May 2015

Deriving critical load functions for nitrogen and sulphur using threshold values of a habitat quality metric
Executive summary

As a signatory party to the Convention on Long Range Transboundary Air Pollution (CLRTAP), the UK has been requested to provide nitrogen and sulphur critical load (CL) functions “taking into account their impact on biodiversity”. These functions should describe the combinations of N and S deposition that are likely to cause immediate or eventual damage. In previous studies, it was established that: a) the mean habitat-suitability for positive indicator-species can be used in this context as an overall indicator of habitat quality (Defra project AQ0828); and b) values for this indicator decline with increases in N pollution at example sites with different habitats (Defra project AQ0832). These studies influenced the decision in 2014 by the CLRTAP Coordination Centre for Effects (CCE) to encourage all signatory parties to calculate habitat-suitability based indicators.

If the mean habitat-suitability for positive indicator-species (referred to in this report as the Habitat Quality Index, HQL) is to be used to define CL for a habitat, it is necessary to define a threshold value for this index below which the habitat should be considered to be damaged. In the current study, threshold values were determined for 40 example sites by calculating HQL using a biogeochemistry and species model (MADOC-MultiMOVE) run forward under a scenario with N deposition set to the empirical Critical Load, Cl_{emp}. The HQL value in 2100 under this scenario was considered to correspond to the threshold or critical value, HQL_{crit}. Once this threshold had been established, different combinations of N and S deposition that caused HQL to decline below HQL_{crit} were determined, and summarised into a simple function for each site.

Initial results of the study were submitted in response to the ‘Call for Data 2014-15’ by the CLTRAP Co-ordination Centre for Effects (CCE), meeting the deadline of 23rd March 2015, and presented at the 25th CCE Workshop in April 2015. The biodiversity-based critical load functions derived for example sites with acid grassland or wet heath were sensible, showing declines in habitat quality with both N and S pollution. Functions for bog sites showed sensitivity to N but not to S, and sensible functions were not obtained for calcareous grassland due to limited data availability. A revised set of results was prepared for only acid grassland and wet heath habitats, and submitted to the CCE on 18th May 2015. Preliminary and revised results are discussed in this report.
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1. Introduction

Air pollution by sulphur (S) and nitrogen (N) causes soil acidification, and nitrogen has additional effects on ecosystems through mechanisms such as eutrophication and formation of ground-level ozone. Substantial reductions in S pollution since the 1980s have led to a widespread recovery from acidification (Emmett et al., 2010) except on some weakly-buffered soils (Evans et al., 2012). Nitrogen pollution has also decreased, but by a smaller proportion. The current approach to assessing effects of N pollution are based on its contribution to acidification, using a comparatively simple mass-balance approach; and on its eutrophying and other effects, which are summarised using the “empirical critical load” approach. Empirical critical loads for N have been established by assessing evidence from experiments and some survey studies (Bobbink and Hettelingh, 2011). However, experimental studies may not capture the medium-term and long-term effects of N, since the effects of N deposition can be persistent and cumulative, and at many sites changes induced by N are likely to have already occurred when the experiment started. Also this approach does not adequately represent the combined effects of N and S pollution. For these reasons, the Coordination Centre for Effects (CCE) of the Convention on Long Range Transboundary Air Pollution (CLRTAP) has encouraged the development of dynamic modelling approaches that capture the combined effects of air pollution on biodiversity (e.g. Hettelingh et al., 2008). Progress was initially slow due to lack of consensus on how the outputs from such models (e.g. changes in habitat-suitability for each of a large set of plant and lichen species) should be interpreted in terms of policy targets such as “no net loss of biodiversity”. However, work funded by Defra under the AQ0828 and AQ0832 projects (Rowe et al., 2014a; Rowe et al., 2014b) has defined an index of Habitat Quality (HQL) for use in this context, i.e. mean habitat-suitability for positive indicator-species. This report describes the application of this index to the dynamic modelling of N and S impacts.

In most years the CCE issues a “Call for Data”, which helps to ensure that scientific efforts under the CLRTAP are coordinated and support the development of policy. The Call for Data 2014-15 was issued in draft form on 22nd April 2014, and officially adopted in October 2014 (http://www.wge-cce.org/Activities/Call_for_Data). The first aim of the Call addresses the grid projection used for data responses, and the second offers an opportunity for National Focal Centres (NFCs) to update data submissions. These aims will not be discussed in this report. The third aim is to “Apply novel approaches to calculate nitrogen and sulphur critical load functions taking into account their impact on biodiversity. For this, National Focal Centres are encouraged to use the ‘Habitat Suitability Index’ (HS - index) agreed at the M&M Task Force meeting”. The metric proposed for UK responses (HQL) is of this type, and indeed the presentation of the UK metric at the CCE Workshop in 2014 was a major factor in the CCE’s decision to encourage the use of metrics of this type.

The objective of the current study was to meet the third aim of this Call for Data by applying the habitat quality metric (HQL) developed in the AQ0828 and AQ0832. The MADOC-MultiMOVE model (Butler, 2010; de Vries et al., 2010; Rowe et al., 2014d) was used to determine combinations of N and S likely to cause habitat quality to decline below a threshold, i.e. biodiversity-based critical load functions. This report outlines the approach taken and illustrates this approach for a set of example sites.
2. Methods

2.1 Overview of methods

The basis of the study is the capacity to predict changes in habitat suitability for species under different pollutant deposition scenarios, which has been developed by linking dynamic models of biogeochemical change with regression models of habitat-suitability for individual species.

