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

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Reactive nitrogen (N) deposition from intensive agricultural and industrial activity has been identified as the third greatest threat to global terrestrial biodiversity, after land-use and climate change. While the impacts of N deposition are widely acknowledged, their magnitude is poorly quantified. We combine N deposition models, empirical response functions, and vegetation mapping to simulate the effects of N deposition on plant species richness from 1900 to 2030, using the island of Great Britain as a case study. We find that current species richness values – when averaged across five widespread habitat types – are approximately one-third less than without N deposition. Our results suggest that currently expected reductions in emissions will achieve no more than modest increases in species richness by 2030, and that emissions cuts based on habitat-specific "critical loads" may be an inefficient approach to managing N deposition for the protection of plant biodiversity. The effects of N deposition on biodiversity are severe and are unlikely to be quickly reversed.

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The recently adopted UN Sustainable Development Goals (SDGs) include a target to halt biodiversity losses from terrestrial ecosystems by 2030. An important but frequently overlooked threat to global biodiversity is the atmospheric deposition of reactive nitrogen (N), which is produced by fossil-fuel combustion and intensive agriculture. Given that many ecosystems have evolved under N-limiting conditions, a long-term increase in N deposition even at low levels can cause eutrophication and acidification, with wide-ranging negative consequences for ecosystem services and biodiversity. Field and laboratory experiments, as well as surveys repeated through time and across pollution gradients, have conclusively shown that long-term elevated N deposition (comprising wet-deposited NH_4^+ [ammonium] and NO_3^- [nitrate] and dry-deposited NH_3 and NO_y) is linked to reduced plant biodiversity in many natural ecosystems (Duprè *et al.* 2010; Maskell *et al.* 2010; Dise *et al.* 2011). Excess N affects plants through direct toxicity, soil acidification, nutrient imbalances, and interspecific competition (Dise *et al.* 2011). Loss of plant biodiversity is known to influence microbial and faunal biodiversity through trophic cascades and to lead to degradation of important ecosystem services (Sutton *et al.* 2011; RoTAP 2012; Erisman *et al.* 2013). National and transnational policy requires this threat to be addressed (DEFRA 2011; United Nations Sustainable Development Knowledge Platform 2015), but the magnitude of effects at regional to national scales has not been quantified and there is inadequate information about how impacts arose in the past and may develop in the future.

In many parts of the developed world, N deposition levels are expected to plateau and decline in the coming decades; one critical question to address is how this will affect biodiversity (Sutton *et al.* 2011; Lamarque *et al.* 2013). Studies of species recovery after reductions in N deposition are limited (Tilman and Isbell 2015), but available evidence suggests three possible trajectories. Some consequences of N may be acute and linked to atmospheric concentrations: for instance, direct damage by gaseous ammonia (NH_3) (Carfrae *et al.* 2004). Recovery from this type of effect may be relatively rapid, with the degree of recovery proportional to the level of deposition reduction. Other impacts may develop more gradually; for example, the long-term accumulation of N in soil may cause ecological changes such as competitive shifts in species abundance. Recovery from these effects will be slower, requiring the removal of stored N from the system by processes such as denitrification, leaching, fire, or harvesting (Dise *et al.* 2011). Ecological recovery may be delayed due to factors such as species' dispersal abilities and seedbank depletion (Basto *et al.* 2015). Of greatest concern is the possibility that chronically elevated N deposition may cause a regime shift, favoring the establishment and invasion of nitrophilic species, which then self-perpetuate through mechanisms such as shading, litter accumulation, and production of chemicals which inhibit competitor growth (Isbell *et al.* 2013). Such regime shifts may be essentially irreversible on human timescales. It is unclear which of these trajectories will dominate, and this is likely to vary between habitats and sites.

For many years, the island of Great Britain (GB) has provided a useful location to conduct pollution-related

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studies. Because GB experienced industrialization relatively early as compared to other regions, studying the consequences of pollution here can provide insight into areas currently undergoing industrialization. As an example region, GB also benefits from having vegetation communities that have been intensively studied, air pollution gradients that encompass the range across most of the developed world, and an extensive air quality monitoring network. UK domestic environmental policy goes beyond the requirements of the SDGs, with aims both to halt biodiversity loss earlier than the UN goal and, ultimately, to reverse previous losses (DEFRA 2011). We use models based on well-established empirical relationships to investigate the potential impacts of N deposition on landscape-scale biodiversity in the past, present, and future.

Materials and methods

We focus on the species richness of five habitats that are widespread in the temperate and sub-boreal zone and are known to be sensitive to N deposition: acid grassland, bog, sand dune, upland heathland, and lowland heathland (Bobbink *et al.* 2010) (Figure 1). Each of these habitats has been surveyed over N deposition gradients across GB in previous studies, which have shown species richness to be significantly negatively related to N deposition after accounting for other major drivers of diversity that were measurable at that scale (Stevens *et al.* 2004; Field *et al.* 2014). The identified relationships are supported by a large body of evidence from additional research and are used here as the best-available basis for modelling (Duprè *et al.* 2010; Maskell *et al.* 2010; Payne *et al.* 2014).

