Prediction of plant species occurrence as affected by nitrogen deposition and climate change on a European scale

G.W.W. Wamelink, J.P. Mol-Dijkstra, G.J. Reinds, J.C. Voogd, L.T.C. Bonten, M. Posch, S.M. Hennekens, W. de Vries

PII: S0269-7491(19)33408-6

DOI: https://doi.org/10.1016/j.envpol.2020.115257

Reference: ENPO 115257

To appear in: *Environmental Pollution*

Received Date: 26 June 2019

Revised Date: 11 July 2020

Accepted Date: 12 July 2020

Please cite this article as: Wamelink, G.W.W., Mol-Dijkstra, J.P., Reinds, G.J., Voogd, J.C., Bonten, L.T.C., Posch, M., Hennekens, S.M., de Vries, W., Prediction of plant species occurrence as affected by nitrogen deposition and climate change on a European scale, *Environmental Pollution* (2020), doi: https://doi.org/10.1016/j.envpol.2020.115257.

G.W.W. Wamelink designed the research and the model and wrote the manuscript,

J.P. Mol-Dijkstra did run and designed the scenarios and wrote part of the results section and made the figures,

G.J. Reinds provided the data for the scenarios and did evaluate the results,

J.C. Voogd provided base data and handled the output data,

L.T.C. Bonten did the math for the model and model design,

M. Posch designed the HSI modeling and reviewed the manuscript,

S.M. Hennekens provided the base data,

W. de Vries overviewed the research and reviewed the manuscript.


Nitrogen Deposition
Climate Change

Prediction of plant species occurrence as affected by nitrogen deposition and climate change on a European scale

G.W.W. Wamelink[1], J.P. Mol-Dijkstra[1], G.J. Reinds[1], J.C. Voogd[1], L.T.C. Bonten[1], M. Posch[2], S.M. Hennekens[1] & W. de Vries[1,3].

[1]Wageningen Environmental Research, Wageningen University and Research, PO Box 47, NL-6700 AA Wageningen, the Netherlands.

[2]International Institute for Applied Systems Analysis (IIASA), Schlossplatz 1, A-2361 Laxenburg, Austria.

[3]Environmental Systems Analysis Group, Wageningen University and Research, PO Box 47, NL-6700 AA Wageningen, the Netherlands.

Abstract

Plant species occurrence in Europe is affected by changes in nitrogen deposition and climate. Insight into potential future effects of those changes can be derived by a model approach based on field-based empirical evidence on a continental scale. In this paper, we present a newly developed empirical model PROPS, predicting the occurrence probabilities of plant species in response to a combination of climatic factors, nitrogen deposition and soil properties. Parameters included were temperature, precipitation, nitrogen deposition, soil pH and soil C/N ratio. The PROPS model was fitted to plant species occurrence data of about 800,000 European relevés with estimated values for pH and soil C/N ratio and interpolated climate and modelled N deposition data obtained from the Ensemble meteo data set and EMEP model results, respectively. The model was validated on an independent data set. The test of ten species against field data gave an average Pearson's r-value of 0.79.

PROPS was applied to a grassland and a heathland site to evaluate the effect of scenarios for nitrogen deposition and climate change on the Habitat Suitability Index (HSI), being the average of the relative probabilities, compared to the maximum probability, of all target species in a habitat. Results for the period 1930-2050 showed that an initial increase and later decrease in nitrogen deposition led to a pronounced decrease in HSI, and with dropping nitrogen deposition to an increase of the HSI. The effect of climate change appeared to be limited, resulting in a slight increase in HSI.

Key-words: biodiversity, climate change, nitrogen deposition, precipitation, soil, EUNIS

1. Introduction

The distribution of plant species over a range of abiotic conditions, such as climate, soil pH and nutrient availability, depends on the response of individual plant species to these local environmental conditions and their ability to disperse and occupy space in environments with those conditions (O'Brien et al., 2000). Apart from land use change and management, species distribution is nowadays strongly influenced by climate change and nitrogen deposition (Alkemade et al., 2009). Climate change affects the distribution of species, the structure and species composition of ecosystems and the phenology of flora (Chapin et al., 2000; Dale et al., 2001; Theurillat and Guisan, 2001; Walther et al., 2002; Thuiller et al., 2005). In addition to land use change, resulting in changes in species composition and structure, ecosystems have also become more vulnerable to climate change (Chapin et al., 2000; Dale et al., 2001). After land use change and climate change, nitrogen (N) deposition is considered the third driver of global biodiversity loss (Sala et al., 2000; Lu et al., 2008), affecting plant growth and distribution through nutrient (N) availability and soil pH (Dale et al., 2001; Theurillat and Guisan, 2001; Pärtel, 2002; Smart et al., 2005; Wamelink et al., 2005). While enhanced nitrogen deposition was initially mainly documented for European and North America, it currently is also documented as a major problem in large parts of Asia and to a lesser extent Latin America, and it is expected to remain so in the future (Gilliam, 2006; Lu et al., 2008).

The impact of N deposition on occurrence, growth and distribution is different for every plant species, but, in general, native species adapted to N-poor circumstances will be outcompeted by species that are more favoured at high N availability (Wilson and Tilman, 1991; Berendse, 1998; Smart et al., 2005; Xiankai et al., 2008; De Vries et al., 2010; Payne et al., 2013). There is evidence that increasing N availability causes an overall increase in plant biomass production, usually associated with an overall decline in plant species diversity (Grime, 2001; Tilman et al., 2006; Bobbink et al., 2010). Effects of N deposition are now recognised in nearly all oligotrophic natural ecosystems in Europe, and include grasslands, heathlands, coastal habitats, oligotrophic wetlands (mires, bogs and fens), forests and aquatic and marine habitats (Achermann and Bobbink, 2003; Bobbink and Hettelingh, 2011; Dise et al., 2011). Recently, Clark et al. (2019) estimated N responses of hundreds of herb species for the united states, showing that many species decline at higher nitrogen deposition levels.

In this paper, we present a newly developed empirical model PROPS, short for PRobability of Occurrence of Plant Species, predicting the occurrence probabilities of plant species in response to a combination of climatic factors, i.e. temperature and precipitation, soil factors, i.e. soil pH and soil C/N ratio, and N deposition.

Until now, only a limited number of models have been developed to assess human-induced changes in biodiversity at European and global scales. One example at the European scale is EUROMOVE, a species-based logistic regression model, calculating the occurrence probabilities of almost 1400 European vascular plant species (Bakkenes et al., 2002; Thomas et al. 2004; Bakkenes et al., 2006). The regression equations describe the relation between six climatic variables and species occurrence (presence/absence) data of higher plants in grid cells of approximately 50 x50 km^2, based on maps in the Atlas Flora Europaeae. The rationale behind this climate-based regression model approach is that broad-scale species distributions are determined by, and in equilibrium with, the prevailing climate, while soil factors, such as pH and nutrient availability (specifically N) indicators play a role on the local scale only. This can be questioned, considering the large-scale impact of N and sulphur deposition on those factors (e.g. De Vries et al., 2003, 2007). Sulphur deposition has for instance a negative impact on tree health and forest floor chemistry (van Breemen et al. 1982; Schulze, 1989). Dirnböck et al. (2014), for example, found that the cover of oligotrophic plant species decreased with an increase in N deposition, based on monitoring data between 1994 and 2011 at 1335 permanent forest floor vegetation plots from northern Fennoscandia to southern Italy.

One example of a model at the global scale is GLOBIO, which describes the response of plant species to changes in direct human influence (land cover, land-use intensity, fragmentation, infrastructure development), climate and atmospheric N deposition (Sala et al., 2000; Alkemade et al., 2009). The model includes response functions with respect to species occurrence and climate, based on relations in EUROMOVE, and empirical response functions between the number of plant species and N deposition (Alkemade et al., 2009), using the mean abundance of species relative to their abundance in undisturbed ecosystems (MSA) as an indicator for biodiversity. The VEG model (Sverdrup et al. 2007) simulates species abundance as a result of a range of parameters including the effect of nitrogen and acid deposition. However, this model is solely based on expert judgement and we wanted to build a model based on field data. The BERN model (Schlutow and Huebener, 2004) and GBMOVE model (Smart et al., 2005 uses the C/N ratio as a critical limit for species occurrence. In the PROPS model we relate, besides C/N, also nitrogen deposition with species occurrence, thus making a direct link between the stressor and the species. The disadvantage of using only N deposition as a driver is the assumed direct impact of deposition changes, whereas the effect is most likely occurring through changes in N availability (Berendse, 1998; Grime, 2001; Tilman et al., 2006), being influenced not only by N deposition but also by variables such as soil C/N ratio that changes slowly in time in response to N deposition.

In the last decades, N deposition is clearly declining in both the US (Du et al.2019; Gilliam et al., 2019) and Europe (Dirnböck et al., 2018; Schmitz et al., 2019). However, potential recovery will likely be slow and will only occur if the nitrogen deposition will decrease substantially and the accumulated nitrogen is removed from the system (Stevens, 2016; Dirnböck et al., 2018; Gilliam et al., 2019; Schmitz et al., 2019). This may have different causes, from the excessive nitrogen still present in the vegetation till the lack of seed sources and dispersal capacity of species.

PROPS has been developed to predict changes in occurrence probabilities of plant species at a European scale. A preliminary version of the model has been applied in combination with the VSD+ model (Reinds et al., 2012), predicting changes in soil pH and soil C/N ratio in response to N and S deposition and climate change, as input for PROPS. The model PROPS was designed for scientists to be used either together with the VSD+ model or as a stand-alone model.

In this paper, we present the PROPS model approach and the plausibility of the model results by comparing modelled and observed plant species probabilities. Furthermore, we illustrate the model behaviour for a wet grassland and a heathland in the Netherlands, by presenting the impacts of changes in N deposition and climate on abiotic conditions and on plant species occurrence. The latter effect is quantified in terms of an overall habitat quality index.

2. Methodological approach

2.1 The PROPS model

The PROPS model estimates the occurrence probability of plant species as a function of variables for temperature, water availability, acidity and nitrogen availability, based on site measurements of both plant species occurrence and these environmental factors. The model is the predecessor of the US-PROPS model (McDonnell et al., 2018; 2020). Potential indicators included were (i) annual mean temperature and effective temperature sum above 5° C for temperature (ETS5), (ii) mean values for total annual precipitation for the growing season (April 1- October 1) for the five years around the year of observation of the plant composition , (iii) pH for soil acidity and (iv) total soil N content, soil C/N ratio, dissolved NO_3 concentration and N deposition for N availability. Note that unlike in EUROMOVE (Bakkenes et al., 2002; Bakkenes et al., 2006), actual (AET) or potential (PET) evapotranspiration were not included as indicators for water availability, as this required modelling at site level with a high uncertainty. Dissolved NO_3 concentration was not used in the final model version, as data were too sparse and confined to regions with high N deposition only.

We tested several models with different combinations of abiotic parameters. The model performance was evaluated by the mean deviance averaged over all relevés, with mean deviance being the difference between the calculated probability response curve and the actual occurrence of a species in a relevé (Figure 1). The lower the mean deviance, the better the model performance for a given species. The combination of abiotic indicators that yielded the lowest mean deviance, was assumed to be the optimal model. It turned out that mean annual temperature, mean annual precipitation, pH, N deposition and soil C/N ratio gave the best fits to species occurrences. Since soil C/N ratio is a reasonable indicator for N mineralization (Janssen, 1996; Manzoni et al., 2008), the combination of both N deposition and soil C/N was thus used as an indicator for N availability to plants.

We used several datasets for different purposes to build and test PROPS. An overview can be found in Table 1.

2.2 Fitting response curves

The model was fitted to presence-absence data using a logistic regression technique (e.g. Ter Braak and Looman, 1986). The problem of fitting a model that estimates probabilities is that you cannot observe a probability in the field. In the observed relevés, the plant species either occurs or is absent. The fitted polynomial is thus an estimate for the occurrence probability of the plant species based on the distribution of data on the occurrence (value equals 1) or absence (value is 0) of plant species in relevés, as illustrated in Figure 1.

The probability *y* of occurrence of a plant species was modelled as:

(1) $$y = \frac{1}{1 + \exp(-z)}$$

where *z* is the sum of quadratic polynomials in the standardized abiotic variables x_k:

(2) $$z = \sum_{k=1}^{n} (a_k + b_k x_k + c_k x_k^2)$$

where *n* is the number of explanatory environmental variables. Every explanatory variable *x* was normalized according to:

(3) $$x_{std} = (x - x_{mean})/x_{stdev}$$

where x is the (log-transformed) value of the explanatory variable, x_{mean} is the mean value of the explanatory variable over the entire data set, and x_{stdev} is the standard deviation of the explanatory variable over the entire dataset. The parameter c_k in the quadratic term was forced to be negative or zero, meaning that the form of the curve was either 'bell shaped' (c_k<0) or linear (c_k=0).

We were able to fit response curves for 4053 species, with at least 25 occurrences in the database, which make up together the PROPS model.

