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Long-term effects of atmospheric deposition on British plant species richness

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Abstract

The effects of atmospheric pollution on plant species richness ($n_{sp}$) are of widespread concern. We carried out a modelling exercise to estimate how $n_{sp}$ in British semi-natural ecosystems responded to atmospheric deposition of nitrogen ($N_{dep}$) and sulphur ($S_{dep}$) between 1800 and 2010. We derived a simple four-parameter equation relating $n_{sp}$ to measured soil pH, and to net primary productivity (NPP), calculated with the N14CP ecosystem model. Parameters were estimated from a large data set ($n = 1156$) of species richness in four vegetation classes, unimproved grassland, dwarf shrub heath, peatland, and broadleaved woodland, obtained in 2007. The equation performed reasonably well in comparisons with independent observations of $n_{sp}$. We used the equation, in combination with modelled estimates of NPP (from N14CP) and soil pH (from the CHUM-AM hydrochemical model), to calculate changes in average $n_{sp}$ over time at seven sites across Britain, assuming that variations in $n_{sp}$ were due only to variations in atmospheric deposition. At two of the sites, two vegetation classes were present, making a total of nine site/vegetation combinations. In four cases, $n_{sp}$ was affected about equally by pH and NPP, while in another four the effect of pH was dominant. The ninth site, a chalk grassland, was affected only by NPP, since soil pH was assumed constant. Our analysis suggests that the combination of increased NPP, due to fertilization by $N_{dep}$, and decreased soil pH, primarily due to $S_{dep}$, caused an average species loss of 39% (range 23 – 100%) between 1800 and the late 20th Century. The modelling suggests that in recent years $n_{sp}$ has begun to increase, almost entirely due to reductions in $S_{dep}$ and consequent increases in soil pH, but there are also indications of recent slight recovery from the eutrophying effects of $N_{dep}$.

Keywords: modelling; net primary productivity; nitrogen deposition; plant species richness; soil pH; sulphur deposition

Capsule

Modelling the long-term effects of atmospheric deposition indicates that both nutrient enrichment and soil acidification reduced plant species richness, which is now recovering from acidification.
1. Introduction

Over the past two centuries, nitrogen (N) and sulphur (S) deposition have impacted terrestrial ecosystems globally (Vitousek et al., 1997; Larssen et al., 1999; Sutton et al., 2011; Fowler et al., 2012). Forms of both deposited elements cause soil acidification (van Breemen et al., 1984), while N also acts as a nutrient (Matson et al., 2002). Among the ecological effects caused by these pollutants, a major concern is plant species loss in natural and semi-natural (i.e. managed but not fertilized) ecosystems (Bobbink et al., 2010; Azevedo et al., 2013).

Empirical field evidence connecting deposition with declines in plant species richness ($n_{sp}$; number of species per unit area) comes largely from spatial surveys, covering locations with different deposition loads ($N_{dep}$, $S_{dep}$). For example, Stevens et al. (2004) and Maskell et al. (2010) related spatial variations in $n_{sp}$ to $N_{dep}$ in Britain. Similar findings were made for sites across NW Europe by Dupré et al. (2010). For the continental USA, Simkin et al. (2016) reported a positive dependence of $n_{sp}$ on $N_{dep}$ at low $N_{dep}$ (up to about 1 gN m$^{-2}$ a$^{-1}$) and a negative dependence over higher ranges of $N_{dep}$. With regard to pH, a number of studies have been published showing a positive dependence of $n_{sp}$ on pH in temperate and boreal ecosystems (e.g. Grime 1973; Gough et al., 2000; Peet et al., 2003; Stevens et al., 2004; Dupré et al., 2010), strongly suggesting that soil acidification reduces $n_{sp}$.

Field evidence for changes in $n_{sp}$ over time, as a result of changes in deposition rates, is comparatively rare. Two exceptions are recent studies by Rose et al. (2016) and Mitchell et al. (2018), which have demonstrated increases in plant diversity over recent decades at several sites in Britain. Rose et al. (2016) attributed the increases principally to the reversal of soil acidification, emphasising reductions in $S_{dep}$, and they identified “a pressing need to distinguish more clearly between the spatial impacts of acidification and eutrophication on species richness.”

Here we address the issue of long-term (1800-2010) temporal change in $n_{sp}$ in Britain using process-based models, driven by measured and modelled deposition rates. We account for soil acidification with CHUM-AM, a model that simulates soil and surface water chemistry, and which has been calibrated and used for long-term simulations at a range of locations to describe responses to both acid and metal deposition (Ashmore et al., 2004; Tipping et al., 2006, 2007, 2010; Tipping & Chaplow, 2012). The nutrient effects of $N_{dep}$ are simulated with the N14CP model (Davies et al., 2016, 2017), which deals with the interlinked biogeochemical cycles of carbon, nitrogen and phosphorus, and has been used to calculate national scale changes in NPP in British semi-natural ecosystems. Because these ecosystems are assumed mostly to be N-limited, like many temperate natural and semi-natural ecosystems (Elser et al. 2007; LeBauer & Treseder 2008; Lee et al. 2010; Field et al. 2017), N14CP-calculated NPP responded strongly to the increases in $N_{dep}$ over the simulation period (Tipping et al., 2016).
The exception was ombrotrophic peatland, which is likely phosphorus-limited (Toberman et al., 2015; Schillereff et al., 2016). The significance of NPP is in providing the mechanism for changes in \( n_{sp} \), primarily via competition effects (Grime, 1973; Huston, 2014, Fraser et al., 2015; Grace et al., 2016), thereby enabling \( n_{sp} \) to be linked with the nutrient effects of \( N_{dep} \).

We analysed plant richness data obtained in the British Countryside Survey of 2007 (http://www.countrysidesurvey.org.uk/) for four vegetation classes, namely acid and neutral grassland, dwarf shrub heath, peatland and broadleaved woodland. We parameterized a simple model relating the values of \( n_{sp} \) to (a) measured soil pH at the sampling sites and (b) NPP calculated with the N14CP model. Then, again employing N14CP-calculated NPP values, we used the model to predict changes of \( n_{sp} \) over time at six field sites to which the CHUM-AM model had been calibrated in previous work. We also performed predictive calculations for a chalkland site at which soil acidification was assumed not to have occurred.

We report simulations of \( n_{sp} \) over the period 1800-2010 for the combined effects of changes in soil pH and NPP, and for each factor separately. The results provide a retrospective account of the paths to present conditions, partition the \( n_{sp} \) changes according to the two drivers (pH, NPP), and offer an approach to forecasting future changes in \( n_{sp} \) for different scenarios of pollutant deposition. In its long-term approach, our study complements that of Clark et al. (2018), who calculated exceedances of Critical Loads of air pollutants for the period 1800-2025 in the USA. Whereas Clark et al. considered changes over time in the vulnerability of various indicators, including plant community composition, to atmospheric pollution, our focus is on the mechanistic biogeochemical effects of pollution and the quantitative responses of plant species richness.
2. Methods

2.1. Plant species richness and soil pH data

Plant species richness data, $n_{sp}$, expressed as the number of different species per quadrat for each vegetation class, and measured soil pH, were obtained from Countryside Survey (CS) results from 1978, 1998 and 2007 (http://www.countrysidesurvey.org.uk/); see Table 1. Bryophytes were excluded because these have not been exhaustively recorded in the CS quadrats. Data from four vegetation classes were analysed, namely unimproved grassland, dwarf shrub heath, peatland, and broadleaved woodland (Jackson, 2000). Peatland includes bog and peat-dominated heathland. Unimproved grassland comprises neutral and acid grassland not subject to agricultural improvement. For brevity, we refer to the vegetation classes, as grassland, heathland, peatland and woodland.

Values of $n_{sp}$ were available for 4 m$^2$ quadrats in 1998 and 2007, and for 200 m$^2$ quadrats in all three of the survey years. These quadrat sizes are appropriate for sampling species richness in the target habitats; 200m$^2$ has been consistently used for British broadleaved woodlands (Smart et al., 2014) while 4m$^2$ is recommended for grassland and dwarf shrub heath (Rodwell, 2006). Sampling was carried out as close as possible to the same date in every survey to avoid seasonal effects. We used data from the most extensive survey, that of 2007, for model fitting, and data from 1978 and 1998 for model testing. Some $n_{sp}$ values in the 4 m$^2$ quadrat data were zero, because at this scale, no live material was present at the time of sampling, at sites with bare rock, areas of bare peat, and dense stands of the rhizomatous fern *Pteridium aquilinum*. For surveys with results for both 4 m$^2$ and 200 m$^2$ quadrats, the $n_{sp}$ values for the two quadrat sizes were strongly correlated, as demonstrated with the 2007 data in Fig. S1.

We also used relevant data from the literature, for comparison. Data on species richness in 1 m$^2$ quadrats as a function of pH in two Derbyshire (UK) valleys, Cressbrookdale and Lathkilldale, came from Grime (1973), samples collected in 1965-1971. Lathkilldale was ungrazed and sporadically burned, and Cressbrookdale was grazed by sheep and cattle. At both locations, sites with a range of pH were sampled. Stevens et al. (2004), reported species richness in 4 m$^2$ quadrats samples collected in 2002 and 2003 from acid grassland sites at 68 locations on a transect of $N_{dep}$ (with varying pH) across Britain.

2.2. The CHUM-AM model

The hydrochemistry model CHUM-AM was described in detail by Tipping et al. (2006, 2007). It deals with hydrology, C, N and S cycling, cation sorption to soil organic matter, mineral precipitation, and
weathering, in a soil-rock system that includes a topsoil compartment. Water and solutes are transferred to surface waters. The model was driven by measured and modelled $N_{\text{dep}}$, $S_{\text{dep}}$, and base cation deposition data from 1975, and for earlier years by deposition estimated from known or assumed emissions, as described in detail by Tipping et al. (2006, 2007, 2010) and Tipping and Chaplow (2012); see Fig. S2. Weathering rate constants are calibrated to match observed soil and water chemistries. The key output for the present work was the annual average pH of topsoil, typically to a depth of 15 cm.

The model outputs used here were from the previous studies referenced above with simulations from 1400 CE to 2010 for a number of small catchments (Fig. 1, Table 2). The CHUM modelling is for the lumped catchment, and therefore we have to use the same pH values for each class of vegetation considered at the site. For example, the River Etherow catchment has both grassland and peatland, and the same pH values were assumed to apply to both.

2.3. The $N14CP$ model

The model is described in detail in Davies et al. (2016), also in Tipping et al. (2017, 2019). It describes plant-soil pools and fluxes of C, N and P, driven by climate, $N_{\text{dep}}$, $S_{\text{dep}}$, base cation deposition, weathering of base cations and P, and vegetation history. The model simulates, on four quarterly time steps within each year, the growth and decay of plant biomass, N fixation, the production of litter and its incorporation into soil organic matter (SOM), the immobilisation of nutrients (N, P) by SOM, SOM turnover, leaching losses, and denitrification. The fixation of N from the atmosphere is positively related to temperature and P availability, but does not depend on vegetation class. It is down-regulated by $N_{\text{dep}}$ such that no additional N from $N_{\text{dep}}$ becomes available until the $N_{\text{dep}}$ rate outstrips the potential fixation rate. The peatland module is described by Janes-Bassett et al. (2020); peatland is assumed to be P-limited, and therefore no effect of $N_{\text{dep}}$ on NPP is predicted.

Within the N14CP formulation, soil pH, calculated from an annual balance of cations and anions, acts as a modifier to organic matter decomposition, and therefore affects N cycling and thereby NPP. However, the resultant pH dependence of decomposition following the model’s parameterization was found to be small, and so in practice variations in soil pH have little influence on the simulated NPP. Because the soil pH estimates with N14CP are highly approximate, the results from the more chemically-detailed CHUM-AM model were preferred.

The N14CP model, driven by vegetation class, climatic variables and modelled atmospheric pollutant deposition, is used to simulate ecosystem C-N-P cycling, including NPP over the Holocene. We assumed that the vegetation classes at the present sites had been constant since the period of tree
clearance in Britain (see Tipping et al. 2017). Annual values of N_{dep} and S_{dep} resolved spatially (5 km x 5 km grid squares) over the period 1800–2010, and taking vegetation class into account, were estimated as in previous modelling reported in Tipping et al. (2017); see Fig. S2. The key outputs for the present work were the average NPP (gC m\(^{-2}\) a\(^{-1}\)) by year for each vegetation class in 5 km x 5 km grid squares across Britain. These are referred to as NPP_{calc}.

2.4. Data analysis

Following Grime (1973) and Peet et al. (2003), in order to establish general trends in the data, we averaged values of n_{sp} according to pH and NPP_{calc}. This was done first with ordered pH values and second with ordered NPP_{calc}. The number of data for each variable in each averaged bin was set to the integer nearest to the square root of the total number of data.

We used Microsoft Excel to perform linear regression analyses. Results were checked for normality using Q-Q plots, and where necessary outliers were identified as points deviating by more than three standard deviations from the expected value.

Data fitting was performed using Microsoft Excel Solver. Models were compared using the Akaike information criterion (\(\Delta AIC\)); Akaike weights (\(w_{AIC}\)) were interpreted as conditional probabilities (Wagenmakers and Farrell, 2004). We estimated model parameter uncertainty using a Monte Carlo method implemented in Microsoft Excel (Hu et al., 2015). This involved repeated resampling of n_{sp} from the values predicted with the best-fit model, adding perturbations from the assumed normal distribution of root mean squared deviations. Each derived set of n_{sp} was then fitted with the model to yield a parameter set. This was done 1000 times, and the parameter standard errors were calculated from the results. To estimate ranges of predicted values, the model was run repeatedly (1000 times) with parameter sets drawn from the normal distribution of values described by the parameter means and standard errors.
3. Results

3.1. Dependence of $n_{sp}$ on pH and NPP$_{calc}$

Trends in $n_{sp}$ with measured soil pH and NPP$_{calc}$ are shown in Fig. 2, by averaged data for the four vegetation classes in 4 m$^2$ quadrat samples collected in 2007. The N14CP model assumes peatland to be P-limited, consequently there is little variation spatial variation in NPP$_{calc}$ for this vegetation class, and so the results are not plotted. Values of $n_{sp}$ clearly increase with pH, and in two cases (heathland, woodland) they clearly decline with NPP$_{calc}$. For grassland, the decline with NPP is less definite. Very similar trends were evident in the 200 m$^2$ quadrat data for 2007 (Fig. S3).

Increasing $n_{sp}$ with pH, and declining $n_{sp}$ with NPP, are expected from the published literature (see Introduction). However, there is no evidence of a positive relationship at low NPP$_{calc}$, as would be expected from a unimodal dependence on NPP (Grime, 1973; Fraser et al., 2015). In case this might reflect the high degree of N enrichment in the ecosystems that had developed by 2007, we plotted the data (200 m$^2$ quadrats) for 1978, when N enrichment would have been less, but again found no evidence for positive relationships in plots of $n_{sp}$ against NPP$_{calc}$ at low NPP$_{calc}$.

The pH dependence of $n_{sp}$ (Fig. 2) is similar in shape to published values for temperate and boreal field sites, with a relatively steep rise in the low pH region, and a flattening off at higher pH (Grime, 1973; Gough et al., 2000; Peet et al., 2003; Schuster and Diekmann, 2003; Vonlanthen et al., 2006; Chytrý et al., 2007; Peppler-Lisbach and Kleyer, 2009; Riesch et al., 2018). Therefore to model the dependence of $n_{sp}$ on pH at constant NPP we adopted an equation of the form

$$n_{sp} = \alpha' (pH-pH_0)^{\beta'}$$

Here $\alpha'$ and $\beta'$ are constants, and $\beta'$ has a value between 0 and 1. The value of pH$_0$ is the pH at which the soil is too acid for significant plant survival. In the above-cited literature, plots of $n_{sp}$ against pH suggest that pH$_0$ has values near to 3, and the plots in Fig. 2 are in line with this. For simplicity, the decline in $n_{sp}$ with NPP$_{calc}$ was assumed to be a linear relationship, requiring one additional parameter $\gamma$. This led to a full model equation as follows

$$n_{sp} = \alpha (pH-pH_0)^{\beta} (1 - \gamma NPP_{calc})$$

We explored how many parameters could be justifiably fitted to describe the $n_{sp}$ values of the four vegetation classes.

The first step was to fit the model to the grassland, heathland and woodland data sets separately for the 4 m$^2$ quadrats sampled in 2007, using individual data points (not the averaged values of Fig. 2). Four versions of the model were tested (Table 3). Version 1 included all four parameters, in version 2 pH dependence was eliminated, in version 3 NPP dependence was eliminated, and in version 4 a linear
pH dependence was forced. Table 3 shows that for each of the three vegetation classes, the values of $w_{AIC}$, interpreted as the probability of the model being correct, are very low for model versions 2 and 3, which means that both pH dependence and NPP dependence need to be included in the best model. Overall, the $w_{AIC}$ values for versions 1 and 4 are similar, making it difficult to choose between them. However, the pH$_0$ values fitted with version 1 are similar for the three vegetation classes (grassland 2.89, heathland 2.90, woodland 3.30), and consistent with observations reported in the literature and shown in Fig. 2. On the other hand, with version 4 ($\beta$ set to 1.0), the pH$_0$ values (0.91, 2.04, -2.02 respectively) vary more, and are less realistic. Therefore we favour version 1 of the model. Table 4 shows the fitted parameters.

In the case of peatland, because there is essentially no dependence of $n_{sp}$ on NPP$_{calc}$, only two model versions were tested, the first with $\beta$ optimised, and the second with $\beta$ set to 1.0. These gave $w_{AIC}$ values of 0.35 and 0.65 respectively. Again these are quite similar, and again the pH$_0$ value of 3.04, obtained with the first version, is close to the values for the other vegetation classes, and more realistic than the value of 1.99 obtained with the second version. The fitted parameters for peatland with the first model version are presented in Table 4.

The second step was to consider whether the total number of fitted parameters could be reduced from the total of 17 required to parameterize the model separately for the four vegetation classes (Table 4). We fitted the entire data set ($n = 1156$) with three models, A, B and C (Table 5). Model A retained the 17 parameters already fitted, while model B had common values of $\alpha$, $\beta$, $\gamma$ and pH$_0$ for all four vegetation classes. For model C, the vegetation classes were distinguished by fitting a specific value of $\alpha$ for each class, with common values of $\beta$, $\gamma$ and pH$_0$. The values of $w_{AIC}$ (Table 5) show that models B and C are both clearly superior to model A, and that model C is preferable to model B. Therefore, we chose model C for the predictive calculations.

Model C accounts for 23.9 % of the total variance in $n_{sp}$ ($n = 1156$). Its parameter values and their standard errors are shown in Table 6. The parameter uncertainties are fairly modest, suggesting that the parameter values are reasonably well defined, bearing in mind the large scatter in the data. A plot of observed against calculated $n_{sp}$ values is shown in Fig. 3. Plots to show what the fitted model predicts for heathland and woodland are shown in Fig. S4; as would be expected from the similar values of $\alpha$ for the non-woodland classes (Table 6), results for grassland and peatland are similar to those for heathland. Parameter values derived from the 200 m$^2$ quadrat data are shown in Table S1.

3.2. Testing the model against independent data
We compared model predictions with values of $n_{sp}$ for different vegetation classes extracted from CS survey results for 1978 and 1998, at sites that had not been surveyed in 2007. Because the 1978 survey did not include 4 m$^2$ quadrats, we restricted the comparisons to 200 m$^2$ quadrat values, using the parameters for Model C shown in Table S1. The observed and predicted values of $n_{sp}$ (Fig. S5) were in reasonable agreement ($r^2_{adj} = 0.161$, $p < 0.0001$, $n = 336$). The slope of 0.92 in a plot of observed vs predicted $n_{sp}$ did not differ from unity.

We also applied the grassland model to two published data sets for $n_{sp}$ in grassland (Fig. 4). For the Derbyshire dales data of Grime (1973) the measured pH values were used to drive the model, with a single modelled NPP value. For the Stevens et al. (2004) data, we used measured pH and modelled NPP values to drive the model. We found highly significant correlations between observed and calculated values (see caption to Fig. 4), but the observed values were appreciably greater than the observed and predicted values for the CS plots; see Discussion.

Another approach was to compare changes in $n_{sp}$ occurring at CS plots between either 1978 and 1998 or 1978 and 2007. We extracted results for 551 sites (237 grassland, 96 heathland, 156 peatland, 62 woodland), and compared observed and calculated changes in $n_{sp}$ (Fig. S6). Both losses and gains of species were expected and found. They were weakly ($r^2_{adj} = 0.049$) but significantly ($p < 0.0001$) correlated.

We also tested the ability of the CHUM-AM model to simulate changes in soil pH, by comparing observed results for the CS sites with the modelled changes for the CHUM-AM sites. We restricted the CS sites analysed to those with an average pH of between 3 and 5, to match the range of CHUM-AM values. The CS and CHUM-AM locations are not the same, and so the comparison is only of general trends across Britain. The average increase in pH between 1978 and 1998 for 174 CS sites was 0.31 (standard error, SE = 0.04), while that for 144 sites from 1978 to 2007 was 0.33 (SE = 0.05). The corresponding average modelled changes for the six CHUM-AM sites were, for 1978-1998, 0.22 (SE = 0.03) and, for 1978-2007, 0.32 (SE = 0.05). The differences between the observed and modelled values are not significant ($p > 0.05$). Another comparison that can be made is with measured changes reported by the National Soil Inventory (NSI) of England and Wales (Kirk et al., 2010). Between 1978 and 2003, average annual increases in soil pH, attributed principally to reductions in acid deposition, were 0.011 for semi-natural grassland (235 sites) and 0.013 for deciduous woodland (104 sites). These correspond to total pH changes of 0.275 and 0.325 respectively, comparable to the modelled average pH change for the six CHUM-AM sites of 0.288 over the same 25-year period.

3.3. Predicted temporal changes 1800-2010
Calculated changes in soil pH (CHUM-AM) and NPP (N14CP) at the study sites (Fig. 1) are shown in Figs. 5 and S7. Except for the South Downs site, soil pH is calculated to have been at its lowest in the 1970s, then to have increased by 0.2 – 0.5 units over the period to 2010. For the South Downs chalk grassland we assumed that there had been no significant change in soil pH, owing to the high buffering capacity of the soil conferred by the calcium carbonate; we assumed a constant pH of 7.5 (Goulding, 2016). We applied Model C, driven by the modelled pH and NPP values, to calculate \( n_{sp} \) for 4 m\(^2\) quadrats from 1800 to 2010 at the sites for which CHUM-AM had been calibrated. Results are plotted in Fig. 5 and Fig. S7, and summarized in Table 7. Fig. S8 shows estimates of uncertainty in the calculated values of \( n_{sp} \).

In two of the nine site/vegetation combinations of Table 7, namely Lochnagar/heathland and Old Lodge/woodland, the NPP\(_{calc}\) values for the early years of the simulations were less than the lowest NPP\(_{calc}\) values for the period (1978-2007) with observed \( n_{sp} \) values, i.e. values used for data fitting. Therefore in these two cases the predictions of \( n_{sp} \) are outside the range of NPP\(_{calc}\) for which Model C is calibrated. However, the 1800 values are only slightly less than the 1978-2007 minima, and so it is unlikely that the effects on predicted \( n_{sp} \) are significant.

The overall pattern of change over the period 1800 to 2010 is of an initial decline in \( n_{sp} \) until around 1980, followed by an increase. The declines were caused both by decreases in soil pH and increases in NPP, whereas the subsequent recoveries are due almost entirely to pH reversal. The River Etherow site is calculated to have responded most in terms of \( n_{sp} \) change, owing to the high levels of atmospheric pollution it has received over a prolonged period. The least sensitive sites are Lochnagar and the South Downs, the former because of its remoteness from pollution sources, the latter because of the lack of change in soil pH.

The comparative effects of variations in soil pH and NPP on the predicted variations of \( n_{sp} \) over time (Table 7, Fig. 5, Fig. S7) vary among the sites, depending upon vegetation class, soil response to acidifying agents, and atmospheric deposition (Table 2). In four cases, Cote Gill, Mosedale Beck, and the two Old Lodge sites, the effects of pH and NPP variations are similar. For Lochnagar and River Etherow/grassland pH effects dominate, but there are contributions from NPP. For the two peatland sites, River Etherow and Great Dun Fell, the effects of NPP variation are near to zero, because of the assumed P limitation, as discussed in Section 3.1, and so soil pH variation is the sole factor. The chalk grassland of the South Downs is calculated to respond only to changes in NPP, since atmospheric deposition of acidifying agents is assumed not to affect soil pH.

The summary data in Table 7 show that all nine site/vegetation combinations are calculated to have suffered declines in \( n_{sp} \) since 1800, the greatest, 100 %, being for both grassland and peatland at the
River Etherow, while the smallest, 23%, was for heathland at Lochnagar. On average, the decline was 39%. Species richness recoveries are calculated for most of the sites over recent years (from about 1990 onwards), the annual rates ranging from zero to 0.095 species a\(^{-1}\) with an average of 0.046 species a\(^{-1}\). The highest rates are estimated for peatland vegetation, and for sites with high S deposition (cf. Table 2).
4. Discussion

4.1. Modelling species richness

The model combines the two distinct drivers, resulting in a model (equation 2) that gives stronger relationships than either driver separately, which is necessary to take into account both acidification and eutrophication effects on $n_{sp}$. The best version (Model C, Table 5), distinguishes vegetation classes only in terms of the parameter $\alpha$, which provides a general measure of species richness in a vegetation class; the $\alpha$ values suggest that woodland tends to be the most species-rich of the four classes, while grassland, heathland and peatland are quite similar.

Ideally, the construction of a model relating $n_{sp}$ to soil pH and NPP would be based on empirical measurements of both driving variables at each site where the richness is determined. We have such data for pH, but NPP estimates have not been part of the CS studies, and therefore we used values modelled as averages over 5 km x 5 km grid cells. Another limitation in the modelling is that the available data for parameterization and testing refer only to relatively recent times, i.e. from 1978 onwards. This means that there are relatively few values of $n_{sp}$ from remote relatively unpolluted sites, that might approach near-pristine conditions. Therefore, application of the model to unpolluted conditions involves some extrapolation, as noted in Section 3.3.

The results of tests on independent data provide support for the parameterizations from 2007 data. Earlier CS data for 1978 and 1998 are predicted quantitatively and without bias, with parameters obtained by fitting the 2007 data (Fig. S5), and changes in $n_{sp}$ at the CS plots are also captured (Fig. S6). However, although the predicted values of $n_{sp}$ are strongly correlated with data reported in two other studies (Fig. 4), the absolute reported values are in the upper range of CS values and so are underpredicted. This is probably because these other studies (Grime, 1973; Stevens et al., 2004) used internally more homogenous examples of each grassland type associated with stable, well-established grazing regimes. The random sampling approach used in CS results in a noisier sample, more representative of the range of variation in the wider countryside where assignment to each grassland habitat type is post hoc rather than predetermined during study design (Maskell et al., 2010).

Additional support for the model, in terms of the structure of equation (2), is that it predicts that slopes of $n_{sp}$ against NPP should become more negative with increasing pH (Fig. S4), behaviour that has been reported for the Park Grass experiments at Rothamsted (Crawley et al., 2005).

We did not find evidence for the operation of the unimodal (hump back) model of Grime (1973), in which lower $n_{sp}$ at low NPP would be expected. This applied to both the 2007 data and the data from 1978, when the ecosystems would have been less enriched in N, and therefore perhaps more likely to
reveal a positive relationship of $n_{sp}$ to $NPP_{calc}$ at low $NPP_{calc}$. The lack of evidence of unimodal behaviour is perhaps not surprising given the crude and highly-averaged nature of our NPP estimates, which do not reflect the considerable small-scale spatial variations in measured values (Tipping et al., 2019). Consequently, our ranges of $NPP_{calc}$ are more restricted than the ranges of productivity in studies that do provide evidence for the unimodal model (Huston, 2014; Fraser et al., 2015; Simkin et al., 2016).

Although the model accounts for a significant amount of the variance in $n_{sp}$, a considerable amount (76.1%) remains unaccounted for, and consequently uncertainty (95% CL) in the predicted values is about ±30%, depending upon the vegetation class (Fig. S8). It must result from controls on $n_{sp}$ other than soil pH and NPP, including land management, grazing, small-scale soil variation, climate and species pool effects, micronutrient levels, predation, competition, pathogens, seed dispersal, and stochastic events or short-range phenomena such as weather-induced population dynamics (Grace et al., 2016). These other controlling factors may cause $n_{sp}$ to be greater or smaller than average. If these other factors are constant over time, then relative changes due to variations in soil pH and NPP might still hold, but if they vary temporally then this will not be true. We therefore cannot claim to be simulating actual $n_{sp}$ over time at any particular place, nor even relative values. The outputs of the calculations are best thought of as estimations of idealised relative change in $n_{sp}$ over time, due to variations in soil pH and NPP, as affected only by $N_{dep}$ and $S_{dep}$.

In our analysis climate plays only a minor role in determining $NPP_{calc}$. This is principally because the N14CP model assumes that NPP is controlled by a single limiting factor, which for semi-natural sites in Britain is N availability. Temperature has only a minor effect via its influence on the turnover of soil organic matter, and the associated modification of N cycling rates (Tipping et al., 2017). With regard to soil pH, the soil chemical reactions assumed in the CHUM-AM model are only slightly affected by temperature. For neither N14CP nor CHUM-AM do trends in rainfall exert much influence. Therefore our estimates of $n_{sp}$ are hardly dependent upon climatic variation.

4.2. Different approaches to understanding atmospheric deposition effects

Previous studies of plant species richness across Britain and in Europe have mainly used modelled estimates of $N_{dep}$, with some studies including $S_{dep}$ as explanatory variables introduced into statistical regression models (Stevens et al., 2004; Maskell et al., 2010; Dupré et al., 2010; Mitchell et al., 2018). There are difficulties with such an approach because the N and S linger in the ecosystem, so that observed $n_{sp}$ at a given point in time may not be directly related to deposition in the same year. In the case of acidification, there is not a general, direct relationship between pollutant deposition and soil pH, since variations in soil chemistry, especially weathering rates, also control pH. Thus whilst
measured pH is a good predictor of $n_{sp}$, $N_{dep}$ and $S_{dep}$ are less effective. In the case of $N_{dep}$, although correlations can be established between species loss and contemporary deposition rates, on a spatial basis, it is less easy to extend these to take temporal change into account. Again, the ecosystem retains deposited N which changes relatively slowly in response to changes in deposition rates. As pointed out by Stevens (2016) the use of cumulative N deposition, while taking into account the long-term enrichment of ecosystems with N, does not allow for N loss and associated ecosystem recovery to occur. This has led to the recent recommendation of a moving 30-year cumulative average (Rowe et al., 2017; Payne et al., 2019).

The modelling reported here is a more fundamental approach, based on process understanding using previously published studies to parameterize a particular function form. Relating richness to biogeochemical cycling permits a starting $n_{sp}$ to be calculated, based on the acquisition of N by fixation in earlier years, which was superseded by $N_{dep}$ during the period of the simulation (1800-2010). By distinguishing the separate dependences of $n_{sp}$ on soil pH and NPP$_{calc}$, equation (2) permits the separate effects of $N_{dep}$ and $S_{dep}$ to be estimated. However, whereas modelling NPP at a large scale is feasible, at least in terms of averages, pH is difficult to predict, since it can be highly spatially variable. Thus the CHUM-AM modelling has depended upon calibration to individual catchments. For both variables, and biogeochemistry as a whole, large scale modelling gives only average values, which will therefore always restrict the accuracy of prediction, until such time as measured data at high resolution become available to drive biogeochemical models. With regard to how plants respond to changes in NPP and pH, we have assumed here that, although changes in NPP and pH result from gradual changes in soil properties, $n_{sp}$ responds to them instantaneously in a given year. It seems likely that there would actually be some lag in the response (Posch et al., 2004; Clark et al., 2013; Rowe et al., 2017), but it is difficult to test this, given the high degree of scatter in the available data.