The biogeochemistry model used in the current study was MADOC (Rowe et al., 2014d), essentially a combination of the Very Simple Dynamic (VSD) acid-base chemistry model (Posch and Reinds, 2009) with a simple model of carbon (C) dynamics (Tipping et al., 2012). It is analogous to the VSD+ model (Bonten et al., 2010) which is being developed using a different model of C dynamics to extend VSD, but in the UK model more emphasis has been placed on processes that are important in upland systems and more C-rich soils, such as the production of dissolved organic C. The MADOC model responds to several environmental drivers such as the deposition loads of N and S, and was used to predict changes in soil pH, soil total C/N ratio, and the annual flux of available N from deposition and release from soil organic matter.

The habitat-suitability model used in the current study was MultiMOVE (Butler, 2010). This predicts the suitability of a site for each of around 1300 plant and lichen species, depending on the current environmental conditions. These conditions are expressed using four indicators that are based on trait-means for the species present (mean “Ellenberg R” for alkalinity; mean “Ellenberg N” for eutrophication; mean “Ellenberg F” for wetness; mean “Grime Height” for vegetation height) and three climate-based indicators (minimum January and maximum July temperature, and annual precipitation). The habitat-suitability values predicted by MultiMOVE were rescaled by prevalence in the training dataset, using the method of Real et al. (2006). Values rescaled in this way are comparable among species and can be used to reconstruct a plausible set of plant species for a given site (Rowe et al., 2014a).

Habitat-suitability for a large set of species could be analysed and interpreted in many different ways. The AQ0828 and AQ0832 studies established that the most suitable indicator of overall habitat quality that can be calculated from these outputs is the mean habitat suitability for positive indicator-species. This conclusion was reached following a detailed consultation with habitat specialists of the Statutory Nature Conservation Bodies (Rowe et al., 2014b). In the current study, species-level model outputs were summarised using this Habitat Quality Index (HQI).

To calculate N and S critical load functions using such an index requires definition of a threshold value below which the site should be considered to be in damaged or unfavourable condition. To establish this threshold, the value of HQI was calculated under a scenario where N deposition was set to the empirical N critical load (CL\textsubscript{empN}), using the ‘mapping value’ for CL\textsubscript{empN} as determined for each site by the UK National Focal Centre, and no anthropogenic sulphur deposition. The CL\textsubscript{empN} was originally set, on the basis of evidence and/or expert judgement, at a level intended to avoid damage in the near- and long-term. By running the model chain forward at the critical load for an extended period, the resulting value of HQI can be assumed to correspond to a threshold or critical value. The model chain was run forward to 2100 as recommended by the CCE. This date is a compromise between capturing the effects of N persisting over many decades (although with diminishing impacts) and the increasing uncertainty associated with predicting effects in future centuries. For comparison, values for HQI in 2100 were also calculated for two other critical load scenarios, with S deposition set to CL\textsubscript{maxS} and N deposition at either zero or CL\textsubscript{minN} (see Figure 1).
Figure 1. Illustration of three Critical Load combinations of nitrogen and sulphur deposition for which the MADOC-MultiMOVE model was run forward to 2100: a) \( S = CL_{\text{maxS}}, N = 0 \); b) \( S = CL_{\text{maxS}}, N = CL_{\text{minN}} \) and c) \( S = 0, N = CL_{\text{empN}} \). Scenario c) was used to define a threshold value for the habitat quality index, \( HQI_{\text{crit}} \).

Using the threshold established in this way, a more complete picture of N and S effects on ecosystems can be obtained, by running the model chain at different rates of N and S deposition to determine which combinations cause \( HQI \) to decline below the threshold. The combinations that give \( HQI = HQI_{\text{crit}} \) were assumed to correspond to the ‘biodiversity-based’ Critical Load function which was the goal of the exercise. Such a CL function is illustrated for a hypothetical site in Figure 2.

A simplified version of the CL function (blue line in Figure 3) was illustrated in the Call for Data instructions (CCE, 2014). Responses were requested in the form of two values on each of the S and N deposition axes: \( CL_{\text{LminN}}, CL_{\text{Smax}}, CL_{\text{Nmax}} \) and \( CL_{\text{Smin}} \). Clearly such a simple function can only be an approximation of a curvilinear function, as shown for the hypothetical example (Figure 2).
Figure 3. Reproduced from CCE (2014). Extension of Critical Load function for nitrogen and sulphur deposition to include biodiversity-based critical loads. The 9 critical load quantities asked for in the Call are: \( CL_{\text{nutN}} \), \( CL_{\text{empN}} \), the 3 quantities defining the acidity CL function (\( CL_{\text{maxS}} \), \( CL_{\text{minN}} \), \( CL_{\text{maxN}} \); in brown) and the 4 quantities defining a new biodiversity CL function (\( CL_{\text{minN}} \), \( CL_{\text{maxS}} \), \( CL_{\text{minN}} \), \( CL_{\text{maxS}} \); in blue). The darkest area shows the ‘minimal critical load function’, i.e. the combinations of \( N \) and \( S \) deposition for which none of the CLs is exceeded.

