Biogeosciences Discuss.,
https://doi.org/10.5194/bg-2017-374-SC2, 2017

Biogeosciences Discussions
Open Access
EGU

Interactive comment on "Annual net primary productivity of a cyanobacteria dominated biological soil crust in the Gulf savanna, Queensland, Australia" *by* Burkhard Büdel et al.

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Received and published: 6 November 2017

Response to Referee 1 (M. Bowker) This paper tackles a challenging measurement problem: estimation of the net C flux of a biocrust community over a year in the field. Also, using a battery of controlled environment treatments, the authors determine the response of these biocrusts to moisture, temperature, and light. Overall, the authors find that biocrusts are a net C-sink in this environment, but net production is only observed for a portion of the year. The strength of the paper is that the authors have amassed an impressive amount of data and are one of only a handful of groups to complete this type of estimate. The weaknesses are perhaps due to a weak expres-

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sion of why it is so important to conduct this measurement, and why other similar measurements have been scarce, and an occasional propensity to dwell on details without clear explanation of why they are important. Below, I provide several suggestions to help revise the paper.

Answer: Thanks for the positive valuation. We tried hard to eliminate the weaknesses in expression and also to explain every detail and why they are important.

Major comments: 1. I understand that this study does not fit the typical hypothesis test framework, but nonetheless the authors could ensure that readers comprehend the more interesting elements of this work in the abstract, introduction and throughout. We can be fairly confident that most persistent biocrusts have a positive C-balance, because if they did not they would cease to exist eventually. Readers may find it intriguing that despite this apparent tautology, it is difficult to actually observe net CO2 uptake in biocrusts. This is distressing given that due to their extent, biocrusts may be non-trivial players in the global C cycle today, and almost certainly were major players in early terrestrial communities. We need this information. The reasons are various, but 2 major ones are that the positive CO2 uptake only occurs during a small part of the year in most studies, and it is difficult to separate C-balance of biocrusts from C-flux from organisms (microbes, roots) or minerals (carbonates) that occur below them. If the study is framed as outlined above, obtaining an annual measurement becomes much more intriguing to the casual reader and the importance of this endeavor is understood.

Answer: We rephrased the referring parts of the abstract, introduction and discussion and tried to make the aims and outcomes unambiguously clear throughout the text. We included every suggestion of the referee and hope we could clarify the unclear or weakly expressed parts.

2. Consider standardizing terminology for the one year monitoring (also called “monitoring of gas exchange”) and the factorial experiment (also called “gas exchange under controlled conditions”). I might suggest “environmental manipulations” and “Field mon-

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itoring".

Accepted, we changed this in the manuscript.

3. Consider placing the material on P4 L8-13 in section 2.3, and P4 L14-21 in section 2.4. It might improve flow and understandability.

Accepted.

4. P 4 L9 – Why were the samples stored frozen? This does not seem like a region where freezing soils are natural. Aren't you worried this exposure could have harmed or otherwise altered the samples?

Answer: we added the following information for better understanding. "....This treatment had been tested in our laboratory many times with lichens of many different geographical origins, including the tropics and resulted in high survival rates (roughly 95%) compared to dry storing in herbarium cabinets or boxes in the laboratory. Earlier gas exchange measurements on biocrusts, cyanobacteria, byrophytes and lichens before freezing and after thawing and re-moistening resulted in identical rates (unpublished laboratory tests)".

5. I could benefit from a few more details about how the 21 samples were used. For example you say 9 were used for the environmental manipulations, and 11 were used for long-term monitoring. What about the 21st sample? Also, I understand you inserted different biocrust samples for different portions of the field monitoring. But why are the samples used for such wildly varying times, I would have thought each would be used about 1.1 months?

Answer: We understood that this graph was confusing, as well as the text. We replaced the figure by Table 1, where we give just the sample and from when to when it was used. We also explained the somehow chaotic seeming randomization of the sample changing mode using the following sentence: "Fourteen samples were used during field monitoring (Table 1) and exposed in a random mode. The "random" mode was

determined by the ability of access (climatic conditions, days off) by one of us to the investigation site during the whole measuring period".