4.3. Long-term changes in $n_{sp}$

The long term simulations of $n_{sp}$ using Model C rely on the estimations of pH and NPP at the different sites over time. The pH values refer to averages over each of the catchments, while the NPP values are averages for each vegetation class over 5 km x 5 km grid cells. Changes of surface water pH calculated with CHUM-AM over 100-200 years are realistic by comparison with estimates of pH change estimated from diatom sediment records (Tipping & Chaplow, 2012). Furthermore, CHUM-AM was calibrated using data covering periods during which surface water pH changed appreciably in most cases, which strengthens belief in the calculations. That soil pH is reasonably estimated is shown from comparisons of changes in CHUM-AM-predicted values for 1978-1998 and 1978-2007 with CS measurements for similarly-acid soils, and with results from the NSI surveys (Section 3.2). Although it
seems logical for continued depositional inputs of N over time to have increased productivity in N-limited ecosystems, such as the grassland, heathland and woodland considered here, empirical evidence of long term change in NPP is lacking. We have previously presented evidence that modelled NPP is compatible with available measured values for sites in Britain, albeit in a correlation with high scatter, and that NPP is related to N$_{dep}$ (Tipping et al., 2019). If space-for-time substitution holds, then it can be assumed that NPP has increased over time. Moreover, increases in soil C over periods of several decades were consistent, through the N14CP model, with a long-term N fertilization effect of N$_{dep}$ on NPP (Tipping et al., 2017).

The long term modelling results (Table 7, Figs. 5 and S7) show declines in $n_{sp}$ of between 23 and 100% from an assumed pristine condition in 1800 to the latter part of the 20$^{th}$ Century, after which recovery took place. In 2010, the simulated $n_{sp}$ values averaged 76% of the 1800 ones, compared to 54% at the times of maximum species loss. Nearly all of the calculated recoveries result from the reversal of soil acidification, although in recent years slight decreases in NPP are simulated, with consequent small upturns in $n_{sp}$. Since peatland NPP is supposed not to depend upon N$_{dep}$, the recovery of $n_{sp}$ at the peatland sites, owing to acidification reversal, is calculated to be nearly complete. Again, we emphasise that these are changes for idealised conditions, driven only by N$_{dep}$ and S$_{dep}$.

These findings are consistent with the results of plant trait analyses in British semi-natural terrestrial ecosystems by Maskell et al. (2010) and Stevens et al. (2010), who concluded that acidification had a greater effect than eutrophication on species decline in acid grasslands and heathlands. Of the five site/vegetation examples that fall into these vegetation categories, soil pH does indeed dominate in two cases (River Etherow, Lochnagar), whereas the pH and NPP effects are about equal for the other three (Cote Gill, Mosedale Beck, Old Lodge). Furthermore, Maskell et al. concluded that eutrophication was the dominant effect in calcareous grassland, and again this is borne out by our results for the South Downs site. Our modelling results are also reasonably consistent with measured changes in $n_{sp}$ over recent decades at sites in the UK Environmental Change Network; Rose et al. (2016) found average increases of 0.14, 0.066 and 0.059 species per year in 4 m$^2$ quadrats as the averages for lowland, upland and woodland respectively over the period 1993 to 2012 (slightly later than in our modelling). The average rate of change from the data of Table 7 is 0.046 species per year, comparable to the values of Rose et al.

The analysis reported here follows applications of the N14CP model to calculate long-term increases in soil C (Tipping et al., 2017) and NPP (Tipping et al., 2019), both driven by N$_{dep}$ fertilization. Despite the coherence of the modelling and results, the evidence for these effects of N$_{dep}$ is not yet conclusive; in particular the prediction of an increase in NPP due to fertilization by N$_{dep}$, although statistically
significant, is tenuous, owing to the extremely noisy data (Tipping et al., 2019). If the trends are
correct, however, they mean that $N_{\text{dep}}$ has promoted C storage while diminishing plant diversity, and
so there is a conflict between two desirable environmental outcomes.

Since $S_{\text{dep}}$ in Britain has declined so markedly in recent decades, variations in $N_{\text{dep}}$ are likely to have
the most effect on $n_{\text{sp}}$ in the future. Our calculations suggest that a slight recovery from eutrophication
has taken place already, reflecting decreases in $N_{\text{dep}}$ in recent years. Continued $N_{\text{dep}}$ at present levels,
or further declines, would be expected to lead to further increases in $n_{\text{sp}}$ at the N-limited non-peatland
sites. This prediction differs from that of Stevens et al. (2016) who forecast continued declines in
richness, based on cumulative $N_{\text{dep}}$. However, their conceptual model did not take account of
 terrestrial N turnover, and the loss of N from ecosystems under lowered $N_{\text{dep}}$, which are features of
the N14CP model, and would also be taken into account by the use of moving average cumulative N
deposition (Rowe et al., 2017; Payne et al., 2019).

4.4 Developments and wider applications

In the work described here, we combined measured soil pH and modelled NPP, both of which are
strongly affected by atmospheric pollution, as drivers of the $n_{\text{sp}}$ model, and used spatial data for
calibration. To improve this analysis, in future work, measurements of NPP at CS sites where $n_{\text{sp}}$ is
determined would provide valuable additional data for model calibration. Another possibility is to
make use of NPP estimated from remote sensing, drawing on high spatial resolution mapping studies
(TEBBS et al., 2017). With regard to further model testing and improved calibration in the British
context, it could be informative to analyse results from the unfertilised experimental plots of the
Rothamsted Park Grass experiment (Crawley et al., 2005; Silvertown et al., 2006), for which time series
data covering more than 150 years on plant species diversity and soil pH are available, together with
measurements of herbage mass, obtained in the management of the site by annual mowing.

The parameterizations of equation (2) reported here cannot be regarded as universal, but specific to
the particular conditions in these British locations. To explore the wider applicability of the model,
analyses might be conducted at larger scales. For example, the large set of species richness and soil
pH data for the USA reported by Simkin et al. (2018) could be analysed, with modelled NPP or NPP
estimated by remote sensing (Zhao et al., 2005). Another possibility is to make use of the data
assembled by Fraser et al. (2015) for grasslands worldwide. These two sets cover wider ranges of $N_{\text{dep}}$
and NPP than experienced by locations in Britain, and so might include low-NPP sites where $n_{\text{sp}}$
increases with NPP. If so, a more complex form of equation (2) would be required, to take account of
the unimodal relationship.
In the present study, to conduct temporal modelling, we took advantage of previous acidification modelling with CHUM-AM at a small number of well-calibrated catchments. To provide a more comprehensive analysis for Britain, it would be necessary to calibrate the topsoil part of CHUM-AM or another dynamic soil acidification model such as VSD (Posch and Reinds, 2009) to individual CS plots, using measured pH and deposition history. This would permit $n_{sp}$ to be simulated at both large spatial and long temporal scales. Similar approaches could be applied more widely, at regional and perhaps global scales; the key is to relate soil pH and NPP to atmospheric deposition, which is rare in current large-scale biogeochemical models or dynamic global vegetation models. Such modelling could lead to useful forecasts of species richness responses to pollution, given appropriate future scenarios of $N_{dep}$ and $S_{dep}$. 
5. Conclusions

- A model of plant species richness ($n_{sp}$) based on simulated NPP and measured soil pH accounts for 24% of the variation in $n_{sp}$ at British semi-natural grassland, heathland, peatland and woodland sites.

- The model is validated through comparison with (a) independent Countryside Survey data, both absolute $n_{sp}$ values, and $n_{sp}$ changes between years, (b) independent published data sets, and (c) observed recent increases in $n_{sp}$ at sites within the UK Environmental Change Network.

- Results for nine site/vegetation cases across Britain suggest that past losses of richness were in the range 23 to 100% (average 39%), depending upon the extent of atmospherically deposited pollution by nitrogen and sulphur, and on soil and vegetation properties.

- In four of the nine cases, $n_{sp}$ was affected about equally by pH and NPP, while in another four the effect of pH was dominant. The ninth site, a chalk grassland, was affected only by NPP, since soil pH was assumed constant.

- Recovery is calculated to have taken place over recent decades, largely due to acidification reversal, with an average increase of 0.046 species per year over the period 1993 to 2010.

- There are indications of recovery from the eutrophying effects of N deposition, with slight increases in predicted $n_{sp}$ in recent years.
Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2021.117017.

Author contributions

Edward Tipping; Conceptualization, Writing - original draft, Project administration, Investigation, Software, Methodology, Funding acquisition, Jessica A.C. Davies; Investigation, Software, Writing - review & editing, Peter A. Henrys; Investigation, Software, Writing - review & editing, Susan G. Jarvis; Investigation, Software, Writing - review & editing, Simon M. Smart; Conceptualization, Investigation, Software, Writing - review & editing.
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Table 1. Summary of Countryside Survey field data; the values are the numbers of plots sampled for species richness and soil pH in each vegetation class, by year of sampling and quadrat size.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>200</td>
<td>200</td>
<td>4</td>
<td>200</td>
</tr>
<tr>
<td>grassland</td>
<td></td>
<td>90</td>
<td>81</td>
<td>573</td>
<td>573</td>
</tr>
<tr>
<td>heathland</td>
<td></td>
<td>218</td>
<td>226</td>
<td>189</td>
<td>189</td>
</tr>
<tr>
<td>peatland</td>
<td></td>
<td>96</td>
<td>216</td>
<td>223</td>
<td>223</td>
</tr>
<tr>
<td>woodland</td>
<td></td>
<td>43</td>
<td>58</td>
<td>171</td>
<td>171</td>
</tr>
</tbody>
</table>
Table 2. Catchments for which CHUM-AM has been calibrated, and used for simulation of long-term variation in $n_{sp}$. The total deposition values (g m$^{-2}$ a$^{-1}$) (non-marine for $S_{dep}$) refer to non-tree vegetation, and are given for years when deposition rates were approximately maximal. The references are to studies in which topsoil pH was modelled; soil chemistry was not modelled for the chalk soil of the South Downs.

<table>
<thead>
<tr>
<th>Catchment</th>
<th>Location</th>
<th>Area (km$^2$)</th>
<th>Vegetation</th>
<th>$N_{dep}$ 1990</th>
<th>$S_{dep}$ 1970</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cote Gill</td>
<td>Central Pennines</td>
<td>5.0</td>
<td>grassland</td>
<td>2.9</td>
<td>6.0</td>
<td>Tipping et al., 2010</td>
</tr>
<tr>
<td>River Etherow</td>
<td>South Pennines</td>
<td>13.0</td>
<td>peatland &amp; grassland</td>
<td>3.4</td>
<td>6.0</td>
<td>Tipping et al., 2010</td>
</tr>
<tr>
<td>Great Dun Fell</td>
<td>North Pennines</td>
<td>0.2</td>
<td>peatland</td>
<td>2.3</td>
<td>2.3</td>
<td>Tipping et al., 2010</td>
</tr>
<tr>
<td>Lochnagar</td>
<td>Cairngorms</td>
<td>0.9</td>
<td>heathland</td>
<td>0.8</td>
<td>2.1</td>
<td>Tipping et al., 2007</td>
</tr>
<tr>
<td>Mosedale Beck</td>
<td>Lake District</td>
<td>3.7</td>
<td>grassland</td>
<td>3.2</td>
<td>5.2</td>
<td>Tipping and Chaplow, 2012</td>
</tr>
<tr>
<td>Old Lodge</td>
<td>Ashdown Forest</td>
<td>2.4</td>
<td>heathland &amp; woodland</td>
<td>2.3</td>
<td>2.1</td>
<td>Ashmore et al., 2004</td>
</tr>
<tr>
<td></td>
<td>South Downs</td>
<td>-</td>
<td>grassland</td>
<td>2.4</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>
Table 3. Comparison of different versions of the equation 2 model, fitted to data for separate vegetation classes. Key:  \( n_{\text{param}} \) = number of parameters, SS = sum of squared deviations, AIC = Akaike Information Criterion, \( \Delta \text{AIC} \) = difference in AIC between a model and the best model, \( w_{\text{AIC}} \) = AIC weight.

<table>
<thead>
<tr>
<th>Version</th>
<th>Parameters fitted</th>
<th>( n_{\text{param}} )</th>
<th>Grassland (n = 573)</th>
<th>Heathland (n = 189)</th>
<th>Woodland (n = 171)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SS</td>
<td>( \Delta \text{AIC} )</td>
<td>( w_{\text{AIC}} )</td>
<td>SS</td>
</tr>
<tr>
<td>1</td>
<td>( \alpha, \beta, \gamma, \text{pH}_0 )</td>
<td>4</td>
<td>18935</td>
<td>0.27</td>
<td>0.466</td>
</tr>
<tr>
<td>2</td>
<td>( \alpha, \gamma ) (( \beta = 0, \text{pH}_0 = 0 ))</td>
<td>2</td>
<td>23395</td>
<td>117.5</td>
<td>0.000</td>
</tr>
<tr>
<td>3</td>
<td>( \alpha, \beta, \text{pH}_0 ) (( \gamma = 0 ))</td>
<td>3</td>
<td>19514</td>
<td>15.54</td>
<td>0.000</td>
</tr>
<tr>
<td>4</td>
<td>( \alpha, \gamma, \text{pH}_0 ) (( \beta = 1 ))</td>
<td>3</td>
<td>18992</td>
<td>0.00</td>
<td>0.534</td>
</tr>
</tbody>
</table>
Table 4. Parameters with model version 1 from Table 3, fitted to vegetation classes separately. The value of γ for peatland was assumed to be the average of the values for the other three vegetation classes.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Grassland</th>
<th>Heathland</th>
<th>Woodland</th>
<th>Peatland</th>
</tr>
</thead>
<tbody>
<tr>
<td>α</td>
<td>10.4</td>
<td>8.1</td>
<td>15.2</td>
<td>10.3</td>
</tr>
<tr>
<td>β</td>
<td>0.557</td>
<td>0.677</td>
<td>0.297</td>
<td>0.573</td>
</tr>
<tr>
<td>$10^3\gamma$</td>
<td>-1.23</td>
<td>-0.92</td>
<td>-1.04</td>
<td>-1.06</td>
</tr>
<tr>
<td>pH₀</td>
<td>2.89</td>
<td>2.90</td>
<td>3.30</td>
<td>3.04</td>
</tr>
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</table>