2.3 Databases

Two different databases were used to parameterize the PROPS model (Table 1). The first dataset includes information on plant species occurrences in approximately 800,000 relevés in Europe (collected in the EU for the BioScore project, Hendriks et al. 2016; Hennekens et al. 2017) without measurements of abiotic parameters. Therefore, we estimated the soil parameters at these sites, using the plant species composition and probability curves fitted from a soil-plant database as described below.

2.3.1 The BioScore database used to parameterize the model

The information on plant species occurrences in approximately 800,000 vegetation relevés in the BioScore database was derived with the Braun-Blanquet method (1964), with surface areas varying from mostly 1-9 m^2 for grassland till 100-200 m^2 for forests. The "BioScore project based" dataset was further augmented with climatic data obtained from a European daily high-resolution gridded data set of surface temperature and precipitation (Ensemble dataset) (Haylock et al. 2008) and N deposition data based on EMEP model (Simpson et al., 2012), using results from Schöpp et al. (2003) to obtain historic N and S depositions. The averaged climate and N deposition data of the five years around the year of observation of the plant composition were taken. The Ensemble dataset (http://eca.knmi.nl/download/ensembles/download.php#datafiles) contains daily gridded observational data on rainfall and air temperature (average, minimum and maximum) for the period 1950-2012 at a 0.25^0 x 0.25^0 grid. Details are given in Haylock et al. (2008) and Van den Besselaar et al. (2011). The climatic data used, i.e. the mean annual temperature and mean values for the annual precipitation and the precipitation in the growing season (April 1- October 1) for the five years around the year of observation were set equal to data from the grid cell corresponding to the location of the relevé and the year of observation. The effective temperature sum above 5°C (ETS5) was calculated from the daily temperature data in the Ensemble dataset. EMEP model results include annual ammonia and NO_x deposition values which were summed to obtain total N deposition and used for relevés whose location corresponded to an EMEP 50 km x 50 km grid cell. The PROPS model was ultimately fitted to plant species occurrence data of about 800,000 relevés with estimated values for pH and soil C/N ratio (see below) and interpolated climate and modelled N deposition data using the logistic regression technique described above.

2.3.2 The soil-plant database used to calculate soil parameters for the BioScore database

The second dataset contains information on plant species occurrence for approximately 12,000 relevés, mainly in the Netherlands, the United Kingdom, Ireland, Denmark and Austria, augmented with data from ICP Forests (see Table 1, Table 2), together with measurements for at least one soil parameter (pH or soil C/N ratio). Soil pH was measured in either water, calcium chloride extract or potassium chloride extract. The pH values in 0.01 M calcium chloride and 1.0M potassium chloride extract were recalculated to pH values in water extract, using the following relationship based on measured data in Austria (pH-H_2O and pH-$CaCl_2$, eq 5) and in the Netherlands (pH-H_2O and pH-KCl based on data from Wamelink et al. 2012, eq 6):

(5) $$pH_{H_2O} = 0.724 + 0.943 \cdot pH_{CaCl2}$$

(6) $pH_{H_2O} = 1.576 + 0.805 \cdot pH_{KCl}$

This dataset with measured soil parameters was split into a calibration part, used for the fitting of the response of species occurrence to soil parameters (90% of the dataset), and a validation part, which was used for the validation of the fitted response curves (10% of the dataset). For each species in the calibration part of the dataset we fitted one-dimensional species occurrence probability curves for the explanatory variables pH and C/N. We were able to fit occurrence probability curves for 949 species with pH and 819 species with C/N as explanatory variable. C/N was log-transformed (Figure 2). We used the occurrence probability curves for pH and C/N ratio to calculate pH and C/N ratio for the BioScore sites where only plant composition was observed. The best estimate for the soil parameters was assumed to be the value at which the modelled occurrence probability of all species is highest, i.e. at the maximum of the product of the probabilities of all occurring plant species in the relevé concerned. It was (arbitrarily) assumed that at least five plant species with a probability curve had to be present at the site to obtain a proper estimate of the soil parameters. Tree species were excluded from the procedure as they react very slowly to (changes in) abiotic conditions.

To evaluate the validity of the approach we back-calculated the pH and C/N ratio at the sites of the validation set from the species composition and compared these values to the measured values at the site. The comparison of calculated to measured soil parameter values in the validation set confirmed that there was a strong correlation ($r^2 > 0.5$) between measured and calculated values for both pH and C/N ratio. At part of the sites, however, there was a substantial deviation between the measured and calculated values (Figure 2).

2.4 Validation of PROPS on observed plant species probabilities

We applied the PROPS model to the validation part of the soil-plant database with measured soil pH and C/N ratio, combined with observations of plant species composition. The validation part of the dataset contained approximately 700 relevés with measured pH and C/N ratio and modelled N deposition, and interpolated precipitation and temperature from the earlier mentioned Ensemble dataset and EMEP model results. With these abiotic factors as input to the PROPS model, we calculated for each of the 700 relevés the probability of occurrence for all species that occurred in the validation part of the soil-plant database.

We compared the predicted probabilities with observed occurrences, which we translated to 'observed' probabilities. The 'observed' probabilities were calculated by dividing the number of occurrences within an abiotic factor class by the total amount of relevés within that abiotic factor class. The abiotic factor class was defined as a discrete combination of abiotic factors. To obtain the abiotic factor classes, we first divided the abiotic factors in two or three classes. Theoretically, when you divide all five abiotic factors into three classes you would have 3^5=243 classes. Since we had only 700 relevés in the validation set, we decided to divide only pH, C/N and temperature in respectively three, three and two classes. The argument was that C/N and pH already includes effect of N deposition and temperature was considered the most important climatic parameter. This resulted in 18 classes of which 11 classes had at least 25 relevés (Table 3). The Class border for Temperature was set at 10 °C, being the average annual temperature in the Netherlands. For pH, class borders were set at 4.5 and 6, being borders for acid soils (pH <4.5) and basic soils (pH>6). Borders for soil C/N ratio were set at 12.5 and 20, being borders for systems that are heavily influenced by nitrogen deposition (CN<12.5) and systems with limited impacts of N deposition (C/N >20). For these 11 classes we compared the average predicted probabilities with the 'observed' probabilities of each species and calculated Pearson's r to quantify the correlation between them. After this overall comparison per class, we analysed the results for the 10 most frequent species separately. Of the 4053 species that were included in the model, only 1325 species occurred in the 700 relevés that occurred in the validation part of the soil-plant database. The 10 most frequent species were selected to illustrate the quality of the fitted plant species responses.

We also did the same comparison for all species with more than 100 occurrences in the validation part of the dataset, but then per abiotic factor separately to test the model performance. We divided each abiotic factor in ten classes and then calculated in the same way the 'observed' probabilities and compared them with the averaged predicted probabilities within each class.

2.6 Evaluation of PROPS behaviour in response to increasing N deposition and climate change

We tested the ecological behaviour of the model by applying the PROPS model in combination with the soil chemistry model VSD+ (Bonten et al., 2016) on a wet rich sandy soil in the eastern part of the Netherlands (Lemselermaten), where a rich fen meadow has developed, and a dry poor sandy soil, in the centre part of the Netherlands (Oud Reemst), where a heathland has developed. The period over which the ecological behaviour was tested was 1930-2050.

The VSD+ model was used to simulate changes in pH and soil C/N-ratio in response to N deposition and climate change, and PROPS was subsequently used to predict the probabilities of plant species in this habitat. The results of all individual species were integrated into a Habitat Suitability Index (HSI, eq 7), being a measure of plant species diversity (Posch et al., 2014). The HSI is defined as the average of the probabilities, normalised with their maximum probability, of all target species in a habitat (as agreed at the 2014 Task Force meeting of the ICP Modelling & Mapping):

$$(7) \qquad HSI = \frac{1}{n}\sum_{k=1}^{n}\frac{p_k}{p_{k,max}}$$

Where *n* is the total number of target species, p_k is the probability of occurrence target species *k* and $p_{k,max}$ the maximum probability of occurrence of that species. Thus, the HSI 'summarizes' the chance of occurrence of selected target species. The higher the HSI the higher the chance that the selected target species occur in the field and thus the more species will be present. The HSI is related to the Habitat Quality index defined by Rowe et al. (2009). The Habitat Quality index also considers the (negative) contribution of unwanted species, which we did not include, because of the lack of a list of such species per vegetation type. Rowe et al. define unwanted species as ‘species that are likely to invade this habitat’. We would like to add to this definition that these species invade as a result of an anthropogenic pressure, e.g. nitrogen deposition or climate change. We would like to add to the list of unwanted species, species that are ‘native’ to the habitat but increase in cover and outcompete other species when under pressure of anthropogenic influence.

2.7 Model input

2.7.1 Site 1: Wet molinia fen meadow (Lemselermaten)

We used readily available input for the Lemselermaten site, since the VSD+ model has already been applied earlier for this ecosystem, as described by Van Hinsberg et al. (2011). Habitat types H6410 (https://www.synbiosys.alterra.nl/natura2000/gebiedendatabase.aspx?subj=habtypen&groep=6&id=6410), Molinia meadows on calcareous, peaty or clayey-silt-laden soils (*Molinion caeruleae*; here further referred to as Molinia meadows), and H7230 (https://www.synbiosys.alterra.nl/natura2000/gebiedendatabase.aspx?subj=habtypen&groep=7&id=7230), alkaline fens, both present at the site, were used for the scenario analyses. The HSI for H6410 was based on *Ophioglossum vulgatum, Silaum silaus, Selinum carvifolia, Cirsium tuberosum, Cirsium dissectum, Crepis paludosa, Inula salicina, Serratula tinctoria, Dianthus superbus, Succisa pratensis, Lotus pedunculatus, Sanguisorba officinalis, Potentilla anglica, Galium uliginosum, Viola palustris, Viola persicifolia, Juncus conglomeratus, Luzula multiflora, Colchicum autumnale* and *Molinia caerulea*. The HSI for H7230 was based on *Equisetum variegatum, Aster bellidiastrum, Parnassia palustris, Pinguicula vulgaris, Primula farinosa, Bartsia alpina, Valeriana dioica, Carex hostiana, Carex dioica, Carex flava, Eleocharis quinqueflora, Eriophorum latifolium, Schoenus ferrugineus, Carex_pulicaris, Carex lepidocarpa, Carex davalliana, Tofieldia calyculata, Dactylorhiza incarnata, Dactylorhiza traunsteineri, Epipactis palustris, Liparis loeselii, Selaginella selaginoides,* *Bryum pseudotriquetrum, Cinclidium stygium, Campylium stellatum, Tomentypnum nitens, Ctenidium molluscum* and *Aneura pinguis*.

Nitrogen and sulphur deposition for the period 1880-2000 was obtained from Schöpp et al. (2003). The first 50 years of the model run were used to initialize the model and are not shown. Base cation and chloride deposition, needed for the prediction of pH, was assumed constant and obtained from Van Jaarsveld et al. (2010), who calculated mean yearly total (wet and dry) deposition at a 5 km × 5 km grid for the years 2000-2005. Temperature and precipitation for the sites were obtained from data sets for the central part of the Netherlands covering the period 1910 up to present, based on data from the Dutch Meteorological Office (CBS et al., 2016, 2018); data between 1880 and 1910 were set to the 1910 values of the data sets. The PROPS input (precipitation, temperature and N deposition) for this site for four different scenarios (see Section 2.8) is given in Appendix 1.

Measured soil properties at the site were bulk density, volumetric water content, cation exchange capacity and organic matter content. Measured soil solution concentrations were used for calibration. Initial base saturation was set to 0.95. For the remaining soil and vegetation parameters, default values for a rich sandy soil and for poor grassland were taken from Kros et al. (2017).

Water fluxes, affecting the element leaching, were calculated with the soil hydrology model SWAP (Van Dam et al., 2008). We used the aggregated results for this location from Jansen (2000). Both temperature and soil moisture affect reduction functions for mineralisation, nitrification and denitrification in VSD+ (Bonten et al., 2016). The reduction factor for denitrification was set to 0.9, reflecting the wet circumstances. Reduction functions for mineralisation and nitrification were calibrated on $NH_4^+$and NO_3^- concentrations in soil water with the Bayesian calibration tool available for VSD+.

In order to simulate changes in pH and soil C/N-ratio in response to N deposition and climate change by VSD+ model, data were needed on the initial value for the carbon pool, the initial C/N ratio, exchange constants of H against Al, Ca, Mg, K and Na and the weathering of Ca, Mg, K and Na. These data were based on measurements (carbon contents, C/N ratios, base saturation) or based on calibration, using those data and soil water concentrations (Ca^{2+}, Mg^{2+}, K^+, Na^+ and Cl^-), with the Bayesian calibration tool available for VSD+.

2.7.2 Site 2: Dry calluna heathland (Oud Reemst)

The second site used for the evaluation of PROPS is 'Oud Reemst', a dry heath (H4030, https://www.synbiosys.alterra.nl/natura2000/gebiedendatabase.aspx?subj=habtypen&groep=4&id=4030) on a sandy soil, situated in the centre part of the Netherlands, with *Calluna vulgaris* as dominant species. The HSI was based on the model results of *Calluna vulgaris*, *Cistus salvifolius*, *Daboecia cantabrica*, *Erica cinerea*, *Genista germanica*, *Genista pilosa*, *Ulex gallii*, *Ulex minor* and *Vaccinium vitis-idaea*.

