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Spatio-temporal trends of nitrogen deposition and climate effects on *Sphagnum* productivity in European peatlands

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ABSTRACT

To quantify potential nitrogen (N) deposition impacts on peatland carbon (C) uptake, we explored temporal and spatial trends in N deposition and climate impacts on the production of the key peat forming functional group (*Sphagnum* mosses) across European peatlands for the period 1900–2050. Using a modelling approach we estimated that between 1900 and 1950 N deposition impacts remained limited irrespective of geographical position. Between 1950 and 2000 N deposition depressed production between 0 and 25% relative to 1900, particularly in temperate regions. Future scenarios indicate this trend will continue and become more pronounced with climate warming. At the European scale, the consequences for *Sphagnum* net C-uptake remained small relative to 1900 due to the low peatland cover in high-N areas. The predicted impacts of likely changes in N deposition on *Sphagnum* productivity appeared to be less than those of climate. Nevertheless, current critical loads for peatlands are likely to hold under a future climate.

1. Introduction

Deposition of reactive nitrogen (N) has increased steadily in many parts of the world since the industrial revolution (Galloway et al., 2003). At present N deposition levels are either stabilizing at a high level (Europe) or continue to increase in other parts of the world (de Vries and Posch, 2011). N effects are numerous, ranging from biodiversity loss to increased leaching of nitrate to aquifers and lakes (e.g. Bergström and Jansson, 2006). To improve risk assessments and support policy decisions, critical N deposition loads have been defined for many ecosystems (Bobbink and Hettelingh, 2011), including *Sphagnum*-dominated peatlands. These extremely nutrient-poor ecosystems are among those most sensitive to N enrichment, and show changes in species composition above N deposition levels of 5–10 kg ha^{-1} yr^{-1} (Bobbink and Hettelingh, 2011). Recent work suggests that N-impacts on *Sphagnum* depends on climatic factors (Heijmans et al., 2008; Limpens et al., 2011), implying critical loads may vary across geographical gradients and may change with climate warming. Our study is the first attempt to explore the spatial distribution of N effects on *Sphagnum* production in peatlands for past, present and future.

Sphagnum-dominated peatlands cover large areas of the boreal-temperate zone and store a substantial amount of the global soil carbon (C) pool (Rydin and Jeglum, 2013). Peat mosses (genus *Sphagnum*) play a key role in these ecosystems as they efficiently engineer an environment that facilitates their own growth while being hostile to vascular plants (van Breemen, 1995). Their unique properties are both directly and indirectly responsible for the long-term C sequestration of northern peatlands. *Sphagnum* directly affects C-sequestration by producing litter that decays at a slower rate than vascular plants (Freeman et al., 2001), thus forming a much greater proportion of the peat than expected from their primary production (Wallén, 1992). *Sphagnum* litter/peat is also responsible for the wet and acidic environment that suppresses decay, thus indirectly facilitating long-term C-sequestration. Thus, *Sphagnum* production and abundance are of vital importance for the functioning and C accumulation of *Sphagnum*-peatlands (Johnson and Damman, 1993). The proportion of annual *Sphagnum* production that is eventually integrated into long-term C storage (peat accumulation) varies between 0 and 10%, depending on

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environmental conditions (Rydin and Jeglum, 2013). This can translate into an average carbon accumulation of circa 20 g C m^{-2} yr^{-1} (Roulet et al., 2007). Although peatland habitats are usually resilient to environmental change (Belyea and Baird, 2006), nutrient alterations can lead to drastic changes in the composition of the vegetation. In general vascular plants benefit from the surplus N and become more dominant while the growth of peat mosses decreases due to litter burial and shading (Berendse et al., 2001). There is also experimental evidence of more direct effects of increased N availability on *Sphagnum* performance, such as increased photosynthesis, P limitation and even toxicity at very high N levels (Granath et al., 2009, 2012; Limpens and Berendse, 2003). Consequently, N deposition has been suggested as a potential threat to C sequestration of boreal and temperate peatlands (Gunnarsson et al., 2008; Dise, 2009). Yet, attempts to quantify this threat are lacking. This is in sharp contrast to forest ecosystems where N deposition effects on C sequestration have been quantified at a European scale (de Vries et al., 2006; de Vries and Posch, 2011).

