Estimating global nitrous oxide emissions by lichens and bryophytes with a process-based productivity model

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We thank the reviewers for useful and thorough comments which helped to improve our manuscript. We have prepared a revised manuscript where we account for all points raised by the reviewers, as described below. We show the reviewers' comments in italic text, while our responses are formatted as standard text.

Response to the comments of reviewer #1

I have reviewed your manuscript "Estimating global nitrous oxide emissions by lichens and bryophytes with a process-based productivity model". In this manuscript, the updated model LiBry is used to estimate global respiration of lichens and bryophytes. Then global nitrous oxide emissions from lichens and mosses are derived from the simulated respiration amounts using a conversion factor. This is an important study, as the role of lichens and bryophytes in global biogeochemical cycles has been understudied. This is especially true for nitrous oxide, as exemplified by the fact that this paper is one of two global estimates for of N2O emissions for lichens and bryophytes. The model seems sound to me, and I appreciate the valid points the authors make about the limitations of their emission estimates. However, there are some issues that need to be addressed within the manuscript.

We are glad that the reviewer appreciates the scientific relevance of our study and we have clarified all issues mentioned below.

General Comments – 1. Conflation of mosses & bryophytes, biological soil crusts and microbial surface communities, and other terms – Please clarify if this paper is about one of these, all of these, or some of these. These terms are not interchangeable. The first paragraph of the introduction begins by talking about microbial surface communities

(specifically biocrusts) in a dryland setting. However, the authors study is seeking to address global N2O emissions of lichens and mosses, as declared in the title. While lichens and mosses occur in biocrusts, the initial focus on biocrusts takes away from the global implications of the study and the potential importance of lichens and mosses to N2O emissions in other ecosystems (as the data later goes on to suggest). What is needed is less conflation of biocrusts with distinct units of lichens and mosses throughout the manuscript. This association of biocrusts with lichens and mosses is true for drylands, but the conflation breaks down very quickly in different ecosystems.

Our study focuses on N_2O emissions by lichens and bryophytes. We agree with the reviewer that this should be made more clear in the introduction and we have therefore rephrased the respective parts in the revised manuscript. We have replaced the first paragraph by the following text:

"Lichens and bryophytes have increasingly been recognized to play a relevant role in global biogeochemical cycles [Elbert et al., 2012, Sancho et al., 2016, Barger et al., 2016]. They are globally abundant, growing on soils, rocks, and epiphytically on trees. At high latitudes, they may form extensive covers on the forest floor and in wetlands, mosses frequently represent the dominant vegetation type. In drylands, lichens and bryophytes form so-called biological soil crusts together with photosynthesizing cyanobacteria, algae, fungi and bacteria. These crusts cover vast areas in arid and semiarid ecosystems."

Throughout the manuscript we have exchanged the term "microbial surface communities" by "lichens and bryophytes" in case we refer to the paper by Lenhart et al. [2015], since their study describes measurements on lichens and bryophytes. When referring to the study by Elbert et al. [2012], we have replaced "microbial surface communities" by "lichens and bryophytes, together with free-living cyanobacteria and algae".

2. Clarify the players in N-cycling processes and the mechanisms early – This paper focuses on emissions of N2O actually sourced from the mosses and lichens themselves, not from nitrifiers or denitrifier microbes. Readers should be better introduced to this idea early on, so they are not confused. In the third, fourth, and fifth paragraph of the introduction, the focus is almost entirely on the fixation of N in microbial communities. These paragraphs are not entirely relevant to your study, and serve to confuse the reader. Mechanisms for how microbial compounds release gaseous nitrogen are included, but there is no mention of the mechanisms for lichens and mosses until Page 9 Line 20. The process should be highlighted in the introduction. As follows, Figure 1 with its focus on the microbial communities mechanisms for N2O emissions is largely irrelevant to this study, and could be replaced by an example of lichen and mosses emission and fixation pathways.

Already in the introductory part of the revised manuscript, we now discuss the potential processes responsible for N_2O emissions from lichens and mosses. In fact, the underlying process causing N_2O emissions from lichens and bryophytes is rather unclear. At the current stage there are two different ideas for this process. One option is that N_2O could be directly released from the mosses and lichens in a similar way as it has been

described for plants [Smart and Bloom, 2001]. A second option is that bacteria growing on lichen and mosses are responsible for the emissions. This hypothesis is supported by a recent publication, where the bacterial species *Burkholderia* was isolated from leaves of the moss *Sphagnum fuscum* and was shown to emit N_2O [Nie et al., 2015]. With the current situation of the emission process being not entirely clear, yet, we decided to do without a figure explaining the emission process.

To illustrate the relevance of lichens and bryophytes for global biogeochemical cycles, we have left the second and third paragraphs of the introduction largely unchanged, which describe fixation of CO_2 and nitrogen. We have then replaced paragraphs 4 to 6 with the following content:

"Recently, lichen- and bryophyte-related nitrogen fluxes other than fixation of nitrogen have been shown to be significant at the global scale. Weber et al. [2015] found that biological soil crusts, which may contain large fractions of lichens or bryophytes, emit considerable quantities of the reactive trace gases NO and HONO, accounting for $\sim$1.7 $(\mathrm{Tg\,N})\,\mathrm{yr}^{-1}$. This corresponds to $\sim$20 % of global nitrogen oxide emissions from soils under natural vegetation [Ciais et al., 2013].

Furthermore, Lenhart et al. [2015] showed that a large variety of lichen and bryophyte species release nitrous oxide (N_2O). They estimated that the organisms emit a total value of 0.45 (0.32 - 0.59) $(\mathrm{Tg\,N_2O})\,\mathrm{yr}^{-1}$ at the global scale, which corresponds to 4 - 9 % of natural terrestrial N_2O emissions [Zhuang et al., 2012]. Since N_2O is an important greenhouse gas and also the main depleting substance of stratospheric ozone which is still emitted today, quantifying all contributing sources is of high importance [Butterbach-Bahl et al., 2013, Ravishankara et al., 2009, Gärdenäs et al., 2011, Ciais et al., 2013].

Absolute values of N_2O release estimated by Lenhart et al. [2015] were highest for lichens and bryophytes living on the ground in the boreal zone and for epiphytic lichens and bryophytes in the humid tropics. The relative contributions of lichens and bryophytes to total ecosystem N_2O emissions, however, were highest in desert and tundra biomes, due to the low emissions by other vegetation and the soil there. The high relevance of lichens and bryophytes for N_2O emissions in drylands and at high latitudes is in accordance with their strong impacts on other components of the nitrogen cycle in these regions. Bryophytes, for instance, have been suggested to be the main source of nitrogen input into boreal forests through fixation from the atmosphere [DeLuca et al., 2002]. Also in drylands, lichens and bryophytes are crucial for input of nitrogen into the ecosystem [Barger et al., 2016], and they may even be essential providers of nitrogen for vascular plants [Stewart, 1967, Hawkes, 2003].

The estimate by Lenhart et al. [2015] is derived from measuring emissions of N_2O by the organisms in the laboratory under a range of environmental conditions. All lichen and bryophyte species analyzed by Lenhart et al. [2015] showed release of N_2O. Lichens and bryophytes were shown to utilize ^{15}N labelled NO_3^- but not NH_4^+, indicating that N_2O is likely formed during denitrification. The exact process of N_2O-formation, however, remains largely unknown. One option is that the organisms themselves release N_2O during the metabolisation of nitrate, in a similar way as suggested by Smart and Bloom [2001] for vascular plants. Another option is, that bacteria growing on lichen and moss cushions are responsible for the emissions of N_2O. This second option is supported

by a recently published study, where several strains of the bacterial genus *Burkholderia*, which were shown to emit N_2O, were isolated from the boreal peat moss *Sphagnum fuscum* [Nie et al., 2015]. While Lenhart et al. [2015] describe that the substrate, which the organisms grew on, was thoroughly removed, further cleaning steps to remove potential bacterial colonies have not been conducted.

Another finding by Lenhart et al. [2015] is that N_2O emissions are related to respiration by a relatively constant factor. By applying this factor and, furthermore, assuming a fixed ratio between respiration and NPP, the authors utilised the global NPP data of Elbert et al. [2012] to obtain globally resolved N_2O emissions by lichens and bryophytes. The reliability of global estimates derived from upscaling of small-scale measurements depends on the variation of the measured fluxes. The field measurements of NPP which were extrapolated to the spatial scale of a biome by Elbert et al. [2012] vary by around two orders of magnitude. Measurements of N_2O emissions by lichens and bryophytes, too, show considerable variation. Regarding biological soil crusts, several studies analyzed denitrification rates to be negligible [Johnson et al., 2007, Strauss et al., 2012], and N_2O production was calculated to constitute only 3-4 % of the N fixation rate [Barger et al., 2013]. Other studies, however, described high denitrification rates that either increased [Brankatschk et al., 2013] or decreased with advancing crust development [Abed et al., 2013]. One possibility to increase the reliability of large-scale estimates of N_2O emissions by lichens and bryophytes is the application of alternative, methodically different approaches.

For this reason, we apply here the process-based non-vascular vegetation model LiBry [Porada et al., 2013] to assess the contribution of these organisms to the global N_2O budget."

3. Make introduction global in scope – The results indicate that nitrous oxide emissions by lichens and bryophytes are highest in humid tropics and subtropics and yet, these regions are not even mentioned in the introduction. There is a lot of text spent on the N-dynamics of drylands, but I think it is more important to broaden the scope of the introduction and address the N-dynamics of the ecosystems that end up being most significant to global N20 emissions of lichens and mosses.

We have extended the introduction of the revised manuscript by a short overview of the relative contributions of lichens and bryophytes to nitrogen fluxes in various ecosystems (see previous point, paragraph 3 of the new text for the introduction).

4. Expand the discussion: the discussion and conclusion focuses almost entirely on comparisons and short-comings of the model, while the introduction focuses heavily on N-cycling and mentions implications of N20 emissions. A paragraph tying the discussion back into the topics covered about lichens and mosses in the introduction, and our increased understanding of N20 emissions based on this study would be more satisfying to the reader. The authors begin to do this on page 9 line 15-18, but expanding on it or emphasizing it at the end of the manuscript would make for a stronger overall narrative.

We have removed paragraph 3 and 6 from the discussion and instead added text on the global implications of our study and our understanding of N_2O emissions by lichens and bryophytes at the end of the revised discussion. Moreover, we rephrased the conclusions (see below, reply to reviewer #2).

"Our simulated global N_2O emissions by lichens and bryophytes of 0.27 (0.19 - 0.35) $(\mathrm{Tg\,N_2O})\,\mathrm{yr}^{-1}$ amount to around 3 % of global N_2O emissions from natural sources on land [Ciais et al., 2013]. This value may sound low at first glance, but it equals about 50 % of the atmospheric deposition of N_2O into the oceans or 25 % of the deposition on land [Ciais et al., 2013]. Considering that N_2O has a strong negative effect on stratospheric ozone and a significant warming potential as a greenhouse gas, also relatively small emissions should not be neglected in global budgets.