For the Oud Reemst site a deposition measurement of total N deposition was available for the year 2005. Thus, the modelled N deposition was scaled such that it matched the measured value of 2005 within 20%. Base cation and chloride deposition, temperature and precipitation were obtained as described above for the Lemselermaten site. The used input for precipitation, temperature and N deposition for PROPS for this site for four different scenarios is given in Appendix 2.

Measured soil properties used for model initialisation were cation exchange capacity and organic matter content. Measured pH and C/N ratio were used for calibration of the VSD+ model. Initial base saturation was determined by the model assuming equilibrium conditions at the start. For the remaining soil and vegetation parameters, default values for a poor sandy soil and for heathland were taken from from Kros et al. (2017).

The water leaching flux was calculated by subtracting default transpiration for heath on poor sandy soil and interception from precipitation (following Kros et al., 2017). The reduction factor for denitrification was set to 0.1, reflecting the dry circumstances at the site. Reduction factors for mineralisation and nitrification were set to 0.9.

C and N fluxes by litter fall were taken from Aerts and Heil (1993). Plant uptake of base cations was set equal to the total input by base cation deposition and weathering. Nitrogen uptake was calculated by a fixed N/base cation ratio according to Kros et al. (2017).

The initial value for the carbon pool, the initial C/N ratio and the weathering of Ca, Mg, K and Na were calibrated with the Bayesian calibration tool of VSD+, using measured carbon pool in the soil, C/N ratios and pH.

2.8 Scenarios

We ran four different scenarios based on the combination of two climate scenarios and two N deposition scenarios for the period 2020-2050. The included climate scenarios were a reference scenario, (http://www.clo.nl/search/topic?nid=20883&stopics[]=Klimaatverandering) taken from the Dutch trend of precipitation and temperature, and the warm humid scenario (Wh), with a precipitation increase of 5% and a temperature increase of 2.3 ^{o}C, both compared to the average over the period 1981-2010 (http://www.klimaatscenarios.nl/kerncijfers/). Part of this change is realised in the period 1986 - 2020. For temperature the rise from 2020 till 2050 is approximately 1.9 ^{o}C (see also Appendix 1). The nitrogen scenarios included a reference (ref) scenario, being continuation of the N deposition in the year 2010 and a Maximum Control Efforts (MCE) scenario. ‘The MCE scenario assumes, in addition to all end-of-pipe emission controls, strict decarbonisation policies for the energy sector and agricultural production responding to a ‘healthy diet’ development’ (Amann, 2012). The combinations of the deposition and climate scenarios led to four different scenarios, Ref (current N deposition and climate trends continued), MCE (reduced N deposition, combined with current trends in climate), Wh (current N deposition with climate change according to the warm humid scenario) and WhMCE (reduced N deposition combined with climate change according to the warm humid scenario). Note that for both sites the nitrogen deposition increases and then decreases, but that there is nitrogen deposition and this nitrogen input is in the system during the whole period and for all scenarios. The nitrogen deposition affects both the soil pH (decrease) and C/N (decrease) in the VSD+ model. Also, higher temperatures and precipitation affects both pH and C/N.

3. Results

3.1 Comparison of predicted and observed plant species probabilities

The predicted and observed probabilities for the eleven abiotic factor classes with more than 25 findings (relevés), with combinations of pH, C/N ratio and temperature levels, are shown in Figure 3. The minimum of 25 findings is arbitraril chosen, it prevents outlier results to influence the result of the analyses. The predicted occurrences are generally lower than the observed occurrences, which is partly due to the fact that species occur more often in the validation database than in the database that was used for the curve fitting. The correlation between the average predicted and 'observed' probabilities of plant species, in terms of Pearson's r, is ranging from 0.287-0.758 (Table 4). Splitting the results per species, shows a good relationship between observed and predicted probabilities (Figure 4). In general, the Pearson's r is lower per abiotic factor class (Table 4) than per species (Table 5) with r values varying from 0.653-0.882. The average r value for the selected species is 0.79 (n=10).

In Figure 5 the results per abiotic factor are shown for *Calluna vulgaris*. The graphs at the left show the responses to the different abiotic factors, whereas the graphs at the right show averaged PROPS calculated probabilities against 'observed' probabilities per abiotic factor class. The explained variances range from 0.53-0.96. The results show the best correlation between predicted and observed probabilities for pH class (0.96) and C/N-ratio class (0.90).

3.2 Impacts of changes in N deposition and climate on the habitat suitability index

Predictions are based on the specific species list for each habitat type (as described in Methods 2.7). The results for the wet grassland site Lemselermaten (site 1) are roughly the same for the Alkaline Fens and the Molinia meadows (Figure 6). The HSI decreases slightly from 1930 till around 1950, then it decreases more strongly till the late eighties and it increases from the nineties till present day, mainly in response to N deposition changes. The MCE (Maximum Control Efforts) and the WhMCE (Warm humid combined with the Maximum Control Efforts) scenarios result in an increasing HSI, continuing the trend from the nineties, whereas the reference (Ref) and the Wh (Warm humid) scenario show a change in the trend of the years before, levelling off the HSI. The differences between the MCE and WhMCE and between the Ref and Wh scenarios are very small, implying a very limited impact of the climate change differences. The absolute HSI is always slightly higher for the alkaline fens compared to the Molinia meadows.

As with Lemserlermaten, the biggest difference for the dry heathland site Oud Reemst (site 2), can be found between the MCE (Maximum Control Efforts) and the WhMCE (Warm humid combined with the Maximum Control Efforts) scenarios and the Ref and Wh scenarios (Figure 6). In the period till 1970 the HSI decreases with an acceleration after 1950. From 1950 till 1970 it is more or less stable after which the HSI increases. The simulation of the past reflects the increasing acid deposition till the 1980s, followed by the successful countermeasures to decrease acid deposition, followed by the increasing effect of N deposition and the countermeasures to mitigate those effects (via sod cutting and grazing by sheep). The WhMCE and the MCE scenario give a continuation of the increase of the HSI, with WhMCE performing slightly better. The Ref scenario causes a halt to the increase of the HSI in the previous years, whereas, the Wh scenario causes a small increase.

4. Discussion

4.1 Predictions and their plausibility

The scenario analyses for the grassland site Lemselermaten and the heathland site Oud Reemst show that both sites benefit from a reduction of nitrogen deposition, in terms of an increase in HSI. A change in HSI indicates a change in the accumulated chance of occurrence of the selected plant species. A higher chance indicates a higher chance of finding the target species in the field. The effect of N reduction is in line with earlier research (e.g. Bobbink et al. 1998, Stevens et al. 2004, Wamelink et al. 2009, Stevens et al. 2010). A decrease in N deposition is expected to increase the number of threatened (red list) species of the habitat types, especially in grasslands. The predicted increase in the number of species, including rare species, in response to an increase in temperature and precipitation (warmer and more humid climate) is typical for a relative cold country like the Netherlands, but the effect of the climate change scenario appears to be limited. The limited effect may be affected by the use of the well-defined habitat types. They all consist of species that were present in the habitats in the past and not of those that could be present in the future. In principle, PROPS, which includes a term for temperature as well as precipitation, is able to predict new species that could arrive at a site as Lemselermaten. The effect of the climate scenario may thus be bigger. Also, the effect of a higher temperature may be clouded by the rise in humidity. The first could have a negative impact while the second could have a positive impact resulting in a less pronounced effect compared with only a raise in temperature.

The predicted HSI in 2050 in response to the Maximum Control Efforts (MCE) energy scenarios is higher than the predicted HSI in 1930. This may seem unexpected. However, in 1930 there was already a negative effect of sulphur deposition on the vegetation which started since the industrial revolution. Also, the effect of climate change and measures to improve the quality of natural areas as defined for the MCE scenario will benefit the occurrence of target species. The wet humid scenario in combination with the MCE scenario gives an even higher HSI, which makes sense since the wetland type species will benefit from a precipitation and a temperature increase.

4.2 Limitations of the model predictions

PROPS predicts the potential occurrence probability of plant species in response to changes in climate and air quality. In practise there are several reasons why predicted changes are not (yet) visible in the field, i.e. PROPS does not (i) account for time delays, (ii) predict persistence of species under unfavourable conditions and (iii) include ‘unwanted’ species in the calculation of the Habitat Suitability Index, as discussed further below.

First, the time that is needed for species to respond to a change in N deposition or climate change is not included. This time period is determined by the ability of plants to disperse and occupy space in environments with suitable conditions. The time delay is different between species and among communities and is highly related to N-use characteristic of each species according to Xiankai et al. (2008). They state that understory vascular plants and cryptogam plants are sensitive and respond fast to N deposition, whereas arboreous plant diversity responds less to N deposition, and needs quite a long time to show changes in diversity.

The effect of disturbances is different in every ecosystem and influenced by adaptations (Dale et al., 2001). There are three ways in which plants may respond to climatic change or other changes: (i) persist in the modified climate, (ii) migrate to more suitable climate or (iii) become locally extirpated (Theurillat and Guisan, 2001). PROPS can simulate the effects of (ii) and (iii). If the circumstances at a given site becomes favourable for a species not yet present, the model will predict the appearance of that species, but only when the species is already selected at the beginning of the model run. The model will predict the disappearance of an existing species when the circumstances at a site become unfavourable for that species. However, predicting the persistence of species under unfavourable conditions cannot be modelled, unless the species boundaries in which it is assumed to persist are adjusted. Predicting the persistence of species in unfavourable circumstances remains a problem. Species diversity, determined by components such as species richness, species evenness, composition and interactions and variations within these components, influences the resilience and resistance to environmental change (Chapin et al., 2000). This may result in species still being present at a site under unfavourable circumstances due to the ‘community’ resilience. PROPS, however, will predict the absence of the species when the circumstances are no longer suitable, while the species, as an individual, may persist within a community. However, often this is only a matter of time. An individual species will persist, but as soon as it dies, e.g. of old age, there will be no recolonization and then the species will become locally extirpated. Therefore, persistence will in most cases only lead to a delay of locally extirpation and thus the model is predicting what will happen at some point in the future. PROPS may also predict the presence of species that are not present at the site yet. Combined with the migration of species due to climate change, this may lead to species compositions that never occurred before. Since the species never coexisted, it is unknown how they will react on each other, e.g. a newcomer may outcompete the other species. These effects cannot be extracted from the databases used and can only be studied in experiments or when it actually occurs.

The abiotic parameters for the sites are predicted by using species indicator values for C/N and pH. The explained variance of the response curves on which the indicator values are based is in general not very high. This introduces an uncertainty in the indicator values and thus in the predictions of the abiotic parameters and consequently in the model results of PROPS. This is also visible in Figure 2 where the predicted pH and C/N are validated on field data. The explained variance of the regression (for pH R^2=0.65 and for C/N R^2 = 0.50) is comparable to other research (Wamelink et al. 2005) and reasonable for such data. But part of the predictions contain major outliers, especially for C/N. It would be possible to decrease this uncertainty by taking more soil samples along plots, thus avoiding the need for the estimation of the soil parameters.

The Habitat Suitability Index, which is the commonly agreed indicator for the comparison of the modelled results of the effects of N deposition scenarios on a European scale (CCE, 2014; Posch et al., 2014) is based on an index proposed by Rowe et al (2009) based on ‘wanted’ or typical species only. However, the effect of increased N deposition on the unwanted species that are either becoming dominant or invasive, such as *Deschampsia flexuosa* in dry heathlands or *Molinia cecaele* in wet grasslands, is not included. Including these species in an index could give a better evaluation of the effects of N deposition. A problem is the definition of these ‘unwanted’ species. A complete list per habitat type is not available at the moment.

A ‘probability’ cannot be measured in the field, making a proper validation of the model difficult. We solved this problem by calculating probabilities for the field data as well, based on the occurrences of species in the field. Though this is not a direct validation of the model predictions, it is as close to a proper validation as is possible. The PROPS model is able to predict probabilities that agree reasonably with the average of the observations in the field (r value varying mostly between 0.25 and 0.75 per abiotic factor class). For the evaluation of the selected species the average r value was 0.79.

The HSI does not give an uncertainty accompanying the predicted value. This makes it difficult to judge the significance of differences in predictions. Therefore, an uncertainty (and sensitivity) analysis is highly desirable.

4.3 Included explanatory variables

The PROPS model includes only five abiotic explanatory variables to predict species occurrence. The advantage is that only a limited amount of data is needed. Nevertheless, it is well known that other abiotic variables, such as phosphorus content of the soil (van Dobben et al. 2016) or light (Ellenberg et al. 1991) can have a significant impact on at least part of the plant species. If enough data becomes available then it is advisable to investigate, whether it is necessary to include these abiotic variables.

The EuroMOVE model (Bakkenes et al., 2002) includes more and different climatic variables , i.e. temperature of the coldest month, effective temperature sum above 5 °C, length of growing season, mean growing season temperature above 5 °C, annual precipitation and the ratio between actual and potential evapotranspiration. The data behind these climatic variables are also available to us and we investigated whether inclusion of the effective temperature sum and the effective precipitation and their interactions would lead to a better model prediction. This was not the case and therefore we omitted these variables in the PROPS model.