The overall workflow is summarised in Figure 4. The MADOC model was set up using values collated by the UK NFC for climate and soil parameters. The model was calibrated to match present-day values of two key observations, soil pH and soil total C/N ratio, by adjusting parameters whose true value is unknown. The target values for pH and C/N used in the current study were mean values for the broad habitat corresponding to the EUNIS class for the site, as observed in Countryside Survey 2007 (Emmett et al., 2010). Soil pH was matched by adjusting calcium weathering rate or the density of exchangeable protons on dissolved organic carbon. Soil total C/N ratio was matched by adjusting the rate of N fixation during the pre-industrial period. The calibrated model was then run again with N and S deposition set, for the period 1980-2100, to each of three Critical Load combinations (i.e. \( CL_{\text{maxS}} \), \( CL_{\text{minN}} \) and either \( CL_{\text{empN}} \) or \( CL_{\text{maxN}} \)). The environmental conditions in 2100 were used to calculate habitat-suitability for positive indicator-species, and thence HQI. The mean HQI for the three Critical Load scenarios was assumed to correspond to a threshold level for the site, \( HQI_{\text{crit}} \). The model chain was then re-run, to find combinations of N and S deposition below which this \( HQI_{\text{crit}} \) value was exceeded.
2.2 Example sites

The aim of the study, as outlined above, was to establish a suitable threshold value for $HQI$ and use this to calculate a critical load function describing combinations of N and S which will prevent loss of biodiversity. This required an assessment of variation in this threshold value – in different habitats, and with geographic variation in species occurrence as explained below. To assess this variation, $HQI_{crit}$ and critical load functions were determined for example sites. For the initial response to the Call for Data, a set of seven sites was chosen covering a range of habitats (Table 1; Figure 5a). The models were set up for these sites using data maintained by the National Focal Centre (NFC, http://cldm.defra.gov.uk/), using the 1 x 1 km grid of soil and vegetation data that is held for each N-sensitive habitat.

After evaluating the results, it was decided to base the final UK Call for Data response on fewer habitats but with more example sites for each (Figure 5b). These sites were chosen from the database of Special Areas for Conservation (SACs) maintained by the NFC. Example SACs with either E1.7 ‘Closed non-Mediterranean dry acid and neutral grassland’ or F4.11 ‘Northern wet heaths’, were selected at random from the database.

These approaches were taken to show that the model chain can be applied to the existing NFC dataset, and also to develop capacity to predict and map biodiversity responses to pollution scenarios across all UK grid squares. Model runs could be refined for specific sites by including local information, where this exists.

<table>
<thead>
<tr>
<th>Site</th>
<th>East</th>
<th>North</th>
<th>NFC code</th>
<th>EUNIS</th>
<th>EUNIS habitat name</th>
</tr>
</thead>
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<tr>
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<td>320</td>
<td>653</td>
<td>452522</td>
<td>D1</td>
<td>Raised and blanket bogs</td>
</tr>
<tr>
<td>Thorne Moor</td>
<td>474</td>
<td>416</td>
<td>618576</td>
<td>D1</td>
<td>Raised and blanket bogs</td>
</tr>
<tr>
<td>Moor House</td>
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<td>535878</td>
<td>D1</td>
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<td>Porton Down</td>
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<td>137</td>
<td>813828</td>
<td>E1.26</td>
<td>Sub-Atlantic semi-dry calcareous grassland</td>
</tr>
<tr>
<td>Newborough</td>
<td>243</td>
<td>364</td>
<td>654745</td>
<td>E1.26</td>
<td>Sub-Atlantic semi-dry calcareous grassland</td>
</tr>
</tbody>
</table>
2.3 Predicting biogeochemical change

Deposition sequences

The MADOC model was set up using deposition sequences for S and N provided by EMEP. After calibrating the model (see above) using these deposition sequences, the model was re-run under three different scenarios corresponding to the three CL combinations of N and S previously established for the site. To reflect the cumulative and persistent effects of N, deposition was set to the CL values from 1980, and MADOC was run forward to 2100 as requested by the CCE. Values for soil pH, soil C/N ratio, available N flux and above-ground plant biomass were used to indicate environmental conditions likely at this date.

2.4 Predicting changes in habitat quality

Changes in habitat suitability for species

The biogeochemical conditions predicted by MADOC for 2100 under three Critical Load scenarios were used to estimate positions on each of the gradients that define habitat-suitability for species in the MultiMOVE model. These gradients are mean values for floristic traits – for wetness ($E_w$),
alkalinity ($E_R$), fertility ($E_N$) and vegetation height ($G_H$). Together with climate variables (maximum July temperature, minimum January temperature and total annual precipitation), these trait-means define the environmental conditions at a site. Biogeochemical conditions were related to trait-means using relationships established from empirical data (Table 2).
Table 2. Conversion equations used to estimate floristic trait-means (used to predict habitat-suitability for species) from biogeochemical conditions. $E_W = \text{mean Ellenberg 'moisture' score for species present}$; $E_R = \text{mean Ellenberg 'alkalinity' score for present species}$; $E_N = \text{mean Ellenberg 'fertility' score for present species}$; $G_H = \text{mean Grime 'height' score for present species}$; $MC = \text{soil moisture content, g water 100 g}^{-1} \text{fresh soil}$; $pH = \text{soil pH}$; $N_{av} = \text{available N, g N m}^{-2} \text{yr}^{-1}$; $CN = \text{CN ratio, g C g}^{-1} \text{N}$; $H = \text{canopy height, cm}$; $C_{plant} = \text{total plant biomass C}$. Mean $G_H$ was weighted by observed cover or occurrence frequency; other trait-means were not weighted.

<table>
<thead>
<tr>
<th>Value to be estimated</th>
<th>Calculated as</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E_W$</td>
<td>$\ln \left( \frac{MC}{100 - MC} \right) + 3.27$</td>
<td>Smart et al. (2010)</td>
</tr>
<tr>
<td>$E_R$</td>
<td>$pH - 2.5$</td>
<td>Smart et al. (2004)</td>
</tr>
<tr>
<td>$E_N$</td>
<td>$0.318 \log_{10} N_{av} + 1.689 + \frac{284}{CN}$</td>
<td>Rowe et al. (2011b)</td>
</tr>
<tr>
<td>$G_H$</td>
<td>$\max (1, 1.17 \times \ln H - 1.22)$</td>
<td>Rowe et al. (2011b)</td>
</tr>
<tr>
<td>$H$</td>
<td>$\left( \frac{C_{plant}}{14.21 \times 3} \right)^{1/0.814}$</td>
<td>derived from Parton (1978) and Yu et al. (2010)</td>
</tr>
</tbody>
</table>

Whether changes in vegetation height should be included is debatable. If management intensity increases to compensate for extra herbage production, the vegetation height may not change. However, faster closure of gaps is probably a key driver of species loss as systems become more productive, since the diversity of strategies for colonising new gaps is an important factor in maintaining overall plant diversity. This argues for the inclusion of an effect on ground-level light availability of extra biomass production, even if the vegetation height changes little, and this approach was taken in the current study, with simulated changes in height taken into account in the species modelling.

The MultiMOVE model was used to determine the suitability of the site for positive indicator-species for the habitat, under the conditions projected to occur in 2100 under the CL scenario. The model predicts habitat-suitability using several statistical modelling techniques in an ensemble approach (Butler, 2010), and for the current study the model-average habitat-suitability was used. Raw suitability predicted by the model were standardised for prevalence in the training dataset using the method of Real et al. (2006). Habitat suitability was estimated for all species that were: a) positive indicator-species for the habitat (see Section 2.4); and b) present in the surrounding 10x10 km square.

**Summary metric**

To calculate HQI, i.e. mean habitat suitability for positive indicator-species, requires definition of the indicator-species relevant for a site. The lists of indicator species used to calculate HQI in the AQ0832 study (Rowe et al., 2014b) were derived from common standards monitoring (CSM) guidance documents (e.g. JNCC, 2006). Judgements were made as to which species to include or exclude as positive indicators. Since that study, lists of positive indicator-species have been made available as a result of a combined effort by the Joint Nature Conservation Committee (JNCC) and the Botanical Society of the British Isles (BSBI) (Kevin Walker, pers. com.) and were used in the current study. However, neither the CSM guidance nor the more recent effort lists species for EUNIS.
habitat classes, which need to be used for the CCE data submission. To obtain suitable lists for these classes we used correspondence tables developed by Ian Strachan under the JNCC AND-UP project (Jones et al., in prep).

At a given site, particular positive indicator-species might not be present due to unsuitable climate rather than because of the effects of pollution. To avoid underestimating the overall habitat-suitability for positive indicator-species, species that had never been recorded from a particular grid-square were excluded when calculating the mean habitat-suitability. The records used for this filtering were obtained from the Botanical Society of the British Isles, the British Lichen Society and the British Bryological Society.

2.5 From habitat quality to critical load functions

Following calibration of MADOC to match the C/N ratio and soil pH values obtained from the NFC database for the soil and vegetation type, this model was run forward to 2100 with deposition set to each of the CL combinations of N and S (see section 2.3). The resultant abiotic conditions were used to predict the value of HQI under each of these CL combinations, and the mean value was used as $HQI_{\text{crit}}$ for the site (see section 2.4).

Ideally, the new CL function would be established by determining the exact combinations of N and S deposition that result in $HQI = HQI_{\text{crit}}$. Routines to do this could be developed, but would require calibration of the whole MADOC-MultiMOVE chain, which would currently be too time-consuming. Instead, the model chain was run using 10 x 10 combinations of N and S deposition, evenly covering ranges from 20% to 200% of $CL_{\text{emp}}$ and $CL_{\text{maxS}}$, respectively (see Figure 3). This allowed the response surface to be plotted, and a contour-fitting routine was applied to interpolate the new CL function. This function was simplified into the two-node form (i.e. $[N=CL\text{Nmin}, S=CLS\text{max}]$ and $[N=CL\text{Nmax}, S=CLS\text{min}]$; see Figure 3) required for responding to the CCE Call for Data, by positioning these nodes so that differences from the interpolated function were minimised within these deposition ranges.
3. Results

3.1 Biogeochemical change

The dynamic effects of different air pollution scenarios extended over the 21st century are illustrated below for the Snowdon acid grassland site. The time course of N and S deposition is shown for i) current legislated emissions, and for three Critical Load combinations: ii) S deposition at Cl_{max S}; iii) S deposition at Cl_{max S} together with N deposition at Cl_{min N}; and iv) the empirical N critical load, Cl_{emp N} (Figure 6). At this site Cl_{emp N} is greater than the current legislated emissions, so the Cl_{emp N} scenario causes relative increases in C/N (due to stimulated production of plant litter with a high C/N), N availability and vegetation height (Figure 7). Sulphur pollution was reduced in all the CL scenarios, so these showed increases in pH, although N leaching in the Cl_{emp N} scenario caused pH to decrease in the longer term.

Figure 6. Deposition rates of a) nitrogen and b) sulphur at Snowdon (a Welsh acid grassland site) under four scenarios: i) deposition predicted with current legislated emissions under the Gothenberg protocol; ii) N = 0, S = Cl_{max S}; iii) N = Cl_{min N}, S = Cl_{max S}; and iv) N = Cl_{emp N}, S = 0.

Figure 7. Simulated responses at Snowdon (a Welsh acid grassland site) of a) soil C/N, g g^{-1}, b) available N, kg N ha^{-1} yr^{-1}, c) soil pH and d) vegetation height, cm, to four N and S deposition scenarios: i) deposition predicted with current legislated emissions under the Gothenberg protocol; ii) N = 0, S = Cl_{max S}; iii) N = Cl_{min N}, S = Cl_{max S}; and iv) N = Cl_{emp N}, S = 0.
The sensitivity of the MADOC-MultiMOVE model chain was explored by varying N deposition over the range of 20-200 % of $C_{\text{LempN}}$ and S deposition over the range of 20-200 % of $C_{\text{LmaxS}}$ (Figure 8). Increases in both N and S caused pH to decline. Soil C/N ratio and plant-available N both increased with greater rates of N deposition but were not affected significantly by S deposition.

![Figure 8](image)

**Figure 8.** Simulated sensitivity of biogeochemical properties: a) pH; b) C/N ratio, g C g$^{-1}$ N; c) plant-available N, g N m$^{-2}$ yr$^{-1}$, to variation in nitrogen and sulphur deposition at the Whim Moss blanket bog site.

### 3.2 Species change

The habitat-suitability for individual species is calculated on the basis of floristic trait-means, the values of which are inferred from biogeochemical properties (see Table 2). The sensitivity of the three trait-means that are most responsive to N and S deposition was assessed over ranges of 20-200 % of $C_{\text{LempN}}$ and 20-200 % of $C_{\text{LmaxS}}$ (Figure 9). The response of the alkalinity trait to N and S was similar to the pH response. Trait-means representing fertility and vegetation height both increased with more N deposition but were hardly affected by S deposition.

![Figure 9](image)

**Figure 9.** Simulated sensitivity of mean values for floristic traits: a) Ellenberg R i.e. alkalinity; b) Ellenberg N i.e. fertility; c) Grime H i.e. height, to variation in nitrogen and sulphur deposition at the Whim Moss blanket bog site.

The trait-mean values calculated above were used to explore the sensitivity of individual species to variation in N and S pollution. Three of the positive indicator-species for blanket bog were selected to illustrate different types of response (Figure 10). Habitat-suitability for all three species declined with more N deposition, steeply in the case of *Drosera rotundifolia*. This species was relatively insensitive to S deposition. The other two species illustrated show contrasting responses to increased S deposition, which made the site more suitable for *Vaccinium myrtillus* but less suitable for *Trichophorum cespitosum*. 

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Figure 10. Simulated sensitivity of habitat suitability (rescaled by prevalence) for selected positive indicator-species: a) Round-leaved sundew; b) Bilberry; c) Deergrass, to variation in nitrogen and sulphur deposition at the Whim Moss blanket bog site.

3.3 Habitat Quality Index

The overall response of the habitat was summarised using the HQI metric, i.e. mean habitat suitability (rescaled by prevalence) for all locally-occurring positive-indicator species. The sensitivity of HQI to variation in N and S deposition was assessed over ranges of 20-200% of CL$_{\text{empN}}$ and 20-200% of CL$_{\text{maxS}}$ for the Whim Moss blanket bog site (Figure 11). Although other positive indicator-species were included, the response is similar to the surface that would be obtained by averaging the responses for the three species illustrated in Figure 10. Clearly positive and negative responses to S deposition (i.e. principally to acidification) cancelled out, and there was no overall response of HQI to variation in S deposition within this range. By contrast there was a strong overall response of HQI to N deposition (i.e. principally to eutrophication and increased vegetation height), with clear decline at greater N deposition rates.

Figure 11. Simulated sensitivity of an overall habitat quality index HQI, the mean habitat-suitability (rescaled by prevalence) for locally-occurring positive indicator-species, to variation in nitrogen and sulphur deposition at the Whim Moss blanket bog site.
3.4 Biodiversity-based Critical Load functions

A threshold value for the habitat quality metric, $HQI_{crit}$, was determined by calculating the HQI value in 2100 under a scenario with N deposition set to the empirical critical load. Combinations of N and S deposition that result in HQI values below this threshold were assumed to be in exceedance of the biodiversity-based critical load. The biodiversity-based CL function was derived as the line of combinations of N and S deposition that gave an HQI value of exactly $HQI_{crit}$. This function is illustrated for examples of four EUNIS habitats in the left-hand and middle columns of plots in Figure 12. An approximation of each function, required for the CCE Call for Data response and made by fitting two points on the N x S plane to minimise differences from the exact function, is shown in the right-hand column of plots in Figure 12.

The responses of HQI to N and S pollution at the wet heath and acid grassland sites illustrated were broadly as expected, in that HQI values declined with both N and S deposition. The response surface for the acid grassland site shows some anomalies – for example, at the pH value corresponding to 60 % of CL$_{max}$ deposition, if the N deposition is at 80 % of CL$_{empN}$, both a decrease to 60 % of CL$_{empN}$ and an increase to 100% CL$_{empN}$ will cause a slight increase in HQI. This illustrates the effect of including many species with responses that depend on the values for all the environmental axes at the particular site, in that overall responses may not always be clearcut. Nevertheless, since HQI mainly declined with increases in both N and S deposition, it was possible to make an approximate function of the form required for the Call for Data response.

At the blanket bog site, HQI declined with N pollution, but changes in S pollution had little effect on HQI. This is presumably due to the combination of two effects. Firstly, the soil pH at the site was calibrated to a typical value for UK blanket bog, 4.51 (Emmett et al., 2010). This is quite acid, and because pH is measured on a negative logarithmic scale, further decreases in pH require substantial additions of acid anions. Secondly, many of the species that are positive condition indicators for blanket bog are typical of acid environments. Although habitat-suitability for such species is expected to decline at very low pH values, these low values were not represented in the MultiMOVE training dataset so the niche models do not show a decline at low pH. It is probably true that naturally-acid habitats are not extremely susceptible to acid pollution, but the model chain may underrepresent the effects of large S loads that reduce pH to unnatural levels.

At the calcareous grassland site, HQI was not affected by S pollution within the range studied. This was expected, since calcareous soils are well-buffered against acid inputs. However, the increase in HQI with more N deposition was not expected. This response is probably an error that results from the lack of low-fertility sites on mineral soils with low C/N ratios in the Countryside Survey dataset that was used to derive the conversion equation to mean Ellenberg N (Table 2). Because the largest values of HQI are not found at low values of N and S deposition, the derived CL function is not sensible for this habitat.
Figure 12. Biodiversity-based Critical Load (CL) functions for example sites with different EUNIS habitats: Glensaugh, F4.11 Northern wet heaths; Snowdon, E1.7 Closed non-Mediterranean dry acid and neutral grassland; Whim Moss, D1 Raised and blanket bogs; and Porton Down, E1.26 Sub-Atlantic semi-dry calcareous grassland. The CL function for each site is illustrated in three ways: Left plot, 3D representation with CL function shown by the boundary between green (protected) and blue (not protected); Middle plot, CL function represented on 2D grid; Right plot, approximation of the CL function using only two points, as required for the response for the CCE Call for Data.
3.5 Response to Call for Data

Following the initial analysis of example sites presented above, it was decided to prepare the revised Call for Data response for only two habitats, E1.7 Dry acid grassland and F4.11 Northern wet heath. This decision was made partly due to time constraints – biodiversity-based CL functions could be developed for other habitats but would require more exploratory work, and in the case of calcareous grasslands may require more empirical evidence to establish relationships between biogeochemical measurements and trait-means. The E1.7 and F4.11 habitats are those for which there is currently most confidence in the simulated responses of HQI and in the derived CL functions.

Critical loads functions were derived and submitted in the Call for Data response for 26 E1.7 Dry acid grassland sites and 14 F4.11 Wet heath sites. A selection of representative examples is shown in Figure 13. Of the wet heathland sites, ten had responses similar to that in Figure 13a (i.e. when N deposition is 20% of CL_{empN}, the CL_{bdiv} function was exceeded with S deposition of less than 200 % of CL_{maxS}) and four had responses similar to that in Figure 13b (i.e. when N deposition is 20% of CL_{empN}, CL_{bdiv} was exceeded only with S deposition > 200 % of CL_{maxS}). Of the dry acid grassland sites, 18 had responses similar to that in Figure 13c, four similar to Figure 13d, and four similar to Figure 13e (i.e. very sensitive to S pollution, such that CL_{bdiv} was exceeded with only 20% of CL_{maxS}).

![Figure 13](image-url)  
**Figure 13.** Examples of biodiversity-based Critical Load functions, defined as the line where a habitat quality index reaches a critical value and shown as the boundary between green and blue areas in the above plots, for: a) & b) a wet heath site; c), d) and e) a dry acid grassland site. See text for discussion of response types.

The CL_{bdiv} functions for all sites were approximated using two points on the N x S plane (see Section 2.5) and the locations of these points were submitted on 18th May 2015 as part of the UK response to the Call for Data 2014-15. The submitted data are reproduced in Table 3.
Table 3. Biodiversity-based Critical Load functions and critical values for the habitat quality metric submitted to the CCE in response to the Call for Data 2014-15. SiteID = UK National Focal Centre code for the 1 x 1 km gridcell and EUNIS habitat; CLNmin, CLSmax = coordinates of first point defining the C\text{bdiv} function (see Figure 3); CLNmax, CLSmin = coordinates of second point defining the CL\text{bdiv} function; HScrit = critical value for the habitat quality metric, referred to as HQI\text{crit} in the text.

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4. Discussion

4.1 Biodiversity-based Critical load functions

The MADOC-MultiMOVE model was successfully applied to the task of deriving simple functions that describe combinations of N and S deposition above which the habitat is likely to be damaged. Inevitably the results are a simplification, in that environmental conditions and pollution history at a site are imperfectly known, species occurrence is affected not only by habitat-suitability but by dispersal and extinction processes, and interpretation of species change in terms of conservation targets is inevitably somewhat subjective. Nevertheless, the approach reproduces to a large extent the expected effects of N and S pollution, with changes to individual species dependent on their sensitivity to acidification, eutrophication and/or shading, and, generally, declines in overall habitat quality with greater rates of pollution.

Nitrogen pollution consistently caused declines in habitat quality, except in calcareous grasslands where the links between floristic trait-means and environmental conditions have a relatively poor evidential basis. Sulphur pollution often had a relatively weak effect, causing little decline in simulated HQI even at rates of 200 % or more of CL\text{max} at some sites. This may be because the habitats studied (dry acid grassland and wet heath) are relatively insensitive to acidification – even though soil pH in these habitats can be pushed to low levels by acid pollution, their positive indicator-species are not greatly affected by low pH. However, an alternative explanation is that the models do not capture the negative impacts of very low pH, in particular when very acid sites have not been included in the datasets used to derive species niche models. More exploration of
individual species’ responses would help in assessing which of these explanations is more correct. However, the negative effects of N via eutrophication and shading seem to be well-captured by the model chain.

