

1 **Nitrogen deposition and plant biodiversity: past, present, and future**

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14 ABSTRACT

15 Reactive nitrogen (N) deposition from intensive agricultural and industrial activity has been
16 identified as the third greatest threat to global terrestrial biodiversity. While the impacts of N
17 deposition are widely accepted, their magnitude is poorly quantified. Here we combine N deposition
18 models, empirical response functions and vegetation mapping to model the impacts of N deposition
19 on plant species richness from 1900 to 2030 using Great Britain as a case study. We find that N
20 deposition is likely to have caused the loss of approximately one-third of species richness from five
21 widespread habitats. Our results suggest that currently-expected reductions in the emission of NO_y
22 and NH₃ will achieve no more than modest increases in species richness by 2030 and that cuts based
23 on habitat critical loads may be inefficient. The impacts of N deposition on plant biodiversity are
24 severe and unlikely to be quickly reversed.

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36 INTRODUCTION

37 The recently-adopted UN Sustainable Development Goals (SDGs) include a target to halt biodiversity
38 loss from terrestrial ecosystems by 2030. An important but frequently-overlooked threat to global
39 biodiversity is deposition of reactive nitrogen (N), produced by fossil fuel combustion and intensive
40 agriculture. Since many ecosystems have evolved under conditions of N limitation, a long-term
41 increase in N deposition at even low levels can cause eutrophication and acidification with wide-
42 ranging impacts on ecosystem services and biodiversity. Field and laboratory experiments and
43 surveys repeated through time and across pollution gradients have conclusively shown that long-
44 term elevated N deposition (comprising wet-deposited NH_4^+ and NO_3^- and dry-deposited NH_3 and
45 NO_y) is linked to reduced plant biodiversity in many natural ecosystems (Dise, et al. 2011, Duprè, et
46 al. 2010, Maskell, et al. 2010). Excess N impacts plants through direct toxicity, soil acidification,
47 nutrient imbalances, and interspecific competition (Dise, et al. 2011). Loss of plant biodiversity is
48 known to impact on microbial and faunal biodiversity through trophic cascades and to lead to an
49 erosion of important ecosystem services (Erisman, et al. 2013, RoTAP 2012, Sutton, et al. 2011).
50 National and trans-national policy requires this threat to be addressed (DEFRA 2011, United Nations
51 2015) but the scale of impacts at regional to national scales has not been quantified and we have
52 little understanding of how impacts have arisen through time and may develop in the future.

53 In many regions of the developed world levels of N deposition are expected to plateau and decline in
54 coming decades and a key question is how this will affect biodiversity (Lamarque, et al. 2013, Sutton,
55 et al. 2011). Studies of recovery from decreased N deposition are limited (Tilman and Isbell 2015),
56 but available evidence suggests three main trajectories. Some impacts of N may be acute and linked
57 to atmospheric concentrations, for instance direct damage by gaseous ammonia (Carfrae, et al.
58 2004). Recovery from such impacts may be relatively rapid, with the degree of recovery proportional
59 to the deposition reduction. Other impacts may develop more gradually with the long-term
60 accumulation of N in soil causing ecological changes such as competitive shifts in species abundance.
61 Recovery from these impacts will be slower, requiring the removal of stored N from the system by
62 processes such as denitrification, leaching, fire, or harvesting (Dise, et al. 2011). There may be
63 considerable hysteresis in ecological recovery due to factors such as species dispersal abilities and
64 the loss of seedbank (Basto, et al. 2015). Most concerningly, chronically elevated N deposition may
65 cause a regime shift with the establishment and invasion of nitrophilic species which then self-
66 perpetuate through mechanisms such as shading, litter accumulation, and allelopathy (Isbell, et al.
67 2013). Such regime shifts may be essentially irreversible on human timescales. Which of these
68 trajectories will dominate is unclear and this is likely to vary between habitats and sites.

69 Great Britain (GB) has been a model for studies of pollution impacts for many years as early
70 industrialisation means that impacts here can often provide early-warning of impacts developing
71 elsewhere. As an exemplar region, GB also benefits from intensively studied vegetation
72 communities, air pollution gradients that encompass the range across most of the developed world,
73 and an extensive air quality monitoring network. UK domestic environmental policy goes beyond the
74 requirements of the SDGs, with aims to both halt biodiversity loss earlier than the UN goal and,
75 ultimately, to reverse previous losses (DEFRA 2011). Here we use models based on well-established
76 empirical relationships to investigate the potential impacts of N deposition on landscape-scale
77 biodiversity in the past, present and future.

78 MATERIAL AND METHODS

79 We focus on the species richness of five habitats that are widespread in the temperate and sub-
80 boreal zone and known to be sensitive to nitrogen deposition: acid grassland, bog, sand dune,
81 upland heathland and lowland heathland (Bobbink, et al. 2010). These habitats have all been
82 surveyed across GB-wide nitrogen deposition gradients in previous studies. These studies showed
83 species richness to be significantly negatively related to N deposition after accounting for other
84 major drivers on diversity that were measurable at that scale (Field, et al. 2014, Stevens, et al.
85 2004). The identified relationships are supported by a large body of other research and are used
86 here as the best-available basis for spatial and temporal up-scaling (Duprè, et al. 2010, Maskell, et al.
87 2010, Payne, et al. 2014).

88 We modelled the change in N deposition from 1900 to 2030 using the UK's national air pollution
89 models C-BED (Smith, et al. 2000) and FRAME (Dore, et al. 2007) with scaling factors for historic
90 emissions (Fowler, et al. 2005). We defined four scenarios of future N deposition: current
91 expectations (CE) based on trends in industrial and agricultural activity anticipated by the UK
92 government; ten (%10) and thirty (%30) percent blanket deposition reductions beyond CE; and a
93 scenario in which local action is taken to reduce deposition to the legally-mandated target (critical
94 load: CL) for each grid cell (Bobbink and Hettelingh 2011).

95 To reflect the considerable uncertainty in how N impacts biodiversity and how species richness will
96 recover from reduced deposition we propose three alternative scenarios spanning the range of
97 possibilities suggested in the literature. In the first scenario, increases in N deposition will produce
98 an instant loss of species richness and reductions in N deposition will produce instant recovery. We
99 reflect this scenario by using current-year annual N deposition as the driver of species richness
100 change. In the second scenario, increases and decreases in N will produce lagged responses as
101 species richness takes time to respond to N deposition due to ecological hysteresis and accumulated
102 N. We reflect this scenario by using a 30 year moving window of N deposition as the driver of species
103 richness change (Rowe, et al. 2016). Finally we consider the possibility that the impacts of N may be
104 irreversible on decadal time-scales as communities undergo fundamental regime shifts. We reflect
105 this scenario by using cumulative N deposition since 1900 as the driver of species richness change.
106 While all of these scenarios are feasible, we consider the lagged scenario to be perhaps the most
107 plausible (Rowe, et al. 2016). We used regression to model the relationship between species
108 richness and each metric of N deposition in the national surveys (current/fully cumulative/30 year
109 cumulative), representing each of the three response scenarios. We quantified the spatial
110 distribution of the five target habitats using data from the UK National Vegetation Classification
111 dataset (Averis 2004). Applying the regression equations to the N deposition trajectories for each
112 10x10km cell containing a specific habitat allowed us to predict change in species richness due to N
113 deposition over time (WebFigure 1). We expressed the output as a percentage relative to the
114 maximum species richness in the absence of N deposition (i.e. the Y-intercept) and summed results
115 across habitats and grid cells to assess impacts across Great Britain (see Supplementary Methods for
116 full detail).

117 RESULTS

118 We find that, across habitats and regardless of the response scenario chosen, modelled species
119 richness for 2015 is approximately two thirds of species richness in the absence of N deposition
120 (range 65-68%; Fig. 1). The largest loss, with species richness around 25% of 1900 levels, is in the
121 south of Britain, coinciding with the highest levels of N deposition. Acid grassland and upland heath
122 are the most impacted communities; bogs show the lowest loss of species richness (WebFigure 2).

123 All models show species richness declines due to N deposition from 1900 through to the late 20th
124 century (Figure 2). The instant response scenario shows species richness at the start of the 20th
125 century to be around three quarters of the 'no N deposition' baseline (due to existing industrial
126 emissions) followed by a steady decline to the 1990s and then some recovery. Models based on
127 cumulative N impacts, by contrast, show species richness gradually declining as N accumulates in the
128 system over time, with no recovery. Results from models based on 30-year cumulative N deposition
129 impacts (where, by definition, responses cannot be modelled until 1930) are between these
130 extremes. Under all response scenarios, the decline in species richness through the twentieth
131 century considerably exceeds estimated errors based on 95% confidence intervals of the underlying
132 regressions. The timing and extent of recovery differs for the different scenarios: under the
133 assumption of instant ecosystem response to N deposition, recovery begins at the end of the 20th
134 century as N deposition declines, assuming a 30-year lagged response to N deposition, impacts
135 increase to the end of the 20th century and then stabilise, and assuming the response is to
136 cumulative N deposition, species richness continues to decline through to 2030 (Fig. 2; WebFigure 3;
137 WebVideo File).

138 DISCUSSION

139 If, as expected, these habitats are representative of N-sensitive ecosystems, and defining
140 biodiversity simply as total plant species richness, it is only under the most extreme assumption of
141 fully-cumulative impacts of nitrogen on species that the UK will fail to meet the SDG target to *halt*
142 biodiversity loss due to N deposition. Other developed countries are likely to follow similar
143 trajectories by reducing N emissions. All models agree that currently-expected N emission
144 reductions will not lead to species richness returning to levels of the early 20th century by 2030. The
145 scale of further deposition cuts that would be required to achieve levels of species richness last seen
146 in the early 20th century (1900-1940 mean) ranges from very large (27.3% cut) for the optimistic
147 instant impact/instant recovery scenario, to vast (92%) for the 30-year lagged impact/lagged
148 recovery. Due to the non-linear relationship between N emission and N deposition, achieving such
149 large deposition reductions might require even larger emission reductions (RoTAP 2012). Clearly this
150 scale of deposition reduction is highly unlikely to be achieved, and therefore the loss of species
151 richness is unlikely to be substantially reversed. The most pessimistic possibility is that no extent of
152 N deposition cuts will lead to the recovery of habitats which have undergone fundamental regime
153 shifts, as shown by the cumulative impact/no recovery scenario. However the most likely outcome is
154 probably only a very modest improvement in GB-wide species richness of the five habitats by 2030
155 (e.g. 3% average increase in species richness with currently expected emissions reductions and the
156 30-year lagged response scenario). Similarly limited recovery is likely in other countries where
157 deposition has peaked. N impacts however are likely to extend into previously-unimpacted regions
158 of the world partly due to the export of industrial and agricultural N emissions from the developed
159 world. Achieving the SDG target in terms of Nitrogen deposition is likely to be extremely challenging.

160 The main policy tool used to control air pollution in Europe, and increasingly the rest of the world, is
161 the *critical load*: a level of pollution loading below which impacts on a specified habitat type are not
162 known to occur (Bobbink and Hettelingh 2011). Critical loads are assigned on the basis of
163 experimental studies and expert opinion, but both the existence of an ‘impact floor’ and the ranking
164 of ecosystem sensitivity have recently been questioned for some habitats (Armitage, et al. 2014,
165 Field, et al. 2014, Payne, et al. 2013). In our models one surprising finding is that blanket cuts in N
166 deposition across Britain achieve a higher GB-wide recovery of species richness than the same
167 overall reduction of N deposition based on the lowest critical load for each grid cell (WebTable 1).
168 This is because the survey data that underlie our models do not support the ranking of habitat
169 sensitivity used by critical loads (Field, et al. 2014). This may give caution to the use and wider
170 adoption of this approach. However it should be noted that critical loads are not used solely for the
171 preservation of plant biodiversity and there are other applications (e.g. ecosystem biogeochemical
172 changes) for which targeted reduction in N deposition on the basis of critical loads may be more
173 effective.

174 Large reductions in N deposition are achievable. For instance, the Netherlands has halved ammonia
175 emissions since 1990, primarily by requiring better agricultural technology (Sutton, et al. 2015). In
176 the United Kingdom, measures such as improvements in manure spreading, manure storage and
177 livestock management have the potential to make a substantive difference for comparatively
178 modest investment (Dragosits 2015). Similarly, there may be a role for active habitat management to
179 remove accumulated N (e.g. burning, grazing, turf cutting) and thereby accelerate recovery (Jones,
180 et al. 2017, Storkey, et al. 2015). Enforcing such options would require considerable political will and
181 funding. Policy-makers often look for rapid ‘quick-win’ results, but our models demonstrate that it is
182 likely to take considerable time for the ecological benefits of reduced N deposition to be realised.
183 There is therefore a key role for appropriate mid-point metrics such as reductions in N leaching or
184 tissue N content, to allow the long-term benefits of N deposition reduction to be communicated on
185 political time-scales (Rowe, et al. 2016). Our results demonstrate the large scale of the N deposition
186 problem, which has built up over many years and over extensive regions, and show that positive
187 outcomes for biodiversity of reducing N deposition are unlikely to be achieved quickly.

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193 Temperature Impacts on Peatland Biodiversity and Biogeochemistry). Thanks to all who contributed
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195 with data collection and provided access permission for sites. Thanks to Laurence Jones for providing
196 additional sand dune distribution data and Ed Rowe for suggesting the use of the 30-year window.
197 The nitrogen deposition data are freely available through the Air Pollution Information System
198 website (<http://www.apis.ac.uk/>).
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200 REFERENCES

- 201 Armitage HF, Britton AJ, van der Wal R, *et al.* 2014. The relative importance of nitrogen deposition as
202 a driver of racomitrium heath species composition and richness across europe. *Biological*
203 *Conservation* **171**: 224-231.
- 204 Averis A, Averis, B., Birks, J., Horsfield, D., Thompson, D., Yeo, M. 2004. Illustrated guide to british
205 upland vegetation. Joint Nature Conservation Committee.
- 206 Basto S, Thompson K, Phoenix G, *et al.* 2015. Long-term nitrogen deposition depletes grassland seed
207 banks. *Nature Communications* **6**: 6185.
- 208 RIVM. 2011. Review and revision of empirical critical loads and dose-response relationships :
209 Proceedings of an expert workshop, noordwijkerhout, 23-25 june 2010. The Netherlands.
- 210 Bobbink R, Hicks K, Galloway J, *et al.* 2010. Global assessment of nitrogen deposition effects on
211 terrestrial plant diversity: A synthesis. *Ecological Applications* **20**: 30-59.
- 212 Carfrae JA, Sheppard LJ, Raven JA, *et al.* 2004. Early effects of atmospheric ammonia deposition on
213 *calluna vulgaris* (l.) hull growing on an ombrotrophic peat bog. *Water, Air, & Soil Pollution: Focus* **4**:
214 229-239.
- 215 DEFRA. 2011. Biodiversity 2020: A strategy for england's wildlife and ecosystem services. London:
216 Department of Environment Food and Rural Affairs.
- 217 Dise NB, Ashmore MR, Belyazid S, *et al.* Sutton M (Ed). 2011. Nitrogen as a threat to european
218 terrestrial biodiversity. In: The european nitrogen assessment: Sources, effects and policy
219 perspectives. Cambridge University Press.
- 220 Dore A, Vieno M, Tang Y, *et al.* 2007. Modelling the atmospheric transport and deposition of sulphur
221 and nitrogen over the united kingdom and assessment of the influence of so₂ emissions from
222 international shipping. *Atmospheric Environment* **41**: 2355-2367.
- 223 Dragosits U, Carnell, E., Misselbrook, T., Stevens, C., Jones, L., Rowe, E., Hall, J., Dise, N., Dore, A.,
224 Tomlinson, S., Sheppard, L., O'Shea, L., Reis, S., Bealey, W., Braban, C., Smyntek, P., Sutton, M. 2015.
225 Identification of potential 'remedies' for air pollution (nitrogen) impacts on designated sites (rapids).
226 Report on defra project aq0834. Edinburgh: Centre for Ecology and Hydrology.
- 227 Duprè C, Stevens CJ, Ranke T, *et al.* 2010. Changes in species richness and composition in european
228 acidic grasslands over the past 70 years: The contribution of cumulative atmospheric nitrogen
229 deposition. *Global Change Biology* **16**: 344-357.
- 230 Erisman JW, Galloway JN, Seitzinger S, *et al.* 2013. Consequences of human modification of the
231 global nitrogen cycle. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*
232 **368**: 20130116.
- 233 Field CD, Dise NB, Payne RJ, *et al.* 2014. The role of nitrogen deposition in widespread plant
234 community change across semi-natural habitats. *Ecosystems* **17**: 864-877.
- 235 Fowler D, O'Donoghue M, Muller JBA, *et al.* 2005. A chronology of nitrogen deposition in the uk
236 between 1900 and 2000. *Water, Air, & Soil Pollution: Focus* **4**: 9-23.
- 237 Isbell F, Tilman D, Polasky S, *et al.* 2013. Low biodiversity state persists two decades after cessation
238 of nutrient enrichment. *Ecology Letters* **16**: 454-460.
- 239 Jones L, Stevens C, Rowe EC, *et al.* 2017. Can on-site management mitigate nitrogen deposition
240 impacts in non-wooded habitats? *Biological Conservation*:
- 241 Lamarque J-F, Dentener F, McConnell J, *et al.* 2013. Multi-model mean nitrogen and sulfur
242 deposition from the atmospheric chemistry and climate model intercomparison project (accmip):
243 Evaluation historical and projected changes. *Atmospheric Chemistry and Physics* **13**: 7997-8018.
- 244 Maskell LC, Smart SM, Bullock JM, *et al.* 2010. Nitrogen deposition causes widespread loss of species
245 richness in british habitats. *Global Change Biology* **16**: 671-679.
- 246 Payne RJ, Caporn SJ, Field CD, *et al.* 2014. Heather moorland vegetation and air pollution: A
247 comparison and synthesis of three national gradient studies. *Water, Air, & Soil Pollution* **225**: 1-13.
- 248 Payne RJ, Dise NB, Stevens CJ, *et al.* 2013. Impact of nitrogen deposition at the species level.
249 *Proceedings of the National Academy of Sciences* **110**: 984-987.

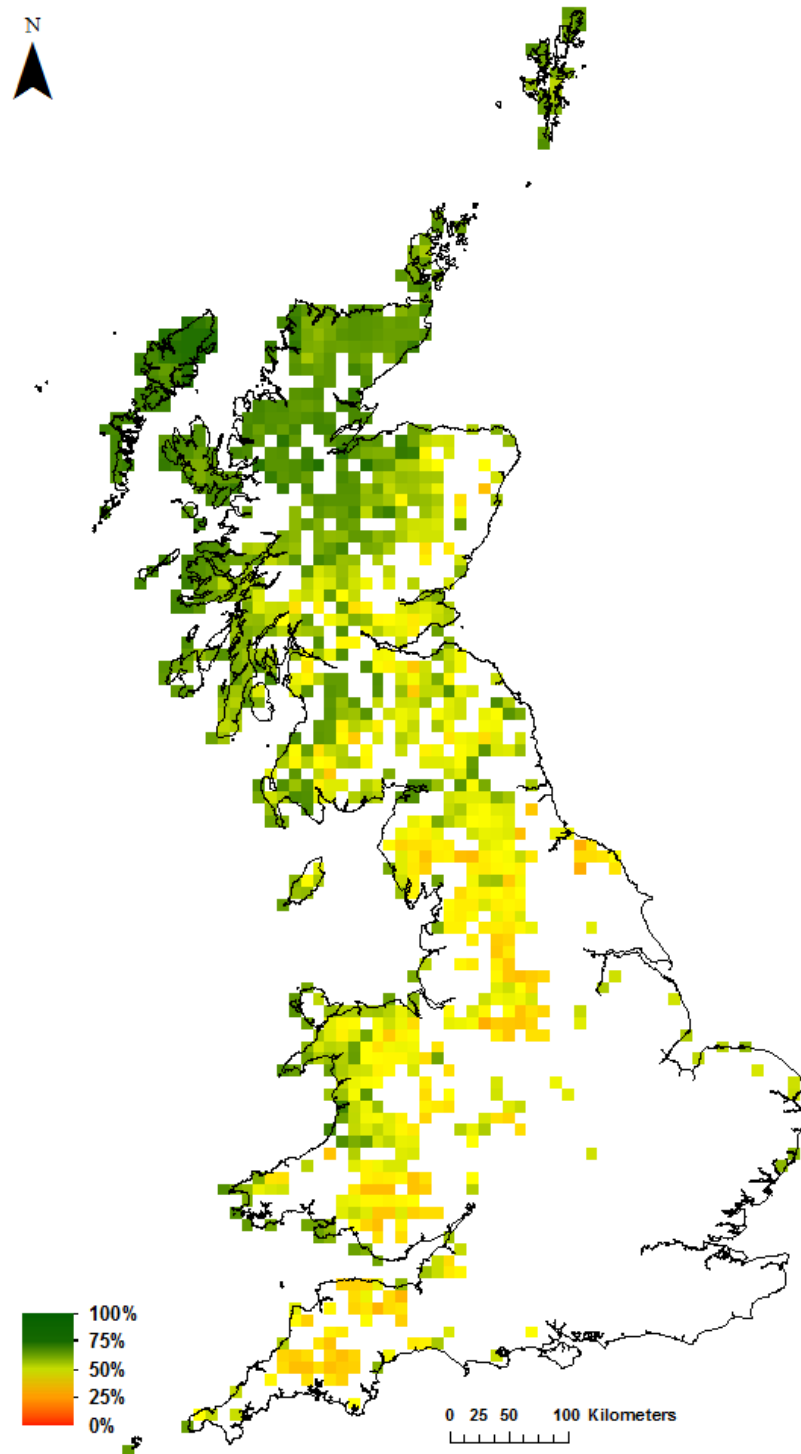
250 RoTAP. 2012. Review of transboundary air pollution (rotap): Acidification, eutrophication, ground
251 level ozone and heavy metals in the uk. Centre for Ecology and Hydrology.
252 Rowe E, Jones L, Dise N, *et al.* 2016. Metrics for evaluating the ecological benefits of decreased
253 nitrogen deposition. *Biological Conservation*:
254 Smith RI, Fowler D, Sutton MA, *et al.* 2000. Regional estimation of pollutant gas dry deposition in the
255 uk: Model description, sensitivity analyses and outputs. *Atmospheric Environment* **34**: 3757-3777.
256 Stevens CJ, Dise NB, Mountford JO, *et al.* 2004. Impact of nitrogen deposition on the species richness
257 of grasslands. *Science* **303**: 1876-1879.
258 Storkey J, Macdonald AJ, Poulton PR, *et al.* 2015. Grassland biodiversity bounces back from long-
259 term nitrogen addition. *Nature* **528**: 401-404.
260 Sutton M, Dragosits U, Geels C, *et al.* 2015. Review on the scientific underpinning of calculation of
261 ammonia emission and deposition in the netherlands. Amsterdam: Government of the Netherlands.
262 Sutton MA, Howard CM, Erisman JW, *et al.* 2011. The european nitrogen assessment: Sources,
263 effects and policy perspectives. Cambridge University Press.
264 Sutton MA, Oenema O, Erisman JW, *et al.* 2011. Too much of a good thing. *Nature* **472**: 159-161.
265 Tilman D and Isbell F. 2015. Biodiversity: Recovery as nitrogen declines. *Nature* **528**: 336-337.
266 United Nations. 2015. Transforming our world: The 2030 agenda for sustainable development.
267 A/res/70/1. New York: United Nations.

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270 CAPTIONS

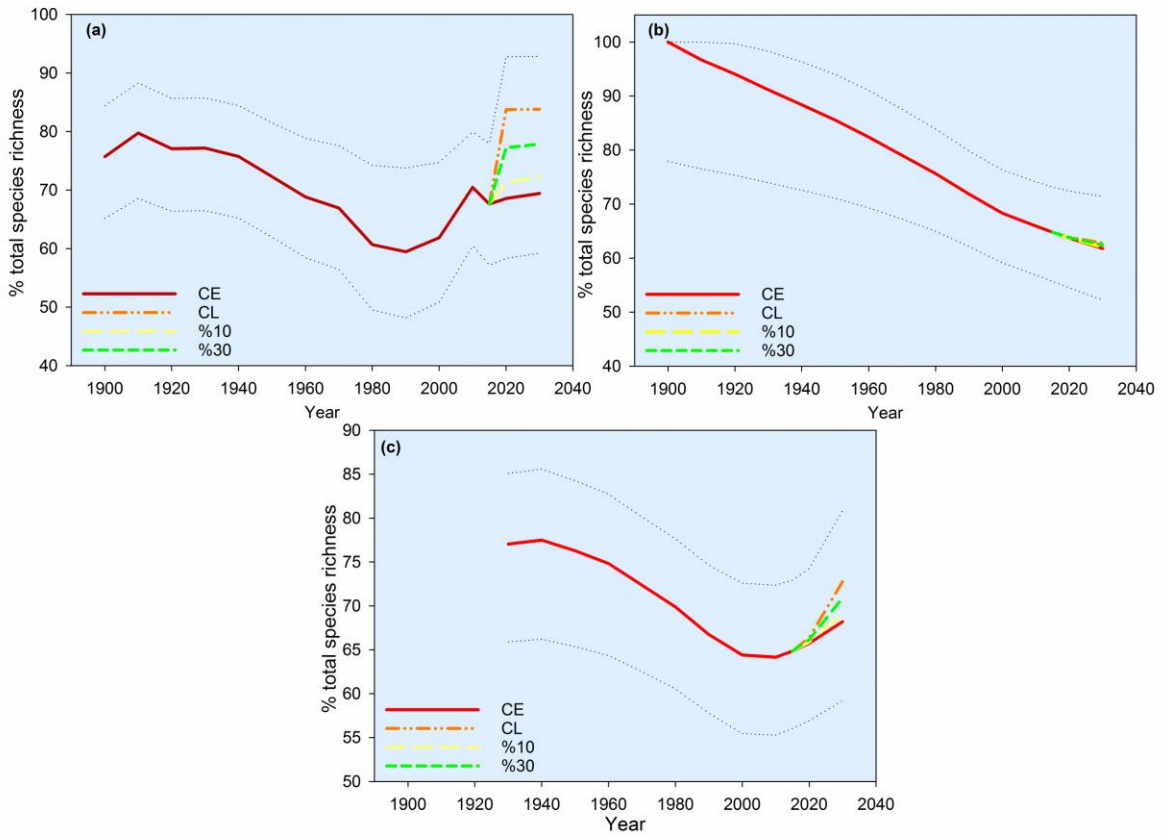
271 Figure 1. Projected species richness for 2015 for five widely-distributed habitats across Great Britain.
272 Figure based on the 30-year lagged response scenario. Shown is the mean species richness of all
273 habitats in each cell, scaled to 100% species richness in the absence of N deposition. Note that there
274 are no data for south-east England due to a low abundance of N-sensitive semi-natural habitats: this
275 region is dominated by agricultural systems and/or habitats on calcareous soils.



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277 Figure 2. Projections of change in overall mean species richness due to N deposition across the five
 278 habitats for 1900-2030 on the basis of a) instant, b) cumulative and c) lagged response scenarios.
 279 Results show projections and estimated uncertainties based on regression 95% confidence bands

280 (dotted envelopes around lines), with four scenarios for future N deposition: currently expected
 281 (CE), 10% or 30% reduction above expectations (%10, %30), and reduction to the critical load (CL).



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283 Table 1. Predictions of mean species richness (as a percentage of expected species richness in the
 284 absence of N deposition) in Great Britain across five habitats for 2030 using three response scenarios
 285 and four N deposition scenarios. Figures in parentheses show uncertainties in predictions based on
 286 95% confidence bands of the underlying regressions.

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292 Table 1. Predictions of mean species richness (as a percentage of expected species richness in the
293 absence of N deposition) in Great Britain across five habitats for 2030 using three response scenarios
294 and four N deposition scenarios. Figures in parentheses show uncertainties in predictions based on
295 95% confidence bands of the underlying regressions.

Response to N deposition	Predicted mean % species richness for 2030 (and uncertainty) based on:			
	Current expectations (CE).	10% reduction above expectation (%10).	30% reduction above expectation (%30).	Deposition reduction to critical load (CL).
Instant	69.4 (59.2-79.4)	72.2 (62.1-81.5)	77.9 (67.3-86.7)	83.8 (71.7-92.9)
Lagged	68.2 (59.2-76.1)	69.1 (60.0-76.9)	70.9 (61.5-78.8)	72.7 (63.2-80.9)
Cumulative	61.8 (52.2-71.0)	62.0 (52.5-71.1)	62.4 (53.1-71.4)	62.8 (53.7-71.5)

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301 SUPPLEMENTAL METHODS

302 N deposition models

303 Total inorganic nitrogen deposition was modelled using the UK's national pollutant deposition
304 models. Different forms and deposition pathways of N (e.g. oxidised vs reduced, wet vs dry) can
305 have different ecological impacts (Sheppard, et al. 2011, Van den Berg, et al. 2008), however at a
306 national scale total inorganic N deposition is a well-defined measure of N load that integrates the
307 impacts of these different N forms and species. Past and present N deposition was estimated using
308 the Centre for Ecology and Hydrology Concentration-Based Estimated Deposition model (C-BED
309 (Smith, et al. 2000)). C-BED predicts N deposition for grid cells (5x5km; aggregated here to 10x10km
310 to match vegetation data) on the basis of monitored atmospheric concentrations and climate data.
311 As C-BED is based on measured data for the past to assess impacts into the future we used the
312 process-based Fine Resolution Atmospheric Multi-pollutant Exchange (FRAME) model (Dore, et al.
313 2007, Fournier, et al. 2004, Fournier, et al. 2005). FRAME is calibrated to C-BED results to generate a
314 self-consistent time series of nitrogen deposition and the two are frequently used in tandem.
315 Comparisons to monitored data and model inter-comparisons show that FRAME performs
316 reasonably well (Chemel, et al. 2011, Dore, et al. 2015, Smith, et al. 2000) and both CBED and FRAME
317 are widely employed in a variety of science and policy contexts. To define the 'current expectations'
318 (CE) scenario for future deposition we use FRAME predictions of total N deposition for 2020 and
319 2030 based on predicted trends in agricultural and industrial N emissions by the UK Department of
320 Environment, Food and Rural Affairs (DEFRA). Scenarios of 10% and 30% N deposition reductions
321 (relative to the CE scenario) assume major national-scale action is taken to produce additional N
322 emissions reductions and that these reductions are implemented evenly across the UK between
323 2015 and 2020 and maintained thereafter. The fourth scenario assumes highly localised action to
324 reduce N deposition to the lower limit of the critical load (CL) range (Bobbink and Hettelingh 2011)
325 for the most sensitive of the habitats we consider in each grid cell. We model this reduction to occur
326 progressively between 2015 and 2020 and for N deposition to be maintained at or below the critical
327 load to 2030.

328 Reconstructing spatial trends in N deposition for the non-recent past is complicated since reliable
329 atmospheric deposition monitoring for the UK only commenced in the 1980s (Fowler, et al. 2005).
330 However, historical data for important variables such as farm animal numbers and coal consumption
331 are available, along with limited N deposition data. Fowler, et al. (2005) have used this information
332 to establish a national-scale deposition chronology and then hind-cast N deposition from 1900 by re-
333 scaling contemporary deposition patterns. This approach has been widely used to calculate
334 historical trends in N deposition and total cumulative N deposition in Great Britain and at a
335 European scale (Duprè, et al. 2010, Payne 2014, Phoenix, et al. 2012). We adopt this methodology
336 here using C-BED data from 1996-1998 as a baseline to calculate total N deposition for each grid cell
337 for the 20th century, with 1900 selected as the start-point to span the total era of direct
338 anthropogenic N fixation (1913 to present). We combine these hind-casted results with C-BED data
339 for the current period of monitoring and predictions to 2030 based on FRAME to give grid cell-
340 specific deposition chronologies as a self-consistent time series.

341

342 Response functions

343 To relate species richness to N deposition we use empirical response functions. We use previous
344 surveys of habitats along national-scale gradients of N deposition to derive regression equations that
345 characterise relationships between plant communities and N deposition. An alternative would be to
346 use relationships based on N-addition experiments (Hettelingh, et al. 2008). However, experimental
347 studies are often limited by small plot sizes, high treatment doses, unrealistic treatment frequency,
348 short duration and high background levels of N deposition, making both temporal and spatial
349 extrapolation extremely problematic. Relationships based on targeted surveys along national N
350 deposition gradients are now widely-accepted as characterising the relationship between plant
351 communities and N deposition (Caporn, et al. 2014, Payne, et al. 2014, Stevens, et al. 2011).

352 We restricted our study to five vegetation communities that are widespread and known to be
353 sensitive to N deposition, and for which targeted survey datasets are available across Great Britain:
354 acid grassland (National Vegetation Classification U4), sand dune (SD8, SD12), blanket bog (M18,
355 M19), upland heath (H12) and lowland heath (H8- H10). We used the dataset of Stevens, et al.
356 (2004) for acid grassland and the datasets of Field, et al. (2014) for the other habitats. We focus on
357 species richness as a meaningful, easily-quantified, and well-understood measure of biodiversity that
358 has been widely used in pollution impact studies (Maskell, et al. 2010, Stevens, et al. 2004). We
359 calculate species richness as the number of species per 2 × 2 m quadrat averaged over five quadrats.
360 In all of these habitats previous research has shown that there is a negative correlation between N
361 deposition and species richness which cannot be adequately explained by other variables such as
362 climate or local site conditions (e.g. pH, soil organic matter, grazing intensity)(Field, et al. 2014,
363 Stevens, et al. 2004). On this basis our models solely consider N deposition and thereby assume any
364 co-variance with other environmental drivers remains constant.

365 Regression models relating species richness to current N deposition have been previously presented
366 by Field, et al. (2014) and Stevens, et al. (2004) and were re-calculated here using a consistent
367 approach. To allow flexibility in the form of the regression we considered a sequence of polynomials
368 of increasing complexity. To avoid over-fitting we only used more complex models where they
369 resulted in a significant improvement in fit (F-test, $P < 0.05$); in practise all selected models were
370 either linear (the majority) or quadratic (WebTable 2). Using current N deposition for prediction
371 implies that when N deposition falls there will be an instant recovery of species richness. As there
372 are many reasons to believe that this will not be the case we also produced regressions based on
373 two alternative N deposition metrics. Firstly, to encompass the possibility that N deposition may
374 force habitats across a 'tipping point' (Isbell, et al. 2013) we considered cumulative N deposition
375 since 1900. Using this metric assumes that impacts accumulate over time with no possibility for
376 recovery however greatly N deposition is reduced. Reality may lie somewhere between these
377 extremes of 'instant recovery' and 'no recovery ever' with some species recovering quickly but
378 others recovering very slowly. To encompass this 'lagged impact/lagged recovery' scenario we also
379 considered N deposition accumulated over the previous thirty years. We selected 30 years as the
380 duration of this moving window following a recent compilation of expert opinion by UK air pollution
381 scientists (Rowe, et al. 2016). For each habitat we therefore produced three alternative regressions
382 based on each of our three N deposition metrics (WebTable 2). Current, cumulative and 30-year
383 cumulative N deposition are highly correlated so there is little statistical reason to prefer any one of

384 the three metrics or any one of the three sets of results. Instead we propose that they are all
385 plausible and can be viewed as representing the range of alternative possible outcomes.

386 Our models are based solely on the data and do not make any *a priori* assumptions about how
387 species richness should respond to N deposition. We recognise that there will be some level of non-
388 anthropogenic nitrogen deposition (due to lightning, volcanism etc.) to which ecosystems will be
389 adapted, but in industrialised regions such as the United Kingdom this will be dwarfed by
390 anthropogenic emission (Galloway, et al. 2004) and can safely be ignored.

391 Vegetation distribution

392 To quantify the spatial distribution of our five target habitats we used the UK Joint Nature
393 Conservation Committee, extended National Vegetation Classification Dataset (NVC (Averis 2004,
394 Rodwell 1991)), supplemented by additional data for sand dunes (Dr Laurence Jones, CEH Bangor).
395 With more than 35,000 records, the NVC dataset is probably the largest survey-based vegetation
396 distribution dataset available for any country. The dataset records the presence of an NVC
397 community within a 10 x 10 km grid cell based on site visits by expert surveyors. This allows us to
398 have confidence that these specific communities are present, and obviates the need for
399 extrapolation across communities which would be required for alternative land cover datasets based
400 on remote sensing. As the dataset combines information from studies made over several decades
401 the distribution of the vegetation communities remains static over time in all our models.

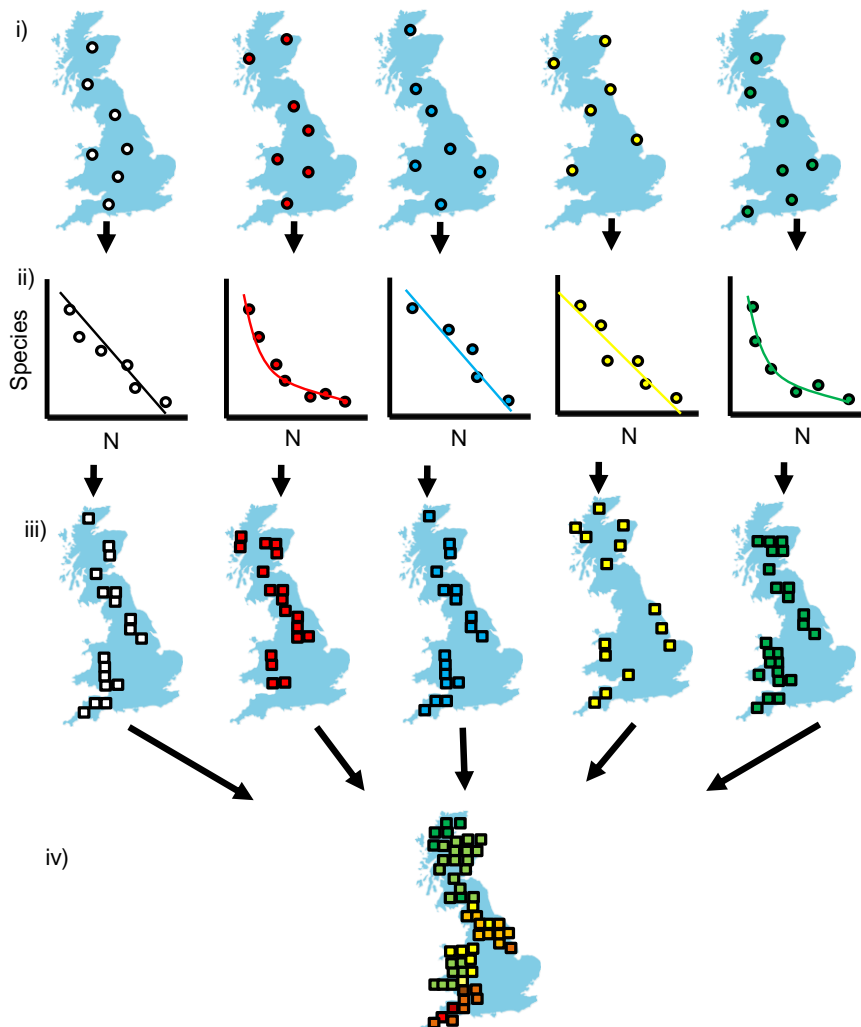
402 Our N deposition modelling allowed us to produce deposition chronologies for every grid cell
403 identified as containing one of our five target habitats. To these grid cell chronologies we applied our
404 habitat-specific response functions to predict changes in species richness for each time step. We
405 repeated this process three times using each of: current, cumulative 1900- and thirty year
406 cumulative N deposition data as the driver of change. To integrate results across habitats we
407 expressed the output on a relative scale as a percentage of species richness in the absence of N
408 deposition (i.e. the Y intercept) with all results constrained to be 100>0%. We mapped the results
409 and by summing across all grid squares and habitat types thereby calculated a figure for percentage
410 loss in national biodiversity. We derived estimates of uncertainty for these figures by using the 95%
411 confidence bands of the regressions to give maximum and minimum estimates for each grid cell.

412 In interpreting the results it should be borne in mind that we focus on five habitats which, while
413 widespread and of conservation importance, are all known to be sensitive to N deposition in terms
414 of species richness. Our results may not apply equally to all other habitats. Our models also do not
415 consider the effect of any drivers other than N deposition. We do not attempt to model change in
416 other drivers of biodiversity change such as landuse or climate change. Our approach is the best
417 currently practicable but large underlying uncertainties mean that results should be viewed primarily
418 as a means to explore plausible scenarios.

419

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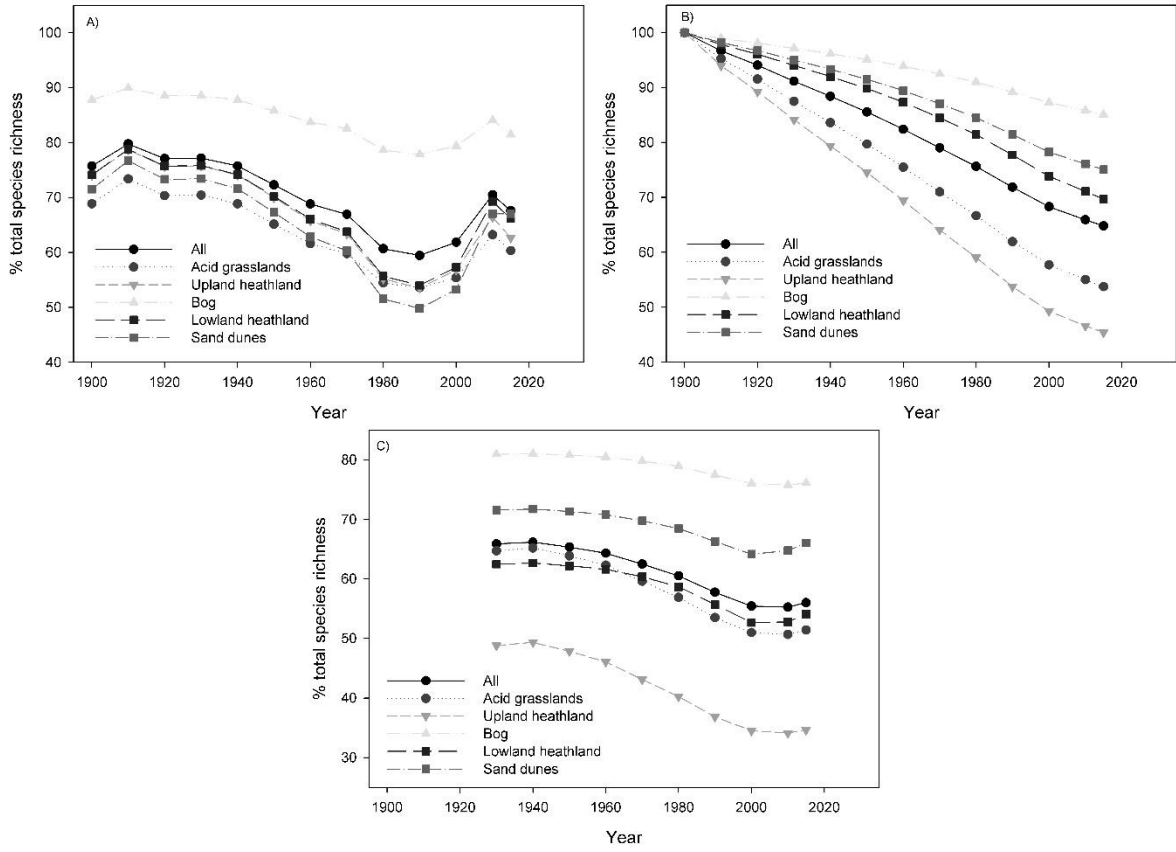
421 WebFigure 1. Schematic diagram demonstrating the principles of our approach. In the first stage (i)
422 national surveys of plant species richness are conducted spanning air pollution gradients (these have
423 been previously published); in the second stage (ii) the relationship between species richness and N
424 deposition is modelled using regression; in the third stage (iii) these regression models are applied to
425 vegetation maps and national N deposition data to predict national impacts on species richness (iv).
426 Stages iii and iv are repeated for multiple time steps and the entire process is repeated using
427 current, cumulative and 30 year cumulative N deposition to give three sets of results (WebFigure 2).



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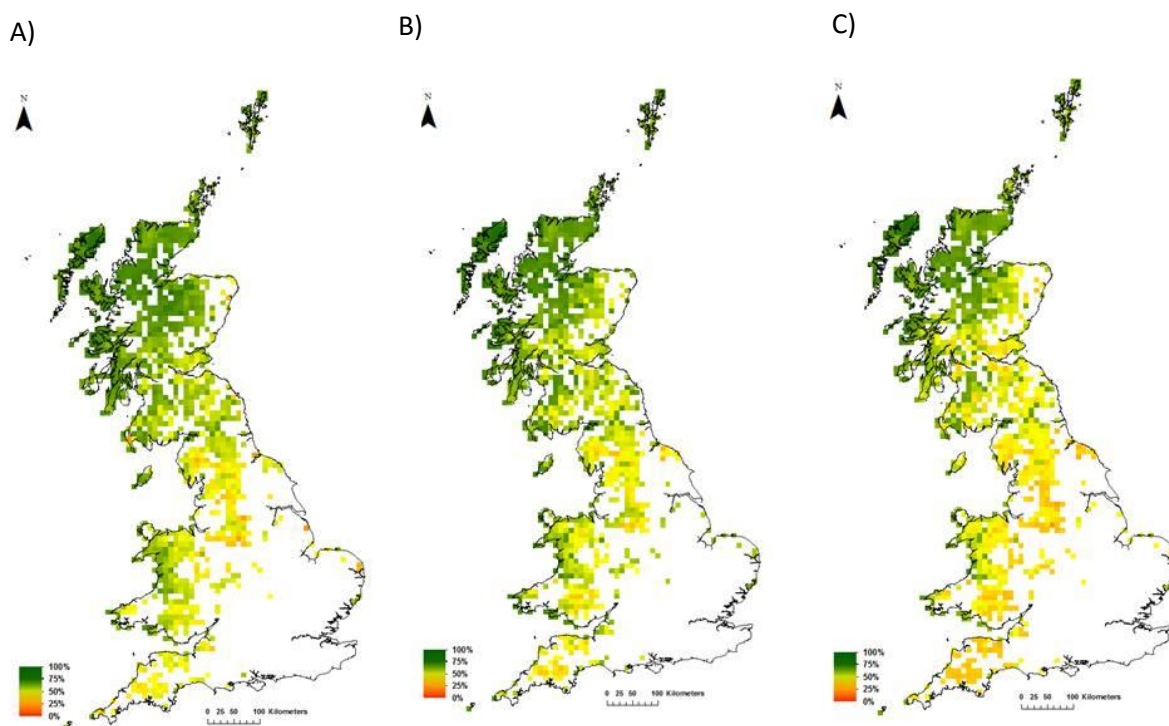
430 WebFigure 2. Hind-casted change in mean species richness by habitat based on a) instant, b)
431 cumulative and c) 30-year lagged response to N deposition.



432

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434 WebFigure 3. Currently expected (CE) 2030 species richness of Great Britain based on a) instant, b)
435 cumulative and c) 30-year lagged response to N deposition scenarios.



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440 WebTable 1. Total deposition reduction required to reach same mean species richness by blanket
441 cuts versus reduction to critical load.

Response to N deposition	Proportion deposition reduction required by blanket cuts versus reduction to critical load
Instant	0.96
Lagged	0.93
Cumulative	0.86

442

443 WebTable 2. R² values showing fit of models based on alternative metrics of N deposition. Best-
444 fitting alternatives shown in bold. Selected models were all linear with the exception of
445 those with values underlined, which were quadratic.

	Current	Lagged	Cumulative
Acid grasslands	<u>0.63</u>	<u>0.63</u>	0.63
Upland heaths	0.39	0.58	<u>0.58</u>
Lowland heaths	0.13	0.20	0.19
Bogs	0.19	0.17	0.15
Sand dunes	0.41	0.30	0.30

446

447 WebVideo File. Change in species richness 1930-2030 based on the 30-year lagged response
448 scenario.



449 Supplementary Video File.wmv

450

451 References

- 452 Armitage HF, Britton AJ, van der Wal R, *et al.* 2014. The relative importance of nitrogen deposition as
 453 a driver of racomitrium heath species composition and richness across europe. *Biological*
 454 *Conservation* **171**: 224-231.
- 455 Averis A, Averis, B., Birks, J., Horsfield, D., Thompson, D., Yeo, M. 2004. Illustrated guide to british
 456 upland vegetation. Joint Nature Conservation Committee.
- 457 Basto S, Thompson K, Phoenix G, *et al.* 2015. Long-term nitrogen deposition depletes grassland seed
 458 banks. *Nature Communications* **6**: 6185.
- 459 RIVM. 2011. Review and revision of empirical critical loads and dose-response relationships :
 460 Proceedings of an expert workshop, noordwijkerhout, 23-25 june 2010. The Netherlands.
- 461 Bobbink R, Hicks K, Galloway J, *et al.* 2010. Global assessment of nitrogen deposition effects on
 462 terrestrial plant diversity: A synthesis. *Ecological Applications* **20**: 30-59.
- 463 Caporn SJ, Carroll JA, Dise NB, *et al.* 2014. Impacts and indicators of nitrogen deposition in
 464 moorlands: Results from a national pollution gradient study. *Ecological Indicators* **45**: 227-234.
- 465 Carfrae JA, Sheppard LJ, Raven JA, *et al.* 2004. Early effects of atmospheric ammonia deposition on
 466 *calluna vulgaris* (l.) hull growing on an ombrotrophic peat bog. *Water, Air, & Soil Pollution: Focus* **4**:
 467 229-239.
- 468 Chemel C, Sokhi RS, Dore AJ, *et al.* 2011. Predictions of uk regulated power station contributions to
 469 regional air pollution and deposition: A model comparison exercise. *Journal of the Air & Waste*
 470 *Management Association* **61**: 1236-1245.
- 471 DEFRA. 2011. Biodiversity 2020: A strategy for england's wildlife and ecosystem services. London:
 472 Department of Environment Food and Rural Affairs.
- 473 Dise NB, Ashmore MR, Belyazid S, *et al.* Sutton M (Ed). 2011. Nitrogen as a threat to european
 474 terrestrial biodiversity. In: The european nitrogen assessment: Sources, effects and policy
 475 perspectives. Cambridge University Press.
- 476 Dore A, Vieno M, Tang Y, *et al.* 2007. Modelling the atmospheric transport and deposition of sulphur
 477 and nitrogen over the united kingdom and assessment of the influence of so₂ emissions from
 478 international shipping. *Atmospheric Environment* **41**: 2355-2367.
- 479 Dore AJ, Carslaw DC, Braban C, *et al.* 2015. Evaluation of the performance of different atmospheric
 480 chemical transport models and inter-comparison of nitrogen and sulphur deposition estimates for
 481 the uk. *Atmospheric Environment* **119**: 131-143.
- 482 Dragosits U, Carnell, E., Misselbrook, T., Stevens, C., Jones, L., Rowe, E., Hall, J., Dise, N., Dore, A.,
 483 Tomlinson, S., Sheppard, L., O'Shea, L., Reis, S., Bealey, W., Braban, C., Smyntek, P., Sutton, M. 2015.
 484 Identification of potential 'remedies' for air pollution (nitrogen) impacts on designated sites (rapids).
 485 Report on defra project aq0834. Edinburgh: Centre for Ecology and Hydrology.
- 486 Duprè C, Stevens CJ, Ranke T, *et al.* 2010. Changes in species richness and composition in european
 487 acidic grasslands over the past 70 years: The contribution of cumulative atmospheric nitrogen
 488 deposition. *Global Change Biology* **16**: 344-357.
- 489 Erisman JW, Galloway JN, Seitzinger S, *et al.* 2013. Consequences of human modification of the
 490 global nitrogen cycle. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*
 491 **368**: 20130116.
- 492 Field CD, Dise NB, Payne RJ, *et al.* 2014. The role of nitrogen deposition in widespread plant
 493 community change across semi-natural habitats. *Ecosystems* **17**: 864-877.
- 494 Fournier N, Dore A, Vieno M, *et al.* 2004. Modelling the deposition of atmospheric oxidised nitrogen
 495 and sulphur to the united kingdom using a multi-layer long-range transport model. *Atmospheric*
 496 *Environment* **38**: 683-694.
- 497 Fournier N, Weston KJ, Dore AJ, *et al.* 2005. Modelling the wet deposition of reduced nitrogen over
 498 the british isles using a lagrangian multi-layer atmospheric transport model. *Quarterly Journal of the*
 499 *Royal Meteorological Society* **131**: 703-722.
- 500 Fowler D, O'Donoghue M, Muller JBA, *et al.* 2005. A chronology of nitrogen deposition in the uk
 501 between 1900 and 2000. *Water, Air, & Soil Pollution: Focus* **4**: 9-23.

502 Galloway JN, Dentener FJ, Capone DG, *et al.* 2004. Nitrogen cycles: Past, present, and future.
503 *Biogeochemistry* **70**: 153-226.

504 Hettelingh J-P, Posch M, Slootweg J, *et al.* 2008. Tentative dose–response function applications for
505 integrated assessment. *CCE status report*: 89.

506 Isbell F, Tilman D, Polasky S, *et al.* 2013. Low biodiversity state persists two decades after cessation
507 of nutrient enrichment. *Ecology Letters* **16**: 454-460.

508 Jones L, Stevens C, Rowe EC, *et al.* 2017. Can on-site management mitigate nitrogen deposition
509 impacts in non-wooded habitats? *Biological Conservation*:

510 Lamarque J-F, Dentener F, McConnell J, *et al.* 2013. Multi-model mean nitrogen and sulfur
511 deposition from the atmospheric chemistry and climate model intercomparison project (accmip):
512 Evaluation historical and projected changes. *Atmospheric Chemistry and Physics* **13**: 7997-8018.

513 Maskell LC, Smart SM, Bullock JM, *et al.* 2010. Nitrogen deposition causes widespread loss of species
514 richness in british habitats. *Global Change Biology* **16**: 671-679.

515 Payne R. 2014. The exposure of british peatlands to nitrogen deposition, 1900–2030. *Mires and Peat*
516 **14**: 1-9.

517 Payne RJ, Caporn SJ, Field CD, *et al.* 2014. Heather moorland vegetation and air pollution: A
518 comparison and synthesis of three national gradient studies. *Water, Air, & Soil Pollution* **225**: 1-13.

519 Payne RJ, Dise NB, Stevens CJ, *et al.* 2013. Impact of nitrogen deposition at the species level.
520 *Proceedings of the National Academy of Sciences* **110**: 984-987.

521 Phoenix GK, Emmett BA, Britton AJ, *et al.* 2012. Impacts of atmospheric nitrogen deposition:
522 Responses of multiple plant and soil parameters across contrasting ecosystems in long-term field
523 experiments. *Global Change Biology* **18**: 1197-1215.

524 Rodwell JS. 1991. British plant communities. Cambridge University Press.

525 RoTAP. 2012. Review of transboundary air pollution (rotap): Acidification, eutrophication, ground
526 level ozone and heavy metals in the uk. Centre for Ecology and Hydrology.

527 Rowe E, Jones L, Dise N, *et al.* 2016. Metrics for evaluating the ecological benefits of decreased
528 nitrogen deposition. *Biological Conservation*:

529 Rowe E, Jones L, Dise N, *et al.* 2016. Metrics for evaluating the ecological benefits of decreased
530 nitrogen deposition. *Biological Conservation*:

531 Sheppard LJ, Leith ID, Mizunuma T, *et al.* 2011. Dry deposition of ammonia gas drives species change
532 faster than wet deposition of ammonium ions: Evidence from a long-term field manipulation. *Global*
533 *Change Biology* **17**: 3589-3607.

534 Smith RI, Fowler D, Sutton MA, *et al.* 2000. Regional estimation of pollutant gas dry deposition in the
535 uk: Model description, sensitivity analyses and outputs. *Atmospheric Environment* **34**: 3757-3777.

536 Stevens CJ, Dise NB, Mountford JO, *et al.* 2004. Impact of nitrogen deposition on the species richness
537 of grasslands. *Science* **303**: 1876-1879.

538 Stevens CJ, Manning P, Van den Berg LJJ, *et al.* 2011. Ecosystem responses to reduced and oxidised
539 nitrogen inputs in european terrestrial habitats. *Environmental Pollution* **159**: 665-676.

540 Storkey J, Macdonald AJ, Poulton PR, *et al.* 2015. Grassland biodiversity bounces back from long-
541 term nitrogen addition. *Nature* **528**: 401-404.

542 Sutton M, Dragosits U, Geels C, *et al.* 2015. Review on the scientific underpinning of calculation of
543 ammonia emission and deposition in the netherlands. Amsterdam: Government of the Netherlands.

544 Sutton MA, Howard CM, Erisman JW, *et al.* 2011. The european nitrogen assessment: Sources,
545 effects and policy perspectives. Cambridge University Press.

546 Sutton MA, Oenema O, Erisman JW, *et al.* 2011. Too much of a good thing. *Nature* **472**: 159-161.

547 Tilman D and Isbell F. 2015. Biodiversity: Recovery as nitrogen declines. *Nature* **528**: 336-337.

548 United Nations. 2015. Transforming our world: The 2030 agenda for sustainable development.
549 A/res/70/1. New York: United Nations.

550 Van den Berg LJJ, Peters CJH, Ashmore MR, *et al.* 2008. Reduced nitrogen has a greater effect than
551 oxidised nitrogen on dry heathland vegetation. *Environmental Pollution* **154**: 359-369.

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