The study by Zhuang et al. [2012] estimates global patterns of N_2O emission from soils and finds that the humid tropics contribute most to global N_2O emission due to high temperature and precipitation. Our simulated pattern of global N_2O emissions by lichens and bryophytes also shows a hotspot in the humid tropics, but the relative contribution of the boreal zone to the global flux seems to be higher than in Zhuang et al. [2012]. This probably results from the high simulated NPP in the boreal zone, particularly on the ground, which compensates for the lower respiration and therefore N_2O emission per productivity due to low temperatures. Relative contributions of lichens and bryophytes to N_2O emissions are highest for ecosystems in desert regions and at high latitudes, which agrees with the results by Lenhart et al. [2015]."

Specific Comments – 1. Page 4 line 8-16 Clarification of methods for relating N20 emissions with respiration – The explanation of how N2O emissions are derived from respiration states that they were converted from values determined experimentally from N2O emissions by microbial surface communities. It is important to note that lichens and mosses are not microbial surface communities. Mosses are plants! Neither are microscopic. I see later that it is stated Lenhart did measure samples of lichens and bryophytes. However, I had to read Lenhart et al to find that these measurements occurred when the lichens and mosses had their substrate (and therefore soil microbial communities) removed. Both of these points (1. Measurements were taken on lichens and bryophytes, not microbial surface communities and 2.removal of substrate during measurement) need to be made abundantly clear. Also the morphological range of lichens and bryophytes used to get this conversion factor should be briefly mentioned. For instance, is respiration and N2O emissions as tightly coupled with rock lichen and epiphytes?

We have made clear in the respective section that measurements were performed on lichens and bryophytes (P. 4, L. 17-33). Moreover, we have added a sentence regarding the removal of substrate: "...the substrate of the samples was removed to avoid biases resulting from N_2O release by microbes in the substrate."

Nevertheless, we think that bacteria may well be involved in N_2O emissions as explained above (reply to general comment 2., paragraph 4 of the text newly inserted in the revised manuscript).

We also inserted information on the morphological range of the samples in the revised

manuscript: "Foliose and fruticose lichens as well as mosses were collected, which grew on soil, rocks, and epiphytically on trees and there was no variation in N_2O emissions depending on the underlying substrate. Endolithic and crustose lichens were not included in that study, as for these growth forms the dry weight, which is needed for calculations, could not be determined in a reliable manner."

2. Page 9, line 12 The Elbert paper that is being cited includes cyanobacteria in its carbon estimates while this one does not. I would have guessed that the inclusion of cyanobacteria should make carbon estimates higher than carbon estimates from LiBry that focuses on just lichens and mosses. Please address this point.

We have added the following to the revised manuscript (P. 10, L. 10-12): "Our new estimate is higher than that by Elbert et al. [2012], although LiBry does not consider free-living cyanobacteria and algae. This may be explained by the small contribution of cyanobacteria and algae to the overall global carbon uptake, which can be compensated by minor relative changes in productivity of lichens and bryophytes."

3. Page 10 line 30-35. This paragraph is again conflating microbial surface communities with lichens and mosses. If the end goal is to assess model-based estimates of N2O emissions by microbial surface communities that contain lichens and mosses, then this paragraph is appropriate. However, that needs to be stated clearly.

We have changed the terms in the revised manuscript to be more clear.

Technical Points: Page 6, line 12 cannot not be simulated, yet change to cannot yet be simulated Page 10, line 17-18 Sentence fragment. Do you mean that the uncertainty you need to discuss involves the methods you used for estimating respiration and deriving N20 emissions from those respiration rates? If so, please state that more clearly.

We have made this sentence more precise (P. 13, L. 21): "These uncertainties mainly result from our method to estimate respiration and from assumptions concerning the empirical relationship between respiration and N_2O emissions."

Response to the comments of reviewer #2

General comments: The authors present a new approach to estimate global N2O emissions from lichens and bryophytes. In this approach they use empirical relationships between N2O and respiration to derive N2O emissions from simulated respiration fluxes. With this combination of modelling and empirical relationship they can represent the effect of climatic conditions on N2O emissions. Relating N2O emissions to climatic conditions is of course particularly interested in light of climate change. They highlight this, while they do not discuss that the sensitives in their N2O fluxes reflects the sensitivity of respiration. A more detailed discussion on potential differences in climatic

sensitivities of N2O emissions vs respiration and related uncertainties is necessary. They discuss the advantage of their new approach vs previous estimates based on NPP and they also discuss shortcomings and general uncertainties related to N2O emissions by lichens and bryophytes. They state that their model does not simulate nitrification and denitrification, however, it does not get clear if the model is capable of simulating N fixation and N deposition. Those fluxes would have a more direct functional link to N2O emissions as compared to respiration. So in addition to referring to an alternative approach of using NPP, it would be beneficial to refer to other alternatives and related advantages or disadvantages of their approach. Another aspect still missing in the discussion is the general uncertainty related to estimates of the global abundance of lichens and bryophytes. With this extension of the discussion and the more specific comments below, I recommend the study for publication.

In the revised manuscript, we point out that our findings regarding the effects of climate on N_2O emissions depend on the climate sensitivity of the relation between N_2O emissions and respiration. We explain that, so far, this relationship seems to be robust under a large range of environmental conditions, but we also mention that the detailed mechanisms of N_2O emissions in lichens and bryophytes are still unclear. Furthermore, we discuss potential alternative approaches to derive N_2O emissions as well as uncertainties regarding the global abundance of lichens and bryophytes.

Specific comments

Page 1
Line 2 and 3: "This finding relies on ... which are combined with ...": It gets not very clear what the authors mean by "combined"; this is explained better later in the paper, but this sentence sounds too vague, please rephrase more clearly.

We have replaced this sentence by (P. 1, L. 2): "This finding relies on ecosystem-scale estimates of net primary productivity of lichens and bryophytes, which are converted to nitrous oxide emissions by empirical relationships between productivity and respiration, as well as between respiration and nitrous oxide release."

Line 21: "In a first ecosystem-based upscaling approach": is this approach based on modelling or measuring on the ecosystem level? So is the alternative approach by Porada et al. (2013) different because they use a model (vs. observations) or because they model at global scale (vs. at ecosystem scale)?

We have clarified this section as follows (P. 1, L. 20): "In a first approach, based on empirical upscaling of field measurements according to ecosystem categories, Elbert et al. [2012] calculated that lichens and bryophytes, together with free-living cyanobacteria and algae, fix around 14.3 $(\mathrm{Gt\,CO_2})\,\mathrm{yr}^{-1}$ (3.9 Gt carbon) at the global scale. This corresponds to about 7 % of the net primary productivity (NPP) by terrestrial vegetation. As an alternative approach to the empirical upscaling of observations, Porada et al. [2013]

utilized a process-based non-vascular vegetation model for lichens and bryophytes, called LiBry, to calculate the NPP of these organism groups at the global scale, obtaining similar results."

Page 2
Line 6: how can they influence weathering by their demand for phosphorous?

We have extended this point (P. 2, L. 7): "Moreover, it was found in the same study that the organisms may contribute significantly to biotic enhancement of global chemical weathering, by release of weathering agents such as organic acids. Their potential for chemical weathering was derived from their phosphorus demand, assuming that they dissolve surface rocks to acquire phosphorus."

General remark: for those organisms fixing N, would it not make sense to link N2O emissions to fixed N? Or in general to N taken up, including fixed N; maybe this approach is not feasible in your case because of technical or modelling issues, but it would still be worth noting why you use respiration and not a N-related flux;

We explain in the discussion section of the revised manuscript why we do not use N uptake to derive rates of N_2O emissions (P. 14, L. 22): "Respiration by lichens and bryophytes is not the only process which can be used to estimate their N_2O emissions. Barger et al. [2013] report a relationship between nitrogen fixation and N_2O release in biological soil crusts, which include lichens and bryophytes, but also soil bacteria and algae. It is possible to estimate the demand for nitrogen by lichens and bryophytes with LiBry with an uncertainty range of around one order of magnitude [Porada et al., 2014]. However, it is not straightforward to derive realised nitrogen uptake or nitrogen fixation from this, since LiBry does not yet include processes related to nitrogen uptake or metabolisation of nitrogen species. Therefore, for this study, we chose the relation between respiration and N_2O release to quantify N_2O emissions by lichens and bryophytes."

Line 8: are uptake into microbial biomass and leaching the only processes? Later you also mention gaseous losses, and your paper is about N2O emissions, so I guess you can expand this list. And is the uptake of fixed N relevant enough for the study for being dedicated one paragraph?

As described in our response to the comments of reviewer #1, we have rearranged this part of the introduction in the revised manuscript and we now focus on N_2O emissions by lichens and bryophytes, their global significance and the associated metabolic processes. We removed those parts of the introduction which were not relevant for our approach, such as the description of various components of the nitrogen cycle in drylands.

Line 11: how likely is it that nitrification and denitrification occur? As you derive global N2O emissions, do you distinguish between microbial communities that are and those that are not capable of nitrification or denitrification? If not, this fact should be dis-

cussed.

As suggested by reviewer #1, we have clarified in the revised version of our manuscript that our estimate is constrained to N_2O emissions by lichens and bryophytes. Moreover, we discuss the source of N_2O emissions in greater detail (P. 2, L. 31): "... Lichens and bryophytes were shown to utilize ^{15}N labelled NO_3^- but not NH_4^+, indicating that N_2O is likely formed during denitrification. The exact process of N_2O-formation, however, remains largely unknown. One option is that the organisms themselves release N_2O during the metabolisation of nitrate, in a similar way as suggested by Smart and Bloom [2001] for vascular plants. Another option is, that bacteria growing on lichen and moss cushions are responsible for the emissions of N_2O. This second option is supported by a recently published study, where several strains of the bacterial genus *Burkholderia*, which were shown to emit N_2O, were isolated from the boreal peat moss *Sphagnum fuscum* [Nie et al., 2015]."

Line 12: what is meant by "surrounding atmosphere"? I suggest to delete "surrounding"

We have deleted this in the revised manuscript.

Line 13: ammonia is not formed during nitrification or denitrification

Due to the restructuring of the introduction in the revised manuscript, the corresponding paragraph has been deleted.

Line 17-19: who used those data?

We made clear in the revised manuscript (P. 3, L. 4-6) that the data were used by Lenhart et al. [2015].

Line 19: N2O is not in general the main ozone depleting substance, but the main ozone depleting substance that is still emitted; Other ozone depleting substances are not emitted any more, but still more destructive for ozone than N2O

We extended this sentence to (P. 2, L. 17): "Since N_2O is an important greenhouse gas and also the main depleting substance of stratospheric ozone which is still emitted today, ..."

Line 22 ff: in this paragraph you focus on denitrification, what about nitrification?

We point out in the revised manuscript that release of N_2O by lichens and bryophytes is likely due to denitrification (P. 2, L. 31). Therefore, we focus in the respective paragraph on denitrification. As explained above, in the revised manuscript we have removed those parts of the introduction which describe processes not related to N_2O emissions by lichens and bryophytes, but by soil organisms.

Line 22 ff: Regarding the upscaling of N2O emitted by lichens: how uncertain are estimates on global lichen and bryophyte occurrence?