4.2 Uncertainties

In this section we review uncertainties at each stage of the model chain. A full statistical analysis of how these uncertainties propagate through the model chain was beyond the scope of the project, but key uncertainties are highlighted. The mechanisms included within MADOC are inevitably a simplification of the many processes and interactions that may be changed by nitrogen pollution. This simplification is intentional and makes the model more general, but it is important to consider other biogeochemical processes that could be included. Some of these are discussed below, and summarised in Table 4. Uncertainties with respect to species responses and calculation of the HQI summary metric are also considered.

**Phosphorus limitation**

Increasing evidence is emerging that productivity responses to N are limited or co-limited by phosphorus availability in many UK semi-natural habitats (e.g. Rowe et al., 2014c). If systems are P-limited rather than N-limited, this implies that a) productivity responses to N will be smaller, and effects on habitat-suitability via increased plant growth, shading and litterfall will be less, but b) N leaching is likely to begin after comparatively little cumulative N deposition, resulting in increased effects on acidification. A version of MADOC that includes P limitation is being developed, which will simulate these effects (Davies et al., submitted).

**Differential effects of reduced and oxidised N**

There have been numerous experiments on the effects of reduced N, including gaseous ammonia, versus oxidised N. Effects of are often explained as resulting from different species’ preference for different forms of N, and certainly species of agricultural environments are better adapted to use nitrate than are species of more infertile environments. However, the ratio of reduced/oxidised N in soil is much more related to soil aeration than to the ratio in deposition, so effects of different ratios in deposition seem likely to be limited. Also in much of the experimental evidence it is difficult to separate the effect of N oxidation state from effects of the counter-ion with which ammonium or nitrate was applied. Different salts can have very different effects on soil pH, and pH change has major effects on habitats. However, survey evidence has recently shown a greater correlation of mean Ellenberg N (a key indicator of eutrophication) with NH₃ deposition than with NO₃ deposition (van den Berg et al., in press). This suggests that including the effects of this ratio in deposition within the model chain should be reconsidered.

Experimental application of dry ammonia is more representative of N pollution, and has been shown to have profound effects at Whim Moss. These effects were initially restricted to areas receiving unrepresentatively high concentrations of NH₃, but have extended further down the transect that runs away from the ammonia emission point, showing that effects accumulate. Ammonia can have effects on sensitive species, in particular foliose lichens, at extremely low concentrations. It is debatable how relevant sensitive lichens are to biodiversity targets for habitats from which they have long been missing due to air pollution. Including direct effects of dry ammonia in the model chain would be informative, but would require careful consideration of indicator-species lists.
Climate change

Both the biogeochemical and the species models incorporate climatic effects. The model chain could be used to explore the effects of climate change, either alone or in combination with atmospheric pollution on habitat-suitability. The effects of climate change have been included in predictions of pollution impacts by the Swedish modelling group (Belyazid et al., 2011) and generally increase the amount of change in species composition (McDonnell et al., 2014). These effects have not been included here, in part because they raise difficult questions about conservation targets under a changed climate that are beyond the scope of the current study. However, it is likely that N pollution will make it more difficult to maintain both current habitats and climate-adapted habitats that are of conservation concern, under a changing climate.

Ozone

Ozone affects plant physiology and productivity, and there is increasing recognition of the risks of increasing concentrations of ground-level ozone. The MADOC model is being extended under the EU-funded ECLAIRE project to include two well-established effects of ozone, decreasing productivity and reducing the translocation of N out of leaves before senescence (Rowe et al., in prep.). Together these effects are likely to increase N leaching rates, but reducing productivity could in principle help reduce the eutrophying effects of N. This may be an oversimplification of the response to ozone. The replacement of ozone-sensitive species by less sensitive species makes it likely that overall ecosystem responses to ozone will be less than suggested in studies of sensitive species. However, this replacement of species itself has implications for biodiversity. Currently there is insufficient evidence on the differential sensitivity to ozone of different species to incorporate species effects in ozone modelling.

Table 4. Biogeochemical processes and effects missing from the current MADOC-MultiMOVE-HQI setup.

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<th>Process/effect</th>
<th>Summary</th>
<th>Next steps</th>
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<td>Phosphorus limitation</td>
<td>Likely to be an important factor protecting some sites from eutrophication.</td>
<td>Obtain more empirical data on P limitation in UK habitats. Finalise N14CP model and incorporate into MADOC.</td>
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<tr>
<td>Different effects of NH₃ and NOₓ</td>
<td>NH₃ may have greater eutrophying effects than NOₓ.</td>
<td>Review evidence and consider incorporating this mechanism into MADOC.</td>
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<tr>
<td>Direct effects of NH₃</td>
<td>Dry NH₃ gas affects sensitive species at low concentrations.</td>
<td>Develop species models, similar to MultiMOVE but trained on atmospheric NH₃ concentration data, for epiphytic bryophytes and lichens.</td>
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<tr>
<td>Climate change</td>
<td>Temperature and precipitation changes will affect habitat-suitability, directly and via biogeochemical processes.</td>
<td>Effects are already included in MADOC-MultiMOVE. Requires definition of biodiversity targets under likely future climate.</td>
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<tr>
<td>Ground-level ozone</td>
<td>Ozone likely to affect N cycling and have direct effects on sensitive species.</td>
<td>Consider including ozone effects in MADOC runs for CCE work. Obtain more empirical data on ozone sensitivity of habitats and species.</td>
</tr>
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Links from biogeochemical conditions to niche models
In the approach taken, individual species are presumed to respond primarily to their abiotic environment, i.e. nutrient, water and light availability, and temperature. Undoubtedly there are biotic influences on habitat-suitability as well, but many of these can be represented by abiotic conditions – for example, adaptation to herbivory is reflected by the height of vegetation where the species typically grows. Particular interactions such as the facilitative effects of a mycorrhizal infection or the detrimental effects of a disease are important in certain cases, but species distribution can largely be accounted for if the abiotic environment is well-characterised.