6. There are 10 figures, are they are really needed? The content of Figure 6 is mentioned by the authors several times, but it is not completely clear to me why the authors ascribe so much importance to these 3 days. Also, figures 9 and 10 could probably be combined into one 2 panelled figure.

Answer: We omitted figure 3 and replaced it by a much clearer table. Figures 9 and 10 were combined as suggested so that the number of figures is now reduced to 8.

7. There are times when I would like to see different pieces of information integrated, and another case where there is integration but I do not have all the information I need to understand it. Fig. 4. Provides plots of biocrust responses to different environmental gradients in a manner often used by this author group and associates. This is fine, but what I haven't ever seen is a plot integrating more than one of these variables in 3 dimensions. This would be a nice addition, if it could be done. Fig. 8 is a valiant attempt at illustrating responses to 2 environmental variables as a surface, but there is no explanation of how this was created (Kriging?); further, the plot contains many inexplicable peaks and valleys, often near each other. Does this suggest overfitting? Maybe more aggressive smoothing is warranted.

Answer: Figure 8, which is now figure 7 is a contour plot made with the SigmaPlot Software and is based on a linear interpolation between measuring points (the same as in line graphs). We changed the figure legend in order to make it more understandable for readers. Each and every data point of net photosynthesis (measurements at daylight) was related with the referring air humidity and amount of light at the time of measurement. The colour indicates CO2 uptake rates (positive) or CO2 loss rates during the day (negative values) or inactivity (0; yellow colour). Here the new legend of figure 8 (formerly 7): "Contour plot of net photosynthesis of the Boodjamulla biocrust based on linear interpolation between measured values. Shown is the active period

from November 2010 to April 2011. Net photosynthesis is related to relative air humidity and photosynthetic active radiation (PAR). No dark respiration values shown! Colour key: yellow = no activity, orange to red = CO2 loss during the day (suprasaturation), light green to violet = CO2 uptake". We find this type of presentation impressive as it really shows how many wet up and dry down cycles a biocrust experiences in its natural environment and how common suprasaturation is.

8. The discussion is not bad as written. You do address a key measurement issue, and hypothesize that the isolation of biocrust samples from underlying soil is the reason some studies find net C-uptake, and some find net C-loss. I would have like to see you more fully develop a few other elements too (several of which you do address to some degree), for example the generality that biocrusts maintain their existence by attaining positive C-balance only during a portion of the year, and that often the gains over a year are marginal. This means that oft-cited slow natural growth rates likely are due to environmental constraints; only a minority of the year is actually suitable for growth. I would have like to see you advance some hypotheses for why different regions have different annual C-flux values. Related to this, one novel aspect of your study is that all other annual flux measurements were conducted in environments with cool season hydration. Finally, you could develop more your hypothesis about how expected climate changes might impact these naturally occurring biocrusts. It might be helpful to break the discussion into a few subsections devoted to distinct discussion topics.

Answer: The discussion is more or less newly written and also separated into several subsections. Here the new discussion: 4. Discussion 4.1 Seasonality and CO2 balances Apart from a clear seasonal activity pattern of the cyanobacterially dominated biocrust from Boodjamulla, Queensland, only a minority of the year was actually suitable for growth during the one year round CO2 gas exchange field monitoring. An inactive winter period with no measurable CO2 gas exchange lasted from July to mid-September 2010 and then from mid-April to end of June 2011. Metabolic activity was found in the summer months only, starting with September 23rd 2010 where the first

