In Fig. 6 it becomes apparent that the ratio of NP per area and NP per chlorophyll content in C-BSC$_{dom}$ and G-BSC$_{dom}$ differ ~~heavily~~substantially, although the ratio should be similar if both reference values were equally suited for gas exchange measurements in those organisms. This difference is most probably ~~owed~~ due to the ~~completely~~ different composition of photoactive pigments in the two organism groups. Terrestrial green algae possess chlorophyll a and b, whereas cyanobacteria only possess chlorophyll a, which is considered in the calculation of chlorophyll content. But cyanobacteria also possess phycobilisomes and super antennae allowing capture of photosynthetically active radiation from low photon flux densities and the green part of the spectrum (Lüttge, 2011), which are not considered in calculations of this reference value. A much more suitable value than chlorophyll content is therefore area, which has been used in this study. Nonetheless, this value is not perfect as there are probably many dead cells still bound to the EPS of living cells that distort area measurements, and of course it is not useful if fruticose lichens are investigated. Additionally, the arrangement of the BSC does have an influence on the photosynthetic signal, considering that *N. commune* is almost flat while *Z. ericetorum* has a more spherical structure as the BSC gets older. It is therefore of immense importance to decide which reference value should be used when comparing the eco-physiological response of BSC systems.

5 Conclusion

In this study, we present the first detailed eco-physiological dataset describing photosynthetic performance of early successional BSCs. A relative temperature independence of NP, as well as late or no water depression and an adaptation to high light intensities was demonstrated for both early successional BSCs and their separated dominant organisms. This broad physiological ~~plasticity~~ amplitude indicates strong stress tolerance in both organism groups and ~~might~~ may be the reason for their success in heavily disturbed areas. The results can be incorporated into global scale carbon cycle models. Additionally, this study emphasizes the importance of measuring a complete BSC rather than their single components, as not only taxonomic composition but also spatial arrangement seems to be an important factor shaping photosynthetic response in BSC systems. ~~The~~ Lastly, the methodological approach demonstrated that a comparison of photosynthetic values in cyanobacteria and green algae should be based on area rather than chlorophyll content.

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Tables

Table 1: Water content at which net photosynthesis is below 75% of maximum net photosynthesis including standard deviations.

	Normalized water content [%]
C-BSC$_{all}$ [a]	**84.3 ± 15.9**
C-BSC$_{dom}$ [a,b]	**71.7 ± 16.5**
G-BSC$_{all}$ [a,b]	**70.9 ± 15.1**
G-BSC$_{dom}$ [b]	**62.8 ± 18.5**

Superscripted letters represent statistical differences.

Table 1: Chlorophyll content per area in *N. commune* and *Z. ericetorum* samples without soil.

Sample	Chlorophyll content per insolated area [mg/cm²]
***N. commune* S1**	0.23
***N. commune* S2**	0.10
***N. commune* S3**	0.49
***N. commune* S4**	1.48
***N. commune* S5**	0.17
***N. commune* S6**	0.36
***Z. ericetorum* S1**	18.13
***Z. ericetorum* S2**	1.11
***Z. ericetorum* S3**	15.79
***Z. ericetorum* S4**	2.68

Figures

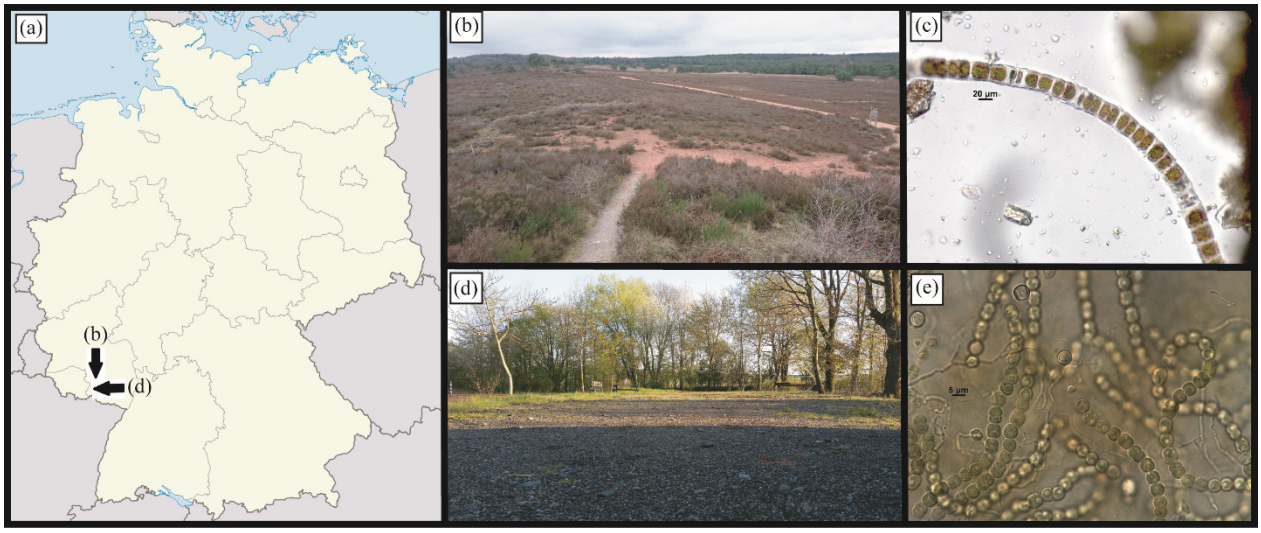


Figure 1: Organisms and map of the study site in Germany, Rhineland–Palatinate (a): Top pictures are from study site 1, Mehlinger Heath viewed from the look-out (b) and microscopic images of the crust dominating organism *Zygogonium ericetorum* (c); bottom depicts study site 2, a parking lot at an equestrian farm near Zweibrücken (d) and microscopic images of the crust dominating organism *Nostoc commune* (e).