This characterisation is unlikely to be perfect, however. The PROPS model has been constructed without using floristic trait-means, by training the niche models using only plots where biogeochemical measurements have been made alongside species records. This reduces the size of the training dataset, and is particularly problematic in the case of N-availability measurements, which are not standardised. The PROPS team are circumventing these issues by relating the occurrence of scarcer species to commoner species for which niches can be defined, and by using measured N deposition rate as an indicator of current N exposure. The MultiMOVE approach of constructing niche models in relation to trait-means allows the use of larger datasets, but introduces uncertainty in that trait-means must then be related to abiotic measurements. The transfer functions used (Table 2) are the result of considerable investigation (e.g. Rowe et al., 2011a; Rowe et al., 2014c; Smart et al., 2010), but uncertainties remain. This is particularly true for less extensive habitats such as calcareous grassland, unimproved neutral grassland, fens and some mires that are poorly represented in the Countryside Survey dataset. A useful focus for future work would be to refine these relationships, for example investigating the use of habitat-specific transfer functions.

**Summarising species responses into an overall quality metric**

Until 2014, the method used to assess predicted habitat responses into an overall assessment of habitat quality or progress towards biodiversity targets was probably the main uncertainty in the model chain. The consensus that habitat quality can be pragmatically assessed as the habitat-suitability for a set of target or ‘positive indicator’ species is a considerable achievement. This consensus may be temporary, since there is continuing pressure to adopt alternative definitions based on species-richness, other taxa, scarce species, functionally important species, etc. (see summary in Rowe et al., 2014a).

Even if it is possible to retain habitat-suitability for locally-occurring positive indicator species as the metric, uncertainty remains as to which species to view as positive indicators. In the initial work that supported the selection of this metric, positive indicator-species were those listed in the Common Standards Monitoring guidance (e.g. JNCC, 2006). In the current study, an updated list was used (see Methods) but this did not include bryophytes or lichens, which are important for some habitats, e.g. *Sphagnum* for bogs. The correspondence between the habitat classification used in preparing the indicator-species lists and EUNIS also introduces uncertainty. Further work to refine the lists of species used for each EUNIS habitat would be useful.

Including many species with responses that depend on the values for all the environmental axes at the particular site, means that overall responses may not be clearcut. The approach means that responses to pollution are not assumed to be negative, but are rather the result of combining understanding of biogeochemical responses of soil, vegetation and individual species. This should be seen as a strength. The HQI metric was shown to mainly decline with increases in pollution, and was particularly strongly affected by N deposition, showing the importance of this environmental driver.

**4.1 CCE Workshop, April 2015**
Results were presented at the CCE Workshop, Zagreb, 20-23rd April 2015, which provided an opportunity for discussion and comparison with results presented by other groups. Biodiversity-based critical load functions were submitted by three Signatory Parties: Germany, Italy and UK. In addition, the coordination team at RIVM had prepared example CL functions using the PROPS model (see presentation ‘Critical loads derived from the PROPS model’ by Maximilian Posch at http://wge-cce.org/Activities/Workshops/Past_workshops/Croatia_2015).

The UK results were similar to those presented by the RIVM team. The PROPS model is analogous to MultiMOVE, but uses floristic data from across Europe to derive the niche models. The PROPS critical load functions are currently calculated without taking into account the dynamics of N retention in soil, using niches defined in part by current N deposition rate. The combined CL function for ‘species of interest’ was often irregular, but generally showed declines in overall Habitat-Suitability at high rates of N and S deposition as expected. The UK and RIVM have used similar approaches to obtain biodiversity-based CL functions. Uncertainties remain, as discussed above, but some success has been achieved by both teams.

4.2 Conclusions

The study demonstrated that a model chain that predicts changes in habitat-suitability for individual species can be used to assess the likelihood of biodiversity loss under different pollution scenarios. The model was applied using data held by the UK NFC, showing that predictions can be obtained for any UK 1 km grid square that has been mapped as containing an acid-sensitive or N-sensitive habitat.

The biodiversity-based Critical Load functions derived in the study are plausible, showing strong effects of N pollution on habitat quality, and effects of S pollution that depend on the site and habitat’s sensitivity to acidification. These effects were not inevitable, but rather emerged from the evidence provided by the responses of individual species. Uncertainties remain with many aspects of the model chain, but a response was made to the CCE Call for Data 2014-15, and considerable progress has been made with applying the MADOC-MultiMOVE model chain, and with summarising outputs into forms that can be used in policy analysis and development.

Acknowledgements

We are grateful to the Botanical Society of the British Isles, the British Bryological Society and the British Lichen Society for allowing the use of distribution data. We are also grateful to David Cooper for supplying the algorithm used to interpolate Critical Load functions.

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