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rains commenced, continuing until April 18th 2011. Due to malfunction of the ACS, measurements from September and October and some days of November and December 2010 were not useable to calculate NP and DR. An estimation based on rainfall data from September and October, together with the referring gas exchange values from November suggests a CO2 loss of roughly 88 mmol m-2. Net primary productivity was determined as 1.7 g C m-2 yr-1 (2.8 g C m-2 yr-1 without Sept.-Oct. correction). Our results showed that the Boodjamulla biocrust exposed a positive net C-uptake after one year field monitoring. This result is in line with the findings of several other studies but differs from all of them in the fact that our study focused to an environment with hot season hydration, whereas all of the other studies were conducted in environments with cool season hydration. For example, a cyanobacterially dominated biocrust in the Mojave Desert, USA had a C gain of 11.5 g m-2 yr-1 (Brostoff et al., 2005), 6.7 times higher than the cyanobacterially dominated Boodjamulla biocrust. Another biocrust dominated by cyanobacteria, algae, lichens and mosses from the Negev Desert, Israel exposed a C gain of 0.7 to 5.1 g m-2 yr-1 (Wilske et al., 2008, 2009) and thus is pretty close to what we observed in our study and also corresponds with the results from biocrust composed of cyanobacteria, lichens and mosses of the Mu Us Desert in China with a C gain of 3.5 to 6.1 g m-2 yr-1 (Feng et al., 2014). However, there are several studies that clearly demonstrate that biological soil crusts loose C to the atmosphere. When studying a cyanobacterially dominated biocrust of the arid grassland in southeast Utah, USA applying the Eddy covariance method, Bowling et al. (2010) could not decide if this biocrust is a sink or a source as there were some grasses involved in the plot and hence their root respiratory CO2 loss influenced the CO2. When these authors applied a top soil chamber for gas exchange measurements, they found the same biocrust a typical C source (Bowling et al. 2011). But still, this does not necessarily mean that overall they are a C-source. A cyanolichen dominated biocrust from the Gurbantungut Desert, China was reported as quite a large C source with a loss of -48.8 $\pm$ 5.4 to - 50.9 $\pm$ 3.8 g C m-2 yr-1 (Su, Y. G. et al., 2012, 2013) and a very similar biocrust type of the arid grassland of the Colorado Plateau, USA that exposed surpris-

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ingly similar values of - 62 ± 8 g C m-2 yr-1 (Darrouzet-Nardi et al., 2015). How can this astonishing and at first glance contradictory fact be explained? Comparing methodology and how measurements were taken, sheds some light on this phenomenon. All investigations, including our own study that showed biocrusts having a net CO2-uptake over the year used gas exchange devices with a separate cuvette where the samples had to be removed from the biocrust (Brostoff et al., 2005; Feng et al., 2014) except the study of Wilske et al. (2008, 2009) that used a top soil chamber measuring the biocrust in situ. All other studies used top soil chambers where the biocrust is measured in situ (Bowling et al., 2011; Su et al., 2013; Darrouzet-Nardi et al., 2015). The main difference we could find in all of this studies was the thickness of the biocrust plus sub-crust (soil) layer used. While those studies revealing biocrusts as CO2 looser used collars penetrating 20 to 35 cm deep into the soil (Bowling et al., 2011; Su et al., 2013; Darrouzet-Nardi et al., 2015), the studies attributing biocrusts as CO2 winners during a one year course either used pieces of biocrusts from 1 to 5 cm thickness (this study, Brostoff et al., 2005; Feng et al., 2014), or a collar penetrating only 5.5 cm into the soil (Wilske et al., 2008, 2009). The metabolic activity of heterotrophic organisms as well as respiration of roots from nearby plants of deeper soil levels apparently influence the CO2 gas exchange measurements accordingly as was already indicated in the investigation of Bowling et al. (2011). Yet, soils are not a perpetual motion machine in terms of carbon balance, the can only respire as much carbon as is introduced into the system. If carbon does not come from the autotrophic part of the soil system, it must be introduced from outside, either via litter transport, blown dust, animals, or with run-on water from the surrounding environment. In a recent study using the Eddy covariance method, Biederman et al. (2017) found a wide range of carbon sink/source function with mean annual net ecosystem productivity (NEP) varying from -350 to +330 g C m-2 across sites with diverse vegetation types in the dryland ecosystems of southwestern North America using evapotranspiration (ET) as a proxy for annual ecosystem water availability. Gross ecosystem productivity (GEP) and ecosystem respiration (Reco) were negatively related to temperature, both interannually within sites and spa-

