

Article (refereed) - postprint

Tipping, E.; Henrys, P.A.; Maskell, L.C.; Smart, S.M. 2013. **Nitrogen deposition effects on plant species diversity; threshold loads from field data**

Copyright © 2013 Elsevier Ltd.

This version available <http://nora.nerc.ac.uk/502141/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

NOTICE: this is the author's version of a work that was accepted for publication in *Environmental Pollution*. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in *Environmental Pollution* (2013), 179. 218-223. [10.1016/j.envpol.2013.04.008](https://doi.org/10.1016/j.envpol.2013.04.008)

www.elsevier.com/

Contact CEH NORA team at
noraceh@ceh.ac.uk

1

2

3 **Nitrogen deposition effects on plant species diversity; threshold loads from**

4 **field data**

5

6

7 E Tipping, PA Henrys, LC Maskell and SM Smart

8

9 Centre for Ecology and Hydrology

10 Lancaster Environment Centre

11 Library Avenue

12 Lancaster LA1 4AP

13 United Kingdom

14

15 Correspondence etc to: Professor Edward Tipping (et@ceh.ac.uk)

16

17

18 **Abstract**

19 National-scale plant species richness data for Great Britain in 1998 were related to modelled
20 contemporary N deposition (N_{dep}) using a broken stick median regression, to estimate thresholds
21 above which N_{dep} definitely has had an effect. The thresholds ($\text{kgN ha}^{-1} \text{a}^{-1}$) are 7.9 for acid grassland
22 14.9 for bogs, 23.6 for calcareous grassland, 7.8 for deciduous woodland and 8.8 for heath. The
23 woodland and heath thresholds are not significantly greater than the lowest N_{dep} , which implies that
24 species loss may occur over the whole range of contemporary N_{dep} . This also applies to acid
25 grassland if it is assumed that N_{dep} has substituted for previous N fixation. The thresholds for bog and
26 calcareous grassland are both significantly above the lowest N_{dep} . The thresholds are lower than the
27 mid-range empirical Critical Loads for acid grassland, deciduous woodland and heath, higher for bogs,
28 and approximately equal for calcareous grassland.

29

30 *Keywords:* Countryside Survey, diversity, nitrogen deposition, plants, species richness

31

32 *Capsule:* Analysis of extensive field data provides estimates of nitrogen deposition rates above which
33 plant species richness is reduced.

34

35

36

37 INTRODUCTION

38 The acidification and eutrophication of terrestrial ecosystems by atmospherically deposited nitrogen
39 (N_{dep}), and resulting biodiversity loss, are of wide concern because of habitat degradation and the
40 possibility that ecosystem impacts are hard to reverse (Bobbink et al., 2010; Strengbom et al. 2001).
41 In Europe, international conventions designed to reduce or reverse unwanted effects of N, notably the
42 Gothenburg Protocol, make use of Critical Loads, i.e. values of N_{dep} above which the effects of
43 atmospherically-deposited N are deemed unacceptable (Bobbink et al., 2010, 2011). Critical Loads of
44 nitrogen are set for different habitats; examples are 3-5 kgN ha⁻¹ a⁻¹ for tundra, 5-10 kgN ha⁻¹ a⁻¹ for
45 raised and blanket bogs, and 10-20 kgN ha⁻¹ a⁻¹ for dry heaths (Bobbink et al., 2011). Their values are
46 derived mainly from the results of experimental studies, usually small-scale field manipulations, in
47 which known added N inputs have been related to observable short-term changes in plant species and
48 growth, and biogeochemical effects. Expert judgement is also applied.

49 The indirect link to long-term biodiversity loss *per se* is seen as a drawback of this approach (van
50 Hinsberg et al, 2008). However, although evidence from field surveys has been used as contextual
51 information to set Critical Loads, its application has proved problematic because low signal-to-noise
52 ratios weaken the ability of the data to identify quantitative thresholds (Bobbink et al., 2010). The
53 importance of other factors in conditioning ecosystem responses to nitrogen deposition has also been
54 emphasised. For example, historical acidification, starting soil pH, land-use intensity and climatic
55 gradients also exert partial unique effects on enrichment indicators such as species richness (Maskell
56 et al., 2010). The contributions of factors other than N deposition on differences in plant species
57 diversity make it difficult to determine effects from conventional (multiple) regression analysis. Some
58 of these factors might be known and quantifiable by survey data but others may not. For example,
59 abiotic factors such as low levels of trace elements, or ecological filters such as species pool effects,
60 are hard to quantify as explanatory variables.

61 Nonetheless, there is mounting field evidence from British and European ecosystems to show that
62 plant diversity decreases with N_{dep} (Stevens et al. 2004; Duprè et al. 2010; Maskell et al. 2010; van
63 den Berg et al. 2011), with N_{dep} assumed to be a proxy for ecosystem N enrichment. Weak but highly
64 significant correlations have been found in cases where plant sampling has been randomised (Maskell
65 et al., 2010), and stronger signals where surveys were optimised by well-replicated sampling along the
66 deposition gradient and controlling for other sources of variation (Stevens et al., 2004).

67 Here we report a new analysis of plant species richness data from nearly 2000 sites in the UK, in
68 which we test for possible thresholds of N_{dep} above which plant species richness can be said to
69 decline. We used data obtained during the Countryside Survey of Great Britain, carried out in 1998
70 (Smart et al., 2003), by the randomised sampling of a large number of spatially representative sites.
71 These data are especially useful for our purposes since they are geographically comprehensive,
72 derived from stratified, random sampling, and recorded at fine resolution. The data are therefore
73 unbiased and also minimise the confounding between alpha and beta diversity (i.e. 'within habitat'
74 versus 'among habitat' diversity) associated with species richness from large grid cells (Huston, 1999).