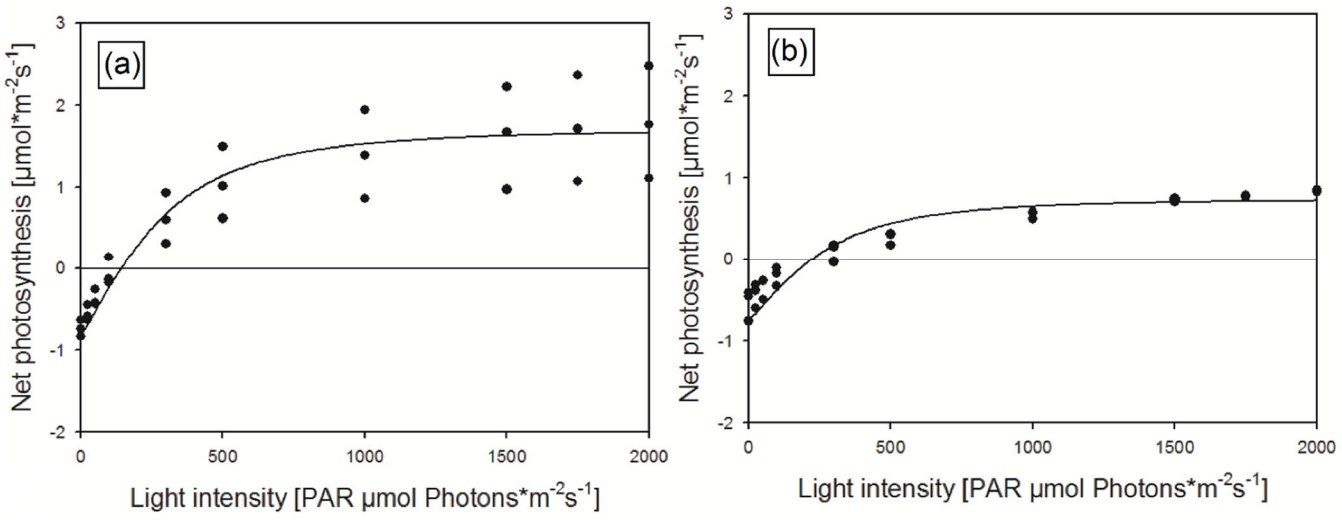
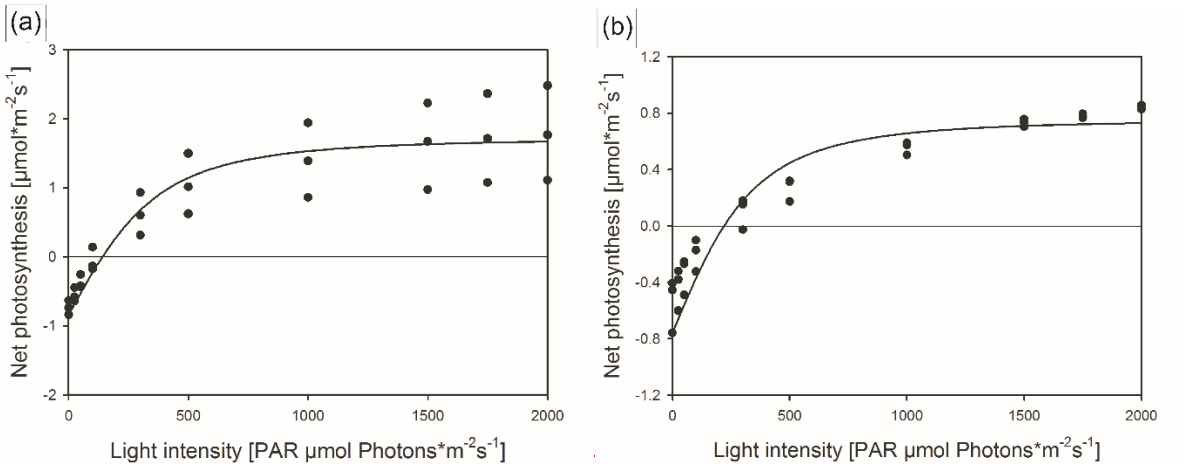


Figure 2: Light dependent photosynthetic response curves of intact BSC with (a) C-BSC$_{all}$ and (b) G-BSC$_{all}$ ~~as the dominating organism~~. n=3.



~~**Figure 2: Light dependent photosynthetic response curves of (a) *Nostoc commune* and (b) *Zygogonium ericetorum*. Net photosynthesis per area is plotted against light intensity as PAR [µmol photons m^{-2} s^{-1}] with n=3 samples.**~~