Related to which abiotic variables to include is the question whether all plant species react similarly to the same set of variables. In our model we assumed that this is the case, but it is well known that species may be indifferent to one of the included parameters, e.g. soil pH (Wamelink et al. 2005). Probably, model performance could be improved to select the most important parameters per species first and then build a species-specific model. This asks for a much more complicated model setup, but could be feasible by collecting more field data, specifically by adding plots from missing niches and regions.

Acknowledgements

The development of the PROPS model has been funded by RIVM-CCE and the European Commission under the project “Effects of Climate Change on Air Pollution Impacts and Response Strategies for European Ecosystems, Grant agreement no: 282910". This research is also part of the strategic research program “Sustainable spatial development of ecosystems, landscapes, seas and regions" funded by the Dutch Ministry of Economic Affairs and carried out by Wageningen University Research Centre (project code KB-14-001-036).

We acknowledge the E-OBS dataset from the EU-FP6 project ENSEMBLES (http://ensembles-eu.metoffice.com) and the data providers in the ECA&D project (http://www.ecad.eu).

References

Achermann, B. & Bobbink, R. (Eds.) (2003). *Empirical critical loads for nitrogen: Expert workshop, Berne, 11-13 November 2002*. Environmental Documentation 164. Swiss Agency for the Environment, Forests and Landscape, Berne, Switzerland.

Aerts, R. & Heil, G.W. (1993). *Heathlands: Patterns and processes in a changing environment.* Kluwer Academic Publishers, Dordrecht.

Alkemade, R. van Oorschot, M., Miles, L., Nellemann, C., Bakkenes, M. & ten Brink, B. (2009). GLOBIO3: A framework to investigate options for reducing global terrestrial biodiversity loss. *Ecosystems,* 12, 374-390.

Amann, M. (Ed.) (2012). *Scenarios of cost-effective emission controls after 2020.* International Institute for Applied Systems Analysis IIASA, Laxenburg, Austria. TSAP Report #7 Version 1.0.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R. & Latour, J.B. (2002). Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Glob. Change Biol.*, 8, 390-407.

Bakkenes, M., Eickhout, B. & Alkemade, R. (2006). Impacts of different climate stabilisation scenarios on plant species in Europe. *Global Environ. Chang.*, 16, 19-28.

Berendse, F. (1998). Effects of dominant plant species on soils during succession in nutrient-poor ecosystems. *Biogeochemistry,* 42, 73-88.

Bobbink, R., Hornung, M. & Roelofs, J.G.M. (1998). The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology,* 85, 717-738.

Bobbink, R. & Hettelingh, J.-P. (2011). *Review and revision of empirical critical loads and dose-response relationships : Proceedings of an expert workshop, Noordwijkerhout, 23-25 June 2010.* Report 680359002/2011, National Institute for Public Health and the Environment (RIVM), Bilthoven, Netherlands.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., ... De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.,* 20, 30-59.

Bonten, L.T.C., Reinds, G.J. & Posch, M. (2016). A model to calculate effects of atmospheric deposition on soil acidification, eutrophication and carbon sequestration. *Environmental Modelling & Software,* 97, 75-84.

Braun-Blanquet, J. (1964): *Pflanzensoziologie, Grundzüge der Vegetationskunde*. (3. Auflage). Springer Verlag, Wien.

CBS, PBL, RIVM & WUR. (2016). *Temperatuur in Nederland en mondiaal, 1906 - 2015 (indicator 0226, versie 12 , 19 februari 2016).* Centraal Bureau voor de Statistiek (CBS), Den Haag; PBL Planbureau voor de Leefomgeving, Den Haag; RIVM Rijksinstituut voor Volksgezondheid en Milieu, Bilthoven; en Wageningen University and Research, Wageningen, www.clo.nl.

CBS, PBL, RIVM & WUR. (2018). *Jaarlijkse hoeveelheid neerslag in Nederland, 1910-2017 (indicator 0508, versie 07 , 25 april 2018)*. Centraal Bureau voor de Statistiek (CBS), Den Haag; PBL Planbureau voor de Leefomgeving, Den Haag; RIVM Rijksinstituut voor Volksgezondheid en Milieu, Bilthoven; en Wageningen University and Research, Wageningen; www.clo.nl.

CCE. (2014). *International cooperative programme on modelling and mapping of critical loads and levels and air pollution effects, risks and trends. Final chair's report of 24th CCE workshop and the 30th meeting of the Programme Task Force, 7th-10th April 2014 in Rome, Italy*. http://www.rivm.nl/media/documenten/cce/Workshops/Rome/ICPMM_CCE_2014-Minutes_2015-04-24.pdf last visited 25-1-2017.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., ... Díaz, S., 2000. Consequences of changing biodiversity. *Nature,* 405, 234-242.

Clark, C.M. Simkin, S., Allen, E., Bowman, W., Belnap, J., Brooks, M., ... Waller, D. (2019). Potential vulnerability of 348 herbaceous species to atmospheric deposition of nitrogen and sulfur in the United States. *Nature Plants,* 5, 697–705.

Dale, V.H. Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., ... Wotton, B.M. 2001. Climate change and forest disturbances. *BioScience*, 51, 723-734.

Davies, C.E. & Moss, D. (2003). *EUNIS habitat classification.* European Topic Centre on Nature Protection and Biodiversity, Paris; https://eunis.eea.europa.eu

De Vries, W., Reinds, G.J., Vel, E. (2003). Intensive monitoring of forest ecosystems in Europe 2: Atmospheric deposition and its impacts on soil solution chemistry. *Forest Ecology and Management* 174, 97-115.

De Vries, W., Van der Salm, C., Reinds, G.J. & Erisman, J.W. (2007). Element fluxes through European forest ecosystems and their relationships with stand and site characteristics. *Environmental Pollution*, 148, 501-513.

De Vries, W., Wamelink, G.W.W, Van Dobben, H. Kros, H. Reinds, G.J, Mol-Dijkstra, J., ... Spranger, T. (2010). Use of dynamic soil–vegetation models to assess impacts of nitrogen deposition on plant species composition: an overview. *Ecological Applications*, 20, 60-79.

Dirnböck, T., Grandin, U., Römermann, M.B., Beudert, B., Canullo, R., Forsius, M., ... Uzięblo, A.K. (2014). Forest floor vegetation response to nitrogen deposition in Europe. *Glob. Change Biol.*, 20, 429-440.

Dirnböck, T., Pröll, G., Austnes, K., Beloica, J., Beudert, B., Canullo, R., ... Forsius, M. (2018). Currently legislated decreases in nitrogen deposition will yield only limited plant species recovery in European forests. *Environmental Research Letters*, 13, 125010.

Dise, N.B., Ashmore, M. R., Belyazid, S., Bobbink, R., De Vries, W., Erisman, J.W., ... Van den Berg, L. (2011). *Nitrogen as a threat to European terrestrial biodiversity.* In: Sutton, M.A., Howard, C.M., Erisman, J.W., Billen, G., Bleeker, A., Grennfelt, P., van Grinsven, H. & Grizzetti, B. (Eds). *The European Nitrogen Assessment.* Cambridge University Press, Chapter 20, Cambridge, UK, pp. 463-494.

Du, E., Fenn, M.E., De Vries, W., & Ok, Y.S. (2019). Atmospheric nitrogen deposition to global forests: Status, impacts and management options. *Environmental Pollution*, 250, 1044-1048.

Ellenberg. H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Pauliβen, D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, 18, 9-166.

Gilliam, F.S., Burns, D.A., Driscoll, C.T., Frey, S.D., Lovett, G.M. & Watmough, S.A. (2019). Decreased atmospheric nitrogen deposition in eastern North America: Predicted responses of forest ecosystems. *Environmental Pollution*, 244, 560-574.

Gilliam, F. (2006). Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology*, 94, 1176 - 1191.

Grime, J.P. (2001). *Plant strategies, vegetation processes, and ecosystem properties.* 2nd ed. Wiley, Chichester, UK.

Haylock, M.R., Hofstra, N., Klein Tank, A. M. G., Klok, E. J., Jones, P. D., & New, M. (2008). A European daily high-resolution gridded dataset of surface temperature and precipitation. *J. Geophys. Res-Atmos.*, 113, D20119.

Hendriks, M., Van Hinsberg, A., Janssen, P. & De Knegt, B. (Eds.). (2016). *BioScore 2.0: A species-by-species model to assess anthropogenic impacts on terrestrial biodiversity in Europe.* PBL Netherlands Environmental Assessment Agency, The Hague.

Hennekens, S.M., Ozinga, W.A. & Schaminée, J.H.J. (2017). *BioScore 3 – Plants. Background and preprocessing of distribution data.* WOt-technical report 106. Statutory Research Tasks Unit for Nature & the Environment (WOT Natuur & Milieu), Wageningen.

Janssen, B.H. (1996). Nitrogen mineralization in relation to C:N ratio and decomposability of organic materials. *Plant and Soil*, 181, 39-45.

Jansen, P.C. (2000). *Aeratie en fluxen in natte natuurterreinen, resultaten van modelberekeningen.* Alterra interne mededeling BWN-01, Wageningen.

Kros, J., Mol-Dijkstra, J.P., Wamelink, G.W.W., Reinds, G.J., van Hinsberg, A. & de Vries, W. (2016). Modelling changes in soil acidity, nitrogen status and plant species diversity in natural ecosystems in response to changes in acid deposition and hydrology. *Ecological Processes,* 5 (1), 22.

Lu, X., Mo, J., & Dong, S. (2008). Effects of nitrogen deposition on forest biodiversity. Acta Ecologica Sinica, 28, 5532-5548.

Manzoni, S., Jackson, R.B., Trofymow, J.A. & Porporato, A. (2008). The global stoichiometry of litter nitrogen mineralization. *Science*, 321, 684-686.

McDonnell, T.C., Reinds, G.J., Sullivan, T.J., Clark, C.M., Bonten, L.T.C., Mol-Dijkstra, J.P., Wamelink, G.W.W. & Dovciak, M. (2018). Feasibility of coupled empirical and dynamic modeling to assess climate change and air pollution impacts on temperate forest vegetation of the eastern United States. *Environmental Pollution,* 234, 902-914.

McDonnell, T.C., Reinds, G.J., Wamelink, G.W.W., Goedhart, P.W., Posch, M., Sullivan, T.J. & Clark, C.M. (2020). Threshold effects of air pollution and climate change on understory plant communities at forested sites in the eastern United States. *Environmental Pollution*, 262, e114351. DOI:10.1016/j.envpol.2020.114351.

O'Brien, E.M., Field, R. & Whittaker, R.J. (2000). Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. *Oikos*, 89, 588-600.

Pärtel, M. (2002). Local plant diversity patterns and evolutionary history at the regional scale. *Ecology*, 83, 2361-2366.

Payne, R.J., Caporn S.J.M., Stevens, C., Carroll, J., Gowing, D.J.G. & Dise, N.B. (2013). Inferring nitrogen deposition from plant community composition. *Ecological Indicators*, 26, 1-4.

Posch, M., Hettelingh, J.P., Slootweg, J. & Reinds, G.J. (2014). *Deriving critical loads based on plant diversity targets*. In: Hettelingh, J.-P., Posch, M., Slootweg, J. (Eds). *Progress in the modelling of critical thresholds, impacts to plant species diversity and ecosystem services in Europe*. CCE Status Report 2014: 41-46; RIVM, Bilthoven, Netherlands.

Reinds, G.J., Bonten, L., Mol-Dijkstra, J.P., Wamelink, G.W.W. & Goedhart, P. (2012). *Combined effects of air pollution and climate change on species diversity in Europe: First assessments with VSD+ linked to vegetation models.* In: M. Posch, J.-P. Hettelingh (Eds.). *CCE Status Report 2012*, pp. 49-61; RIVM, Bilthoven, Netherlands.

Rowe, E., Emmett, B. & Smart, S. (2009). *A single metric for defining biodiversity damage using Habitats Directive criteria.* In: Hettelingh, J.-P., Posch, M., Slootweg, J. (Eds.). *Progress in the modelling of critical thresholds, impacts to plant species diversity and ecosystem services in Europe.* CCE Status Report 2009: 101-106, RIVM, Bilthoven, Netherlands.

Sala, O.E. Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., ... Wall, D.H. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774.

Schlutow, A., & Huebener, P. (2004). *The BERN model: bioindication for ecosystem regeneration towards natural conditions. Umwelt bundesamt*. Research Report 20085221. Umweltbundesamt, Berlin, Germany.

Schmitz, A., Sanders, T.G.M. Bolte, A., Bussotti, F., Dirnböck, T., Johnson, J., Peñuelas, J., Pollastrini, M., Prescher, A.K., Sardans, J., Verstraeten, A. & De Vries, W. (2019). Responses of forest ecosystems in Europe to decreasing nitrogen deposition. *Environmental Pollution*, 244, 980 - 994.

Schöpp, W., Posch, M., Mylona, S. & Johansson, M. (2003). Long-term development of acid deposition (1880–2030) in sensitive freshwater regions in Europe. *Hydrology and Earth System Sciences* 7, 436-446.

