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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 net primary productivity of lichens and bryophytes, which are combined with ecosystem-scale values of their productivity. 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 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 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 nitrous oxide emissions to respiration may be helpful.

1 Introduction

Microbial surface communities 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 on soils, rocks, and epiphytically on trees. In drylands, they widely cover surface soils forming so-called biological soil crusts.

In a first ecosystem-based upscaling approach, Elbert et al. (2012) calculated that these communities fix around 14.3 Gt yr^{-1} of carbon dioxide (3.9 Gt carbon). This corresponds to about 7 % of the net primary productivity (NPP) by terrestrial vegetation. In an alternative approach, 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.

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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 nitrogen fixation was estimated to sum up to a global value of ∼49 Tg 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 yr^{-1}, based on the nitrogen requirements of lichens and bryophytes determined by (Porada et al., 2014). Moreover, it was found in the same study that the organisms may contribute significantly to global chemical weathering, according to their phosphorus demand.

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 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. 1 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, biological soil crusts were shown to emit large quantities of the reactive trace gases NO and HONO, accounting for ∼1.7 Tg 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 nitrous oxide (N_2O) was measured on a large variety of microbial organisms (Lenhart et al., 2015). Utilizing fixed ratios between N_2O emissions, respiration and NPP, the global NPP data of Elbert et al. (2012) were used to obtain globally resolved data on N_2O emissions by microbial organisms and communities. Since N_2O is an important greenhouse gas and also the main depleting substance of stratospheric ozone, 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).

Upscaling of small-scale measurements to global N_2O emissions by lichens and bryophytes, however, is complicated by the considerable variation of the measured fluxes. There have been only few studies investigating N_2O emissions and denitrification processes of biological soil crusts, obtaining differing results. 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 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.

For this reason, we apply here the process-based non-vascular vegetation model LiBry (Porada et al., 2013) to provide an alternative estimate of N_2O emissions associated with lichens and bryophytes. 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.

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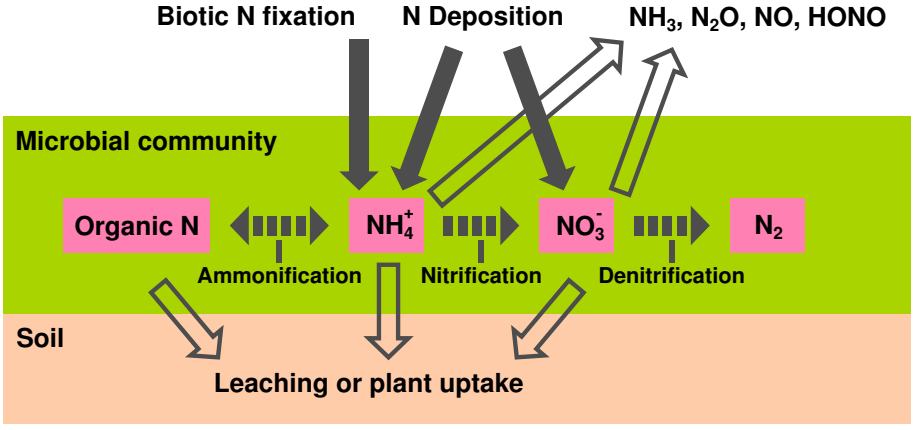

Figure 1. Nitrogen balance of microbial communities. Gains (solid arrows), losses (empty arrows) and transformation processes (dashed arrows) of nitrogen compounds in microbial communities. The community may consist of cyanobacteria, algae, lichens, mosses, fungi and bacteria.

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

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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 are related to their respiration by a conversion factor of 16 ng $N_2O\,(\text{mg } CO_2)^{-1}$. The conversion factor has a 90 % confidence interval of 11 to 21 ng $N_2O\,(\text{mg } CO_2)^{-1}$. 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 to estimate N_2O emissions, since global upscaled data on respiration of these communities 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 % of net photosynthesis. 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 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.

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.

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3 Results

The global distribution of net primary productivity simulated by the updated version of LiBry is shown in Fig. 2. 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 it is assumed in LiBry that lichens and bryophytes cannot grow together with crops, growth is low in these regions 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.

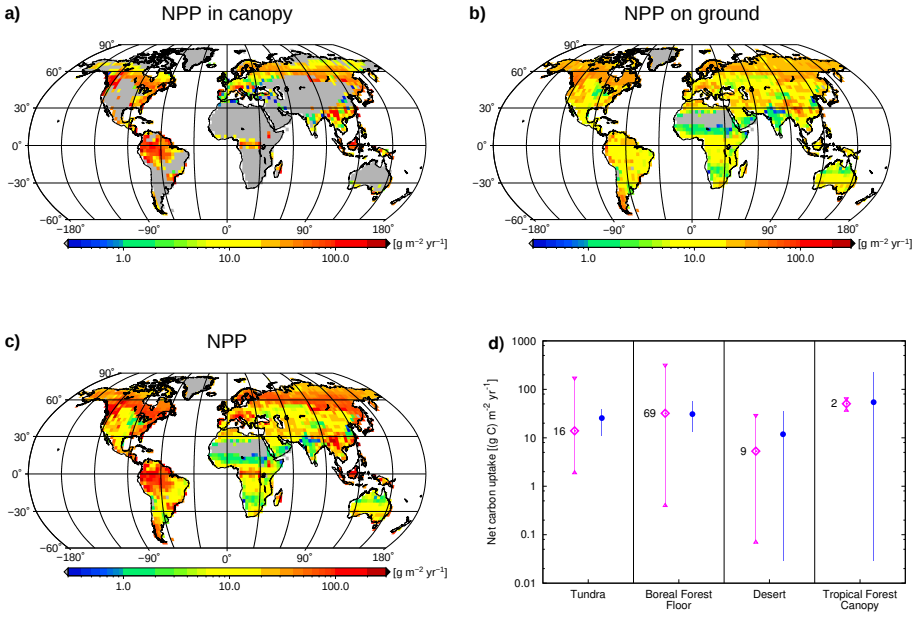

Figure 2. Global patterns of NPP. Lichen and bryophyte NPP estimated by LiBry for a) the canopy, b) the ground and c) all locations of growth. The estimates are in grams of carbon per m^2 and they are average values over the last 50 years of a 600-year simulation with 3000 initial species. d) NPP estimated 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

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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 yr^{-1} of carbon estimated by the new LiBry compares well to the value of 3.9 Gt 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. 2 d). 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 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. 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 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 m^{-2} yr^{-1} of N_2O. Dry regions show lowest values of nitrous oxide emissions, in general less than 1 mg m^{-2} yr^{-1} of N_2O. Considering only lichens and bryophytes which grow as epiphytes in the canopy (Fig. 3 c), 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 m^{-2} yr^{-1} of N_2O (Fig. 3 e). 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 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.

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. 3 b). 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 may be low. Respiration by lichens and bryophytes in the canopy shows a slightly weaker latitudinal gradient, which can be explained by efficient evaporative cooling in the canopy (Fig. 3 d). For the same reason, respiration on the ground in the tropics is markedly higher than at high latitudes (Fig. 3 f), since lichens and bryophytes on the ground usually grow within the surface boundary layer. This increases the relative effect of radiation on the surface temperature of the organisms. 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

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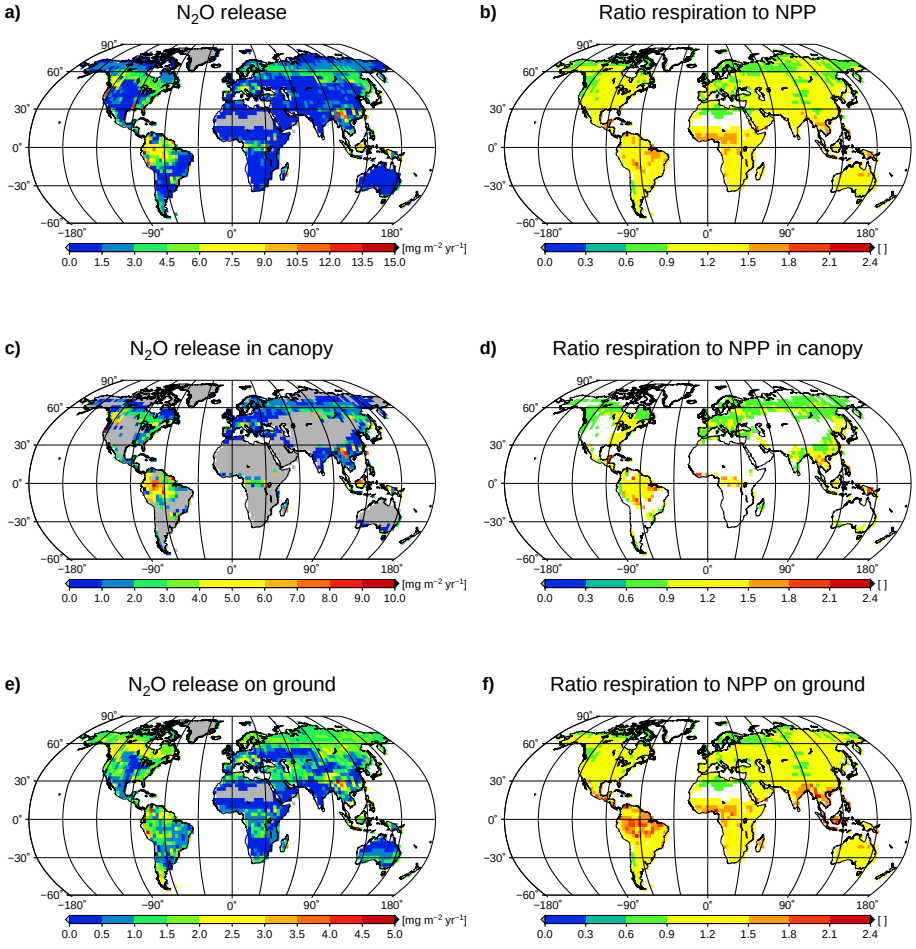

Figure 3. Global patterns of N_2O-release and the ratio of respiration to NPP. Nitrous oxide emissions by lichens and bryophytes estimated by LiBry for a) all locations of growth, c) the canopy and e) the ground. Note the differing ranges of the color bars. Ratio of respiration to NPP for b) all locations of growth, d) the canopy and f) the ground.

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 global variation in emissions due to climatic

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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.

	N_2O-emissions Tg 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 classes are shown: Tropical forest, Extratropical forest, Steppe & Savannah, Desert and Tundra. These classes are based on the categories from Olson et al. (2001), which we aggregate in the same way as 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).

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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 yr^{-1} of carbon while the original version of LiBry predicted a range of 0.34 to 3.3 Gt 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 (Elbert et al., 2012) amounts to 3.9 Gt yr^{-1} of carbon. 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 within a biome and further assumptions are made about the surface coverage and active time of the organisms. Nevertheless, this comparison 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 is at the lower end of the range of 0.32 to 0.59 Tg yr^{-1} calculated by Lenhart et al. (2015). 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 N_2O emissions. Hence, the reason for the differing estimates of N_2O emissions may be that LiBry predicts a value of around 1 for the ratio of respiration to NPP, while Lenhart et al. (2015) assume a higher value of 2. 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. 3). 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). However, observed ratios of respiration to NPP of lichens and bryophytes vary

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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 physiological differences between species as well as heterogeneity in climatic conditions. We examine the relative importance of these two factors with LiBry, since the model simulates various physiological strategies and represents variation in climatic conditions at the global scale. 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 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 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. 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). To analyse the relation between the production of N_2O and respiratory CO_2 in greater detail, measurements of both fluxes in the field 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, 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 underes-

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timation 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). Thirdly, depending on the experimental setup, 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 conditions under which the measurements were made and to restrict natural emission data to those assessed under typically occurring natural conditions.

5 Conclusions

To conclude, we estimate global emissions by N_2O 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' N_2O emissions and we determine the share of functional diversity and climatic heterogeneity on variation in N_2O emissions. The simulated estimates can be complemented by flux measurements of N_2O emissions and respiration in the field, allowing an extended validation of our approach.

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