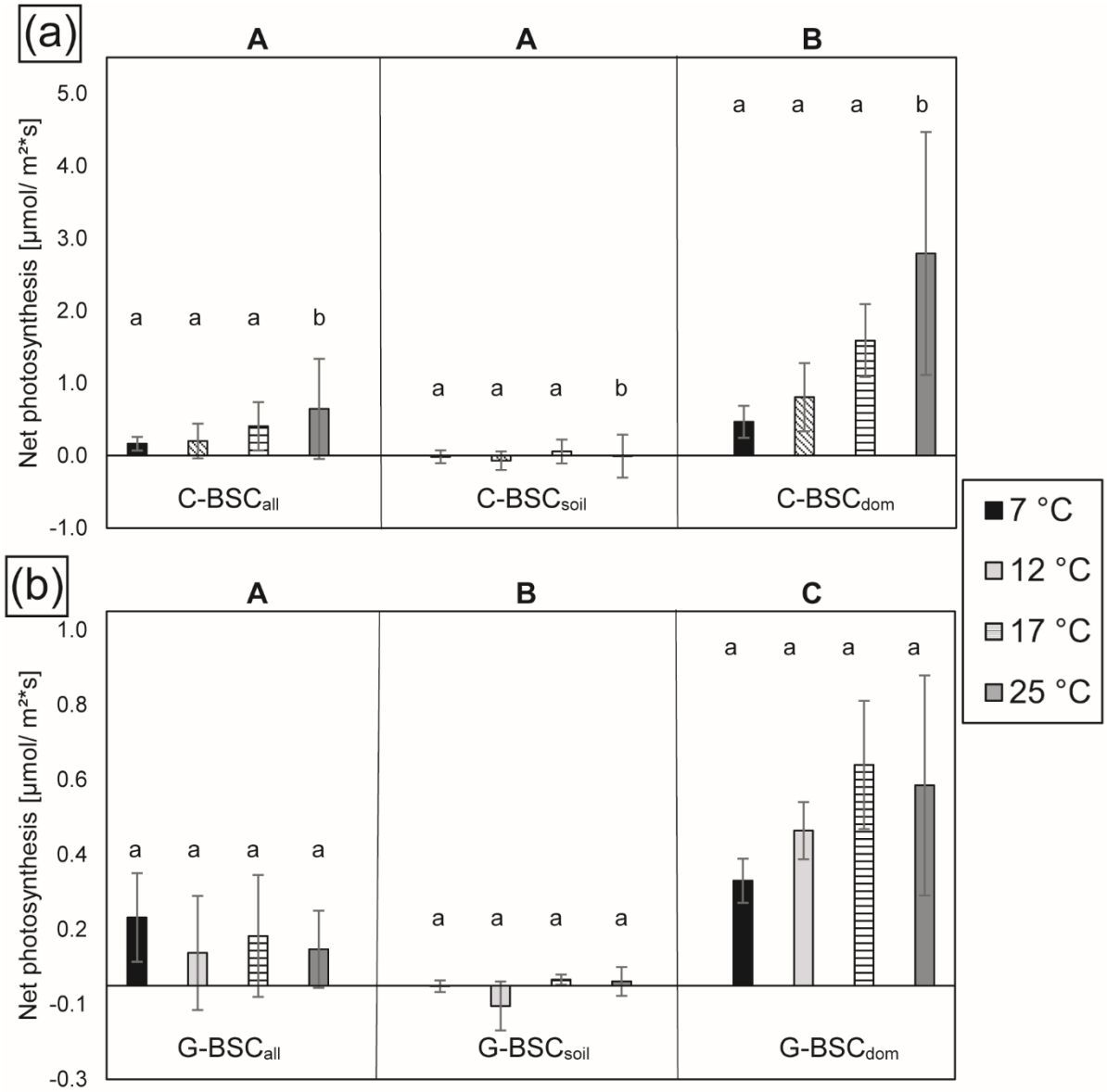


Figure 3: Temperature dependent net photosynthesis per area in (a) *N. commune* and (b) *Z. ericetorum* dominated BSCs, separated dominant organism and separate soil. Capital letters indicate significant differences in organization level between BSC, organism and soil; lower case letters compare temperature differences of one of the organization groups only. Sample size was n=6 for *N. commune*; n=4 for *Z. ericetorum*.

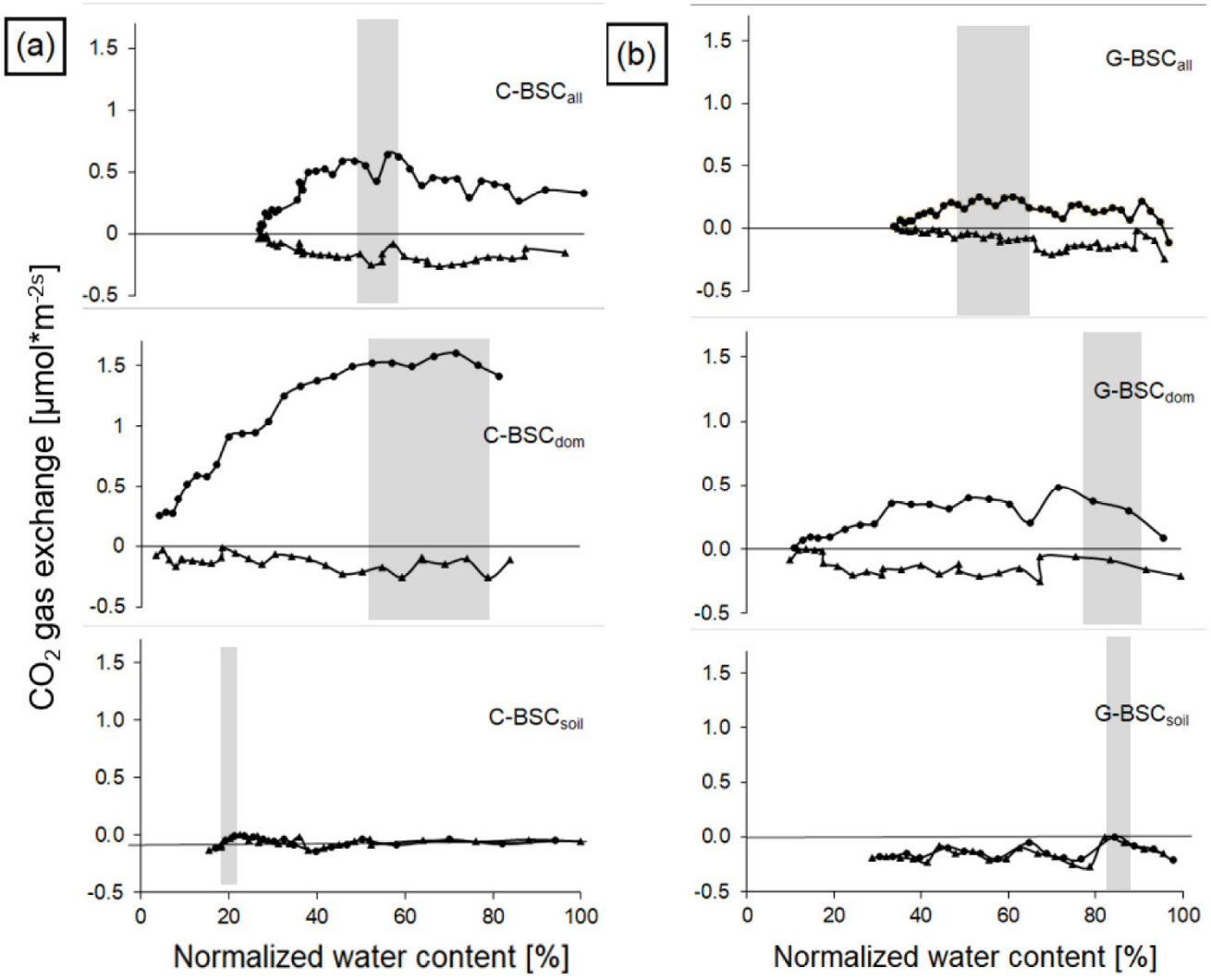
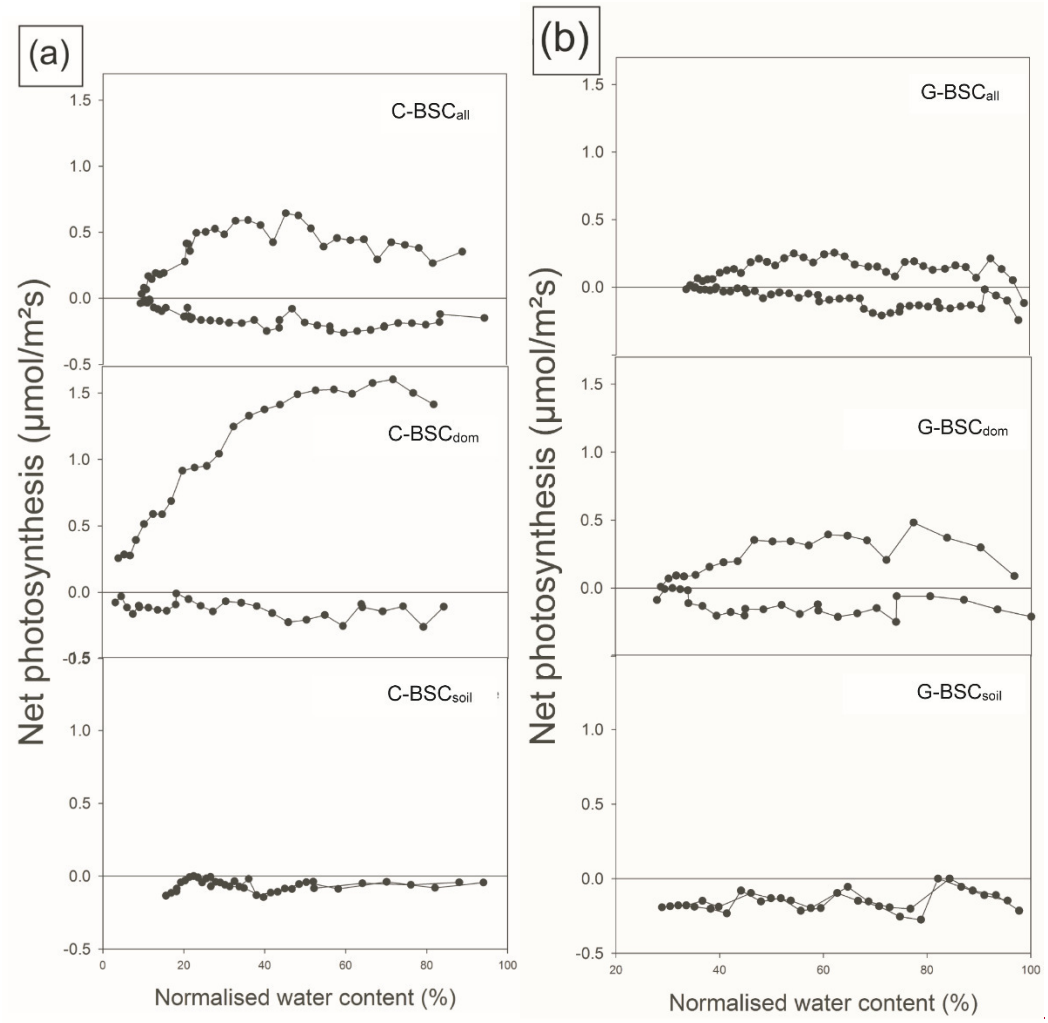


Figure 4: Responses of net photosynthesis (dots) and dark respiration (triangles) to normalized water content for intact BSC, the isolated dominant organisms and in soil at 12°C. Measurements were taken at saturating light and a temperature of 12°C. (a) C-BSC (985 µmol photons m^{-2} s^{-1}) and (b) G-BSC (1260 µmol photons m^{-2} s^{-1}). Grey bars indicate optimum water content.



~~**Figure 4: Differences in water content dependent photosynthetic response in an intact BSC, the isolated dominant organism and in soil. Net photosynthesis is plotted against normalized water content for (a) *N. commmune* and (b) *Z. ericetorum*, both at 12 °C**~~

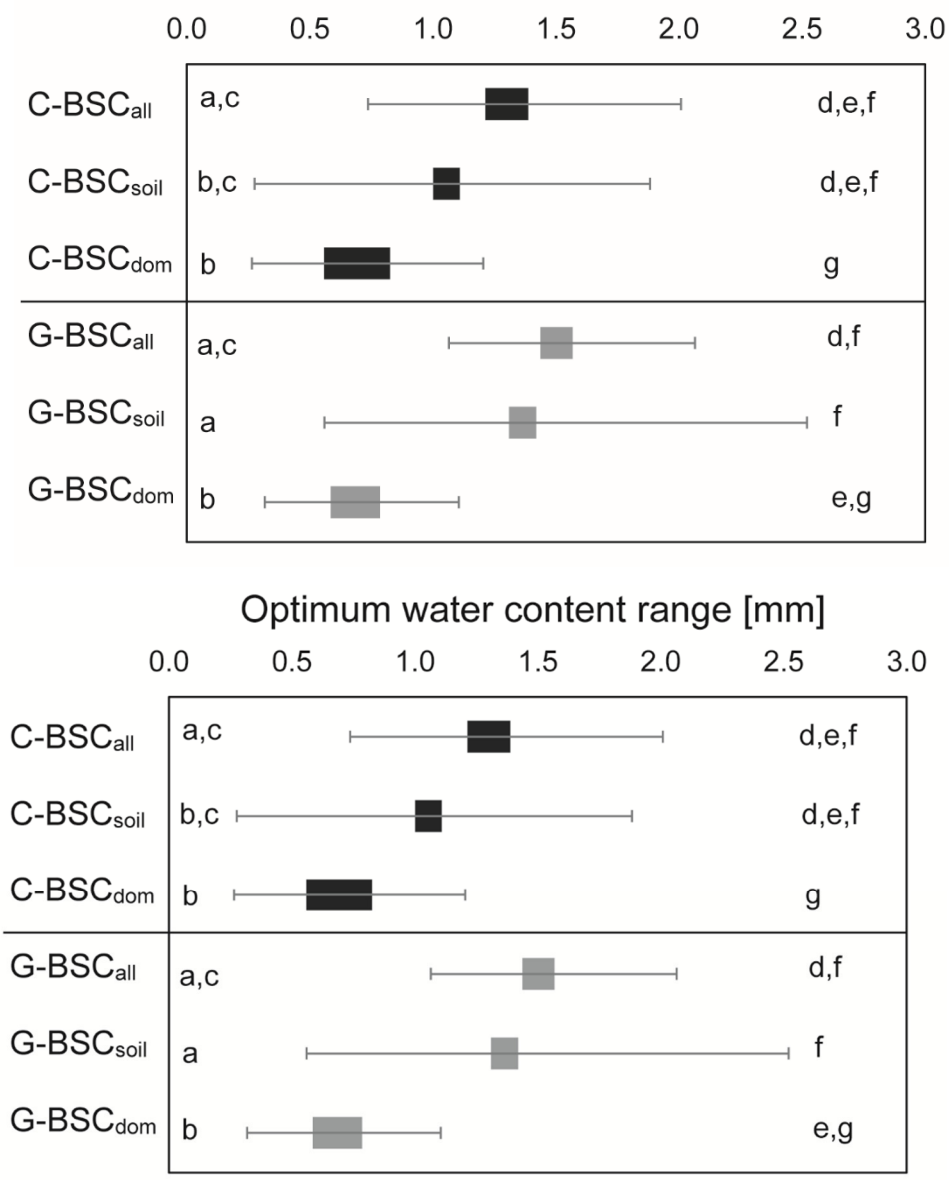


Figure 5: Optimum water content range, in mm precipitation, of a cyanobacteria dominated BSC (upper three; black bars) and a green algal dominated BSC (lower three; grey bars) and their respective separated components. Sample size is n=24 for all C-BSC and 16 for all G-BSC.

~~Figure 5: Optimum water content range, in mm precipitation, of a cyanobacteria dominated BSC (upper three; black bars) and a green algal dominated BSC (lower three; grey bars) and their respective separated components. Sample size is always n=24.~~

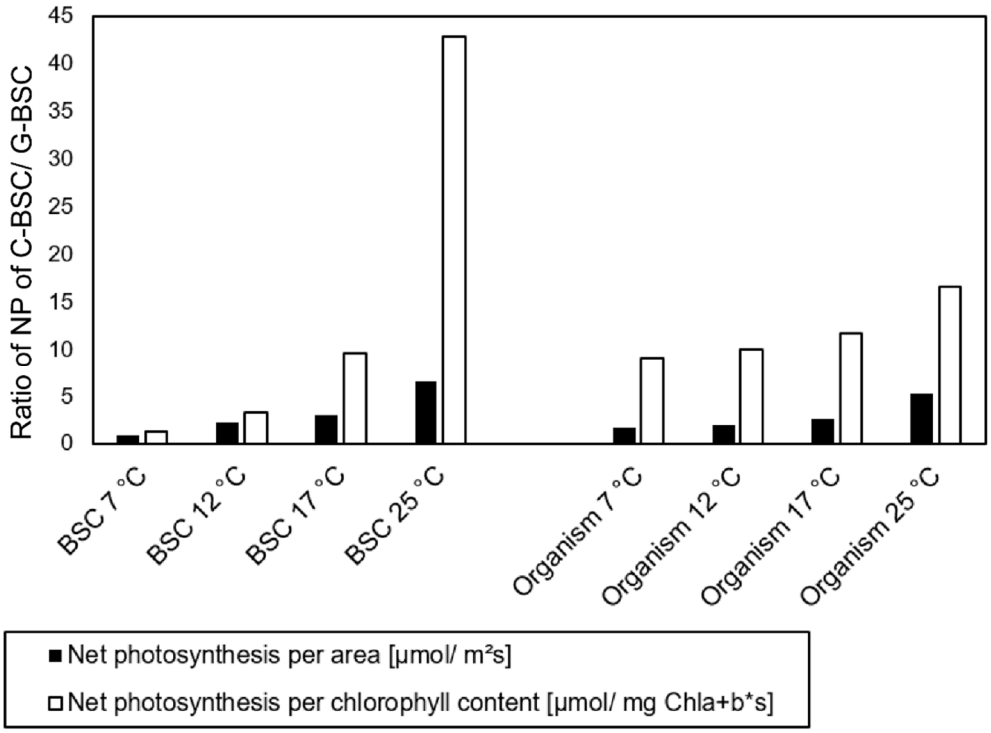
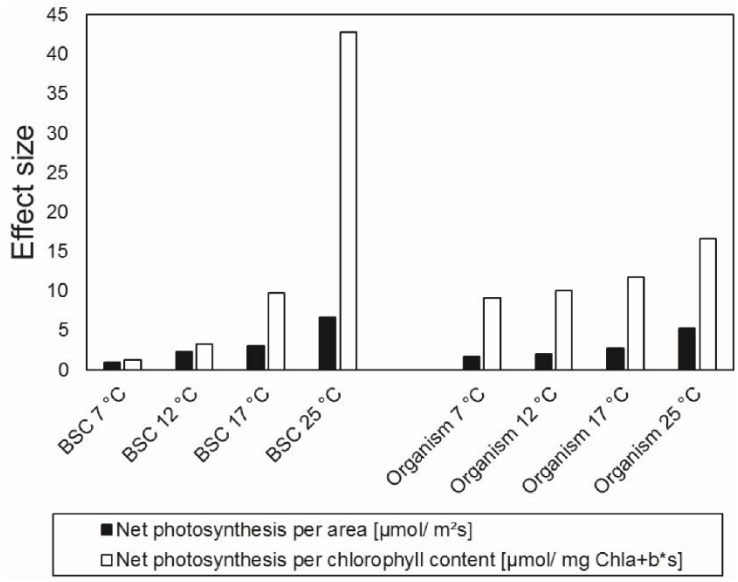


Figure 6: Difference in the ratio of net photosynthesis based on either area or chlorophyll content between C-BSC$_{dom}$ and G-BSC$_{dom}$ (organism) and also between C-BSC$_{all}$ and G-BSC$_{all}$, (BSC) measured at different temperatures.