Schulze, E.D. (1989). Air pollution and forest decline in a spruce (Picea abies) forest. *Science* 244, 776-783.

Simpson, D., Benedictow, A., Berge, H., Bergström, R., Emberson, L.D., Fagerli, H., ... Wind, P. (2012). The EMEP MSC-W chemical transport model - technical description. *Atmospheric Chemistry and Physics*, 12, 7825-7865.

Smart, S., Evans, C., Rowe, E., Wamelink, W., Wright, S., Scott, A., ... Maskell, L. (2005). *Atmospheric nitrogen pollution impacts on biodiversity: Phase 1–Model development and testing (CR0289)*. CEH, Lancaster, United Kingdom.

Stevens, C.J., Dise, N.B., Mountford, J.O. & Gowing, D.J. (2004). Impact of nitrogen deposition on the species richness of grasslands. *Science*, 303, 1876-1879.

Stevens, C. J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D.J.G., Bleeker, A. ... Dise, N.B. (2010). Nitrogen deposition threatens species richness of grasslands across Europe. *Environmental Pollution*, 158, 2940-2945.

Stevens, C.J. (2016). How Long do Ecosystems Take to Recover From Atmospheric Nitrogen Deposition? *Biol. Conserv.* 200, 160–167.

Sverdrup, H., Belyazid, S., Nihlgard, B., & Ericson, L. (2007). Modelling change in ground vegetation response to acid and nitrogen pollution, climate change and forest management at in Sweden 1500–2100 A.D. *Water, Air, and Soil Pollution, Focus* 7, 163–179.

Ter Braak, C.J.F. & Looman, C.W.N. (1986). Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio*, 65, 3–11.

Theurillat, J.-P. & Guisan, A. (2001). Potential impact of climate change on vegetation in the European Alps: A review. *Climatic Change*, 50, 77-109.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F. N., ... Williams, S.E. (2004). Extinction risk from climate change. *Nature* 427, 145-148.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005). Climate change threats to plant diversity in Europe. *PNAS*, 102, 8245-8250.

Tilman, D., Reich, P.B. & Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature,* 441, 629-632.

van Breemen, N., Burrough, P.A., Velthorst, E.J., van Dobben, H.F., de Witt, T., Ridder, T.B. & Reijnders, H.F.R. (1982). Soil acidification from atmospheric ammonium sulphate in forest canopy throughfall. *Nature* 299, 548-550.

Van den Besselaar, E.J.M., Haylock, M.R., Van der Schrier, G. & Klein Tank, A.M.G. (2011). A European daily high-resolution observational gridded data set of sea level pressure. *J. Geophys. Res.*, 116, D11110.

Van Dam, J.C., Groenendijk, P., Hendriks, R.F.A. & Kroes, J.G. (2008). Advances of modeling water flow in variably saturated soils with SWAP. *Vadose Zone Journal*, 7, 640-653. doi:10.2136/vzj2007.0060.

Van Dobben, H.F., Wamelink, G.W.W., Slim, P.A., Kamiński, J. & Piórkowski, H. (2016). Species-rich grassland can persist under nitrogen-rich but phosphorus-limited conditions. *Plant and Soil*, 411, 451-466.

Van Hinsberg A., Reinds, G.J. & Mol, J. (2011). *NFC-reports, Netherlands.* In: M. Posch, J. Slootweg & J.-P. Hettelingh (Eds.), *CCE Status Report 2011*, pp. 127-134, RIVM, Bilthoven, Netherlands.

Van Jaarsveld, J.A., Reinds, G.J., Van Hinsberg, A., van Esbroek, M.L.P. & Buijsman, E. (2010). *De depositie van basische kationen in Nederland.* PBL, Bilthoven, Netherlands.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., ... Bairlein, F. (2002). Ecological responses to recent climate change. *Nature,* 416, 389-395.

Wamelink, G.W.W., Goedhart, P.W., Van Dobben, H.F. & Berendse, F. (2005). Plant species as predictors of soil pH: Replacing expert judgement with measurements. *Journal of Vegetation Science*, 16, 461-470.

Wamelink, G.W.W., Van Dobben, H.F., Mol-Dijkstra, J.P., Schouwenberg, E.P.A.G., Kros, J., De Vries, W. & Berendse, F. (2009). Effect of nitrogen deposition reduction on biodiversity and carbon sequestration. *Forest Ecology and Management*, 258, 1774–1779.

Wamelink, G.W.W., Adrichem, M.H.C. Van, Dobben, H.F., Van, Frissel, J.Y., Held, M., Den, Joosten, V., ... Wegman, R.M.A. (2012). Vegetation relevés and soil measurements in the Netherlands; a database. *Biodiversity and Ecology*, 2012, 125-132.

Wilson, S.D. & Tilman, D. (1991). Components of plant competition along an experimental gradient of nitrogen availability. *Ecology,* 72, 1050-1065.

Table 1. Datasets used to build and test PROPS. Given are the number of relevés or species used. Where a dataset with species was used the number is given in bold.

Dataset	Number of relevés/species	Table/figure	purpose	Source
BioScore project	800,000		To fit the PROPS model	Hendriks et al. 2016; Hennekens et al. 2017
EU soil-plant database	12,000	Table 2	Estimation of response curves per species for abiotic parameters pH and C/N	Database is not published
EU soil-plant database validation set	700	Table 3, 4, 5, Fig. 2, Fig. 3	Validation of PROPS on relevés with measured C/N and pH and modelled nitrogen deposition, temperature and precipitation	Database is not published
PROPS	**4053**		species fitted in PROPS	BioScore project
PROPS	**1325**		fitted response in the EU soil-plant database validation set	
EUROMOVE	**1400**		EUROMOVE model	(Bakkenes et al., 2002; Thomas et al. 2004; Bakkenes et al., 2006
PROPS	**10**	Table 5, Fig. 4, (fig. 5 only *Calluna vulgaris*)	Most frequent species that are evaluated in addition to the general validation	

Table 2. Number of sites with plant composition data and measured abiotic soil parameters in the soil-plant database. The data on pH and/or C/N were used to assess indicators for acidity and N availability at the BioScore sites (Hennekens et al. 2017).

Country	Number of measurements						
	pH	NO_3	**C/N**	N_{tot}	pH + NO_3	**pH + C/N**	pH + N_{tot}
The Netherlands	6955	1447	2538	3060	1399	2474	2989
UK	240	0	240	240	0	240	240
Ireland	411	429	430	430	410	411	411
Denmark	2849	0	2823	0	0	2823	0
Austria	630	0	630	630	0	630	630
ICP Forests (Europe)	530	0	518	530	0	518	530
Other sites	189	54	102	112	54	102	112
Total	11804	1930	7281	5002	1863	7198	4912

Table 3. Number of relevés per abiotic factor class in the validation set with observed data on pH and soil C/N-ratios and interpolated data on N deposition, precipitation and temperature. The Temperature was split into two classes, while pH and soil C/N-ratios were each split into three classes. Combinations of L (low), M (medium) and H (high) for pH, C/N ratio and temperature are used in the Tables 4 and 5 and Figure 3.

	Temperature					
	L ≤ 10			H >10		
	C/N			C/N		
pH	L ≤ 12.5	M 12.5-20	H >20	L ≤ 12.5	M 12.5-20	H >20
L ≤ 4.5	28	93	110	6	24	39
M 4.5-6	92	74	12	20	35	9
H >6	34	38	8	25	48	5

Table 4**.** The correlation (Pearson's r) between the average predicted and 'observed' probabilities of plant species for the 11 abiotic factor classes considered**.** The characters for the abiotic factor class refer to levels of pH, C/N ratio and temperature. LLL means low in pH, C/N ratio and temperature, LML low pH, medium C/N and low temperature etc. For the ranges per class see Table 2.

Abiotic factor class	Pearson's r
LLL	0.648
LML	0.620
LHL	0.758
LHH	0.742
MLL	0.699
MML	0.342
MMH	0.500
HLL	0.474
HLH	0.382
HML	0.379
HMH	0.287

Table 5. The correlation (Pearson's r) between the average predicted and 'observed' probabilities of the 10 most frequent individual plant species (see also Figure 4).

Species	Pearson's r
Agrostis capillaris	0.859
Holcus lanatus	0.703
Festuca rubra	0.804
Rumex acetosa	0.730
Plantago lanceolata	0.826
Deschampsia flexuosa	0.882
Anthoxanthum odoratum	0.862
Calluna vulgaris	0.855
Trifolium repens	0.742
Poa trivialis	0.653

Figure 1. Example of possible occurrences of plant species against an abiotic parameter x. A species either occurs (value is 1) or does not occur (value is 0), with the fitted polynomial being an estimate for the occurrence probability of the plant species.

Figure 2. Comparison of calculated and measured values for pH, C/N ratio, nitrogen (N total, mg/kg) and NO_3 (mg/kg) in the validation set of the soil plant database. The red line indicates the ideal 1:1 line, the black line the regression between estimated and observed values. Both C/N and NO_3 were log-transformed before the regression was carried out.

Figure 3. Predicted plant species probabilities against observed probabilities for each of the 11 considered combinations of pH, soil C/N ratio and temperature classes. The characters in the title of each graph refer to levels of pH, C/N ratio and temperature as given in Table 2. LLL means low in pH, C/N ratio and temperature etc.

Figure 4. Predicted against observed plant species probabilities for the ten most frequent species in the validation data set with measured abiotic factors.

Figure 5. Predicted and observed average probability of *Calluna vulgaris* in response to pH, soil C/N ratio, N deposition, precipitation and temperature (left) and PROPS predicted against observed probabilities (right). The red line indicates the 1:1 line.

Figure 6. Predicted changes in the Habitat suitability index (HSI) for Alkaline Fens (H7230) in the wet grassland site Lemselermaten (left), Molinia meadows on calcareous, peaty or clayey-silt-laden soils

(H6410) in the wet grassland site Lemselermaten (middle) and Dry Heath (H4030) modelled in the dry heathland site Oud Reemst (right). The future predictions are for the reference scenario (Ref), a continuation of the current nitrogen deposition with the current climate, the Maximum Control Efforts (MCE) energy scenario, the Warm humid scenario (Wh) and the WhMCE scenario combining the Wh scenario with the MCE scenario. Predictions are based on the specific species list for each habitat type (as described in Methods 2.7).

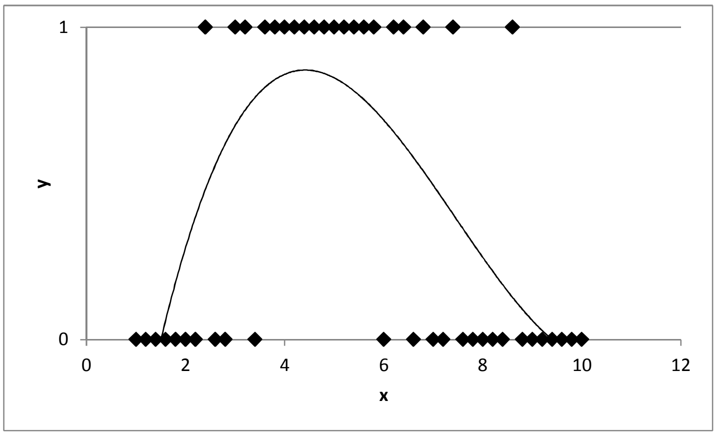


Figure 1. Example of possible occurrences of plant species against an abiotic parameter x. A species either occurs (value is 1) or does not occur (value is 0), with the fitted polynomial being an estimate for the occurrence probability of the plant species.