We have added the following to the discussion (P. 12, L. 14): " . . . In the study of Elbert et al. [2012], for instance, it is assumed that productivity and active time are uniform within a biome. Furthermore, Elbert et al. [2012] use a globally uniform value of surface cover fraction to scale up local field measurements of productivity to the global scale. However, values of surface coverage by lichens and bryophytes compiled by Elbert et al. [2012] vary largely at the small scale, which makes upscaling to larger scales challenging.

While productivity estimated by LiBry is evaluated in this study, large-scale surface coverage of lichens and bryophytes simulated by LiBry has been evaluated for regions north of 50° N in Porada et al. [2016a]. It was shown that LiBry predicts realistic values of cover fraction. Moreover, values of surface cover predicted by LiBry for other regions of the world [Porada et al., 2016b] are in agreement with the estimate of Elbert et al. [2012]. In spite of uncertainties regarding productivity and abundance of lichens and bryophytes, comparing the empirical and process-based approaches gives confidence in the order of magnitude of the LiBry simulation results."

Line 25: relation between N2O and fixation rate seems to be available from the study by Barger et al. 2013, why not using this relationship instead of linking N2O to respiration?

As we explained above (Reply to "General remark", Page 2), we have added to the revised manuscript an explanation why we use respiration instead of N uptake to estimate N_2O emissions (P. 14, L. 22).

Page 3
Figure 1: Figure 1 shows nitrification and denitrification, and the dependence of N2O emissions to NH4 and NO3 concentrations; It also shows that NH4 and NO3 depend on fixation and deposition; In contrast to Figure 1, you derive N2O emissions from respiration; Is there a link between respiration and other N fluxes such as fixation? Is it pure coincidence that respiration and N2O fluxes show an empirical relationship?

Unfortunately, the exact link between respiration and other N fluxes is not known, yet. Lenhart et al. [2015] worked with the empirical relationship between respiration and N_2O fluxes and we adopted that for the current study. As suggested by us in the conclusion of the revised manuscript (P. 15, L. 23), "it would be useful to perform field measurements of N_2O emissions and respiration to test the effect of climatic conditions on the relationship between N_2O release and respiration. Furthermore, using alternative approaches to estimate N_2O emissions by lichens and bryophytes may be helpful to constrain our approach."

Page 4
Line 8 ff: ; is the relationship between N2O and respiration not driven by temperature

change? Also moisture dependency of respiration might be different to N2O, especially as nitrification and denitrification have different optimum ranges; respiration differs between species. . . does N2O/respiration not differ across species? From what I found in cited literature, moisture dependency of respiration stays 1 for moisture values exceeding an upper limit; this is not true for N2O, as under very anoxic conditions, N2O is reduced further to N2: so here, the sensitivity of N2O on moisture differs from the one of respiration! This needs to be discussed at least.

We have added the following to the discussion section of the revised manuscript (P. 13, L. 23):

"...our results rely on the laboratory incubation measurements and the calculated ratio of N_2O emissions to respiration presented in Lenhart et al. [2015]. Furthermore, our approach considers effects of variation in climatic conditions on N_2O emissions by lichens and bryophytes. Hence, it is necessary to discuss the sensitivity of the relationship between respiration and N_2O emissions to a range of climatic conditions. As shown in Lenhart et al. [2015, Fig. 3], the relationship between respiration and N_2O emissions seems to be insensitive to temperature changes for the tested species. Likewise, variations in water content have no clear effect on the relationship between N_2O release and respiration [Lenhart et al., 2015, Fig. S3]. Although the sensitivities of N_2O release to temperature and water content are similar to those of respiration across species, the relationship between N_2O release and respiration shows interspecific variation. However, in spite of a large number of around 40 sampled species, the relationship shows a relatively narrow 90 % confidence interval of 11.3 to 20.7 ng N_2O (mg CO_2)$^{-1}$ [Lenhart et al., 2015]. This suggests that the mechanism of N_2O release by lichens and bryophytes is similar between different species."

Line 22: "...variation in climatic conditions": in the approach used in this study, the sensitivity of N2O emissions on climatic conditions mirrors the sensitivity of respiration; the authors do not discuss potential differences in sensitivities and arising uncertainties in their results, please add this to the discussion

We added two sentences on the potentially different sensitivities of respiration and N_2O emissions on climatic conditions to the methods section of the revised manuscript (p. 5, L. 9):

"It should be pointed out that LiBry does not compute directly N_2O emissions by lichens and bryophytes, but it derives them from simulated respiration through an empirical linear relationship. Hence, differences in the sensitivities of respiration and N_2O emissions to climatic conditions may lead to uncertainties in our predicted effects of climate on N_2O emissions."

Moreover, we extended the discussion of the revised manuscript by a paragraph on the sensitivity of the relationship between respiration and N_2O emissions to environmental conditions (see previous point).

Line 25: the variations in N2O emissions simulated in the study mirrors the variation in

respiration; hence, claiming that their study helps to assess the variation in N2O emissions is a bit of a long shot; some clarification on this, and also on how reliable the linear relationship they are using is under different climatic conditions would be necessary

In the revised manuscript, we have pointed out potential effects of climatic conditions on the relationship between respiration and N_2O emissions. We also have discussed these effects and their implications for our results (see previous two points).

Page 5
Line 4: "Since it is assumed in LiBry that lichens and bryophytes cannot grow together with crops, growth is low in these regions ...": why do they grow at all, if it is stated that they cannot grow together with crops?

In the revised manuscript, we have clarified this (P. 5, L. 16): "In LiBry, it is assumed that lichens and bryophytes only grow on the area fraction of a grid cell which is not occupied by crops. Therefore, on a grid cell basis, regions with a high fractional cover of cropland show low productivity by lichens and bryophytes, in spite of favourable climatic conditions. "

Figure 2: d) Tropical Forest Canopy: It seems like the small values come mainly from very few grid cells at the edge of the tropics; if those few grid cells were excluded, range, and average value would look different; maybe I get this impression only due to the chosen color range, but I still think it wold be worth checking

It is true that the low values of productivity come from a few grid cells at the edge of the biome. However, it seems a bit arbitrary to us to change the boundary of the biome, which is derived from the map by Olson et al. [2001], to exclude some specific values. Since the number of grid cells per biome is very large (hundreds to thousands), excluding a few low values would not significantly shift the average value marked by the blue dot.

Figure 2: what is the difference between organisms growing on ground or on leaves and how is this represented in the model? Here, that distinction comes up for the first time, if it is important to distinguish those two groups, then please add more explanation on it already in the introduction

We added a short description of the different locations of growth simulated by LiBry to the introduction of the revised manuscript (P. 3, L. 17): "LiBry simulates photosynthesis, respiration and growth of lichens and bryophytes as a function of environmental conditions. To distinguish global patterns of productivity on the ground and in the canopy, the model represents these locations and their differing environmental conditions separately. "

Figure 2: values for desert regions are presented, while the Sahara is grey: please explain

In the revised manuscript, we have added to the caption of Fig. 2: "Grey colour denotes regions where no simulated species is able to survive, such as ice shields and the driest regions of deserts." Since we rearranged the figures in the revised manuscript, Fig. 2 is now Fig. 1

Page 9: The authors showed the ratio between respiration and NPP, however, they do not explain in how far respiration is dependent on NPP in the model; as N2O is somehow calculated from respiration, the link between N2O and NPP does not get clear; given this, the authors have a rather large focus on the NPP evaluation while it is not obvious how NPP affects N2O emissions in their approach

We explain in the methods section that NPP is calculated as the difference between photosynthesis and respiration and that respiration is calculated independently, as a function of temperature (P. 3, L. 29-31). To make this more clear, and to explain why we evaluate NPP, we have extended and changed the respective section of the discussion in the revised manuscript (P. 12, L. 25): "... we estimate total N_2O emissions by lichens and bryophytes of 0.27 (0.19 - 0.35) ($Tg\,N_2O$)\,yr^{-1}, which is at the lower end of the range of 0.32 to 0.59 ($Tg\,N_2O$)\,yr^{-1} calculated by Lenhart et al. [2015]. The evaluation of LiBry regarding simulated NPP shows that our global patterns and total values of NPP are very similar to the empirical estimate by Elbert et al. [2012]. Since Lenhart et al. [2015] use this NPP estimate by Elbert et al. [2012] to derive N_2O emissions, differences in NPP are most likely not the reason for our lower estimate of N_2O emissions compared to Lenhart et al. [2015]. Instead, this may be explained by differing methods to compute respiration: While Lenhart et al. [2015] assume a globally uniform ratio of respiration to NPP of the value 2 to estimate respiration, LiBry simulates respiration independently as a species-specific function of temperature and water status. This results in a lower global average value of around 1 for the ratio of respiration to NPP predicted by LiBry. Our estimated ratio of respiration to NPP agrees well with laboratory measurements, but it is in general difficult to compare a global, ecosystem-scale value to small-scale and short-term observations. "

Page 10
Line 9 ff: Diversity of estimated N2O emissions driven respiration, please add notes and discussions on that

We have added the following to the revised manuscript (P. 13, L. 12): "... We examine the relative importance for respiration of differences between species compared to climatic differences with LiBry, since the model simulates various physiological strategies and represents variation in climatic conditions at the global scale. Thereby, we assume that the relationship between respiration and N_2O emissions is relatively insensitive to climatic conditions and physiological differences between species, as suggested by the experiments by Lenhart et al. [2015]."
As explained above, we have added a short discussion of potential effects of climatic

conditions on the relationship between respiration and N_2O emissions to the revised manuscript.

Line 15: "functional diversity of lichens": I guess there are many kind of functional diversities and not all are related to N2O. . .. phrasing is a bit vague

In the revised manuscript, we rephrased this sentence to (P. 13, L. 18): "Modelling approaches in this direction should probably account for both interspecific variation in processes associated with N_2O release by lichens and bryophytes as well as variation in climatic conditions."

Line 16: "considers the most important sources of variation. . .": this might be true for respiration, but you do not explicitly calculate N2O emissions, they mirror the sensitivity of respiration

In the sentence following the quoted one, we refer to this potential uncertainty in our approach. To make this more clear, we have rephrased the sentence (P. 13, L. 21): "These uncertainties mainly result from our method to estimate respiration and from assumptions concerning the empirical relationship between respiration and N_2O emissions."

Line 23 ff: one option to assess the uncertainty regarding wfps for N2O anyway could be to add a sensitivity of the linear relationship between N2O and respiration on water content and test different ranges

As explained above, we have added a discussion on the sensitivity of the linear relationship to water content to the revised manuscript (P. 13, L. 32).

Line 32: I assume not the measurements suffer from uncertainties, but that rather the results presented to not provide any information regarding uncertainties

In the manuscript, our best estimate for N_2O emissions is 0.27 $(\mathrm{Tg\,N_2O})\,\mathrm{yr}^{-1}$. In addition to that, we give an uncertainty range, i.e., 0.19 - 0.35 $(\mathrm{Tg\,N_2O})\,\mathrm{yr}^{-1}$.

Page 11
Line 2: another shortcoming of manual chamber measurements is the limited temporal resolution which can make a huge difference in cumulated fluxes (Barton et al. 2015, Sampling frequency affects estimated of annual nitrous oxide fluxes, Scientific Reports)

We have added this point to the revised manuscript (P. 14, L. 17): "...Furthermore, the limited temporal resolution of chamber measurements may affect estimated N_2O emissions [Barton et al., 2015]."

