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

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12 KEYWORDS: Vegetation; Global change; Air pollution; Species richness

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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<sub>y</sub>  
22 and NH<sub>3</sub> 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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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  $\text{NH}_4^+$  and  $\text{NO}_3^-$  and dry-deposited  $\text{NH}_3$  and  
45  $\text{NO}_y$ ) 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 20<sup>th</sup>  
124 century (Figure 2). The instant response scenario shows species richness at the start of the 20<sup>th</sup>  
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 20<sup>th</sup>  
134 century as N deposition declines, assuming a 30-year lagged response to N deposition, impacts  
135 increase to the end of the 20<sup>th</sup> 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 20<sup>th</sup> 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 20<sup>th</sup> 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.

188

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190

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193 Temperature Impacts on Peatland Biodiversity and Biogeochemistry). Thanks to all who contributed  
194 to the datasets we use here, including the Terrestrial Umbrella project partners, and all who assisted  
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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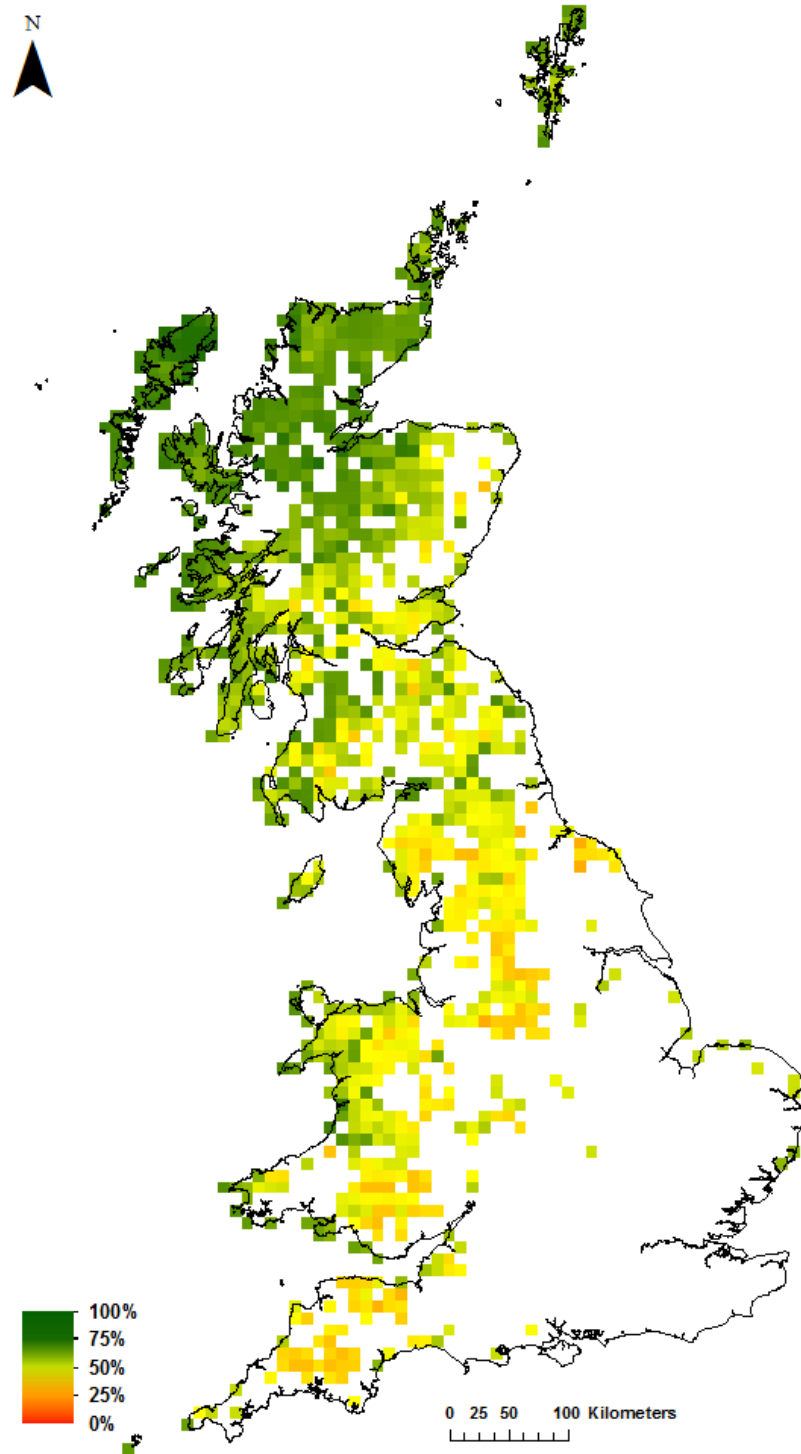
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270 CAPTIONS

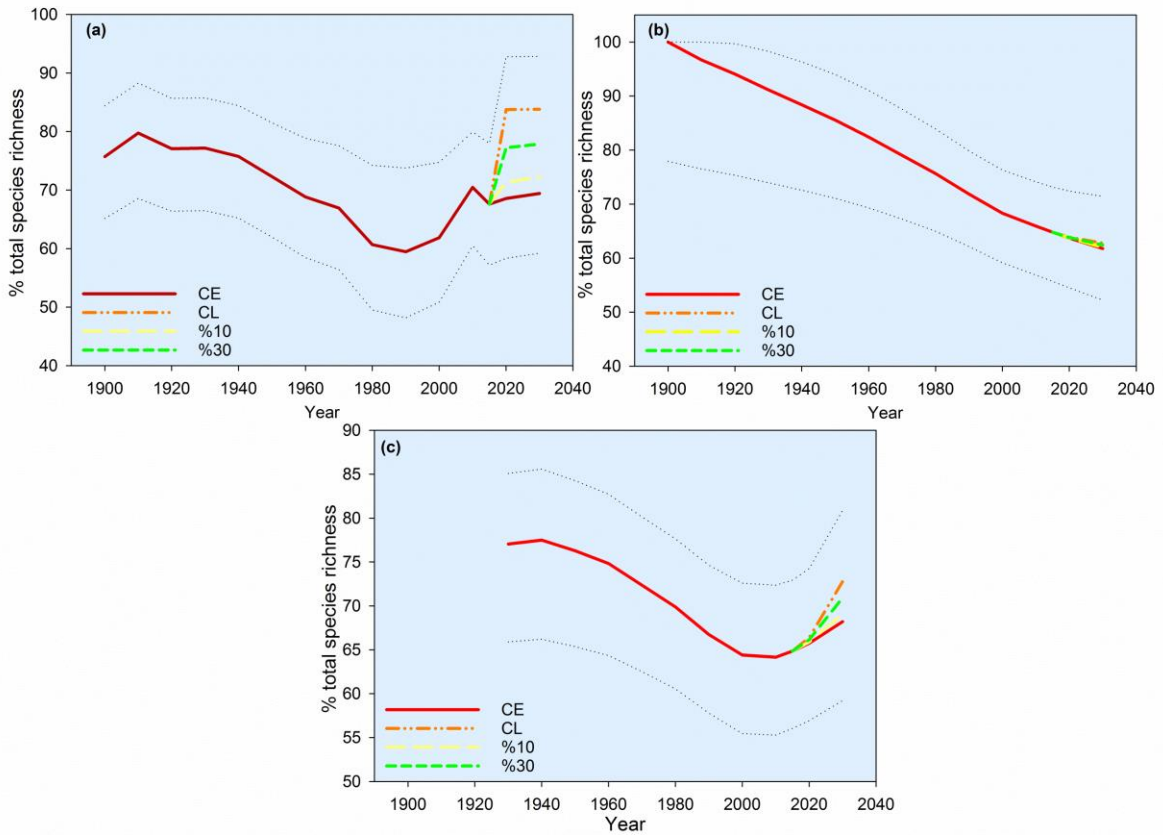
271 Figure 1. Projected species richness for 2015 for five widely-distributed habitats across Great Britain.  
272 Figure based on the 30-year lagged response scenario. Shown is the mean species richness of all  
273 habitats in each cell, scaled to 100% species richness in the absence of N deposition. 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).



282

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 20<sup>th</sup> 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.

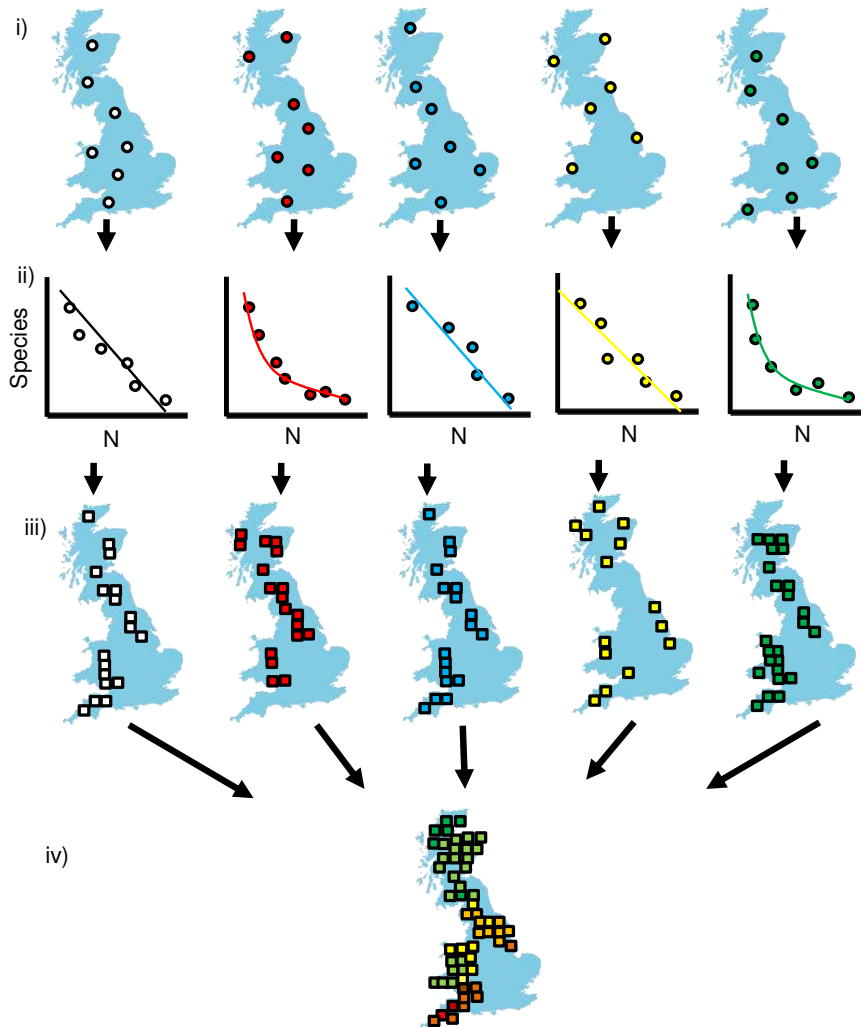
402 Our N deposition modelling allowed us to produce deposition chronologies for every grid cell  
403 identified as containing one of our five target habitats. To these grid cell chronologies we applied our  
404 habitat-specific response functions to predict changes in species richness for each time 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

420

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).

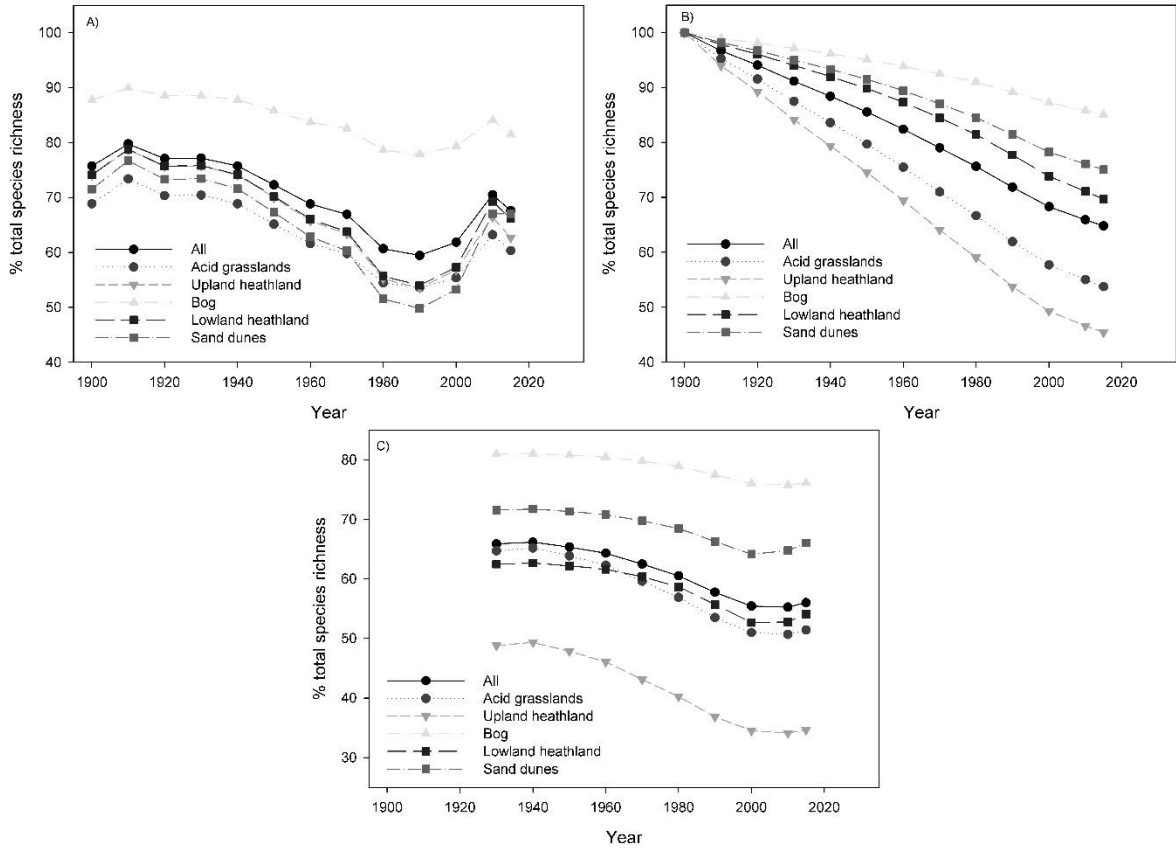


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430 WebFigure 2. Hind-casted change in mean species richness by habitat based on a) instant, b)

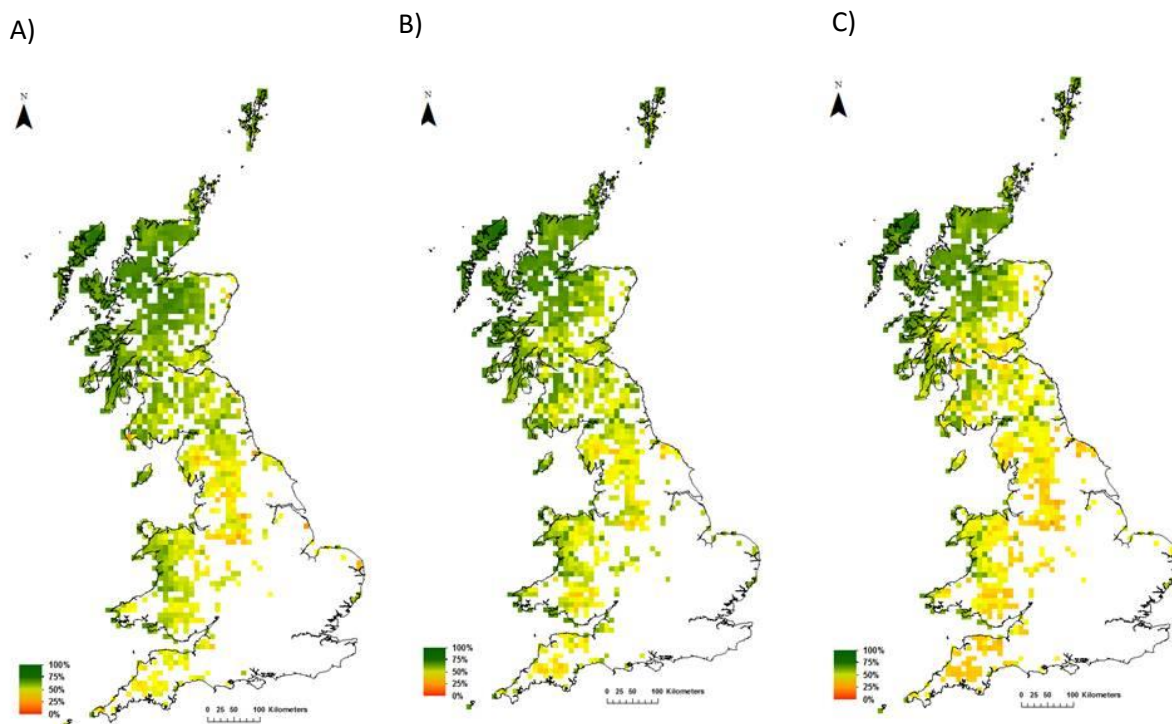
431 cumulative and c) 30-year lagged response to N deposition.



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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. R<sup>2</sup> 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>	<b>0.63</b>
Upland heaths	0.39	<b>0.58</b>	<u>0.58</u>
Lowland heaths	0.13	<b>0.20</b>	0.19
Bogs	<b>0.19</b>	0.17	0.15
Sand dunes	<b>0.41</b>	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

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