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tially across sites and sites demonstrated a coherent response of GEP and NEP to anomalies in annual ET. Their investigation sites included one region having a noteworthy biocrust cover not accompanied by a dense vascular plant vegetation, the La Paz region of Baja California with an annual C-uptake (NEP) of roughly 90 g m-2. Approximating annual C gain based on the maximal CO2 uptake rates of four biocrust types composed of cyanobacteria, cyanolichens and chlorolichens measured by Büdel et al. (2013) from Baja California, we approach an annual C gain of those biocrusts of 11 $\pm$ 4 g m-2 (calculation based on 90 active days per year with 34 of them having a sub-optimal CO2 uptake rate of only 25% of maximum due to suprasaturation. Daily rates were calculated by maximum NP for 5 hours per day minus 10 hours R + DR). This is 6.5 times more than our pure cyanobacterially dominated biocrust from Boodjamulla but still 8 time less than found for the Baja California site in the study of Biederman at al. (2017). It could well be that later successional biocrusts with a wealth of different species groups, including bryophytes, lichens and green algae besides of cyanobacteria, might reach even higher annual carbon fixation rates. This should be in the focus of further studies. 4.2 Carbon dioxide uptake rates and biocrust type Maximum net CO2 uptake rates of the Boodjamulla biocrust (8.3 μmol CO2 m-2 s-1) clearly exceeded those of a comparable cyanobacterially dominated biocrust from the Negev Desert, Israel reaching maximal values of 1.1 μmol CO2 m-2 s-1 (Lange et al., 1992) and from the Colorado Plateau, USA with 2.0 μmol CO2 m-2 s-1 (Darrouzet-Nardi et al., 2014). The higher NP rates of the Boodjamulla biocrust are probably related to the felt like structure on the soil surface offering a higher surface for gas exchange (Fig. 2a-d), while the Negev Desert biocrust was a thin layer of cyanobacterial filaments slightly beneath the surface. Annual carbon fixation rates of cyanobacterially dominated arid region biocrusts are generally lower (this study; Brostoff et al., 2005; Feng et al., 2014; Wilske et al., 2009) compared with biocrusts including lichens and bryophytes (see summarizing table 15.2 in Sancho et al., 2016; Elbert et al., 2012; Porada et al., 2013) or the carbon gain of isolated biocrust organisms as for example the green algal lichen Lecanora muralis (Schreber) Rabenh. from a rock crust with 21.5 g C m-2 yr-1 (Lange

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2002, 2003a, b). The developmental stage of a biocrust might be an important factor for photosynthetic performance too. This view is supported by the results of a study determining NP rates depending on successional stages rather than developmental stages. In this study the authors classified biocrusts as early successional (Microcoleus) or later successional stages (Nostoc/Scytonema or Placidium/Collema) and differences in NP, which was on average 1.2-2.8-fold higher in later successional crusts compared to the early successional stages (Housman et al., 2006). Considering the Boodjamulla biocrust as a mid-successional type, where an increase in carbon gain might be expected in the future when lichens and bryophytes establish to form a later successional soil crust. Dealing here with a cyanobacterially dominated biocrust of a mid-successional type might explain the low C-uptake rates and also the seeming discrepancy to the values calculated for the global NPP by cryptogamic covers of Elbert et al. (2012). 4.3 Active times and water relation The Boodjamulla biocrust had metabolic activity for only 25% of the year, made up of 12.3% NP and 12.8% DR (Fig. 8a). In 29.2% of the photosynthetic active time CO2 fixation was considerably lowered by water suprasaturation. For comparison, the lichen L. muralis from temperate climate was active for 35.5% of year, made up of 16.7% NP and 18.9% DR. During periods of photosynthesis, the lichen was heavily depressed by water suprasaturation at 38.5% (Lange, 2003a). It is obvious that the strict seasonal rainfall pattern is a major reason for the considerably lower metabolic activity of the savannah-type biocrust from Boodjamulla compared to the rock crust lichen L. muralis in a temperate climate with rainfall expanding over the whole year. As characteristic for poikilohydric organisms, both the Boodjamulla biocrust as well as the rock crust lichen suffer considerably from water suprasaturation causing waterlogged gas diffusion channels and thus drastically limiting CO2 gas exchange (see Green et al., 2011 and references therein). Because metabolic activity is strictly bound to the presence of water it is important to know the role of water content on photosynthetic and respiratory CO2 exchange. The Boodjamulla biocrust achieved maximum NP values at 0.5-0.8 mm WC and had a lower compensation point for NP at 0.1 mm WC. Comparable values were found for

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the Negev biocrust studied by Lange et al. (1992) and the rock crust lichen L. muralis (Lange, 2002). In the chlorolichens of a biocrust biocrust from Utah, Diploschistes diacapsis (Ach.) Lumbsch, Psora cerebriformis W. Weber, and Squamarina lentigera (Weber) Poelt photosynthetic metabolism was activated by extremely small amounts of moisture. The lower compensation point for NP is between 0.05 and 0.27 mm WC. Maximal NP occurred between 0.4 and 1.0 mm WC (Lange et al., 1997). The values for the cyanobacterial soil crust lichen Collema tenax (Swartz) Ach. however, were considerably higher with the lower NP compensation point at 0.2 mm WC and maximal NP between 0.8 to 1.2 mm WC, but performed NP under much higher temperatures than the above mentioned green algal lichens (Lange et al., 1998). Almost all gas exchange activity of the Boodjamulla biocrust occurred at air relative humidity above 42% (Fig. 7). This however, must be taken with care as it does not mean that the biocrust is active at this value and above. Like all cyanobacteria investigated so far, the cyanobacteria of the Boodjamulla biocrust are also not activated by air humidity alone (unpublished results). The value of 42% relative humidity is merely a good indicator for the right combination of WC (rainfall dependent), temperature and light. A comparable observation has been made by Raggio et al. (2017), who found air relative humidity (« 50%) and air temperature as the best predictors of metabolic activity duration for four different biocrust types across Western Europe. In a number of cases we found activation of the Boodjamulla biocrust without any measurable precipitation (Fig. 5, supplementary figure S3, January 4th-5th). This is likely explained by dew formation, a non-rainfall water source found playing in important role in biocrusts (Lange et al., 1994; Ouyang and Hu, 2017) and also observed at Boodjamulla during wet season. There are a number of studies that found dew formation in biocrust systems, for example the study of Jacobs et al. (2000), where in a desert environment of Israel daily amounts of dew ranged between 0.1 mm/night and 0.3 mm/night. Dew formation determined for an inland dune biocrust community in Germany formation ranged from 0.04 kg/m^2 and 0.18 kg/m^2 within 2 days (Fischer et al., 2012). Even fog was identified as a major source of non-rainfall water driving biocrust productivity in the Atacama Desert of

Chile, where approximately 8% to 24% of the fog water flux available to the BSCs at the soil surface (Lehnert et al., 2017). 4.4 Reestablishment and resurrection after the dry season What are the reasons for negative C-balances of the biocrust during the first active months after start of the rainy season? We suggest that in contrast to eukaryotic poikilohydric photoautotrophs such as liverworts, mosses or lichens, that resuscitate their complete thallus compartments after hydration, prokaryotic cyanobacteria show considerable die back rates during longer dry periods or drought events. For example in the terrestrial, colony-forming unicellular genus Chroococcidiopsis the number of viable cells decreased with age of the colony and the length of exposure to drought (Grilli Caiola et al. 1993; Grilli Caiola and Billi, 2007). Desiccation-tolerant Chroococcidiopsis cells must either protect their components from desiccation-induced damage or repair it after rehydration. It was found that desiccation survivors limit genome fragmentation, preserve intact plasma membranes, and have spatially reduced reactive oxygen species accumulation and dehydrogenase activity whereas damaged cells do not (Billi, 2008). In the abundant biocrust cyanobacterium Microcoleus vaginatus Gomont ex Gomont immediate, but transient induction of DNA repair and regulatory genes signalled the hydration event and recovery of photosynthesis occurred within 1 hour accompanied by upregulation of anabolic pathways (Rajeev et al., 2013). In general, during the desiccated period homoiochlorophyllous (maintain their chlorophyll during desiccation) cyanobacteria still suffer from photoinhibition induced by the typical high light intensities of their habitat. Nevertheless, resurrection of photosynthesis after desiccation occurs within hours or days, depending on the degree of damage (Lüttge, 2011), while regrowth takes days or weeks, largely depending on the availability of water, but also needs a positive C input. Our field monitoring uncovered numerous events of suprasaturation during daylight combined with low NP rates after the onset of the active season. Suprasaturation events later in the season are easily compensated by high NP rates (Fig. 4). We interpret the early C-loss phase after the drought, at least partly as a reestablishment period of the biocrusts structure, enabling the biocrust diminishing suprasaturation events by means of erect cyanobacterial filament bundles,

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standing out of a covering water film and thus probably improve CO2 gas diffusion (Fig. 2c, d). 4.5 Influence of temperature and global warming In the experimental manipulation setup the Boodjamulla biocrust did respond to air higher air temperature (20 - 47°C) with a continuous increase of both, NP and DR, with NP increasing a slightly higher rates than DR (Fig. 3b). Even at 47°C, CO2 uptake did not show any reduction nor did DR show a considerably stronger CO2 release and NP still exceeded DR five times. However, in our field measurements we did not observe biocrust activity above air temperatures of 43°C (Fig. 6b), at this temperatures the biocrust was dry and inactive. During field monitoring the optimal temperature for positive NP was around 35°C (Fig. 6b). Applying an experimental air temperature increase of 2–3°C, Maestre et al. (2013) observed a drastic reduction in biocrust cover of ca. 44% in 4 years in a dryland ecosystem in Spain. Soil CO2 efflux was increased and soil net CO2 uptake was reduced with the additional warming. According to the field monitoring gas exchange rates of the Boodjamulla biocrust, we would expect even shorter activity periods under the scenario of global warming and related to that, probably lower C-uptake or even C-loss resulting in a pronounced reduction of biocrust coverage. Another indirect effect of warming could be expected when it influences rainfall amount and regime. It could be speculated that less, but heavier rain events would certainly effect the Boodjamulla biocrust by increasing suprasaturation periods resulting in lower or even no carbon gain probably also causing a pronounced reduction in coverage. 5. Conclusion The Boodjamulla biocrust showed a highly seasonal photosynthesis-related metabolic activity divided into four major periods: 1) a metabolically inactive winter time; 2) onset of the photosynthetic active period, starting with roughly three month of reestablishment, limited CO2-uptake due to suprasaturation, and a hypothesized increased activity of heterotrophic organisms decomposing organic matter from old biocrusts; 3) a four-month period of net C-uptake; and 4) about one month with C-loss until a complete cease of activity. During the four periods, NP and NPP rates vary strongly and thus seasonality plays an important role. It is absolutely crucial in which period of the year biocrust material is sampled for eco-physiological experiments. The cyanobacterially

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dominated Boodjamulla biocrust turned out to be a small but consistent sink of carbon as it grows and possibly also contributes to the soil organic matter (SOM). From the magnitude of values it is clear that the observed C fluxes are not at all close to what a plant community can do. Methodological approaches analysing the carbon cycling of biocrusts need to critically reflect, that including or excluding sub-biocrust partitions might influence the status of the biocrust as being either considered as a sink or a source. There is an urgent need for more long-term measurements on different biological soil crust types and developmental stages from all climatic regions of the world.