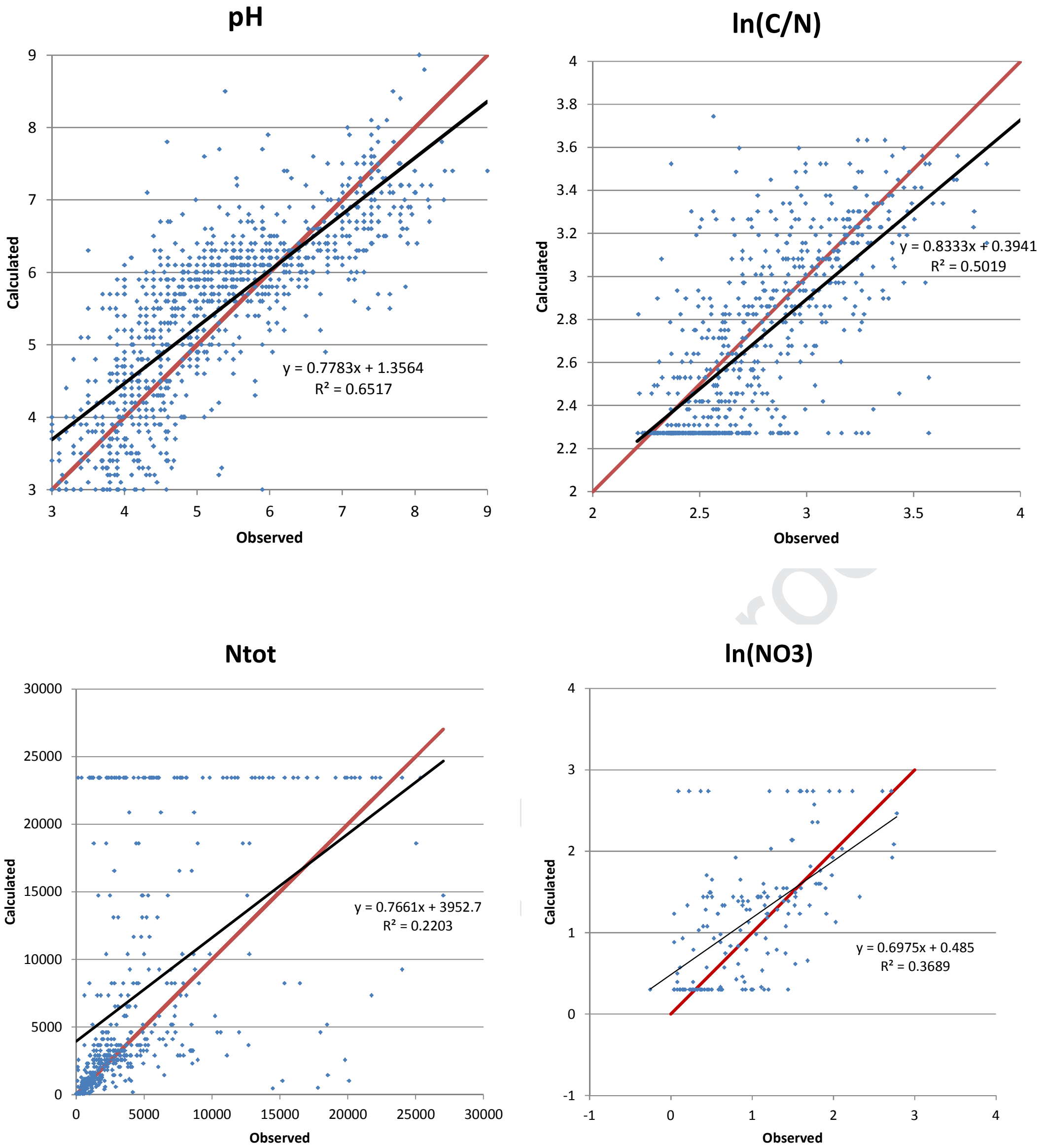


Figure 2. Comparison of calculated and measured values for pH, C/N ratio, nitrogen (N total, mg/kg) and NO_3 (mg/kg) in the validation set of the soil plant database. The red line indicates the ideal 1:1 line, the black line the regression between estimated and observed values. Both C/N and NO_3 were log-transformed before the regression was carried out.

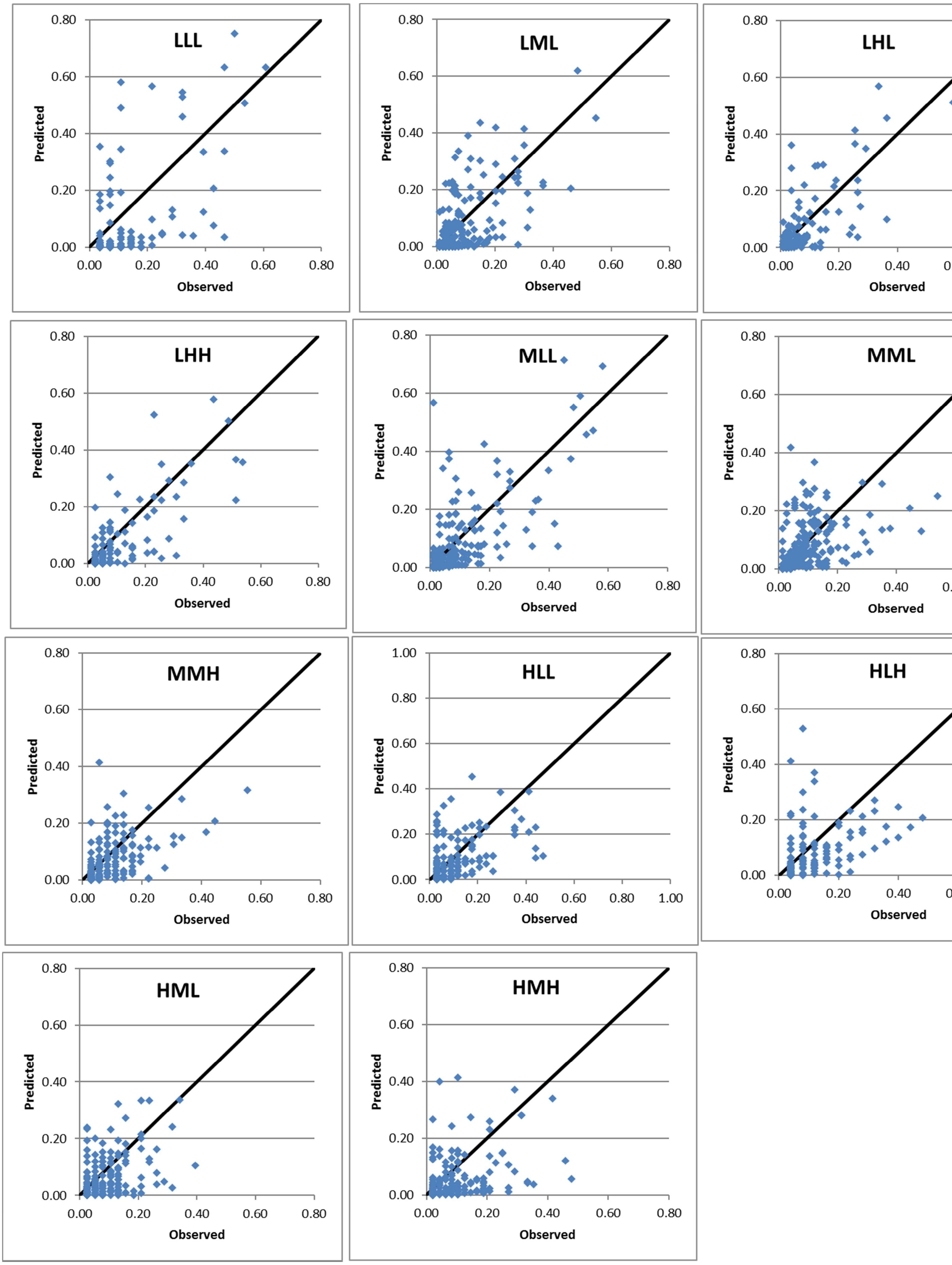

LLL
LML
LHL
LHH
MLL
MML
MMH
HLL
HLH
HML
HMH
Predicted
Observed
0.00
0.20
0.40
0.60
0.80
1.00

Figure 3. Predicted plant species probabilities against observed probabilities for each of the 11 considered combinations of pH, soil C/N ratio and temperature classes. The characters in the title of each graph refer to levels of pH, C/N ratio and temperature as given in Table 2. LLL means low in pH, C/N ratio and temperature etc.

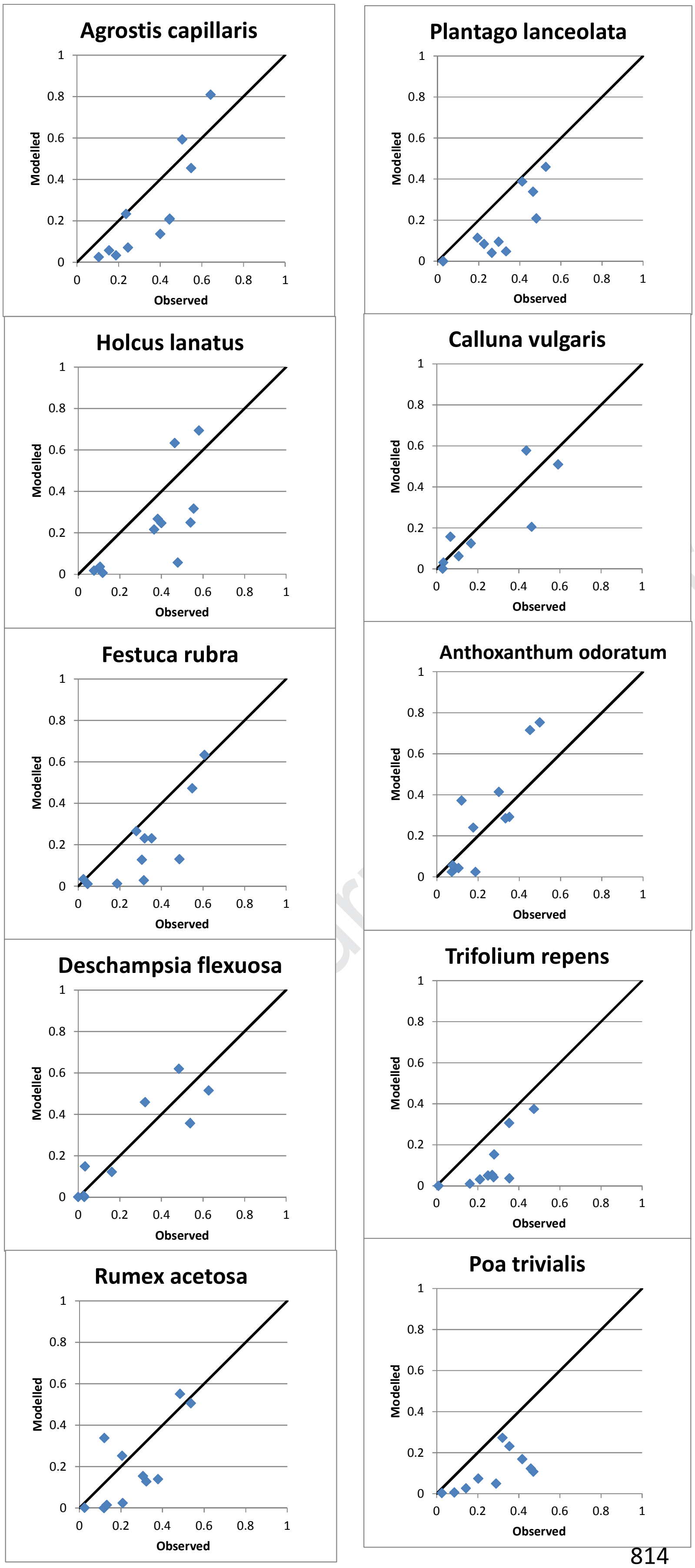
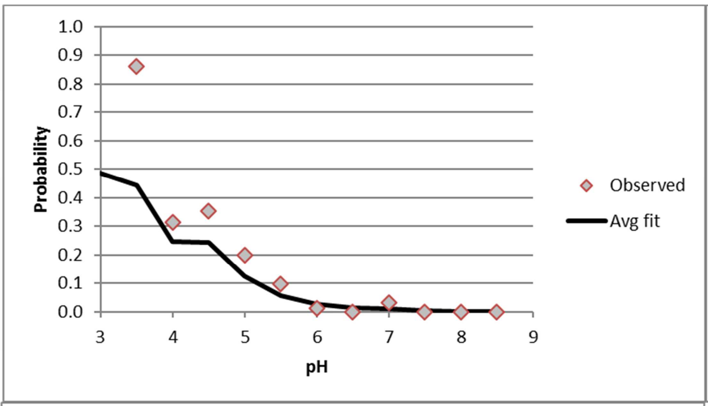
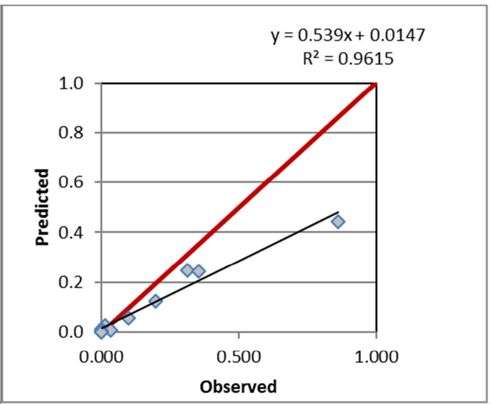
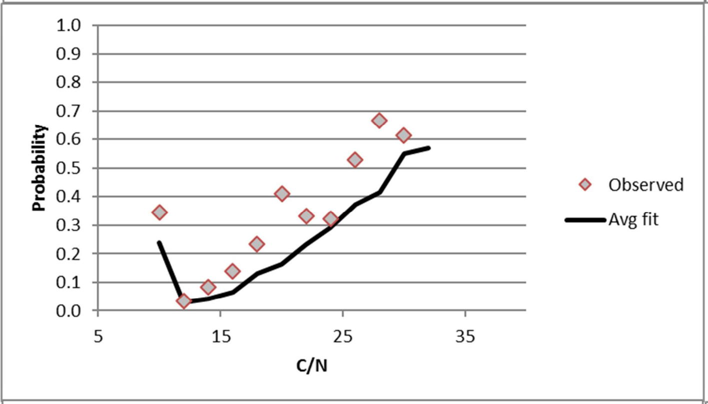
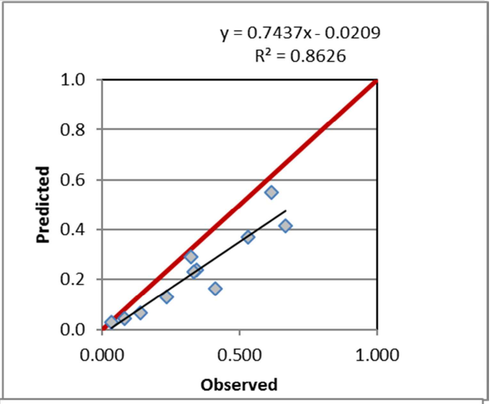

Agrostis capillaris
Plantago lanceolata
Holcus lanatus
Calluna vulgaris
Festuca rubra
Anthoxanthum odoratum
Deschampsia flexuosa
Trifolium repens
Rumex acetosa
Poa trivialis
Modelled
Observed
0
0.2
0.4
0.6
0.8
1

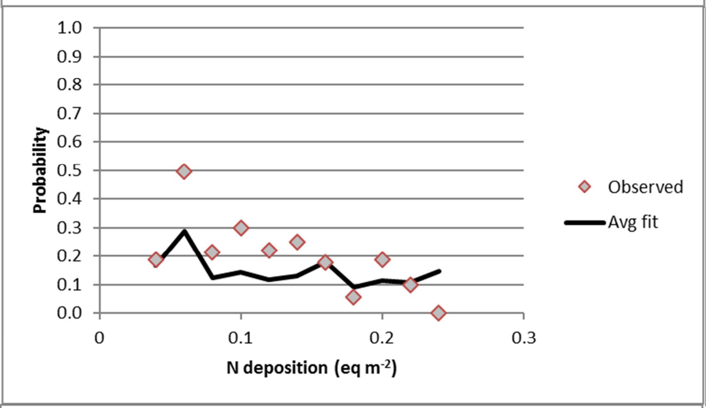
Figure 4. Predicted against observed plant species probabilities for the ten most frequent species in the validation data set with measured abiotic factors.