Table 5. Results of fitting equation (2) to the combined data set ($n = 1156$). See Table 3 for key to abbreviations.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameters fitted</th>
<th>$n_{param}$</th>
<th>SS</th>
<th>ΔAIC</th>
<th>wAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>α, β, γ, pH₀ for each class</td>
<td>15</td>
<td>28100</td>
<td>8.95</td>
<td>0.08</td>
</tr>
<tr>
<td>B</td>
<td>common α, β, γ, pH₀</td>
<td>4</td>
<td>28472</td>
<td>2.15</td>
<td>0.252</td>
</tr>
<tr>
<td>C</td>
<td>α for each class; common β, γ, pH₀</td>
<td>7</td>
<td>28272</td>
<td>0.00</td>
<td>0.739</td>
</tr>
</tbody>
</table>

Table 6. Parameters adopted for predictive modelling with model C. The standard errors were obtained from Monte Carlo analysis (Section 2.4). SE = standard error.

<table>
<thead>
<tr>
<th>parameter</th>
<th>value</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>α grassland</td>
<td>11.7</td>
<td>1.3</td>
</tr>
<tr>
<td>α heathland</td>
<td>11.2</td>
<td>1.3</td>
</tr>
<tr>
<td>α peatland</td>
<td>11.6</td>
<td>1.3</td>
</tr>
<tr>
<td>α woodland</td>
<td>13.9</td>
<td>2.0</td>
</tr>
<tr>
<td>β</td>
<td>0.458</td>
<td>0.070</td>
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<tr>
<td>$10^3\gamma$</td>
<td>-1.12</td>
<td>0.097</td>
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<tr>
<td>pH₀</td>
<td>3.20</td>
<td>0.25</td>
</tr>
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</table>
Table 7. Summary of long-term simulations of average $n_{sp}$. Recent increases in $n_{sp}$ refer to the period 1993-2010.

<table>
<thead>
<tr>
<th>Site</th>
<th>Vegetation</th>
<th>$n_{sp}$ 1800</th>
<th>minimum $n_{sp}$</th>
<th>$n_{sp}$ 2010</th>
<th>maximum fractional decrease</th>
<th>recent increase $n_{sp}$ yr$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cote Gill</td>
<td>grassland</td>
<td>13.2</td>
<td>7.8</td>
<td>9.3</td>
<td>0.41</td>
<td>0.047</td>
</tr>
<tr>
<td>River Etherow</td>
<td>grassland</td>
<td>8.0</td>
<td>0.0</td>
<td>5.3</td>
<td>1.00</td>
<td>0.083</td>
</tr>
<tr>
<td>River Etherow</td>
<td>peatland</td>
<td>6.8</td>
<td>0.0</td>
<td>6.1</td>
<td>1.00</td>
<td>0.095</td>
</tr>
<tr>
<td>GDF</td>
<td>peatland</td>
<td>8.7</td>
<td>6.1</td>
<td>8.5</td>
<td>0.30</td>
<td>0.067</td>
</tr>
<tr>
<td>Lochnagar</td>
<td>heath</td>
<td>9.5</td>
<td>7.3</td>
<td>8.1</td>
<td>0.23</td>
<td>0.017</td>
</tr>
<tr>
<td>Mosedale Beck</td>
<td>grassland</td>
<td>13.0</td>
<td>7.5</td>
<td>8.5</td>
<td>0.42</td>
<td>0.038</td>
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<td>Old Lodge</td>
<td>heathland</td>
<td>6.4</td>
<td>3.5</td>
<td>4.7</td>
<td>0.45</td>
<td>0.034</td>
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<tr>
<td>Old Lodge</td>
<td>woodland</td>
<td>7.8</td>
<td>3.6</td>
<td>4.8</td>
<td>0.54</td>
<td>0.032</td>
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<tr>
<td>South Downs</td>
<td>grassland</td>
<td>18.7</td>
<td>14.1</td>
<td>14.5</td>
<td>0.25</td>
<td>0.000</td>
</tr>
</tbody>
</table>
Figure captions

Fig. 1. Location map, showing the sites for which CHUM-AM model has been calibrated.

Fig. 2. Averaged data for samples from 4 m² quadrats in 2007. The numbers of values averaged were: grassland 24, heathland 14, peatland 15, woodland 13. The error bars are standard deviations; when they are not visible in the x-axis data, they fall within the points.

Fig. 3. Observed \( n_{sp} \) vs \( n_{sp} \) calculated with Model C, for 4 m² quadrats, sampled in the 2007 Countryside Survey. Results for all four vegetation classes are shown. The 1:1 line is shown.

Fig. 4. Observed \( n_{sp} \) for grassland published by Grime (1973) for two dales in Derbyshire, and for the British survey of Stevens et al. (2004), vs values predicted with Model C, compared with the CS data for 2007 (from Fig. 3). Linear regression results: Lathkilldale, slope = 1.76, \( r^2_{adj} = 0.42, p < 0.0001, n = 39 \); Cressbrookdale, slope = 3.07, \( r^2_{adj} = 0.71, p < 0.0001, n = 34 \); Stevens’ survey, slope = 1.71, \( r^2_{adj} = 0.64, p < 0.0001, n = 61 \).

Fig. 5. Long-term variations in soil pH, NPP\(_{calc}\) and calculated \( n_{sp} \) (4 m² quadrats) at four sites. In the right-hand \( n_{sp} \) panels, the thick solid line refers to variations driven by both pH and NPP\(_{calc}\), the thin solid line is for constant pH (1800 value) and the dotted line is for constant NPP\(_{calc}\) (1800 value). Constant pH was assumed for the South Downs site, because the chalk soil has high buffering capacity (Section 3.3). Plots for the other five site/vegetation combinations are shown in Fig. S7.
Fig. 1
Fig. 2.
Fig. 3.
Fig. 4.
Fig. 5