Line 4: I dont really understand this sentence. How is water, temperature and nutrient

conditions influenced by experimental setup? N2O emissions are driven by those factors, so it is quite logic that N2O emissions show a similar heterogeneity, independent of the experimental setup

We have replaced "experimental setup" by "environmental conditions under which the experiment is performed"

Line 6: This sounds as if you refer to experiments with for instance application of fertilizer, that would in fact influence nutrient conditions by the experimental setup; if so then please phrase it more clearly

With that statement, we had natural environmental conditions in mind. Hence, we state now (P. 14, L. 19): "... Thus, it is indispensable to report and consider the exact environmental conditions under which the measurements were made and to restrict natural emission data to those assessed under typically occurring natural conditions."

Conclusions: There are hardly any conclusions in the conclusion section; The first three sentences are a short summary of the study, the last sentence emphasizes vaguely how additional measurements could be beneficial; In my opinion you can draw more conclusions from your study, so please take a bit more care about this section. It is the last thing people read, and the way it reads now, it leaves at least me with an unsatisfied feeling about what actually your main conclusions are

In the revised manuscript, we have rephrased the conclusions as follows: "We estimate large-scale spatial patterns and global values of N_2O emissions by lichens and bryophytes from a process-based model of their productivity and respiration. Our results suggest a significant contribution of lichens and bryophytes to global N_2O emissions, albeit at the lower end of the range of a previous, empirical estimate. Since both approaches use respiration to derive N_2O emissions, our lower estimate likely results from a different method to predict respiration, compared to the empirical approach. Hence, while estimates of productivity are relatively well constrained, evaluating models with regard to estimated respiration may improve predictions of N_2O emissions by lichens and bryophytes. One important finding derived from our simulation is that the ratio of respiration to NPP by lichens and bryophytes shows spatial variation and a latitudinal gradient at the global scale. This means that productivity and N_2O emissions by the organisms are not necessarily correlated and that tropical regions may show higher emissions than polar regions given the same NPP. Furthermore, we show that both physiological variation among species as well as variation in climatic conditions are relevant for variation in respiration and, consequently, N_2O emissions. Ecosystem-scale estimates of N_2O emissions by lichens and bryophytes should therefore include sufficient ranges of species and climatic conditions to avoid biased results. Our results build on the empirical finding that N_2O emissions by lichens and bryophytes are linearly related to their respiration. This relationship is relatively insensitive to climatic conditions and shows no large variation between species. However, the relationship is based on closed chamber measurements.

Therefore, it would be useful to perform online flux measurements of N_2O emissions and respiration to test the effect of climatic conditions on the relationship between N_2O release and respiration. Furthermore, using alternative approaches to estimate N_2O emissions by lichens and bryophytes may be helpful to constrain our approach."

Technical comments
Line 8: units Tg N2O yr-1 or Tg N2O-N yr-1 ? - please specify the units regarding N2O emissions throughout the manuscript

In the revised manuscript, we have replaced "Tg ... of N_2O" or similar terms by "Tg N_2O".

Line 19: units: Gt C yr-1 or Gt CO2 yr-1 ?

In the revised manuscript, we have replaced "Gt ... of carbon" or similar terms by "Gt C".

Page 2
Line 5: citation style

We have corrected this.

Line 17: N2O is already explained in line 13

We have corrected this.

Page 5: Figure 2: units: change from [g m-2 yr-1] to [g C m-2 yr-1]

We have changed this figure accordingly.

Page 9: Line 15: again unit: Tg N or Tg N2O; Line 17: add blank after 25 %

We have corrected this.

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Estimating global nitrous oxide emissions by lichens and bryophytes with a process-based productivity model

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Abstract. Nitrous oxide is a strong greenhouse gas and atmospheric ozone-depleting agent, which is largely emitted by soils. Recently, also lichens and bryophytes have been shown to release significant amounts of nitrous oxide. This finding relies on ~~empirical relationships between nitrous oxide emissions, respiration and~~ ecosystem-scale estimates of net primary productivity of lichens and bryophytes, which are ~~combined with ecosystem-scale values of their productivity .~~ converted to nitrous oxide emissions by empirical relationships between productivity and respiration, as well as between respiration and nitrous oxide release Here we obtain an alternative estimate of nitrous oxide emissions which is based on a global process-based non-vascular vegetation model of lichens and bryophytes. The model quantifies photosynthesis and respiration of lichens and bryophytes directly as a function of environmental conditions, such as light and temperature. Nitrous oxide emissions are then derived from simulated respiration assuming a fixed relationship between the two fluxes. This approach yields a global estimate of 0.27 (0.19 - 0.35) (Tg N_2O) yr^{-1} ~~of nitrous oxide~~ released by lichens and bryophytes. This is lower than previous estimates, but corresponds to about 50 % of the atmospheric deposition of ~~N_2O~~ nitrous oxide into the oceans or 25 % of the atmospheric deposition on land. Uncertainty in our simulated estimate results from large variation in emission rates due to both physiological differences between species and spatial heterogeneity of climatic conditions. To constrain our predictions, ~~field observations of respiration in combination with a more process-based approach for relating~~ combined online flux measurements of respiration and nitrous oxide emissions ~~to respiration~~ may be helpful.

1 Introduction

~~Microbial surface communities~~ Lichens and bryophytes have increasingly been recognized to play a relevant role in global biogeochemical cycles ~~(Sancho et al., 2016; Barger et al., 2016). These communities comprise photosynthesizing cyanobacteria, algae, lichens and mosses, which, together with fungi and bacteria, grow~~ (Elbert et al., 2012; Sancho et al., 2016; Barger et al., 2016). They are globally abundant, growing on soils, rocks, and epiphytically on trees. At high latitudes, they may form extensive covers on the forest floor and in wetlands, mosses frequently represent the dominant vegetation type. In drylands, ~~they widely cover surface soils forming~~ lichens and bryophytes form so-called biological soil crusts together with photosynthesizing cyanobacteria, algae, fungi and bacteria. These crusts cover vast areas in arid and semiarid ecosystems.

In a first ~~ecosystem-based upscaling approach,~~ approach, based on empirical upscaling of field measurements according to ecosystem categories, Elbert et al. (2012) calculated that ~~these communities~~ lichens and bryophytes, together with free-living cyanobacteria and algae, fix around 14.3 (Gt CO_2) yr^{-1} ~~of carbon dioxide~~ (3.9 Gt carbon) at the global scale. This corresponds to about 7 % of the net primary productivity (NPP) by terrestrial vegetation. In an alternative approach to the empirical upscaling of observations, Porada et al. (2013) utilized a process-based non-vascular vegetation model for lichens and bryophytes, called LiBry, to calculate the NPP of these organism groups at the global scale, obtaining similar results.

Additionally to photosynthetic carbon uptake, ~~several organism groups within the microbial communities, i.e. cyanobacteria, cyanolichens and other bacteria are capable of fixing nitrogen (N) (Pepe-Ranney et al., 2015; Barger et al., 2016). Their~~ lichens and bryophytes are able to fix nitrogen through a symbiosis with cyanobacteria (DeLuca et al., 2002; Barger et al., 2016). Together with free-living cyanobacteria, their nitrogen fixation was estimated to sum up to a global value of ∼49 (Tg N) yr^{-1} (Elbert et al., 2012), which accounts for nearly half of the biological nitrogen fixation on land. The LiBry model yielded a similar estimate of up to 34 (Tg N) yr^{-1}, based on the nitrogen requirements of lichens and bryophytes determined by ~~(Porada et al., 2014)~~Porada et al. (2014). Moreover, it was found in the same study that the organisms may contribute significantly to biotic enhancement of global chemical weathering, ~~according to~~ by release of weathering agents such as organic acids. Their potential for chemical weathering was derived from their phosphorus demand~~.~~ , assuming that they dissolve surface rocks to acquire phosphorus.

~~After fixation, nitrogen compounds are partly incorporated into the biomass of the microbial surface communities, and they can also be leached out by rain (Thiet et al., 2005; Veluci et al., 2006; Coxson, 1991). An uptake of cyanobacteria-fixed N by vascular plants has been proven in a ^{15}N isotope experiment almost 50 years ago (Stewart, 1967). Nitrogen fixed by biological soil crusts has~~ Recently, lichen- and bryophyte-related nitrogen fluxes other than fixation of nitrogen have been shown to be ~~taken up by plants only 15 days after initial fixation (Hawkes, 2003).~~

~~If nitrification and denitrification processes occur within the microbial communities, different gaseous nitrogen compounds may be formed and released into the surrounding atmosphere (see Fig. **??** for an overview). Examples for such compounds are ammonia (NH_3), nitric oxide (NO), nitrous acid (HONO), and nitrous oxide (N_2O) (Barger et al., 2016). In a recent study,~~ significant at the global scale. Weber et al. (2015) found that biological soil crusts~~were shown to emit large~~ , which may contain large fractions of lichens or bryophytes, emit considerable quantities of the reactive trace gases NO and HONO, accounting for ∼1.7 (Tg N) yr^{-1}~~of nitrogen (Weber et al., 2015)~~. This corresponds to ∼20 % of global nitrogen oxide emissions from soils under natural vegetation (Ciais et al., 2013). ~~In a different follow-up study, the emission of~~

Furthermore, Lenhart et al. (2015) showed that a large variety of lichen and bryophyte species release nitrous oxide (N_2O)~~was measured on a large variety of microbial organisms (Lenhart et al., 2015). Utilizing fixed ratios between N~~. They estimated that the organisms emit a total value of 0.45 (0.32 - 0.59) (Tg N)$_2$O~~emissions, respiration and NPP, the global NPP data of Elbert et al. (2012) were used to obtain globally resolved data on~~ yr^{-1} at the global scale, which corresponds to 4 - 9 % of natural terrestrial N_2O emissions ~~by microbial organisms and communities~~(Zhuang et al., 2012). Since N_2O is an important greenhouse gas and also the main depleting substance of stratospheric ozone which is still emitted today, quantifying all con-

tributing sources is of high importance (Butterbach-Bahl et al., 2013; Ravishankara et al., 2009; Gärdenäs et al., 2011; Ciais et al., 2013).

~~Upscaling of small-scale measurements to global~~ Absolute values of N_2O release estimated by Lenhart et al. (2015) were highest for lichens and bryophytes living on the ground in the boreal zone and for epiphytic lichens and bryophytes in the humid tropics. The relative contributions of lichens and bryophytes to total ecosystem N_2O emissions, however, were highest in desert and tundra biomes, due to the low emissions by other vegetation and the soil there. The high relevance of lichens and bryophytes for N_2O emissions ~~by~~ in drylands and at high latitudes is in accordance with their strong impacts on other components of the nitrogen cycle in these regions. Bryophytes, for instance, have been suggested to be the main source of nitrogen input into boreal forests through fixation from the atmosphere by cyanobacterial partners (DeLuca et al., 2002). Also in drylands, lichens and bryophytes are crucial for input of nitrogen into the ecosystem (Barger et al., 2016), and they may even be essential providers of nitrogen for vascular plants (Stewart, 1967; Hawkes, 2003).

The estimate by Lenhart et al. (2015) is derived from measuring emissions of N_2O by the organisms in the laboratory under a range of environmental conditions. All lichen and bryophyte species analyzed by Lenhart et al. (2015) showed release of N_2O. Lichens and bryophytes were shown to utilize ^{15}N labelled NO_3^- but not NH_4^+, indicating that N_2O is likely formed during denitrification. The exact process of N_2O-formation, however, ~~is complicated by the considerable variation of the measured fluxes. There have been only few studies investigating~~ remains largely unknown. One option is that the organisms themselves release N_2O during the metabolisation of nitrate, in a similar way as suggested by Smart and Bloom (2001) for vascular plants. Another option is, that bacteria growing on lichen and moss cushions are responsible for the emissions of N_2O. This second option is supported by a recently published study, where several strains of the bacterial genus *Burkholderia*, which were shown to emit N_2O, were isolated from the boreal peat moss *Sphagnum fuscum* (Nie et al., 2015). While Lenhart et al. (2015) describe that the substrate, which the organisms grew on, was thoroughly removed, further cleaning steps to remove potential bacterial colonies have not been conducted.

Another finding by Lenhart et al. (2015) is that N_2O emissions ~~and denitrification processes of~~ are related to respiration by a relatively constant factor. By applying this factor and, furthermore, assuming a fixed ratio between respiration and NPP, the authors utilised the global NPP data of Elbert et al. (2012) to obtain globally resolved N_2O emissions by lichens and bryophytes. The reliability of global estimates derived from upscaling of small-scale measurements depends on the variation of the measured fluxes. The field measurements of NPP, which were extrapolated to the spatial scale of a biome by Elbert et al. (2012), vary by around two orders of magnitude. Measurements of N_2O emissions by lichens and bryophytes, too, show considerable variation. Regarding biological soil crusts, ~~obtaining differing results. Several~~ several studies analyzed denitrification rates to be negligible (Johnson et al., 2007; Strauss et al., 2012), and N_2O production was calculated to constitute only 3-4 % of the N fixation rate (Barger et al., 2013). Other studies, however, described high denitrification rates that either increased (Brankatschk et al., 2013) or decreased with advancing crust development (Abed et al., 2013). ~~Consequently, reliable~~ One possibility to increase the reliability of large-scale estimates of N_2O emissions by lichens and bryophytes ~~are needed to assess the contribution of these organisms to the global N_2O budget~~is the application of alternative, methodically different approaches.

For this reason, we apply here the process-based non-vascular vegetation model LiBry (Porada et al., 2013) to ~~provide an alternative estimate of~~ assess the contribution of these organisms to the global N_2O ~~emissions associated with~~ budget. LiBry simulates photosynthesis, respiration and growth of lichens and bryophytes as a function of environmental conditions. To distinguish global patterns of productivity on the ground and in the canopy, the model represents these locations and their differing environmental conditions separately. We calculate respiration by lichens and bryophytes directly as a function of environmental conditions and we derive N_2O-emissions based on the simulated respiration. By doing this, we obtain physiologically driven and spatially resolved data on the N_2O-emissions by lichens and bryophytes at the global scale. Since we estimate respiration with LiBry, we do not need to make assumptions regarding the ratio of NPP to respiration, contrary to Lenhart et al. (2015). Furthermore, we quantify different sources of variation in N_2O emissions and determine their relative importance.

~~Nitrogen balance of microbial communities. Gains (solid arrows), losses (empty arrows) and transformation processes (dashed arrows) of nitrogen compounds in microbial communities. The community may consist of cyanobacteria, algae, lichens, mosses, fungi and bacteria.~~

2 Methods

The non-vascular vegetation model LiBry estimates global patterns of photosynthesis, respiration and net primary productivity of lichens and bryophytes (Porada et al., 2013). The model calculates these physiological processes as a function of climate and additional environmental conditions, which are provided in form of time series of global gridded maps. Photosynthesis in LiBry is determined by ambient levels of light, CO_2 and temperature according to the Farquhar-approach (Farquhar and von Caemmerer, 1982). Respiration is simulated as a function of temperature via a Q_{10}-relationship. Both processes also depend on the water status of the simulated lichens and bryophytes, which includes limitation of CO_2-diffusion at high water content. NPP is derived from the difference between gross photosynthesis and respiration. A unique feature of LiBry is that functional diversity of lichens and bryophytes is represented by a large number of artificial species, instead of being aggregated into one or a few average functional types. The advantage of this approach is that adaptation of the organisms to differing environmental conditions is simulated in a more realistic way. Physiological processes such as photosynthesis and respiration are calculated separately for each artificial species. LiBry has been successfully applied to estimate global NPP by lichens and bryophytes (Porada et al., 2013) and other impacts of these organisms on global biogeochemical cycles (Porada et al., 2014, 2016b).

The model version presented here contains several extensions compared to the original version: First, an NPP-based weighting scheme was introduced, which assigns relative abundances to all artificial species that survive in a grid cell of the model in the steady state (Porada et al., 2016b). This allows to derive an average grid cell value of NPP based on the relative abundances of the simulated species in that cell. In the original version, grid cell NPP could only be predicted in form of a range of values, due to unknown abundances of the species. The average grid cell NPP is close to the upper end of the range of productivity values, since the most productive simulated species are assumed to be the most abundant ones. Secondly, a dynamic disturbance scheme was implemented, which replaces the equilibrium computation of surface coverage by a monthly update of coverage

(Porada et al., 2016a). This makes the new model applicable to transient scenarios of climatic and environmental change, while the original model required the assumption of a steady state to compute coverage.

For this study, we run LiBry with an initial value of 3000 artificial species in each grid cell for a period of 600 years to reach steady state, with climatic fields and other forcing data from Porada et al. (2013). Our global estimates are based on average values over the last 50 years of the simulation. We evaluate the new version of LiBry in the same way as the original one (Porada et al., 2013), by comparing simulated NPP to field measurements on a biome basis.

LiBry does not include an explicit representation of processes that directly result in emission of nitrous oxide. However, it has been determined experimentally by Lenhart et al. (2015) that N_2O emissions by ~~microbial surface communities~~ lichens and bryophytes are related to their respiration by a conversion factor of 16 ng N_2O (mg CO_2)$^{-1}$. The conversion factor has a 90 % confidence interval of 11 to 21 ng N_2O (mg CO_2)$^{-1}$. Since LiBry explicitly calculates respiration by lichens and bryophytes, we derive N_2O emissions from simulated respiration using the conversion factor of Lenhart et al. (2015).

The study by Lenhart et al. (2015) uses NPP of ~~microbial surface communities as a basis~~ lichens and bryophytes, together with free-living cyanobacteria and algae, to estimate N_2O emissions, since global upscaled data on respiration of these ~~communities~~ organisms are not available from Elbert et al. (2012). Thereby, Lenhart et al. (2015) assume a fixed ratio of respiration to NPP. To determine this ratio, they ~~measure both quantities in the laboratory on samples of lichens and bryophytes (Lenhart et al., 2015, Tab. S5). The median of their measured values of respiration is 43~~evaluate literature data, obtaining a rate of respiration relative to net photosynthesis of ~49 ~~% of net photosynthesis~~ % (Lenhart et al., 2015, Tab. S6). Since measurements have been made in the sunlight, but respiration continues in the dark, respiration is multiplied by a factor of 2, assuming a 12-hour day. This leads to an estimated ~~respiration of 86 % of net photosynthesis, which suggests that the~~ ratio of respiration ~~and NPP~~ to NPP which is roughly 1 : 1. To evaluate LiBry further, we compute the ratio of respiration to NPP in LiBry to assess if the model is in agreement with these observations.

In the study of Lenhart et al. (2015), the substrate of the samples was removed to avoid biases resulting from N_2O release by microbes in the substrate. Foliose and fruticose lichens as well as mosses were collected, which grew on soil, rocks, and epiphytically on trees and the authors found no variation in N_2O emissions depending on the underlying substrate. Endolithic and crustose lichens were not included in that study, as for these growth forms the dry weight, which is needed for calculations, could not be determined in a reliable manner.

Variation in field measurements of N_2O emissions may result from physiological differences between species, but also from variation in climatic conditions, which can be significant at small scale. To upscale emissions from point measurements to the large scale, it is important to quantify the relative contributions of these different sources of variation. If, for instance, the variation between species regarding their N_2O emissions was small, it would suffice to sample a low number of species to obtain an average emission for a certain climatic condition. LiBry can provide an indication of the relative importance of these sources of variation, since the model not only represents climate variability, but also simulates diverse physiological strategies. Each grid cell of the model contains a range of surviving species at the end of the simulation and, consequently, shows a range of N_2O emissions. LiBry does not simulate spatial variation in climatic conditions within a grid cell. However, by comparing average emission rates of grid cells from different climates it is possible to assess the relative importance of

climatic conditions for variation in N_2O emissions. We select five model grid cells from different ecosystem classes to analyse the relative importance of differences between species and climatic heterogeneity on variation in N_2O emissions. It should be pointed out that LiBry does not compute directly N_2O emissions by lichens and bryophytes, but it derives them from simulated respiration through an empirical linear relationship. Hence, differences in the sensitivities of respiration and N_2O emissions to climatic conditions may lead to uncertainties in our predicted effects of climate on N_2O emissions.

3 Results

The global distribution of net primary productivity simulated by the updated version of LiBry is shown in Fig. 1. Productivity by lichens and bryophytes is highest in forested regions and lowest in deserts and agricultural regions. Hence, the spatial pattern is mainly controlled by water availability, except for cropland. ~~Since~~ In LiBry, it is assumed ~~in LiBry~~ that lichens and bryophytes ~~cannot grow together with crops, growth is low in these regions~~ only grow on the area fraction of a grid cell which is not occupied by crops. Therefore, on a grid cell basis, regions with a high fractional cover of cropland show low productivity by lichens and bryophytes, in spite of favourable climatic conditions. The high productivity in the humid tropics mainly results from epiphytic lichens and bryophytes in the canopy, while in the boreal zone, the larger fraction of productivity stems from the ground.

~~Global patterns of NPP. Lichen and bryophyte NPP estimated by LiBry for a) the canopy, b) the ground and c) all locations of growth. The estimates are in grams of carbon per m^2 and they are average values over the last 50 years of a 600-year simulation with 3000 initial species. d) NPP estimated by LiBry compared to field measurements from four biomes, defined after Olson et al. (2001). The blue dots show the average simulated NPP for each biome and the blue vertical bars show the range of NPP values between the different grid cells in a biome. The magenta diamonds correspond to the median of NPP values measured in the field on the small scale, the magenta vertical bars denote the range of the field measurements. Left to the magenta diamonds the number of field measurements is shown that is considered for the respective biome. Details can be found in Porada et al. (2013).~~

As a result of the dynamic surface coverage, the spatial patterns of NPP differ slightly between the new and the original version of LiBry, but the large scale gradients remain the same. Comparing the global pattern of lichen and bryophyte NPP simulated by the new version of LiBry to an empirical estimate by Elbert et al. (2012) shows good agreement, similar to the original version. Furthermore, the total global NPP predicted by the new LiBry differs from the original estimate due to the updated calculation of coverage. The main difference is found for the tropical forest canopy, where simulated NPP increases significantly. The total global NPP of 4.3 (Gt C) yr^{-1} ~~of carbon~~ estimated by the new LiBry compares well to the value of 3.9 (Gt C) yr^{-1} ~~of carbon~~ calculated by Elbert et al. (2012).

Comparison of simulated NPP to field measurements on a biome basis suggests that LiBry predicts realistic values of NPP for a range of ecosystems (Fig. ~~1 d~~2). In particular, simulated NPP in the tropical and the boreal forest matches well with observations, while the original version of LiBry seemed to underestimate NPP in these biomes. In the biomes desert and, to a lesser extent, tundra, LiBry seems to overestimate productivity, which may have also been the case with the original

version. A potential explanation for this is that productivity in dry and cold areas may ~~be not only~~ not only be limited by climatic factors, but also by nutrient availability (Porada et al., 2016b). Since photosynthesis and growth are only controlled by climatic factors in LiBry, the effect of spatial variation in nutrient availability on productivity cannot ~~not be simulated, yet~~yet be simulated. It should be pointed out however, that, except for the boreal biome, the number of field measurements is quite low and, consequently, the observation-based characteristic values for each biome are subject to considerable uncertainty.

Figure ~~??~~ 3 shows simulated global patterns of nitrous oxide emissions by lichens and bryophytes~~, together with the spatial distribution of the ratio of respiration to NPP~~. Nitrous oxide emission is highest in the humid tropics and subtropics with values up to 10 (mg N_2O) m^{-2} yr^{-1} ~~of N_2O~~ (Fig. ~~??~~ 3 a). A second region of high emissions is the boreal zone with values up to 8 (mg N_2O) m^{-2} yr^{-1}~~of N_2O~~. Dry regions show lowest values of nitrous oxide emissions, in general less than 1 (mg N_2O) m^{-2} yr^{-1}~~of N_2O~~. Considering only lichens and bryophytes which grow as epiphytes in the canopy (Fig. ~~?? c~~3 b), emissions in the humid tropics are around three times higher than in the boreal and temperate zones. Lichens and bryophytes on the ground show highest values of nitrous oxide emissions in the boreal zone, with values around 3 (mg N_2O) m^{-2} yr^{-1} ~~of N_2O~~ (Fig. ~~?? e~~3 c). Regarding the ground, tropical and subtropical regions only partly show N_2O emissions comparable to those of the boreal zone. The reason for this is ~~the~~ low simulated productivity and coverage of lichens and bryophytes on the ground in tropical and subtropical climates, which also leads to low respiration on a grid cell level and hence to low N_2O emissions.

~~Global patterns of N_2O-release and the ratio of respiration to NPP. Nitrous oxide emissions by lichens and bryophytes estimated by LiBry for a) all locations of growth, c) the canopy and e) the ground. Note the differing ranges of the color bars. Ratio of respiration to NPP for b) all locations of growth, d) the canopy and f) the ground.~~

Figure 4 shows the simulated global spatial distribution of the ratio of respiration to NPP. The assumption of a globally constant ratio of respiration to NPP is used by Lenhart et al. (2015) to derive ecosystem-scale N_2O emissions by lichens and bryophytes from their NPP. Alternatively, this ratio can be derived from the independent LiBry estimates of NPP and respiration. The simulated ratio shows a latitudinal pattern with increasing values towards the tropics (Fig. ~~?? b~~4 a). This results from the influence of surface temperature on respiration in combination with high nighttime temperatures in the humid tropics, which cause high respiration rates during the night. Note that high respiration relative to NPP of tropical lichens and bryophytes does not necessarily mean high respiration at the grid cell level, since ~~overall productivity~~ net productivity and coverage may be low. Respiration by lichens and bryophytes in the canopy shows a slightly weaker latitudinal gradient than the ground, which can be explained by efficient evaporative cooling in the canopy (Fig. ~~?? d). For the same reason, respiration on the ground in the tropics is markedly higher than at high latitudes (Fig. ?? f), since~~ 4 b). In contrast, lichens and bryophytes on the ground usually grow within the surface boundary layer~~. This increases the relative effect of radiation on the surface temperatureof the organisms.~~ , which reduces cooling by turbulent heat transfer, leading to a strong influence of incoming radiation on surface temperature. Since radiation input increases toward the equator, the ratio of respiration to NPP on the ground in the tropics is markedly higher than at high latitudes (Fig. 4 c). The ratio of respiration to NPP varies from less than 1 to around 2, while most values are around 1. This means that gross primary productivity (GPP) is partitioned roughly equally into NPP and respiration, which agrees well with the observational data from Lenhart et al. (2015).

An overview of global total values of N_2O emissions, respiration, NPP and the ratio of respiration to NPP estimated by LiBry is shown in Tab. 1.

Table 2 shows N_2O emissions by lichens and bryophytes for individual grid cells from five different ecosystem classes (see also Tab. 1). Variation in emissions between species within a grid cell is large, it can exceed three orders of magnitude. The variation due to climatic conditions is smaller, but it still amounts to almost two orders of magnitude based on the grid cells with the highest and lowest average emission rates. Comparing Tab. 2 to the global range of N_2O emissions by lichens and bryophytes (Fig. ??3) shows that the five selected grid cells represent well the global variation in emissions due to climatic conditions. Thus, both functional diversity of the artificial species and different climatic conditions are important for variation of N_2O emissions, according to the LiBry simulation.

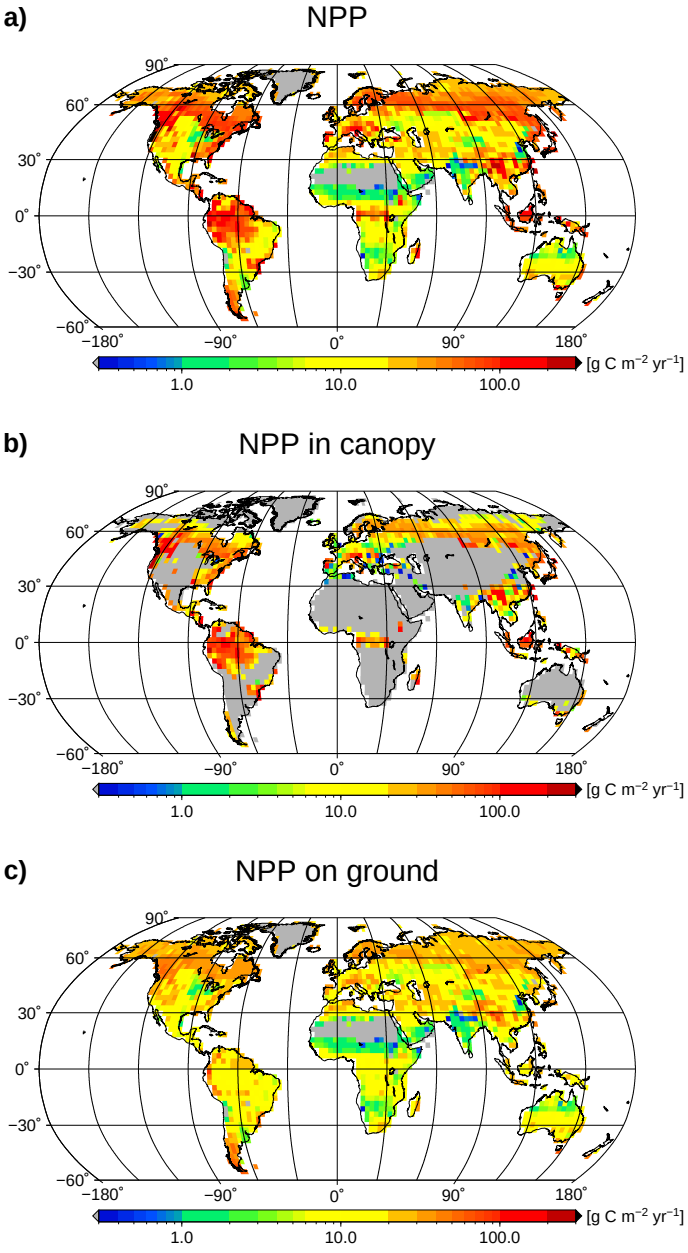

Figure 1. Global patterns of NPP. Lichen and bryophyte NPP estimated by LiBry for a) all locations of growth, b) the canopy and c) the ground. The estimates are in grams of carbon per m^2 and they are average values over the last 50 years of a 600-year simulation with 3000 initial species. Grey colour denotes regions where no simulated species is able to survive, such as ice shields and the driest regions of deserts.

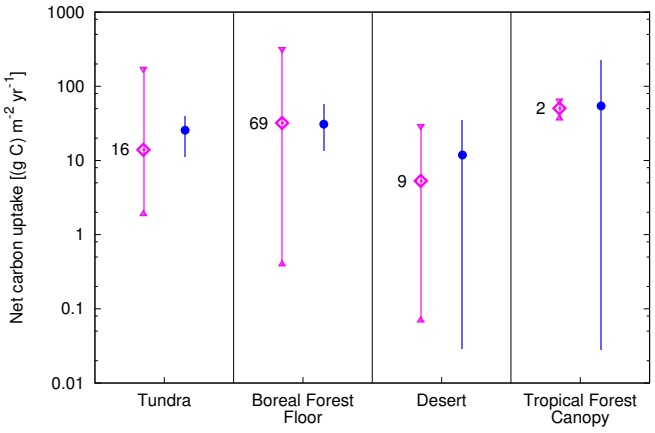

Figure 2. Comparison of LiBry estimates to field measurements. NPP estimated by LiBry compared to field measurements from four biomes, defined after Olson et al. (2001). The blue dots show the average simulated NPP for each biome and the blue vertical bars show the range of NPP values between the different grid cells in a biome. The magenta diamonds correspond to the median of NPP values measured in the field on the small scale, the magenta vertical bars denote the range of the field measurements. Left to the magenta diamonds the number of field measurements is shown that is considered for the respective biome. Details can be found in Porada et al. (2013).

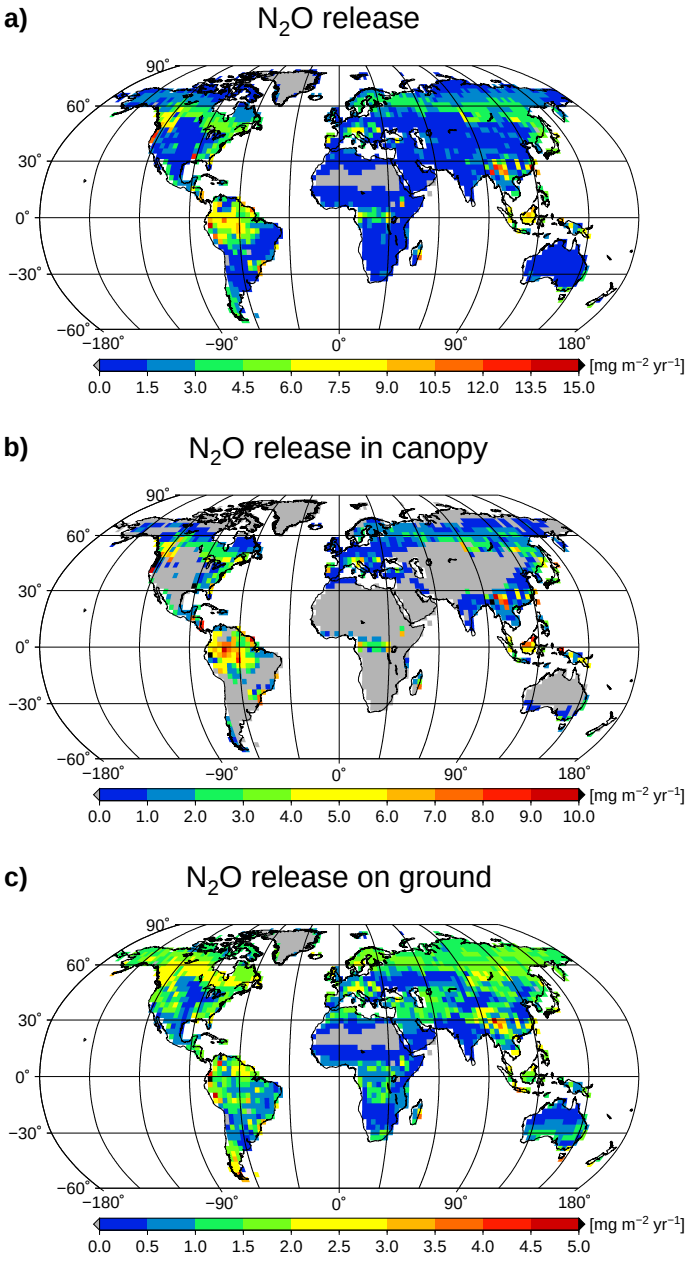

Figure 3. Global patterns of N_2O-release. Nitrous oxide emissions by lichens and bryophytes estimated by LiBry for a) all locations of growth, b) the canopy and c) the ground. Note the differing ranges of the color bars. Grey colour denotes regions where no simulated species is able to survive, such as ice shields and the driest regions of deserts.

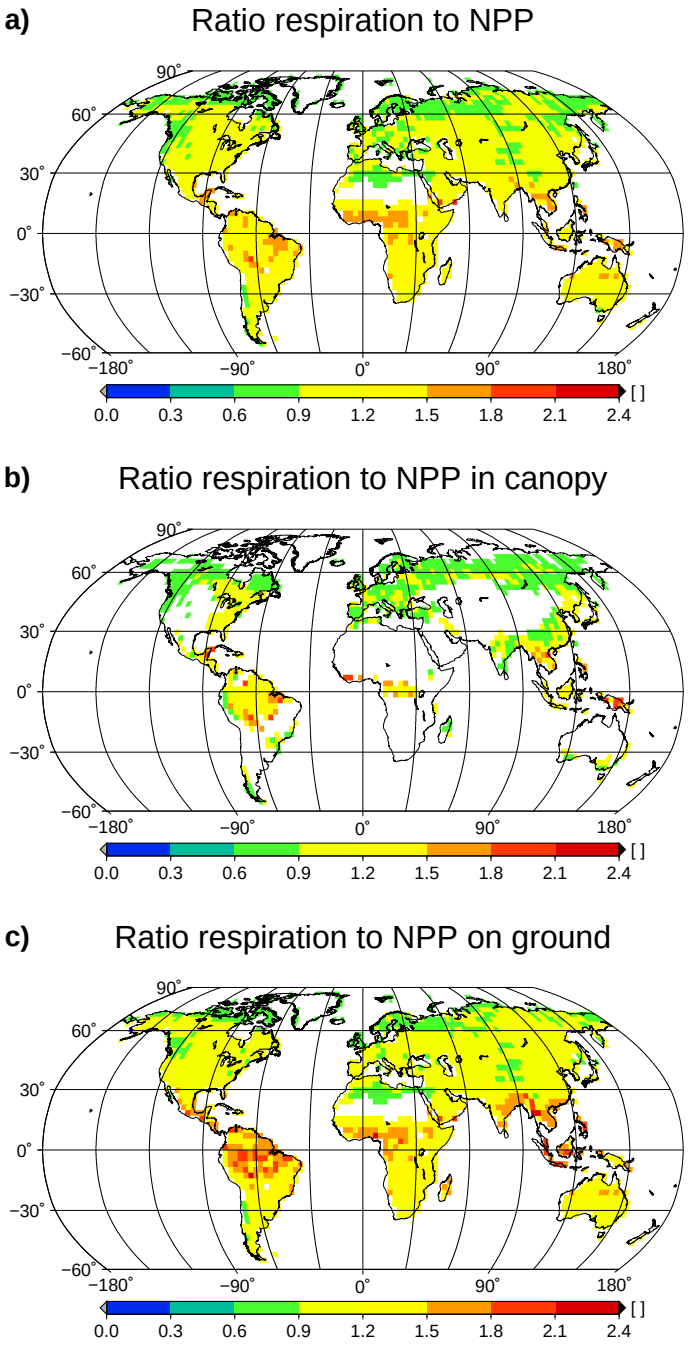

Figure 4. Global patterns of the ratio of respiration to NPP. Ratio of respiration to NPP of lichens and bryophytes estimated by LiBry for a) all locations of growth, b) the canopy and c) the ground.

	N_2O-emissions ($Tg\ N_2O$) yr^{-1}		NPP (Gt C) yr^{-1}	Respiration (Gt C) yr^{-1}	Respiration : NPP [ ]
Canopy + ground					
Global	0.27	(0.19 - 0.35)	4.3	4.5	1.10
Tropical forest	0.11	(0.08 - 0.14)	1.5	1.8	1.33
Extratropical forest	0.11	(0.08 - 0.14)	2.0	1.8	0.93
Steppe & Savannah	0.03	(0.02 - 0.04)	0.4	0.4	1.21
Desert	0.02	(0.01 - 0.03)	0.4	0.4	1.05
Tundra	0.01	(0.007 - 0.013)	0.2	0.2	0.87
Canopy, global	0.13	(0.09 - 0.17)	2.1	2.2	1.01
Ground, global	0.14	(0.10 - 0.18)	2.2	2.3	1.16

Table 1. Annual global total values of N_2O emissions, NPP, respiration and the ratio of respiration and NPP estimated by LiBry and separated into lichens and bryophytes living in the canopy and on the ground. The values in brackets in the first column show the uncertainty in N_2O emissions due to the conversion of released CO_2 to N_2O (90 % confidence interval from Lenhart et al. (2015)). ~~Moreover, values for five different ecosystem~~ Ecosystem classes ~~are~~ shown ~~: Tropical forest, Extratropical forest, Steppe & Savannah, Desert and Tundra. These classes~~ are based on the categories ~~from~~ made by Olson et al. (2001), which ~~we aggregate~~ were aggregated by us in the same way as in Elbert et al. (2012). "Gt C" stands for gigatons of carbon.

Ecosystem class	Location		Minimum	Average	Maximum
Tropical forest	Central Amazon	ground	0.31	0.59	0.88
		canopy	0.081	3.3	8.2
Extratropical forest	West Siberia	ground	0.023	1.7	4.8
		canopy	0.0040	2.1	6.2
Steppe & Savannah	Central Sahel		0.0095	0.088	0.32
Desert	Central Australia		0.019	1.6	5.5
Tundra	North Alaska		0.012	0.095	0.17

Table 2. Simulated nitrous oxide emissions by lichens and bryophytes in [(mg N_2O) m^{-2} yr^{-1}] for individual grid cells of the LiBry model. The values are averages over the last 50 years of a 600-year simulation with 3000 initial species. Grid cells are selected from five different ecosystem classes. In the two forest classes, emissions are separated into canopy and ground. In the other classes, the model does not represent lichens and bryophytes in the canopy. The range of N_2O emissions based on all surviving artificial species in a grid cell is shown. The average value for all species in a grid cell is derived by an NPP-based weighting scheme (see Sect. 2).

4 Discussion

In this study we estimate nitrous oxide emissions by lichens and bryophytes with the global, process-based non-vascular vegetation model LiBry. Thereby, we derive N_2O emissions from respiration fluxes which are, together with photosynthesis and net primary productivity, simulated by LiBry.

We use an updated version of LiBry which contains significant modifications with regard to the original version published in Porada et al. (2013). Regarding NPP, the new version estimates 4.3 (Gt C) yr^{-1} ~~of carbon~~ while the original version of LiBry predicted a range of 0.34 to 3.3 (Gt C) yr^{-1}. The increase in predicted NPP is mainly attributed to a higher simulated productivity in the tropical forest canopy, since a new disturbance scheme allows for a higher surface coverage of lichens and bryophytes there. An empirical global estimate of NPP by ~~microbial surface communities~~ lichens, bryophytes, free-living terrestrial cyanobacteria and algae (Elbert et al., 2012) amounts to 3.9 ~~Gt~~ (Gt C) yr^{-1} ~~of carbon~~. Our new estimate is higher than that by Elbert et al. (2012), although LiBry does not consider free-living cyanobacteria and algae. This may be explained by the small contribution of cyanobacteria and algae to the overall global carbon uptake, which can be compensated by minor relative changes in productivity of lichens and bryophytes. It is ~~, however,~~ not straightforward to determine which number is closest to reality, since both the process-based estimate by LiBry as well as the empirical one by Elbert et al. (2012) are subject to uncertainty. In the study of Elbert et al. (2012), for instance, it is assumed that productivity ~~is more or less homogeneous~~ and active time are uniform within a biome~~and further assumptions are made about the surface coverage and active time of the organisms. Nevertheless, this comparison~~ . Furthermore, Elbert et al. (2012) use a globally uniform value of surface cover fraction to scale up local field measurements of productivity to the global scale. However, values of surface coverage by lichens and bryophytes compiled by Elbert et al. (2012) vary largely at the small scale, which makes upscaling to larger scales challenging.

While productivity estimated by LiBry is evaluated in this study, large-scale surface coverage of lichens and bryophytes simulated by LiBry has been evaluated for regions north of 50° N in Porada et al. (2016a). It was shown that LiBry predicts realistic values of cover fraction. Moreover, values of surface cover predicted by LiBry for other regions of the world (Porada et al., 2016b) a in agreement with the estimate of Elbert et al. (2012). In spite of uncertainties regarding productivity and abundance of lichens and bryophytes, comparing the empirical and process-based approaches gives confidence in the order of magnitude of the LiBry simulation results.

As a 50-year steady-state average value, we estimate total N_2O emissions by lichens and bryophytes of 0.27 (0.19 - 0.35) (Tg ~~yr^{-1}, which amounts to around 3 % of global~~ N_2O~~emissions (Ciais et al., 2013). This value may sound low at first glance, but it equals about 50 % of the atmospheric deposition of N_2O into the oceans or 25~~) ~~%of the deposition on land (Ciais et al., 2013). In soils, which are the major source of naturally formed N_2O, the greenhouse gas can be formed by various processes, including nitrification, denitrification, nitrifier denitrification, and co-denitrification in the process of biological nitrogen cycling (Butterbach-Bahl et al., 2013). In the study of Lenhart et al. (2015), the cryptogamic organisms were shown to utilize ^{15}N labelled NO_3^- but not NH_4^+, indicating that N_2O is likely formed during denitrification.~~

~~Our estimate~~ yr^{-1}, which is at the lower end of the range of 0.32 to 0.59 (Tg N_2O) yr^{-1} calculated by Lenhart et al. (2015). ~~Global~~ The evaluation of LiBry regarding simulated NPP shows that our global patterns and total values of NPP ~~simulated by LiBry, however,~~ are very similar to the ~~estimate used in Lenhart et al. (2015) to quantify~~ empirical estimate by Elbert et al. (2012). Since Lenhart et al. (2015) use this NPP estimate by Elbert et al. (2012) to derive N_2O emissions~~. Hence,~~ , differences in NPP are most likely not the reason for ~~the differing estimates~~ our lower estimate of N_2O emissions ~~may be that LiBry predicts a~~ compared to Lenhart et al. (2015). Instead, this may be explained by differing methods to compute respiration: While Lenhart et al. (2015) assume a globally uniform ratio of respiration to NPP of the value 2 to estimate respiration, LiBry simulates respiration independently as a species-specific function of temperature and water status. This results in a lower global average value of around 1 for the ratio of respiration to NPP ~~, while Lenhart et al. (2015) assume a higher value of 2.~~ predicted by LiBry. Our estimated ratio of respiration to NPP agrees well with laboratory measurements, but it is in general difficult to compare a global, ecosystem-scale value to small-scale and short-term observations.

Our simulated global pattern of N_2O emissions is slightly different than that shown in Lenhart et al. (2015), who estimate highest values in the boreal zone and only intermediate values in the humid tropics. This can be explained by their assumed constant ratio of respiration to NPP, which makes their global pattern of N_2O emissions identical to that of NPP, which is shown in Elbert et al. (2012). In LiBry, however, the simulated ratio of respiration to NPP increases towards higher surface temperatures in the tropics (Fig. ~~??~~4). Furthermore, it can be seen that the ratio shows large spatial variation. Evaluating this simulated pattern is difficult~~since spatially explicit data of respiration by lichens and bryophytes are not available at the global scale, contrary to NPP (Elbert et al., 2012).~~ , since estimates which are extrapolated to the large scale, such as the NPP estimate by Elbert et al. (2012), are not available for respiration by lichens and bryophytes. However, observed ratios of respiration to NPP of lichens and bryophytes vary considerably at the species level, as shown by e.g. Lenhart et al. (2015). Using a constant ratio of respiration to NPP may therefore introduce a bias in the estimated spatial distribution of N_2O emissions.

~~The study by Zhuang et al. (2012) estimates global patterns of N_2O emission from soils and finds that the humid tropics contribute most to global N_2O emission due to high temperature and precipitation. Our simulated pattern of global N_2O emissions by lichens and bryophytes also shows a hotspot in the humid tropics, but the relative contribution of the boreal zone to the global flux seems to be higher than in Zhuang et al. (2012). This probably results from the high simulated NPP in the boreal zone, particularly on the ground, which compensates for the lower respiration and therefore N_2O emission per productivity due to low temperatures.~~

Small-scale measurements of N_2O emissions by lichens and bryophytes may show considerable variation. The sources of this variation ~~are~~ may be physiological differences between species, variation of associated microbial communities, as well as heterogeneity in climatic conditions. We examine the relative importance ~~of these two factors~~ for respiration of differences between species compared to climatic differences with LiBry, since the model simulates various physiological strategies and represents variation in climatic conditions at the global scale. Thereby, we assume that the relationship between respiration and N_2O emissions is relatively insensitive to climatic conditions and physiological differences between species, as suggested by the experiments by Lenhart et al. (2015). Table 2 shows that both differences between artificial species as well as different climatic conditions are important for variation of N_2O emissions. Upscaling of N_2O emission rates measured in the field

may therefore be subject to considerable uncertainty. Modelling approaches in this direction should probably account for both ~~functional diversity of~~ interspecific variation in processes associated with N_2O release by lichens and bryophytes as well as variation in climatic conditions.

Although our approach considers the most important sources of variation in N_2O emissions by lichens and bryophytes, it is associated with uncertainties that should be discussed further. These ~~are mainly our estimate of respiration and the method to derive~~ uncertainties mainly result from our method to estimate respiration and from assumptions concerning the empirical relationship between respiration and N_2O emissions~~from respiration rates~~.

Respiration and the ratio of respiration to NPP simulated by LiBry are difficult to validate, since the number of laboratory or field studies which measure not only NPP, but also GPP and respiration is ~~relatively low~~not very high. Moreover, long-term measurements of respiration would be required to determine the ratio of respiration to NPP. Otherwise, assumptions about the contribution of respiration in the dark to total respiration are necessary.

To obtain N_2O emissions from respiration, our results rely on the laboratory incubation measurements and the calculated ratio of N_2O emissions to respiration presented in Lenhart et al. (2015). Furthermore, our approach considers effects of variation in climatic conditions on N_2O emissions by lichens and bryophytes. Hence, it is necessary to discuss the sensitivity of the relationship between respiration and N_2O emissions to a range of climatic conditions. As shown in Lenhart et al. (2015, Fig. 3), the relationship between respiration and N_2O emissions seems to be insensitive to temperature changes for the tested species. Likewise, variations in water content have no clear effect on the relationship between N_2O release and respiration (Lenhart et al., 2015, Fig. Although the sensitivities of N_2O release to temperature and water content are similar to those of respiration across species, the relationship between N_2O release and respiration shows interspecific variation. However, in spite of a large number of around 40 sampled species, the relationship shows a relatively narrow 90 % confidence interval of 11.3 to 20.7 ng N_2O (mg CO_2)$^{-1}$ (Lenhart et al., 2015). This suggests that the mechanism of N_2O release by lichens and bryophytes is similar between different species.

To analyse the relation between the production of N_2O and respiratory CO_2 in greater detail, measurements of both fluxes ~~in the field~~ by means of online flux measurements would be needed, which then could be linked to the observed water status of the organisms. Since LiBry explicitly represents the dynamic water saturation of lichens and bryophytes, this would allow a more process-based prediction of the duration and magnitude of N_2O emissions. In this way, the uncertainty associated with our approach would be reduced, facilitating an improved estimate of global N_2O emissions by lichens and bryophytes.

In order to assess model-based estimates of N_2O emissions by ~~microbial surface communities~~lichens and bryophytes, a relatively large number of field measurements are necessary. Currently, most N_2O measurements, independently of the substrate or organisms measured, generally suffer from major uncertainties, additionally to variation from functional diversity and differing climatic conditions: first, the majority of these studies have been conducted using the acetylene inhibition technique. The idea of this method is to inhibit the last denitrification step, so that the measured N_2O-amounts should reveal the sum of N_2O and N_2 release during denitrification under natural conditions. It has, however, been shown quite a while ago that this method leads to an underestimation of denitrification under oxic conditions (Bollmann and Conrad, 1997). Secondly, the most widely used measuring technique has been the closed chamber method, which is inexpensive and easy to use. This, however, has major

shortcomings, as environmental conditions are hard to control and only limited surface areas can be measured (Butterbach-Bahl et al., 2013; Groffman, 2012). Furthermore, the limited temporal resolution of chamber measurements may affect estimated N_2O emissions (Barton et al., 2015). Thirdly, depending on the ~~experimental setup~~environmental conditions under which the experiment is performed, particularly water, temperature, and nutrient conditions, the obtained N_2O emission rates could differ widely. Thus, it is indispensable to report and consider the exact environmental conditions under which the measurements were made and to restrict natural emission data to those assessed under typically occurring natural conditions.

Respiration by lichens and bryophytes is not the only process which can be used to estimate their N_2O emissions. Barger et al. (2013) repo a relationship between nitrogen fixation and N_2O release in biological soil crusts, which include lichens and bryophytes, but also soil bacteria and algae. For this approach, however, reliable nitrogen fixation data are sparse. It is also possible to estimate the demand for nitrogen by lichens and bryophytes with LiBry with an uncertainty range of around one order of magnitude (Porada et al., 2014). However, it is not straightforward to derive realised nitrogen uptake or nitrogen fixation from this, since LiBry does not yet include processes related to nitrogen uptake or metabolisation of nitrogen species. Therefore, for this study, we chose the relation between respiration and N_2O release to quantify N_2O emissions by lichens and bryophytes.

~~To conclude, we estimate global emissions by~~ Our simulated global N_2O emissions by lichens and bryophytes of 0.27 (0.19 - 0.35) (Tg N_2O) yr^{-1} amount to around 3 % of global N_2O emissions from natural sources on land (Ciais et al., 2013). This value may sound low at first glance, but it equals about 50 % of the atmospheric deposition of N_2O into the oceans or 25 % of the deposition on land (Ciais et al., 2013). Considering that N_2O has a strong negative effect on stratospheric ozone and a significant warming potential as a greenhouse gas, also relatively small emissions should not be neglected in global budgets.

The study by Zhuang et al. (2012) estimates global patterns of N_2O emission from soils and finds that the humid tropics contribute most to global N_2O emission due to high temperature and precipitation. Our simulated pattern of global N_2O emissions by lichens and bryophytes also shows a hotspot in the humid tropics, but the relative contribution of the boreal zone to the global flux seems to be higher than in Zhuang et al. (2012). This probably results from the high simulated NPP in the boreal zone, particularly on the ground, which compensates for the lower respiration and therefore N_2O emission per productivity due to low temperatures. Relative contributions of lichens and bryophytes to N_2O emissions are highest for ecosystems in desert regions and at high latitudes, which agrees with the results by Lenhart et al. (2015).

5 Conclusions

We estimate large-scale spatial patterns and global values of N_2O emissions by lichens and bryophytes from a process-based model of their productivity and respiration. Our results suggest a significant contribution of lichens and bryophytes to global N_2O emissions, albeit at the lower end of the range of a previous~~estimate. We quantify large-scale spatial patterns of the organisms'~~, empirical estimate. Since both approaches use respiration to derive N_2O emissions, our lower estimate likely results from a different method to predict respiration, compared to the empirical approach. Hence, while estimates of productivity are relatively well constrained, evaluating models with regard to estimated respiration may improve predictions of N_2O emissions ~~and we determine the share of functional diversity and climatic heterogeneity on variation in~~ by lichens and

bryophytes. One important finding derived from our simulation is that the ratio of respiration to NPP by lichens and bryophytes shows spatial variation and a latitudinal gradient at the global scale. This means that productivity and N_2O emissions by the organisms are not necessarily correlated and that tropical regions may show higher emissions than polar regions given the same NPP. Furthermore, we show that both physiological variation among species as well as variation in climatic conditions are relevant for variation in respiration and, consequently, N_2O emissions. ~~The simulated estimates can be complemented by~~ Ecosystem-scale estimates of N_2O emissions by lichens and bryophytes should therefore include sufficient ranges of species and climatic conditions to avoid biased results. Our results build on the empirical finding that N_2O emissions by lichens and bryophytes are linearly related to their respiration. This relationship is relatively insensitive to climatic conditions and shows no large variation between species. However, the relationship is based on closed chamber measurements. Therefore, it would be useful to perform online flux measurements of N_2O emissions and respiration ~~in the field, allowing an extended validation of~~ to test the effect of climatic conditions on the relationship between N_2O release and respiration. Furthermore, using alternative approaches to estimate N_2O emissions by lichens and bryophytes may be helpful to constrain our approach.

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