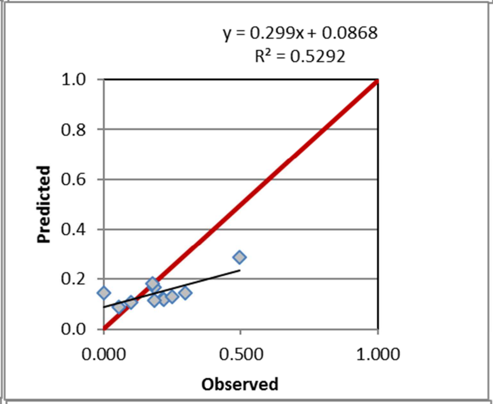

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability
3
4
5
6
7
8
9
pH
Observed
Avg fit

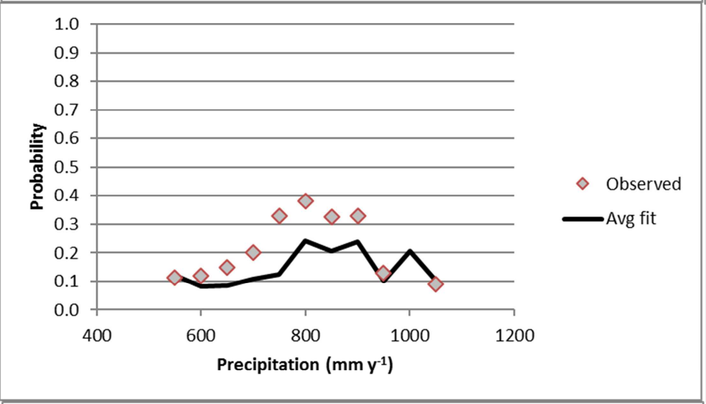

y = 0.539x + 0.0147
R² = 0.9615
1.0
0.8
0.6
0.4
0.2
0.0
Predicted
0.000
0.500
1.000
Observed

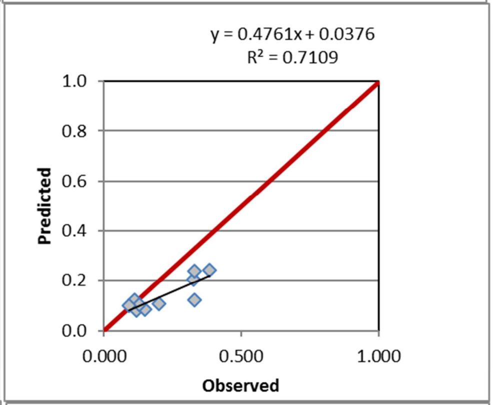

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability
5
15
25
35
C/N
Observed
Avg fit

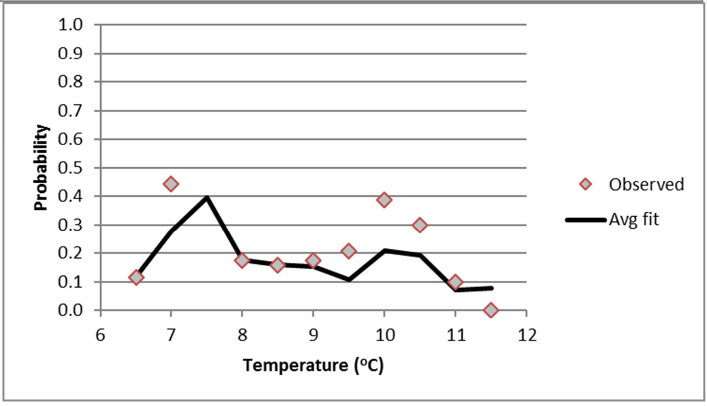

y = 0.7437x - 0.0209
R² = 0.8626
1.0
0.8
0.6
0.4
0.2
0.0
Predicted
0.000
0.500
1.000
Observed


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability
0
0.1
0.2
0.3
N deposition (eq m-2)
Observed
Avg fit


y = 0.299x + 0.0868
R² = 0.5292
1.0
0.8
0.6
0.4
0.2
0.0
Predicted
0.000
0.500
1.000
Observed


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability
400
600
800
1000
1200
Precipitation (mm y-1)
Observed
Avg fit


y = 0.4761x + 0.0376
R² = 0.7109
1.0
0.8
0.6
0.4
0.2
0.0
Predicted
0.000
0.500
1.000
Observed


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability
6
7
8
9
10
11
12
Temperature (oC)
Observed
Avg fit

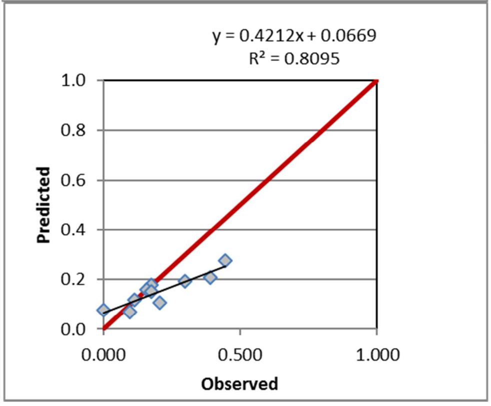

y = 0.4212x + 0.0669
R² = 0.8095
1.0
0.8
0.6
0.4
0.2
0.0
Predicted
0.000
0.500
1.000
Observed

Figure 5. Predicted and observed average probability of *Calluna vulgaris* in response to pH, soil C/N ratio, N deposition, precipitation and temperature (left) and PROPS predicted against observed probabilities (right). The red line indicates the 1:1 line.

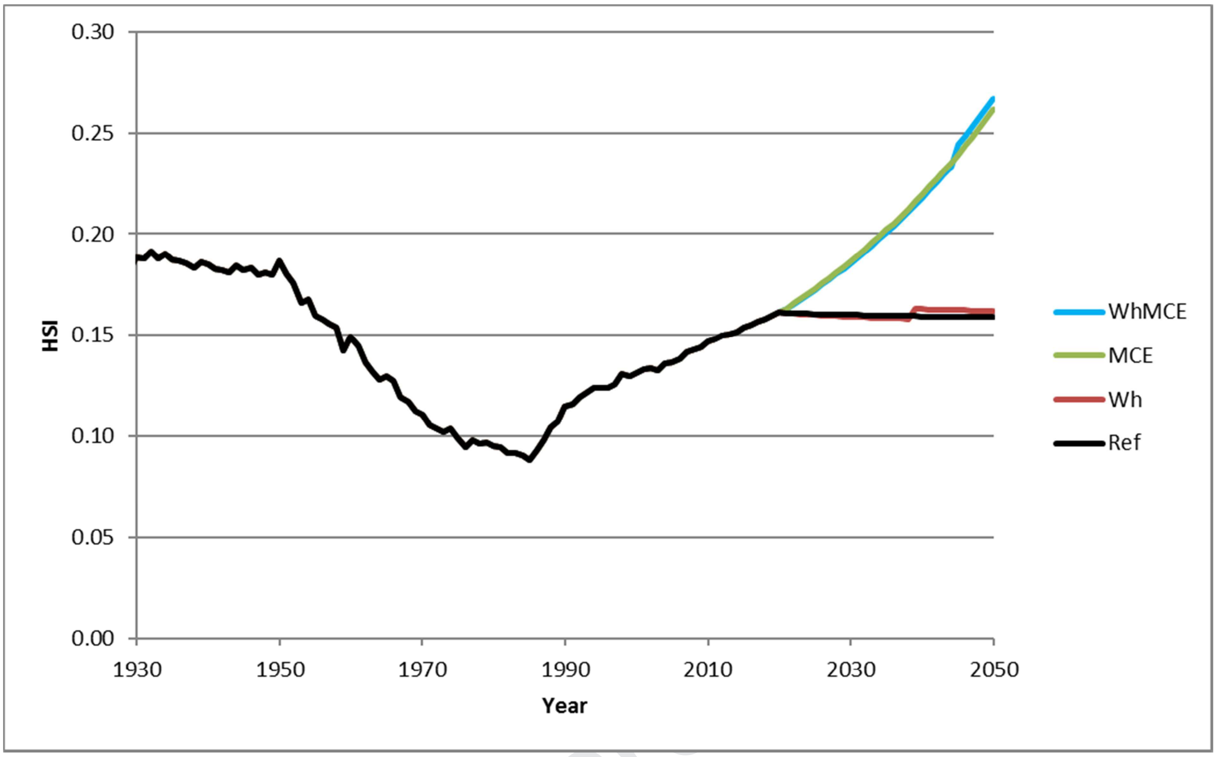
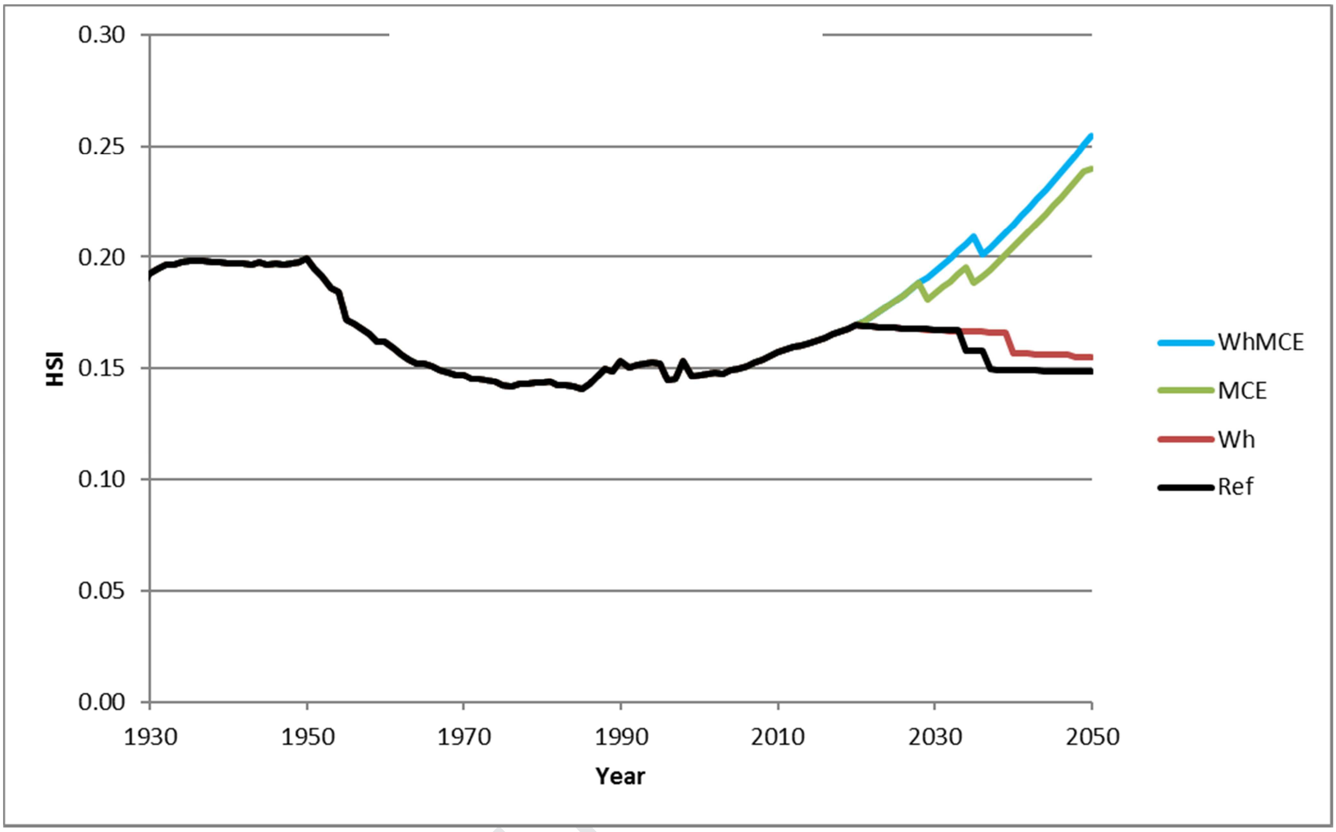

0.30
0.25
0.20
0.15
0.10
0.05
0.00
HSI
1930
1950
1970
1990
2010
2030
2050
Year
WhMCE
MCE
Wh
Ref

Fig. 6 left.