A modelling approach is necessary to quantify the effects of N deposition at a larger scale, and until recently, no model was available for *Sphagnum*. A recent meta-regression analysis (Limpens et al., 2011), was an important step forward in the process of understanding and quantifying the effect of N on *Sphagnum* growth in peatlands. Using results of N application experiments across the northern hemisphere, the authors identified some of the variables that may affect *Sphagnum* growth response to N deposition. This analysis resulted in a statistical model that describes the impact of N deposition on *Sphagnum* production in interaction with climatic factors. By combining this statistical model with N deposition and climate data for European peatlands for the past, present and future (1900–2050) we investigated, i) how N deposition has affected *Sphagnum* production, temporally and spatially across Europe, over the 20th century, ii) the effect of future N deposition on *Sphagnum* production, given future climatic and N deposition projections, and iii) the overall consequences for *Sphagnum* production and potential C-uptake at European scale.

2. Methods and materials

2.1. Modelling the effect of nitrogen deposition on Sphagnum

We adapted the meta-regression model of Limpens et al. (2011), further referred to as Limpens–Granath model, to model the effect of N deposition on *Sphagnum* productivity under different climatic conditions. Our adapted model is expressed as:

$$\log_e(P_{treat}/P_{control}) = \mu + a \times N_c + b \times N_{add} + c \times T_j + d \times P_a + C + Error \qquad (1)$$

where μ is the intercept, N_c is the current mean annual N deposition (g m^{-2} yr^{-1}) at the site at the time of treatment, N_{add} is the annual added N at treatment plots, T_j is the mean July temperature in °C (which is strongly correlated with mean summer temperature, June–August), P_a is mean annual precipitation (mm), $P_{control}$ is the *Sphagnum* productivity at the control plots receiving only N_c, and P_{treat} is the *Sphagnum* productivity at the treatment plots, receiving $N_c + N_{add}$. C and a, b, c, d are regression coefficients, where C also includes the effects of phosphorus application and presence of vascular plants. The *Error* term captures the unexplained between-experiment variation.

Adaptations to the Limpens–Granath model included the use of more recent climate and background N deposition data, and a further simplification of parameters and adaptation of N_c and N_{add} to make the model suitable for comparing N effects over different time periods instead of between treatments. These adaptations are discussed below.

2.2. Parameterization

The model was parameterized using the same experimental data as in Limpens et al. (2011). The most important details are given in Table S1 (sources, location, species, N application rate). In contrast to Limpens et al. (2011), we used more recent climate and background N deposition data. For the adapted model (1) we used gridded average climate data for a 10-year period encompassing the timing of the experiments based on the Climate Research Unit (CRU) data base (Mitchell et al., 2004). Furthermore, annual total background N deposition (i.e. wet plus dry) was used instead of only wet deposition as in Limpens et al. (2011). Most N application experiments were conducted in Europe and wet and dry N depositions for the years of the experimental duration were extracted from the European Monitoring and Evaluation Programme (EMEP MSC-W model results, http://www.emep.int/mscw/index_mscw.html). For non-European sites, N deposition was retrieved from original publications. More details on N deposition and climate data can be found in the methods section below. The model was fitted using a Bayesian approach in the R package MCMCglmm (Hadfield, 2010) to more easily include parameter uncertainties in the spatial models. For parameterization, we ran the model for 140 000 iterations after a burn-in of 30 000 iterations, using non-informative priors. Changing the priors did not alter the results and ensures little influence of the priors on the posterior (see Limpens et al. (2011, 2012) for details on fitting hierarchical meta-regression models accounting for within-study dependence).

The Limpens–Granath model included the effect of microhabitat (moist lawn vs. dry hummocks) and an interaction between microhabitat and temperature. As the proportions of microhabitats in peatlands are not well-documented, we removed the terms involving microhabitat in the model, generalizing our predictions. In addition, the Limpens–Granath model included variables that were manipulated in the experiments: phosphorus application and presence of vascular plants (some experiments removed vascular plants). In our predictions we assumed that phosphorus was not added and vascular plants were not removed.

To test if the adapted Limpens–Granath model would lead to a loss of predictive value, we compared both the original and adapted models using the experiment data set of Limpens et al. (2011). Our simpler model performed as well as the original model, with predictors explaining 51% (present model) and 53% (Limpens–Granath model) of the variation among experiment outcomes (log response ratio), respectively. Model parameters estimated for our revised model are given in Table 1.

Our model was applied on a 0.5 × 0.5° longitude–latitude grid (8539 grid cells with peatlands) covering Europe except for the most eastern parts where the peatland distribution is not available (Ukraine, Belarus, Moldova and Greece, see Fig. 2). To make spatial predictions, we used July temperature, annual precipitation and annual N deposition data for each grid cell. Model uncertainty (parameter uncertainty and random variation) was incorporated by performing random draws of parameter estimates from the joint distribution of the meta-regression model. We made 5000 random draws for predicting the outcome at each grid cell and time period. From these 5000 predictions we calculated the mean and the 90% and 50% uncertainty intervals.

Including all model uncertainties gave wide uncertainty intervals. A large part of that uncertainty comes from the unexplained between-study variation (Table 1), which is mainly a result of large within-peatland variation in *Sphagnum* species and vascular plant cover. Since we were not interested in the within-peatland variation but rather in the aggregated response of the whole peatland to N deposition, we removed the uncertainty related to *Sphagnum* species for the uncertainty graphs. To this end we first analysed a subset of the data used in Limpens et al. (2011) that only contains studies with more than one species (see Table S1). From this data we estimated that the species component explained about 25% of between-study variation. This variation was removed when prediction intervals were created for the graphs presented in the Supporting information (see figures in Appendix S1 in Supporting information).

To summarize the effect over Europe we calculated weighted means of predictions using proportions of peatlands in each grid cell as weights. The estimation of the peatland cover is described later in the methods section. Effects on carbon uptake were calculated by assuming a mean annual *Sphagnum* production of 200 g dry matter m^{-2} yr^{-1}. This value is derived from a meta-analysis of *Sphagnum* production (Gunnarsson, 2005) enhanced by the production rates observed in the control plots of the N addition experiments that formed the basis of our model. The 200 g m^{-2} yr^{-1} is a representative, albeit conservative (e.g. Wieder et al., 2010), estimate of long-term production values and thus highly suitable for the 50-year time step adopted in our study. To convert the dry matter production to C-uptake we assumed a dry tissue carbon content of 50% (Rydin and Jeglum, 2013).

Table 1

Results of the Hierarchical Bayes Linear Models (HBLM) with $\log_e$ response ratio. Negative coefficients indicate that an increase in the predictor depresses the response of *Sphagnum* to adding N. Categorical levels are compared to the intercept which is set to without P addition and without vascular plants. Upper and lower 95% credible intervals are given. Residual heterogeneity represents between study variation not explained by predictors. Of the total between study variation, 51% was explained by the included predictors. $N = 107$.

	Coefficients	Lower-95%	Upper-95%
Intercept	1.491	0.847	2.124
Nitrogen (N) application rate	−0.032	−0.056	−0.009
Background N deposition	−0.200	−0.393	−0.009
Mean July temperature	−0.049	−0.083	−0.014
Mean annual precipitation	−0.000372	−0.000741	−0.000013
Presence of vascular plants	−0.377	−0.585	−0.181
Phosphorus application	0.225	0.023	0.432
Residual heterogeneity (τ^2)	0.062	0.032	0.097