Minor comments Throughout: I suggest using “cyanobacterially dominated” (adverb modifying adjective) or “cyanobacteria-dominated” (noun functioning to modify adjective), not “cyanobacteria dominated”(no hyphen, no adverb)

Accepted, all changed to “Cyanobacterially dominated”

P1L18 - remove “at”

Done

P1L19 - remove “during”, suggest replacement of “referring” with “corresponding”

Done

P2L21-23 – standardize terminology for net C-uptake, 3 different synonyms are used here

Done

P2L27 – This would be a good place to mention that apparent C-source behavior is probably due to the challenges of properly measuring biocrust C-flux

Accepted and included

P4L15 – your meaning is unclear in the phrase “making sure that the area related..range”

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Taken into regard and replaced by a new sentence: “All samples used were tested for a comparative large NP and DR rate under the given environmental conditions for two measurements (1 hour) in the cuvette system and only those were used that had more or less identical NP and DR rates”.

P4L18 – suggest “drainholes” rather than “borings”

Done

P7L1 – suggest “monitoring” rather than “investigation” Done

P7L29 – suggest “continuing” rather than “continued”

Done

P8L12 – that biocrusts are typically losing C does not mean that overall they are a C-source.

Accepted and expressed accordingly

P8L15 – Omit “When”

Done

Thank you Matthew for your very helpful comments.

Interactive comment on Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-374, 2017.

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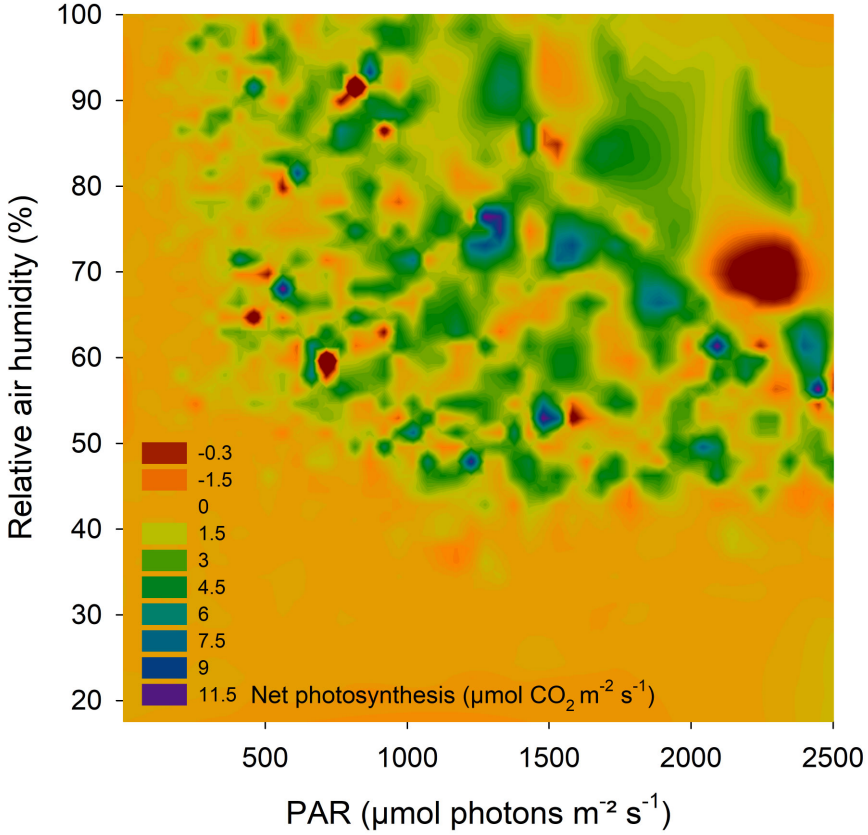

Fig. 1. New figure 7

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