827



828

829 Fig. 6 middle.

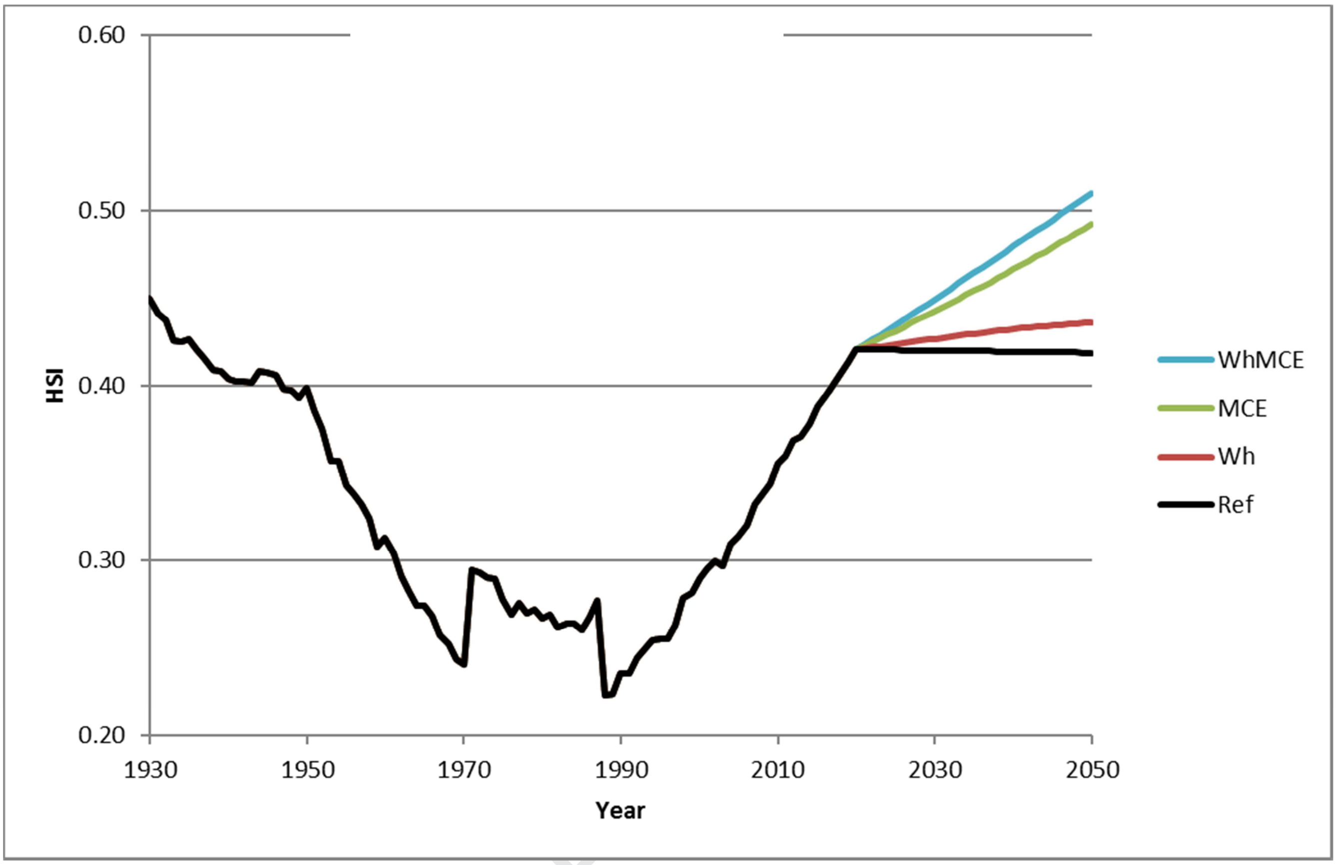
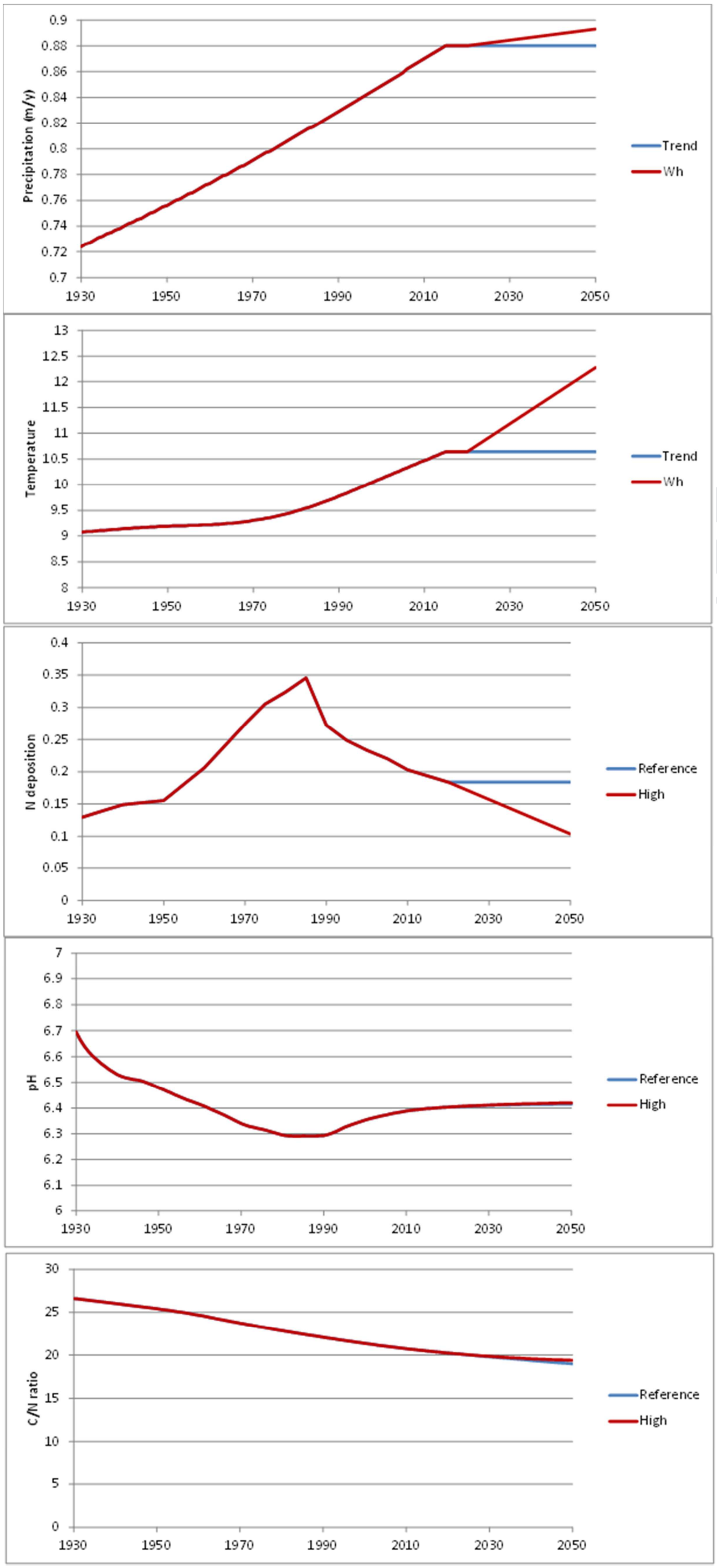


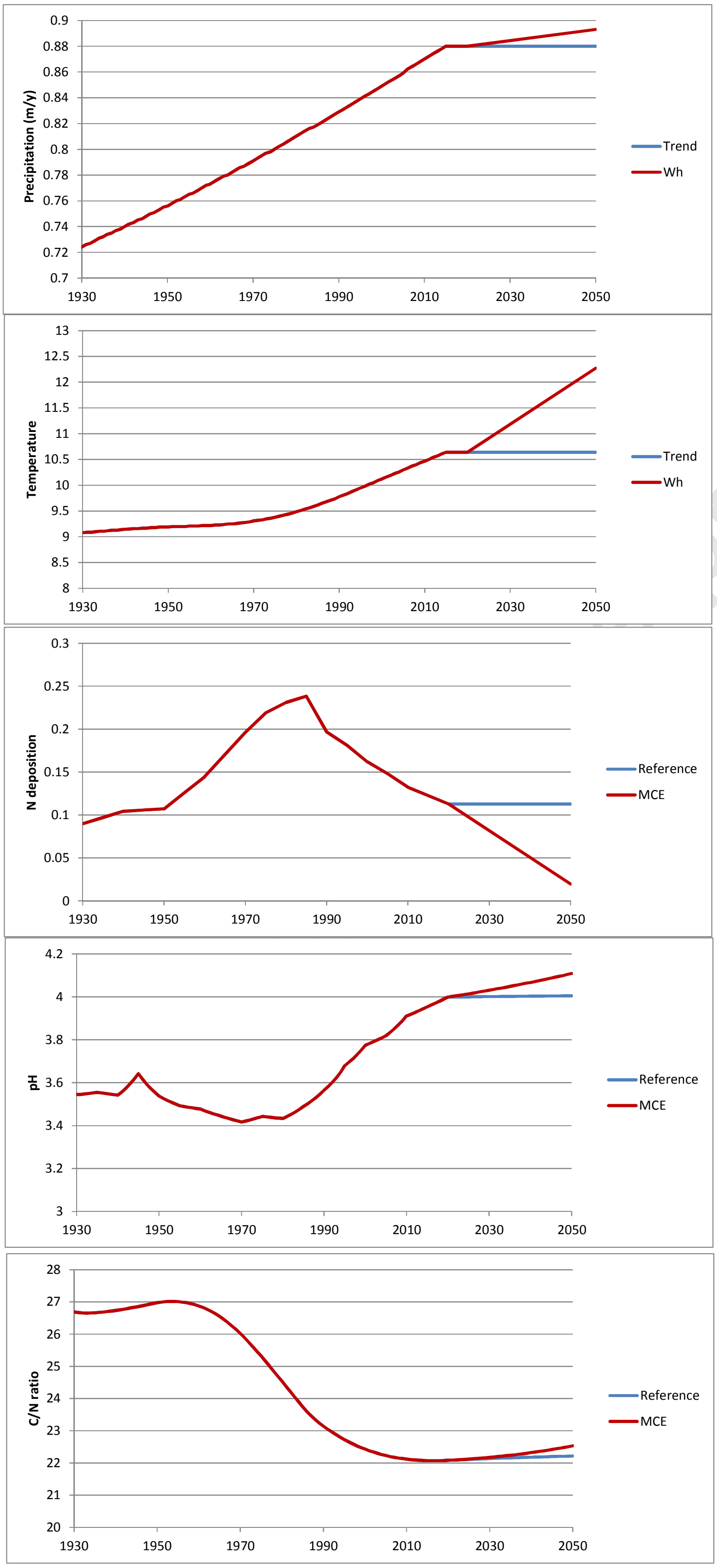
Fig. 6 right.

Figure 6. Predicted changes in the Habitat suitability index (HSI) for Alkaline Fens (H7230) in the wet grassland site Lemselermaten (left), Molinia meadows on calcareous, peaty or clayey-silt-laden soils (H6410) in the wet grassland site Lemselermaten (middle) and Dry Heath (H4030) modelled in the dry heathland site Oud Reemst. The future predictions are for the reference scenario (Ref), a continuation of the current nitrogen deposition with the current climate, the Maximum Control Efforts (MCE) energy scenario, the Warm humid scenario (Wh) and the WhMCE scenario combining the Wh scenario with the MCE scenario.

Appendix 1. Input for PROPS: Temporal changes in precipitation, temperature and N deposition under the scenarios and calculated pH and C/N ratio by VSD+ for wet grassland (Lemselermaten).



Appendix 2. Input for PROPS: Temporal changes in precipitation, temperature and N deposition under the scenarios and calculated pH and C/N ratio by VSD+ for dry heath (Oud Reemst).



Highlights

1. The probability of Plant species on an European scale can be simulated by new model named PROPS
2. Increase of nitrogen deposition leads to a significant decrease of biodiversity
3. The effect of climate change seems relatively small
4. Climate change leads to a slight increase of biodiversity in the Netherlands
5. The habitat suitability index calculation should be updated with unwanted species

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: