

Response to Referee's Comments : bg-2017-157

Hydration status and diurnal trophic interactions shape microbial community function in desert biocrusts

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We thank the reviewer for the constructive comments and suggestions for the manuscript. In the following we provide a point-by-point response to all comments.

In their manuscript, Kim and Or introduce a mechanistic biocrust model, which describes the functioning of biocrust communities with a special emphasis on carbon and nitrogen cycling within these systems. This is a highly relevant topic and the authors made large efforts to include many factors relevant in biocrusts. The results look logic and reasonable and will be relevant for many aspects of biocrust research. Nevertheless, there are some aspects of biocrust functioning, as e.g. leaching of nutrients, erosion processes and more complex N cycling mechanisms, which were not considered in the model and which at least should be mentioned/discussed in the discussion section.

We thank the reviewer for the kind and encouraging comments. Indeed the present biocrust model is a very reduced version of real biocrusts with a focus on microbial interactions in space and time using a few external variables. We will add a discussion that places the proposed model in context of more general processes that were not included here to highlight limitations and complexity of these unique ecosystems.

Page 2, line 10 ff.: The settlement of photoautotrophic organisms is followed by other phototrophic, heterotrophic and chemoautotrophic microorganisms. Here, the publication by Pepe-Ranney et al. may be considered, where settlement of non-cyanobacterial diazotrophic bacteria prior to cyanobacteria is described.

Following the suggestion, the reference will be added.

Page 2, line 26 ff.: Here, you should consider introducing the work of Porada and co-authors, where lichens and mosses as important biocrust compounds have been modelled.

We thank the reviewer for bringing this interesting work to our attention. We have stated in the original manuscript that the proposed model focuses on the early stages of biocrust formation prior to establishment of lichens and mosses. Nevertheless, for completeness, we will add this reference and highlight the simplifications made in this study (considering bacteria only).

Fig. 1: The uppermost millimeters of a biocrust clearly differ from the rest, as e.g. the soil texture is finer etc.. It seems to me that this has not been considered, but on the other hand, the uppermost millimeter or two are shown in a different color. What does the different color imply? Please clarify

We apologise for the confusion in the representation. A different colour was introduced to the upper most region (up to around 5 mm) to indicate a region of interest in this work (see Figure 7). It is correct that the pre-assigned physical structure was statistically identical to the below crust (A finer soil texture is not assigned at the surface, i.e. same roughness parameters and porosity were used.). The caption will be rewritten accordingly.

Page 5, line 18 ff.: Gas diffusion is most probably affected by finer soil at the surface and by extracellular polysaccharides (EPS). This at least needs to be discussed in a proper way as a potential source of error.

We thank for your constructive comments. We certainly agree that these factors greatly modify gas diffusion and water holding capacity across biocrusts. The possible modifications by finer soil texture at the surface and by EPS will be discussed in the revised manuscript.

Page 7, equation R3: The minus in $\text{CO}_3\text{2-}$ needs to be written in superscript.

This has been amended.

Page 8, line 15: As I understand from the later text, diazotrophic photoautotrophs, i.e. cyanobacteria capable of fixing atmospheric nitrogen are forming the first group. This has to be made clear.

We will clarify the first group as diazotrophic photoautotrophs.

Page 14, line 21 ff.: The oxygen profile shows no major variation with depth or time of the day. I am quite sure that this does not reflect natural conditions in biocrusts under unsatu-

rated water conditions, but that higher oxygen contents occur in the uppermost millimeters of a biocrust during daytime. As stated above, multiple scientific results have shown that 1. Soil texture of biocrusts is much finer in the uppermost layer, and 2. There is a dense layer of EPS in the uppermost millimeters, both causing a constrained exchange of gases with the atmosphere. This definitely has to be discussed in an appropriate manner and should be improved in a follow-up version of the model.

The profile of dissolved oxygen was appeared relatively stable due to the mass transfer between gas and liquid in unsaturated soils which is assumed to be very rapid (instantaneous equilibration by Henry's law, see section 2.3.2). This assumption is reasonable because of large liquid-vapour interfacial area and thin water film thickness of unsaturated soils. As the reviewer pointed out, we agree that biocrusts loaded with EPS and finer texture at the surface would affect the exchange of gases. These factors can retard the mass transfer between soil water and the atmosphere by decreasing interfacial area at a relatively wet condition (finer soil texture) and by sustaining thick water film thickness after wetting (swelling of EPS or increase in water holding capacity).

In terms of the current modelling approach, assigning a finer soil texture is possible by using a low porosity or a higher fractal dimension on the uppermost part of biocrusts. As an extended model of biocrusts, local EPS contents can be related to waterfilm thickness at a given matric potential (This would be interesting to investigate the role of EPS in wet-dry cycles that was not included in this work.). Overall, these factors change the water retention behaviour at the surface and the gas percolation that changes boundary conditions for Henry's law. This implies gas diffusion can be hindered even under unsaturated biocrusts at a certain range of hydration conditions as the reviewer mentioned. We greatly appreciate the comment and this aspect will be discussed in the revised manuscript.

Page 14, line 24 ff.: It is hard to recognize a diurnal cycle in the nitrate profile in Fig. 4, as stated by the authors. This has to be clarified. It also does not become clear, why a nitrate accumulation below 4-5 mm should be caused by inhibited denitrification. One normally would expect this inhibition to take place at shallower depth, also due to the occurrence of oxygen. Please clarify!

We thank the reviewer for the insightful comment, and recognise issues with the distribution of nitrate. Figure 4 was meant to show that the nitrate profile does NOT exhibit clear diurnal patterns which differ from the nitrate profile under saturated biocrusts (See Figure S4 in Supplementary text). The accumulation of nitrate below 4-5 mm was clearly due to the lack of denitrification and the activity of nitrite oxidising bacteria producing nitrate (see Figure 5,

denitrification (purple) only occurs locally at the shallow depth while NOB (light blue) appears through out the depth.). We attribute this local denitrification to the creation of local anoxic region, where aerobic organisms scavenge oxygen at the certain region that is disconnected from the percolating cluster of gas phase. High abundance of aerobic organisms (HET, AOB, NOB) yield these local anoxic regions above 4 mm depth (These were already described in the manuscript, Pg 15 Ln.17-20 and Pg 18 Ln 30-32). We will revise the incorrect description from the main text and the caption.

Page 15, line 7 ff.: Some things are striking in the distribution of organism groups along the profile and need explanations. First, there are only very few denitrifiers present and they occur at only 2-3 mm depth. This looks strange, as one would expect more of them occurring at larger depth. Second, there is a pronounced organism gap at 4-6 mm depth. Can you please give explanations for these features.

As we stated above, under unsaturated conditions, denitrification occurs at local anoxic region supported by oxygen scavenging aerobic organisms at patches that are disconnected from the atmosphere. This is not necessarily a 1-D stratified structure and may occur as hot spots for denitrification in this context. The absence of denitrification at larger depth was due to the inhibition by oxygen. In the model, the low activity of aerobic organisms cannot create local anoxic region because of the fast gas transport from the atmosphere overriding their consumptions (i.e., instantaneous equilibration of Henry's law). Regarding the second point, we note that Fig. 5 is a typical result of the DBM simulation (not an averaged result from multiple simulations like Fig. 6). We chose to show this way to put an emphasis on the spatial variability even within at the micro-scale (such as the arise of local anoxic region) under unsaturated conditions. However, due to the light penetration, the vertical stratification was still observed from all the simulations in a similar manner. The microbial activity below around 4 mm is anyway sparse and the gap of activity is domain-specific (randomly created spatial heterogeneity of the physical soil domain). We would like to focus on the high abundance of organisms above 4 mm that are supported by diffusion of fixed carbon and nitrogen at the surface by diazotrophic phototrophs. We apologise for the confusion and will revise the manuscript to clarify this.

Page 15, line 32 ff.: Although the simulation has been made for fully saturated water conditions, which indeed only rarely occur within biocrusts under natural conditions, I still expect it to more closely reflect the actual distribution and activity patterns in biocrusts with a dense surface especially constraining the gaseous surface exchange.

We certainly agree that we gain valuable knowledge about microbial distributions and activities within biocrusts under fully saturated conditions. However, these conditions (especially, soils fully immersed in water) are rarely encountered in desert biocrusts even if fine soil texture and EPS can prolong such conditions. Therefore, understanding biocrusts under unsaturated or dynamic hydration (wetting-drying) is important to quantify microbial interactions and their role for carbon and nitrogen cycling. We are aware of that there is a limit to directly observe microbial activities under unsaturated soils. This modelling work attempts to predict physical and chemical micro-environments to figure out how microbial trophic interactions can be influenced by saturation degree. For instance, aerobic heterotrophs and nitrifiers that would benefit within moderately unsaturated soils thanks to oxygen transport from gas phase. On the other hand, fully saturated conditions favour anaerobic processes, such as denitrification. This implies that studies on fully saturated biocrusts might underestimate or overestimate certain aspects of biocrusts for its role for carbon and nitrogen cycling under natural conditions.

MINIOR ISSUES:

- Page 1, Line 9: assemblies instead of assembly Page 1, Line 12: remove “the” Page 1, Line 18: remove comma Page 1, Line 20: include “the” → protects the soil surface
 - Amended.
- Page 3, line 22: Matrix potential instead of matric potential
 - To be consistent with other modelling papers published along with this work, we decided to keep the term matric potential instead of matrix potential.
- Page 12, line 13 ff.: This sentence is incomplete and needs to be corrected
 - The sentence will be corrected.
- Page 12, line 26 ff.: Formatting of this sentence has to be corrected with regard to brackets. Errors like that occur also in other parts of the manuscript and need to be corrected. There are many, many more of these minor language issues. Thus, the manuscript needs to be thoroughly checked and corrected by a native speaker.
 - We have made every effort to correct the grammar and language issues in the revised manuscript.