75 We analysed the plant species richness data for five broad habitats (acid grassland, bog, calcareous
76 grassland, deciduous woodland and heath), in terms of N deposition estimated from national-scale
77 measurement and spatial interpolation (Smith *et al.*, 2000; NEG-TAP, 2001). Rather than analyse the
78 data by conventional regression, as done in previous work (Stevens *et al.*, 2004, 2010; Maskell *et al.*,
79 2010), we applied a “broken stick” model, the break in which corresponds to the threshold in N_{dep} . The
80 results were assessed for statistical significance in order to estimate the deposition rate above which
81 reductions in species diversity can confidently be said to occur, and to estimate species loss per
82 additional unit of N_{dep} above the threshold. Comparisons of the thresholds with empirical Critical
83 Loads were made.

84

85 **METHODS**

86 The Countryside Survey (CS) samples a large number of 1 km x 1 km squares randomly located
 87 within defined environmental strata across Great Britain to provide statistically representative
 88 coverage of the wider countryside and its habitat composition. Each square contains smaller subplots
 89 where detailed information on vegetation composition (both vascular plants and bryophytes) is
 90 recorded. Surveys have been carried out in 1978, 1984, 1990, 1998 and 2007. In this analysis, we
 91 used CS data collected in 1998 that had previously been assembled and analysed by Maskell et al.
 92 (2010). Further information is available from the Countryside Survey website
 93 (<http://www.countrysidesurvey.org.uk/>).

94 Vegetation plots were classified to the phyto-sociological units of the British National Vegetation
 95 Classification (NVC) (Rodwell, 1992). We used a new assignment of CS plots to the NVC based on
 96 the pseudo-quadrat approach (Critchley et al., 2002 and Supplementary Material). Plots were selected
 97 that were classified with a Jaccard similarity coefficient of >0.5 into one of five NVC habitat types; acid
 98 grassland (U1–9), calcareous grassland (CG2, 3, 4, 6, 8, 10, 11), heathland (H1–19 except H5, 6 and
 99 17), bogs (M1-M4, M6, M15-M21, M25, H9, H12 (bog on deep peat)), and deciduous woodlands
 100 (included W4-W25 with no plots from W20 or W21). Plots were also assigned to the UK Biodiversity
 101 Action Plan Broad Habitat classification (Jackson, 2000) by referencing the habitat assignment of the
 102 mapped unit of land area within which each plot was located.

103 The data employed in this study are summarised in Table 1. Figure 1 shows the coverage of each of
 104 the habitats across Great Britain using data from Land Cover Map 2000 and also the distribution of the
 105 Countryside survey 1km sample squares. This highlights the comprehensive spatial coverage
 106 provided by Countryside Survey. The number of CS plots available for each of the five habitats were
 107 873 (acid grassland), 92 (calcareous grassland), 457 (heathland), 203 (bog) and 361 (deciduous
 108 woodland). The numbers of sites are roughly proportional to the areal distribution of each habitat.

109 For N deposition we used estimates at the 5 x 5 km scale provided by CEH Edinburgh (Smith et al.,
 110 2000; NEG-TAP, 2001;), calculated as the mean of the estimates for 1996-1998 from the CBED model
 111 for deposition to the appropriate habitat type. The ranges of N deposition covered by each of the
 112 habitats are given in Table 1 (see also Figure 2). The distribution of N_{dep} is approximately normally
 113 distributed for all habitats except bog, where there is a clear peak at low N_{dep} . The analysis is helped
 114 by the wide ranges of N_{dep} across GB.

115 We used non-parametric quantile regression to estimate the relationship, including a threshold,
 116 between N_{dep} and species richness. Using this method, one would estimate the parameters of a
 117 standard multivariate linear model by minimising the following function:

$$\arg \min_{\beta} \left\{ \sum_{i=1}^n \rho_{\tau}(Y_i - \beta X_i) \right\}$$

118

119

120 where $\rho_\tau(z) = z(\tau - I(z < 0))$ with $I(\cdot)$ representing the indicator function and τ the quantile estimate. The
121 main analysis was performed with τ set to 0.5, i.e. a median regression. The median is less sensitive
122 to extreme values than the mean and provides a robust estimate of the underlying relationship. We
123 also carried out comparative analyses with τ set to 0.25 and 0.75.

124 As we are seeking to estimate a threshold from the field data, rather than fitting a standard linear
125 slope, we fit a model that includes a breakpoint, which defines the point at which a constant
126 relationship changes into a declining linear trend. We therefore seek to minimise the quantile error
127 (defined in above) between the observed data and a function expressed by three variables that control
128 the constant value up to the breakpoint (n_{max}), the breakpoint location ($N_{dep,T}$) and the slope of decline
129 after the breakpoint, known as species loss rate (r_{sl}). As this function is a three parameter equation, it
130 is minimised using a numerical based technique, in this case we used the Nelder-Mead algorithm
131 (Nelder and Mead, 1965).

132 Because we estimate the regression coefficients non-parametrically by minimising the quantile error,
133 with no distributional assumptions placed on the data or the parameters, we are unable to directly
134 obtain estimates of upper and lower limits for the estimated threshold values. Therefore, in order to
135 estimate a confidence interval on the estimated threshold load, we use a bootstrap based procedure
136 (Efron and Tibshirani, 1993). This involves randomly sampling n observations from the data with
137 replacement, where n is the total sample number. The quantile regression function as described
138 above is then fitted to this new pseudo data set to obtain estimates for each of the three parameters.
139 Estimated parameters are stored and then the whole process is repeated 999 times, producing
140 (including the original data) 1000 sets of breakpoints. Confidence intervals for the breakpoint
141 parameter are then obtained simply by taking the 2.5th and 97.5th percentile from these estimates.

142

143 **RESULTS AND DISCUSSION**

144 Median regression analysis was carried out on each of the five habitats separately, firstly including all
145 species and secondly only vascular species. There were only minor differences in the derived
146 thresholds with or without the bryophytes, and we report only the results for the combined data (Table
147 1). Figure 2 shows the fitted relationships using the mean parameters. Confidence intervals around
148 the threshold value are also plotted with the upper and lower 95% interval values. For acid grassland,
149 bog and calcareous grassland, the lower 95% limit of the threshold is greater than the lowest N_{dep} ,
150 indicating that a significant threshold value is identified. But this does not apply to deciduous
151 woodland and heath, for which the lower 95% confidence limits are less than the lowest N_{dep} ; therefore
152 for these two habitats it appears that species richness is reduced at all current values of N_{dep} .

153 The other information that comes from the fitting is the decrease in species number per additional
154 N_{dep} , r_{sl} . This varies among the habitats, ranging in absolute terms from 0.19 species per $\text{kg N ha}^{-1} \text{yr}^{-1}$
155 in deciduous woodland to 0.85 species per $\text{kg N ha}^{-1} \text{yr}^{-1}$ in calcareous grassland. When expressed as
156 a relative percentage to the maximum species number (n_{max}), the range is from 1.3 – 3.0 % per kg N
157 $\text{ha}^{-1} \text{yr}^{-1}$ again from deciduous woodland to bog.

158 The high scatter in the data (Figure 2) reflects the numerous factors that influence species richness
159 (Grace 1999; Dodd et al 1994). As well as variables that may be affected by N_{dep} , principally soil
160 fertility and acidity, other factors include seed bank availability, species-area and species pool effects,
161 grazing and other disturbances, climate, land-use legacies and the acidifying effect of (non-marine)
162 sulphur deposition (which is likely to have different effects than N_{dep} because the two are not strongly
163 correlated; $r^2 = 0.33$).

164 The use of median (0.5 quantile) regression implies that combinations of these other factors both
165 increase and decrease diversity, on average equally. But bias in one or other direction may exist,
166 which would mean that other quantiles might be more suitable for data fitting (cf. Cade and Noon,
167 2003). Fitting the data to the 0.75 quantile produced thresholds and confidence ranges similar to the
168 median regression values (Table 2). The same is true for the 0.25 quantile for acid and calcareous
169 grasslands and heath, but for bog and deciduous woodland the thresholds are higher. Of course the
170 absolute slopes of the diversity- N_{dep} relationship differ, but the relative slopes do not.

171 Although N_{dep} is an obvious choice for the independent variable, being the driving variable of interest
172 and subject to emission control, it presents some problems with respect to interpretation. Firstly, the
173 effects on diversity are mediated through biogeochemical processing of additional N inputs due to
174 deposition. In the case of acidification, this is by the generation of excess nitrate, when the soil cannot
175 immobilise nitrogen (Emmett, 2007), so that soil pH is decreased which reduces diversity (Grime,
176 2001). Eutrophication depends upon the rate of cycling of N, and control of net primary productivity,
177 potentially producing both increases in diversity at low levels of input and decreases at high levels
178 (Grime, 2001). While both of these effects will depend upon N_{dep} they will be separate.

179 Secondly, although N_{dep} may be a guide to N enrichment, the relationship must be time dependent,
180 due to the accumulation of N in the ecosystem. Therefore, a plot like those in Figure 2 for earlier
181 years would be expected to show a higher threshold and perhaps a lower slope, while a future plot
182 might have a lower threshold and steeper slope. The use of cumulative N_{dep} as employed by Dupre et
183 al. (2009) resolves this to some extent, although not completely if the evolution of the soil N status is
184 nonlinear with respect to N_{dep} . The thresholds of Figure 2 are therefore time-dependent, determined
185 more by historical N build-up than contemporary N_{dep} . A more precise statement of their meaning is
186 that, for N_{dep} values below the current threshold, there is no evidence for diversity loss due to N
187 enrichment brought about by cumulative N_{dep} .

188 A third confounding issue is the relationship between N_{dep} and inputs from N fixation, which will have
189 been the main supply prior to the recent decades and centuries of elevated N_{dep} . According to DeLuca
190 et al. (2008) N fixation is down-regulated by N deposition, so that at N_{dep} below or equal to the
191 “pristine” N fixation rate, the total N input is approximately unchanged. A representative “pristine” N
192 fixation rate of $3 \text{ kg ha}^{-1} \text{ a}^{-1}$ has been estimated for NW Europe (Tipping et al., 2012). Therefore
193 “excess N_{dep} ” thresholds might be derived by subtracting this value from the thresholds of Table 1, i.e.
194 only this excess N_{dep} will have enriched the soils. This suggests that for acid grassland, deciduous
195 woodland and heath, effects are seen at all N_{dep} values above the N fixation rate, whereas for bog and
196 calcareous grassland there is evidence only at higher thresholds.

197 Empirical Critical Loads are derived from short term treatments, usually focused on measurable single
198 processes or effects (Bobbink et al., 2010, 2011). Such experiments in themselves will not have
199 added as much N to the systems as long-term accumulation over decades or centuries, although the
200 systems under study will often have experienced loads higher than our thresholds, i.e. the applied
201 loads will operate to increase the rate of enrichment. By the same arguments as above, empirical
202 loads must be time-dependent, but with a different time constant; thus Hornung et al (1995) suggested
203 that empirical Critical Loads might be applicable on a time scale of only 20-30 years. Therefore one
204 perhaps should not expect agreement in absolute values, although Table 1 and Figure 3 show that the
205 thresholds and empirical Critical Loads are of similar magnitude. However, it might be expected that
206 the order of habitats should be the same in the two systems, and this is the case for deciduous
207 woodland, heath and calcareous grassland, with acid grassland quite close. The one habitat that does
208 not fit well into the pattern is bog, for which the threshold deposition is considerably higher than the
209 empirical Critical Load, and is significantly greater than the lowest N_{dep} . Differences between the
210 thresholds and Critical Loads must arise because the latter are set on the basis of changes in species
211 composition, physiology and biogeochemical variables, as well as in diversity, the exact combination
212 varying amongst habitats. It may therefore be significant that the two habitats for which the threshold
213 and Critical Load agree best (acid and calcareous grasslands) are the only two of the five habitats for
214 which changes in plant species richness were used to set the Critical Load, whereas for bogs
215 changes in plant species composition was the principal criterion (Bobbink et al., 2011).

216 Interpretation of the large-scale spatial results presented here would likely be enhanced by the use of
217 dynamic biogeochemical modelling (see De Vries et al., 2010) to translate the primary driving variable

218 N_{dep} to more direct predictors of species diversity, for example the N cycling flux through the soil, net
219 primary production and soil pH. By taking into account differences in climatic and soil properties, as
220 well as habitat type and deposition, this could distinguish the acidifying and eutrophying effects of N,
221 and, through space-for-time substitution, provide insights into the temporal evolution of effects on
222 biodiversity. Such modelling could further draw together the different kinds of information about
223 ecosystem N enrichment to provide a more comprehensive and robust assessment of the relationship
224 between N deposition and species richness decline.

225

226 **CONCLUSIONS**

- 227 ▪ Threshold N_{dep} values above which plant species diversity is reduced have been derived from field
228 observations for five terrestrial British habitats.
- 229 ▪ In two cases, deciduous woodland and heath, the thresholds (7.8 and $8.8 \text{ kgN ha}^{-1} \text{ a}^{-1}$ respectively)
230 are not significantly greater than the lowest N_{dep} , which implies that species loss has occurred over
231 the whole range of contemporary N_{dep} . This also applies to acid grassland (threshold $7.8 \text{ kgN ha}^{-1} \text{ a}^{-1}$
232 ¹) if it is assumed that N_{dep} has substituted for previous N fixation. For bog and calcareous
233 grassland, the thresholds of $14 \text{ kgN ha}^{-1} \text{ a}^{-1}$ and $24 \text{ kgN ha}^{-1} \text{ a}^{-1}$ respectively are both significantly
234 above the lowest N_{dep} .
- 235 ▪ Median species numbers at N_{dep} below the thresholds are; acid grassland 18, bog 18, calcareous
236 grassland 28, deciduous woodland 14, and heath 13.
- 237 ▪ The average relative loss of species with increasing N_{dep} is 2% per ($\text{kgN ha}^{-1} \text{ a}^{-1}$). The values range
238 from 1.3% for deciduous woodland to 3.0% for calcareous grassland. Absolute losses range from
239 0.19 species per ($\text{kgN ha}^{-1} \text{ a}^{-1}$) for deciduous woodland to 0.85 species per ($\text{kgN ha}^{-1} \text{ a}^{-1}$) for
240 calcareous grassland.
- 241 ▪ The derived thresholds are broadly similar in magnitude to empirical Critical Loads, assigned from
242 collated manipulation studies. The thresholds are lower than the mid-range Critical Loads for acid
243 grassland, deciduous woodland and heath, higher for bogs, and approximately equal for calcareous
244 grassland.

245

246 **ACKNOWLEDGEMENTS**

247 We thank CEH staff and CS surveyors who have helped with collection, organization and analysis of
248 Countryside Survey data. The Countryside Survey of 2007 was funded by a partnership of nine
249 government funded bodies led by the Natural Environment Research Council (NERC) and the
250 Department for Environment, Food and Rural Affairs (Defra). This study was partially funded by the
251 NERC Macronutrient Cycles Programme (Project LTLS). We are grateful to JR Hall (CEH) and a
252 referee for their helpful comments.

253

254 **REFERENCES**

- 255 Achermann, B., Bobbink, R., 2003. Empirical Critical Loads for Nitrogen. Proceedings of Expert
256 Workshop held in Berne, Switzerland 11 - 13 November 2002. Environmental Documentation
257 No. 164. Air. Swiss Agency for the Environment, Forests and Landscape SAEFL, Berne.
- 258 Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M.,
259 Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F.,
260 Nordin, A., Pardo, L., de Vries, W., 2010. Global assessment of nitrogen deposition effects on
261 terrestrial plant diversity: a synthesis. *Ecological Applications* 20, 30-59.
- 262 Bobbink, R., Braun, S., Nordin, A., Power, S., Schütz, K., Strengbom, J., Weijters, M., Tomassen, H.,
263 2011. Review and Revision of Empirical Critical Loads and Dose-Response Relationships.
264 Proceedings of an Expert Workshop, Noordwijkerhout, 23-25 June 2010. RIVM report:
265 680359002.
- 266 Cade, B.S., Noon, B.R., 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in*
267 *Ecology and Environment* 1, 412-420.
- 268 Critchley, C.N.R., Chambers, B.J., Fowbert, J.A., Sanderson, R.A., Bhogal, A., Rose, S.C., 2002.
269 Association between lowland grassland and soil properties. *Biological Conservation* 105, 199-
270 215.
- 271 DeLuca, T.H., Zackrisson, O., Gundale, M.J., Nilsson, M.-C., 2008. Ecosystem feedbacks and
272 nitrogen fixation in boreal forests. *Science* 320, 1181.
- 273 De Vries, W., Wamelink, G.W.W., van Dobben, H., Kros, J., Reinds, G.J., Mol-Dijkstra, J.P., Smart,
274 S.M., Evans, C.D., Rowe, E.C., Belyazid, S., Sverdrup, H.U., van Hinsberg, A., Posch, M.,
275 Hettelingh, J.-P., Spranger, T., Bobbink, R., 2010. Use of dynamic soil-vegetation models to
276 assess impacts of nitrogen deposition on plant species composition: an overview. *Ecological*
277 *Applications* 20, 60-79.
- 278 Dodd, M.E., Silvertown, J., McConway, K., Potts, K.J., Crawley, M., 1994. Stability in the plant
279 communities of the Park Grass Experiment: the relationships between species richness, soil
280 pH and biomass variability. *Philosophical Transactions of the Royal Society B* 346, 185-193.
- 281 Dupre, C., Stevens, C.J., Ranke, T., Bleeker, A., Pöppeler-Lisbach, C., Gowing, D.J., Dise, N.B.,
282 Dorland, E., Bobbink, R., Diekmann, M., 2009. Changes in species richness and composition
283 in European acidic grasslands over the past 70 years: the contribution of cumulative
284 atmospheric nitrogen deposition. *Global Change Biology* 16, 344-357.
- 285 Efron, B., Tibshirani, R., 1993. *An Introduction to the Bootstrap*. Chapman and Hall, New York.
- 286 Emmett, B.A., 2007. Nitrogen saturation of terrestrial ecosystems: some recent findings and their
287 implications for our conceptual framework. *Water Air Soil Pollution Focus* 7, 99-109.
- 288 Grace, J.B., 1999. Factors controlling species density in herbaceous plant communities. *Perspectives*
289 *in Plant Ecology, Evolution and Systematics* 2, 1-28.
- 290 Grime, J.P., 2001. *Plant Strategies, Vegetation Processes and Ecosystem Properties*. 2nd Edition,
291 Wiley, Chichester
- 292 Hall, J., Emmett, E., Garbutt, A., Jones, L., Rowe, E., Sheppard, E., Vanguelova, E., Pitman, R.,
293 Britton, A., Hester, A., Ashmore, M., Power, S., Caporn, S., 2011. UK Status Report July

- 294 2011: Update to Empirical Critical Loads of Nitrogen. Centre for Ecology and Hydrology Report
295 to Defra.
- 296 Hornung, M., Sutton, M.A., Wilson, R.B., 1995. Mapping and modelling of critical loads for nitrogen –
297 a workshop report. Report of a workshop held at Grange-over-Sands, Cumbria, UK, under the
298 auspices of the UN-ECE Convention on Long Range Transboundary Air Pollution, Working
299 Group on Effects, 24-26 October 1994. Institute of Terrestrial Ecology, Edinburgh.
- 300 Huston, M.A., 1999. Local processes and regional patterns: appropriate scales for understanding
301 variation in the diversity of plants and animals. *Oikos* 86, 393–401.
- 302 Jackson, D.L., 2000. Guidance on the interpretation of the Biodiversity Broad Habitat Classification
303 (terrestrial and freshwater types): Definitions and the relationship with other habitat
304 classifications. JNCC Report No. 307. Peterborough, UK: Joint Nature Conservation
305 Committee.
- 306 Maskell, L.C., Smart, S.M., Bullock, J.M., Thompson, K., Stevens, C.J., 2010. Nitrogen deposition
307 causes widespread loss of species richness in British habitats. *Global Change Biology* 16,
308 671-679.
- 309 NEG-TAP 2001, National Expert Group on Transboundary Air Pollution: Acidification, Eutrophication
310 and Ground Level Ozone in the UK. First Report, UK Department of the Environment,
311 Transport and the regions and the devolved administrations, Retrieved
312 from: www.nbu.ac.uk/negtap/finalreport.htm.
- 313 Nelder, J.A., Mead R., 1965. A simplex method for function minimization. *Computer Journal* 7, 308–
314 313.
- 315 Rodwell, J., 1992. *British Plant Communities. Grasslands and montane communities. Volume 3.*
316 Cambridge: Cambridge University Press.
- 317 Smart, S.M., Clarke, R.T., van de Poll, H.M., Robertson, E.J., Shield, E.R., Bunce, R.G.H., Maskell,
318 L.C., 2003. National-scale vegetation change across Britain; an analysis of sample-based
319 surveillance data from the Countryside Surveys of 1990 and 1998. *Journal of Environmental*
320 *Management* 67, 239-254.
- 321 Smith, R. I., Fowler, D., Sutton, M. A., Flechard, C., Coyle, M., 2000. Regional estimation of pollutant
322 gas dry deposition in the UK: Model description, sensitivity analyses and outputs. *Atmospheric*
323 *Environment* 34, 3757–3777.
- 324 Stevens, C.J., Dise, N.B., Mountford, J.O., Gowing, D.J., 2004. Impact of nitrogen deposition on the
325 species richness of grasslands. *Science* 303, 1876-1879.
- 326 Stevens, C.J., Duprè C., Dorland, E., Gaudnik, C., Gowing, D.J.G., Bleeker, A., Diekmann, M., Alard,
327 D., Bobbink, R., Fowler, D., Corcket, E., Mountford, J.O., Vandvik, V., Aarrestad, P.A., Muller,
328 S., Dise, N.B., 2010. Nitrogen deposition threatens species richness of grasslands across
329 Europe. *Environmental Pollution* 158, 2940-2945.
- 330 Stevens, C.J., Manning, P., Van den Berg, L.J.L., De Graaf, M.C.C., Wamelink, G.W., Weiger, B.,
331 Andries, W., Bleeker, A., Vergeer, P., Arroniz-Crespo, M., Limpens, J., Lamers, L.P.M.,
332 Bobbink, R., Dorland, E., 2011. Ecosystem responses to reduced and oxidized nitrogen
333 impacts in European terrestrial habitats. *Environmental Pollution* 159, 665-676.

- 334 Strengbom, J., Nordin, A., Nasholm, T., Ericson, L., 2001. Slow recovery of boreal forest ecosystem
335 following decreased nitrogen input. *Functional Ecology* 15, 451-457
- 336 Tipping, E., Rowe, E.C., Evans, C.D., Mills, R.T.E., Emmett, B.A., Chaplow, J.S., Hall, J.R., 2012.
337 N14C: a plant-soil nitrogen and carbon cycling model to simulate terrestrial ecosystem
338 responses to atmospheric nitrogen deposition. *Ecological Modelling* 247, 11– 26.
- 339 Van den Berg, L.J.L., Vergeer, P., Rich, T.C.G., Smart, S.M., Guest, D., Ashmore, M.R., 2011. Direct
340 and indirect effects of nitrogen deposition on species composition change in calcareous
341 grasslands. *Global Change Biology* 17, 1871–1883.
- 342 Van Hinsberg, A., Reijnen, R., Goedhart, P., de Knegt, B., van Esbroek, M., 2008. Relation between
343 Critical Load Exceedance and Loss of Protected Species. Chapter 5 CCE Status Report
344 2008, pp 73-81.
- 345
- 346

347 Table 1. Summary of data and fitting results. Key: n_{\max} maximum species number; $N_{\text{dep},T}$ threshold N
 348 deposition; r_{sl} no. of species lost per unit N_{dep} ; $\%r_{\text{sl}}$ % species lost per unit N_{dep} . The 95% confidence
 349 limits of $N_{\text{dep},T}$ are given.

| | unit | acid grassland | bog | calcareous grassland | deciduous woodland | heath |
|---------------------------|--|-------------------|-------------------|-------------------------|-----------------------|-----------------|
| EUNIS code | - | E1.7 | D1 | E1.26 | G1 | F4.2, F4.11 |
| no. of sites | - | 883 | 203 | 92 | 361 | 457 |
| range of N_{dep} | $\text{kg ha}^{-1} \text{a}^{-1}$ | 4.9-40 | 5.3-40 | 4.9-36.5 | 6.9-56.7 | 4.9-40 |
| range of critical load* | $\text{kg ha}^{-1} \text{a}^{-1}$ | 10-15 | 5-10 | 15-25 | 10-20 | 10-20 |
| n_{\max} | - | 18.0 | 18.0 | 28.0 | 14.0 | 13.0 |
| $N_{\text{dep},T}$ | $\text{kg ha}^{-1} \text{a}^{-1}$ | 7.8 6.3-8.1 | 14.3 13.2-15.9 | 23.6 15.5-29.3 | 7.8 6.8-15.0 | 8.8 4.7-10.1 |
| r_{sl} | $(\text{kg ha}^{-1} \text{a}^{-1})^{-1}$ | 0.28 | 0.31 | 0.85 | 0.19 | 0.30 |
| $\%r_{\text{sl}}$ | $(\text{kg ha}^{-1} \text{a}^{-1})^{-1}$ | 1.6 | 1.7 | 3.0 | 1.3 | 2.3 |

350 * values employed for national mapping of Critical Loads in the UK (Hall et al., 2011)

351

352

353 Table 2. Threshold values and 95% confidence limits for different quantiles.

| quantile | acid grassland | bog | calcareous grassland | deciduous woodland | heath |
|----------|-------------------|-----------|-------------------------|-----------------------|----------|
| 0.25 | 7.8 | 20.0 | 23.7 | 19.3 | 7.8 |
| | 6.7-8.8 | 5.7-22.8 | 11.1-25.8 | 14.9-20.2 | 4.7-24.8 |
| 0.50 | 7.8 | 14.3 | 23.6 | 7.8 | 8.8 |
| | 6.3-8.1 | 13.2-15.9 | 15.5-29.3 | 6.8-15.0 | 4.7-10.1 |
| 0.75 | 8.0 | 14.1 | 25.8 | 8.0 | 7.8 |
| | 4.7-9.1 | 11.1-16.9 | 18.9-26.6 | 6.7-29.9 | 6.0-10.4 |

354

355 **Figure captions**

356 Figure 1. Map of sites

357 Figure 2. Variation of species richness with N_{dep} and broken-stick model fits. The vertical dashed
358 lines are the 95% limits.359 Figure 3. Plots of contemporary (1998) thresholds against empirical Critical Loads. Key: AG acid
360 grassland, B bog, CG calcareous grassland, DW deciduous woodland, H heath. The points
361 for AG and DW lie very close and so appear as a single point. The ranges for the threshold
362 values are 95% confidence limits. The Critical Load ranges are from Table 1, and the
363 centre-range values are plotted as points.

364

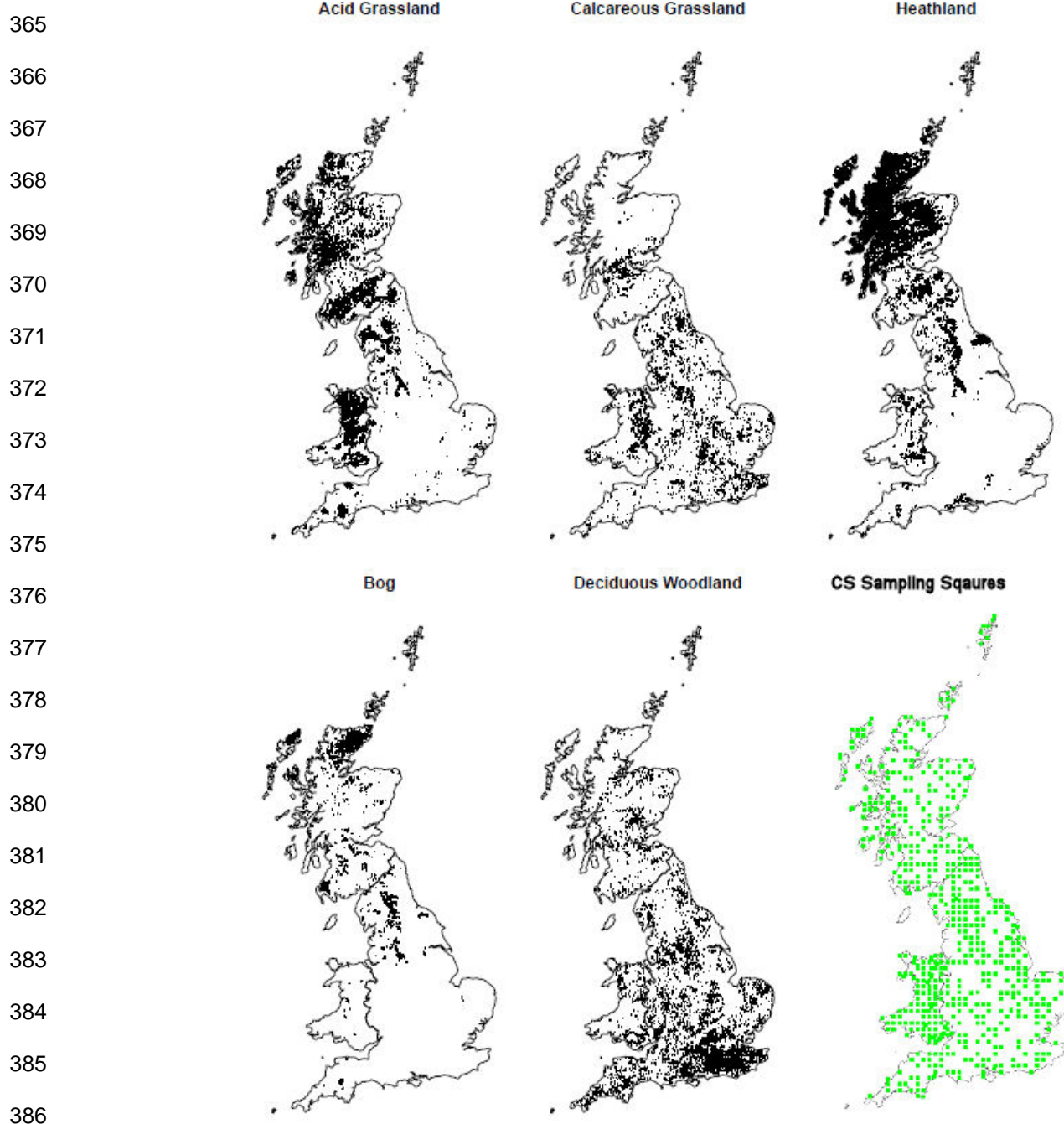


Figure 1.

390

391

392

393

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

410

411

412

413

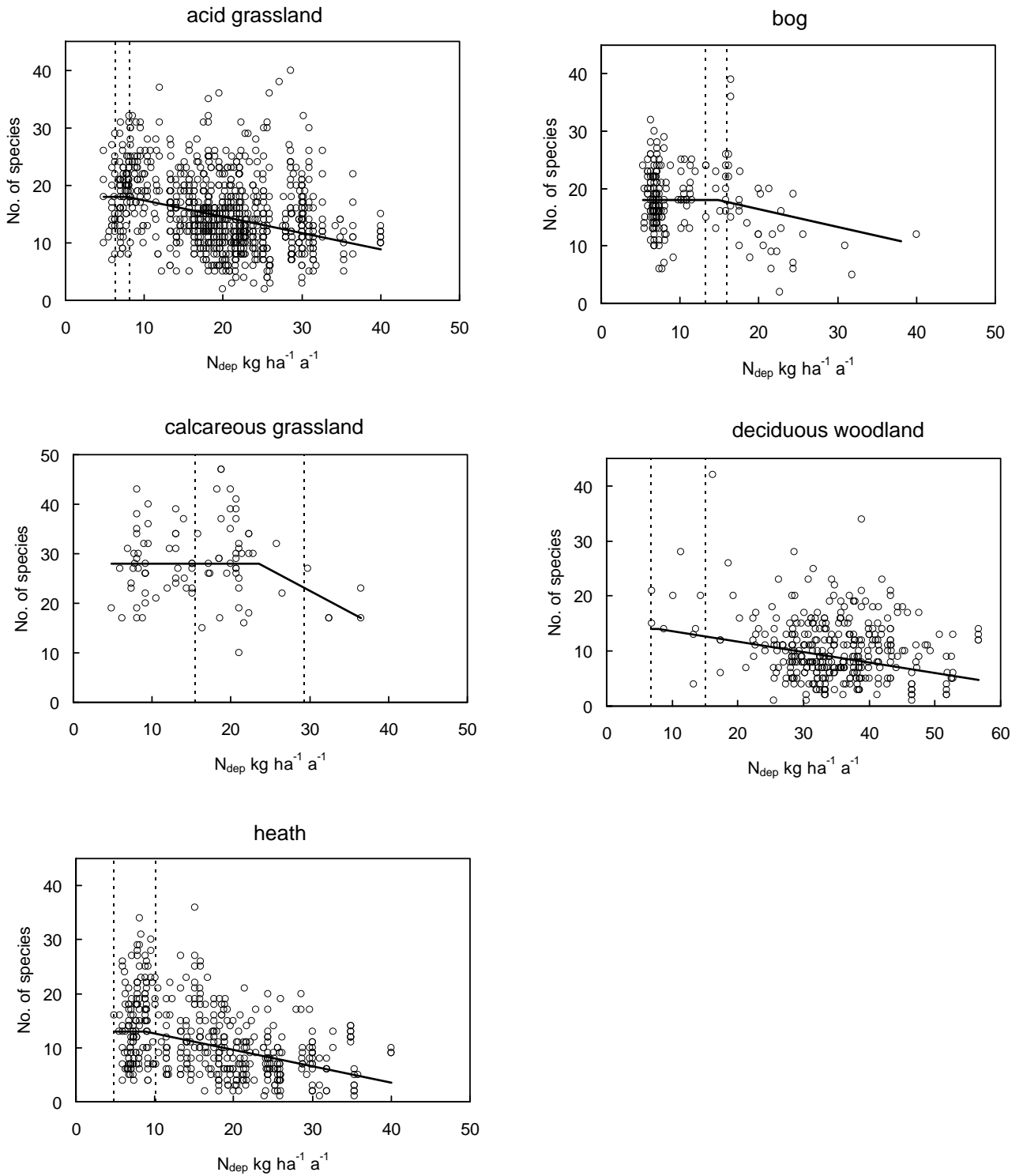
414

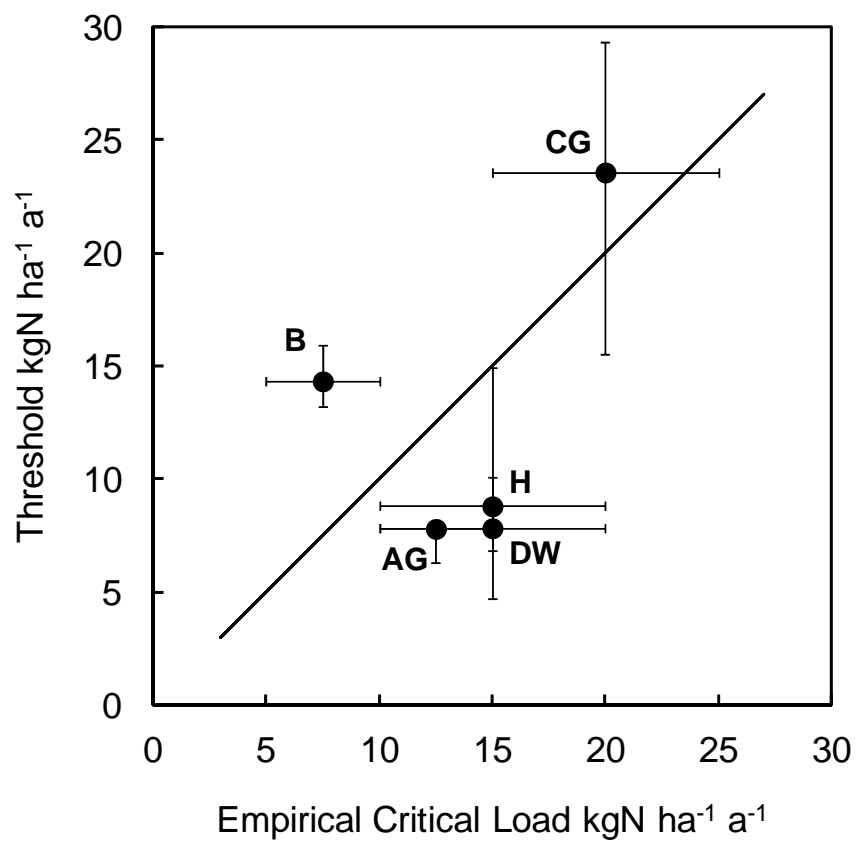
415

416

417 Figure 2.

418





419

420 Figure 3.