~~**Figure 6: Difference in the ratio of net photosynthesis based on either area or chlorophyll content between *N. commune* and *Z. ericetorum* and their respective BSCs, dependent on temperature.**~~

Supplement tables

Table S1: Statistical significance of organization level, temperature and interaction of those effects on NP of C-/G-BSC$_{all}$, C-/G-BSC$_{dom}$, and C-/G-BSC$_{soil}$

Effect	df	F	p
N. commune			
Organization level	2	38.06	0.000~~000~~
Temperature	3	9.41	0.000~~035~~
Organization level * Temperature	6	5.03	0.000~~035~~
Z. ericetorum			
Organization level	2	53.61	0.000~~000~~
Temperature	3	1.64	0.198~~7700~~
Organization level * Temperature	6	1.81	0.125~~4760~~

Table S2: P-values of a tukey post-hoc test for NP depending on organization level (on top) and temperature (below) in a C-BSC.

Organization level	BSC	Soil	*N. commune*
BSC		0.089~~400~~	0.000~~117~~
Soil	0.089~~400~~		0.000~~117~~
N. commune	0.000~~117~~	0.000~~117~~	

Temperature	7 °C	12 °C	17 °C	25 °C
7 °C		0.946~~163~~	0.079~~124~~	0.000~~210~~
12 °C	0.946~~163~~		0.240~~197~~	0.001~~0565~~
17 °C	0.079~~124~~	0.240~~197~~		0.099~~8648~~
25 °C	0.000~~210~~	0.001~~0565~~	0.099~~8648~~	

Table S3: P-values of a tukey post-hoc test for NP depending on organization level in a G-BSC.

Organization level	BSC	Soil	*Z. ericetorum*
BSC		0.026~~302~~	0.000~~119~~
Soil	0.026~~302~~		0.000~~119~~
Z. ericetorum	0.000~~119~~	0.000~~119~~	

Table S4: Statistical analysis of upper limits of optimum water content of both BSC-Systems and their respective separate organisms. Shown are p-values of the tukey post-hoc test.

	C-BSC$_{all}$	**G-BSC$_{all}$**	**C-BSC$_{soil}$**	**G-BSC$_{soil}$**	**C-BSC$_{dom}$**	**G-BSC$_{dom}$**
C-BSC$_{all}$		0.82	0.65	0.14	0.00	0.02
G-BSC$_{all}$	0.82		0.11	0.86	0.00	0.00
C-BSC$_{soil}$	0.65	0.11		0.00	0.15	0.38
G-BSC$_{soil}$	0.14	0.86	0.00		0.00	0.00
C-BSC$_{dom}$	0.00	0.00	0.15	0.00		1.00
G-BSC$_{dom}$	0.02	0.00	0.38	0.00	1.00	

Table S.5: Statistical analysis of lower limits of optimum water content of both BSC-Systems and their respective separate organisms. Shown are p-values of the tukey post-hoc test.

	C-BSC$_{all}$	**G-BSC$_{all}$**	**C-BSC$_{soil}$**	**G-BSC$_{soil}$**	**C-BSC$_{dom}$**	**G-BSC$_{dom}$**
C-BSC$_{all}$		0.94	0.52	0.39	0.04	0.06
G-BSC$_{all}$	0.94		0.14	0.95	0.01	0.01
C-BSC$_{soil}$	0.52	0.14		0.01	0.81	0.79
G-BSC$_{soil}$	0.39	0.95	0.01		0.00	0.00
C-BSC$_{dom}$	0.04	0.01	0.81	0.00		1.00
G-BSC$_{dom}$	0.06	0.01	0.79	0.00	1.00	

Table S6: Mean values of maximum respiration rate per area of soil of both study sites. Sample size is n=3 in both cases.

	Parking Lot	Standard deviation	Mehlinger Heide	Standard deviation
Max. respiration before autoclaving [µmol/ m²s]	-0.23	0.20	-0.43	0.24
Max. respiration after autoclaving [µmol/ m²s]	-0.06	0.01	-0.09	0.01

Table S7: Statistical significance of organization level, temperature and interaction of those effects on DP of C-/G-BSC$_{all}$, C-/G-BSC$_{dom}$, and C-/G-BSC$_{soil}$

Effect	df	F	p
N. commune			
Organization level	2	0.14	0.8721999
Temperature	3	6.27	0.0010930
Organization level * Temperature	6	0.12	0.993160
Z. ericetorum			
Organization level	2	1.01	0.376154
Temperature	3	2.92	0.047354
Organization level * Temperature	6	0.63	0.705086

Table S8: P-values of a tukey post-hoc test for DP depending on temperature in a C-BSC.

Temperature	7 °C	12 °C	17 °C	25 °C
7 °C		0.9943744	0.815237	0.0010847
12 °C	0.9943744		0.9265885	0.0021784
17 °C	0.815237	0.9265885		0.0110604
25 °C	0.0010847	0.0021784	0.0110604	

Table S9: P-values of a tukey post-hoc test for NP depending on temperature in a G-BSC.

Temperature	7 °C	12 °C	17 °C	25 °C
7 °C		0.40875~~09~~	0.079~~389~~	0.041~~412~~
12 °C	0.40875~~09~~		0.803~~020~~	0.63879~~84~~
17 °C	0.079~~389~~	0.803~~020~~		0.9921~~1962~~
25 °C	0.041~~412~~	0.63879~~84~~	0.9921~~1962~~	

Table S10: Chlorophyll content per area in *N. commune* and *Z. ericetorum* samples without soil.

Sample	Chlorophyll content per insolated area [mg/cm²]
***N. commune* S1**	0.23
***N. commune* S2**	0.10
***N. commune* S3**	0.49
***N. commune* S4**	1.48
***N. commune* S5**	0.17
***N. commune* S6**	0.36
***Z. ericetorum* S1**	18.13
***Z. ericetorum* S2**	1.11
***Z. ericetorum* S3**	15.79
***Z. ericetorum* S4**	2.68

Supplement figures

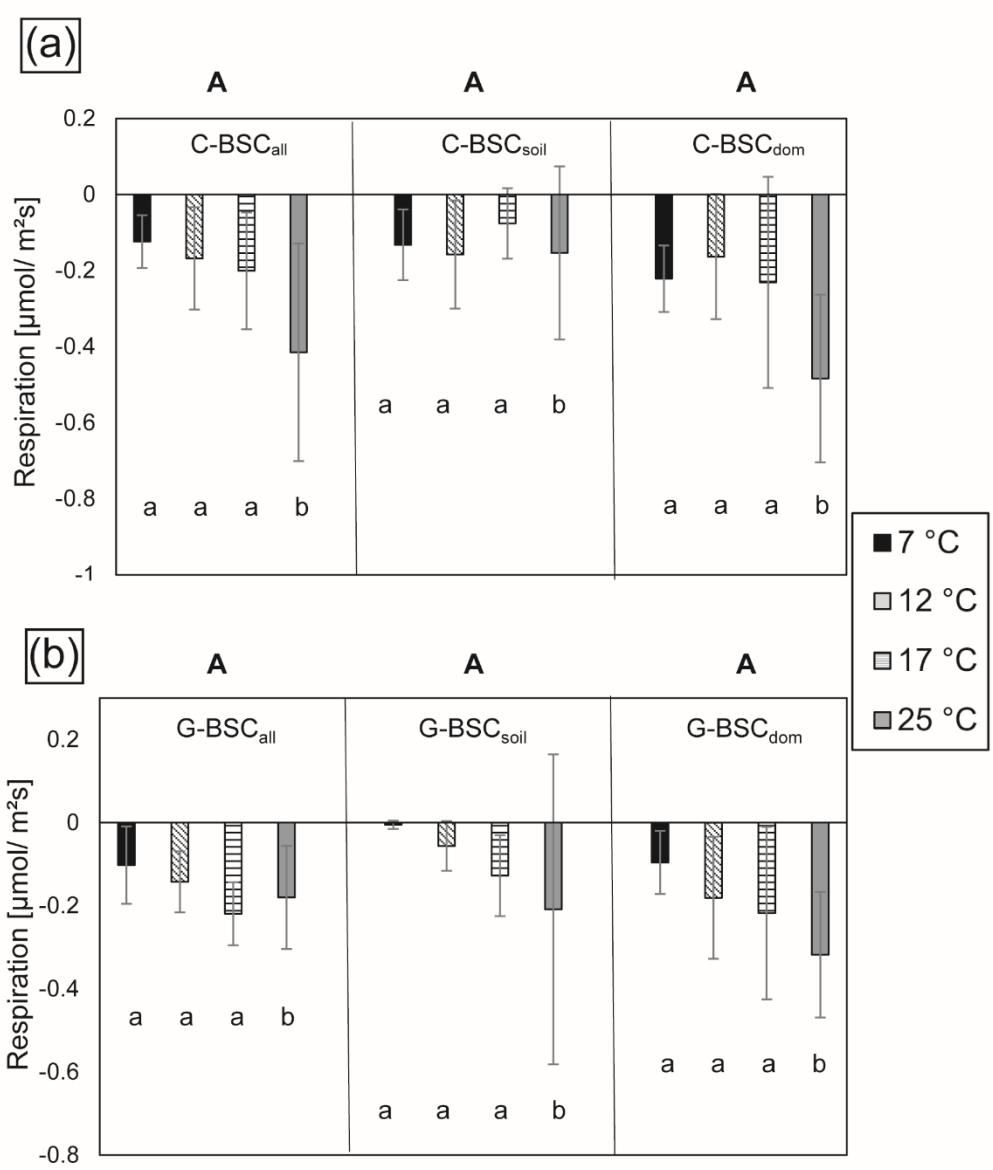
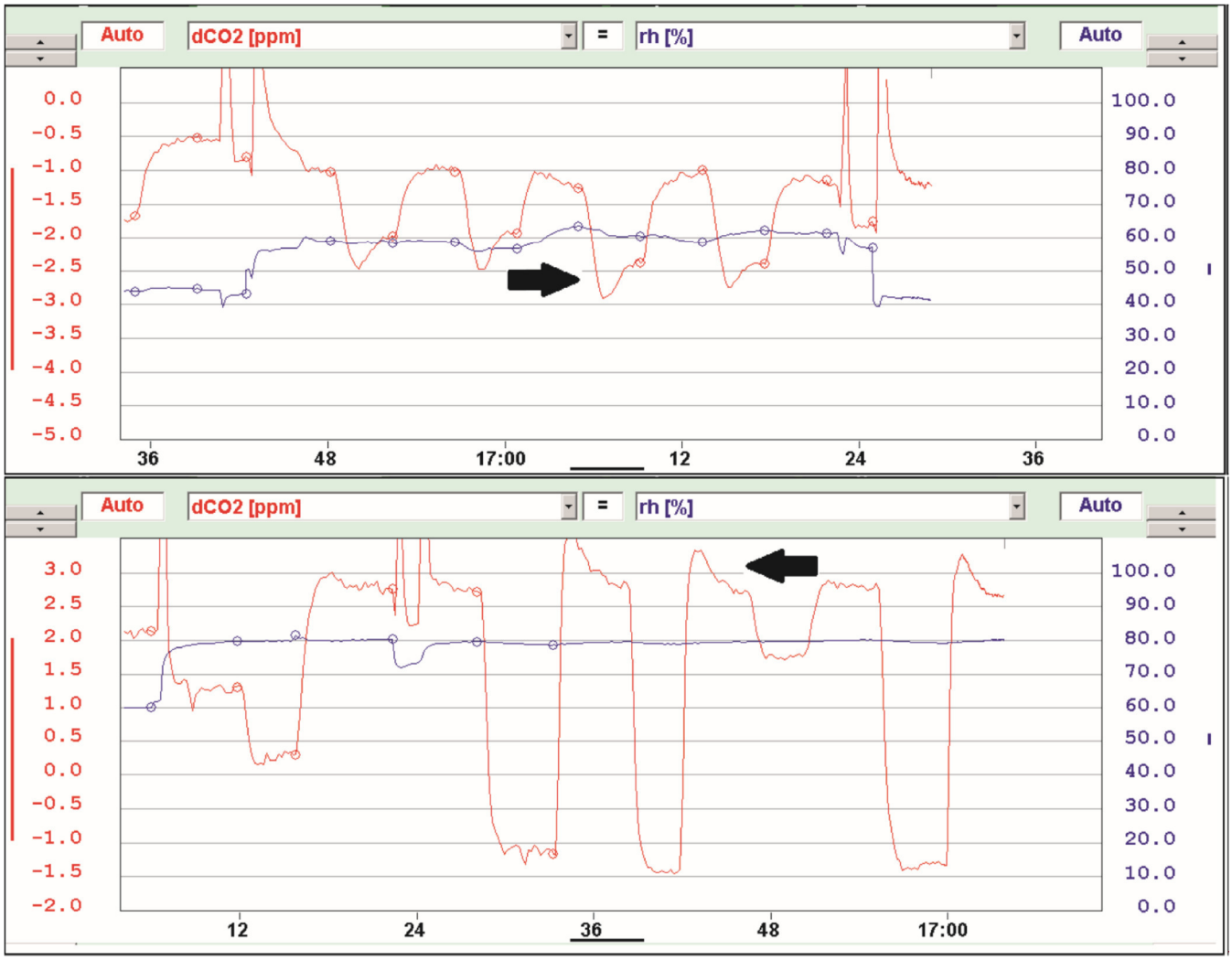


Figure S1: Temperature dependent dark respiration per area in (a) *N. commune* and b) *Z. ericetorum* (dominated BSCs, as well as separated organism and soil. Capital letters describe significant differences in organization level between BSC, organism and soil, whereas lower case letters compare temperature differences in one of the groups only. Sample size: n=6 for *N. commune,* n=4 for *Z. ericetorum*.



~~**Figure S2: CO2 exchange pattern of *N. commune* at 7 °C with optimal water content. The blue line represents relative humidity at the moment of measurement, while the red line represents the difference of CO2 between reference and sampling gas in the GFS 3000. The graph points downward when light is turned on. Abscise is the time. The black arrow marks one example of a sudden increase of CO2 uptake as soon as the light was turned on (a), or release as soon as the light was shut off (b).**~~

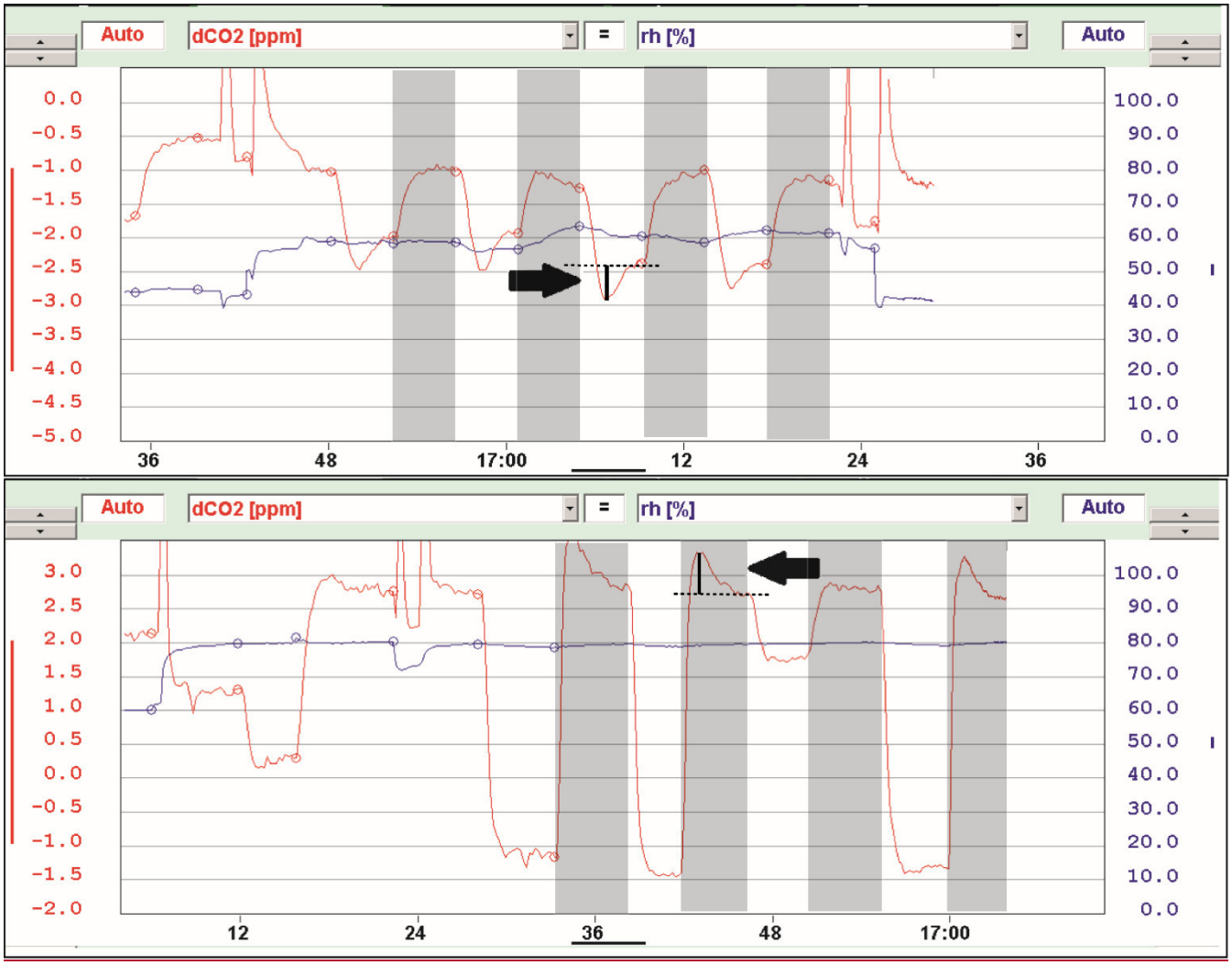


Figure S2: CO_2 exchange pattern of *N. commune* at 7 °C with optimal water content. The blue line represents relative humidity at the moment of measurement in percent, while the red line represents the difference of CO_2 between reference and sampling gas in the GFS 3000 in ppm. Abscise is the time in minutes. Grey underlay represents light being turned off. The black arrow marks one example of a sudden increase of CO_2 uptake as soon as the light was turned on (a), or release as soon as the light was shut off (b). The dotted line indicates the normal gas exchange pattern without a CCM being active in a light-dark-cycle. Here, after a sudden drop (light being turned on) or increase (light being turned off), the red line should flatten immediatley and result in a straight line. When a CCM is present, this is not the case: the solid line represents a CCM being active. Here, the uptake of CO_2 is much higher than the normal NP answer would be, while the line flattens itself only after a couple of minutes.