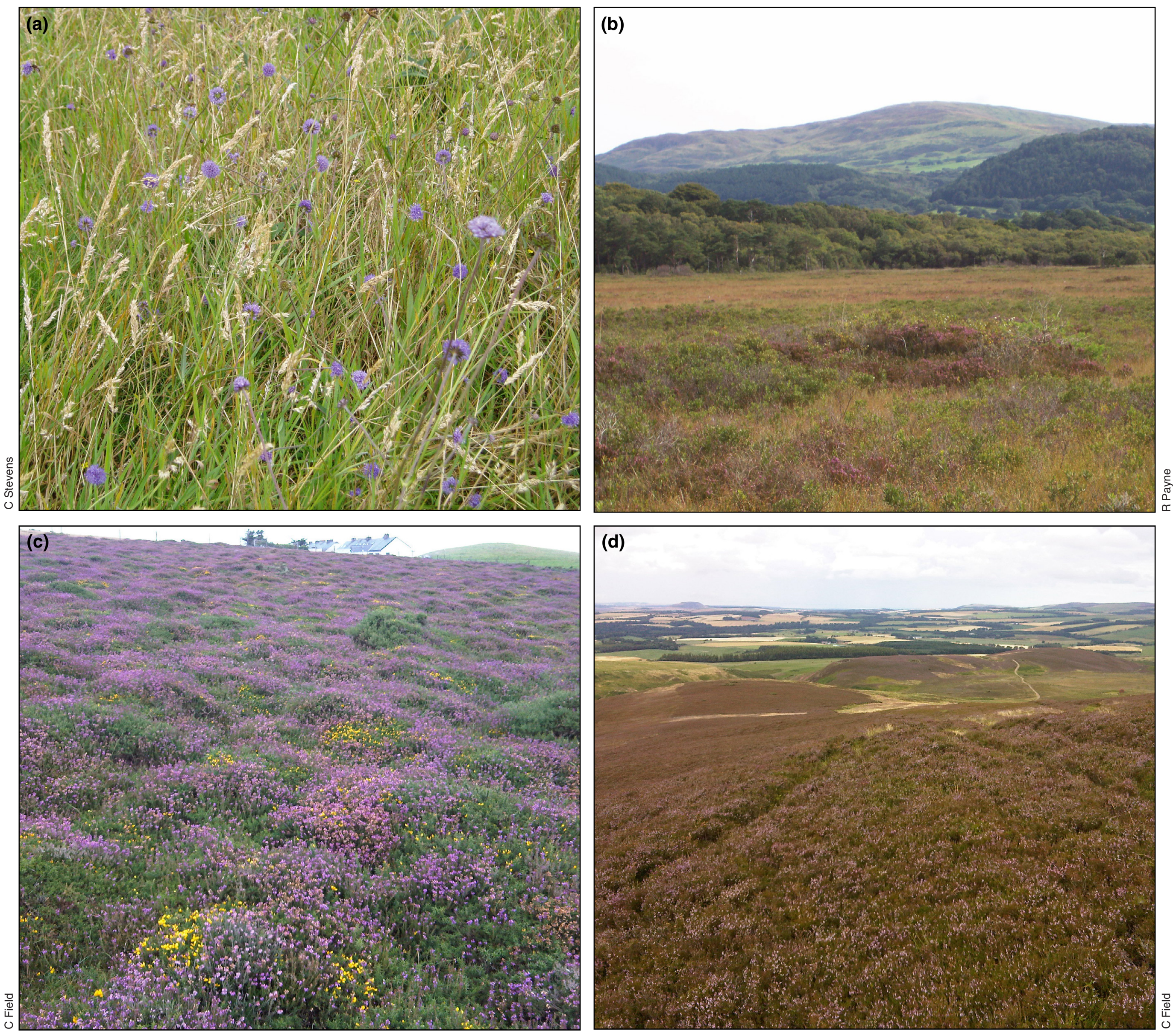

Figure 1. *Habitats investigated in the plant community surveys: (a) acid grassland; (b) bog; (c) lowland heath; (d) upland heath*

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

To account for the considerable uncertainty in how N affects biodiversity and how species richness will recover from reduced deposition, we propose three alternative scenarios spanning the range of possibilities suggested in the literature. In the first scenario, increases in N deposition will produce an instant loss of species richness, and reductions in N deposition will produce instant recovery. We model this scenario by using current-year annual N deposition as the driver of species richness change. In the second scenario, increases and decreases in N will produce lagged responses, where species richness takes time to respond to N deposition due to ecological hysteresis and accumulated N. We model this scenario by using a 30-year moving window of N deposition as the driver of species richness change (Rowe *et al.* 2016). Finally, we consider the possibility that the effects of N deposition may be irreversible on decadal timescales as communities undergo fundamental regime shifts. We simulate this scenario by using cumulative N deposition since 1900 as the driver of species richness change. Although all three scenarios are feasible, we consider the lagged scenario to be the most plausible (Rowe *et al.* 2016). We used regression to model the relationship between species richness and each metric of N deposition in the national surveys (current, fully cumulative, and 30-year cumulative), representing each of the three response scenarios. We quantified the spatial distribution of the five target habitats using data from the UK National Vegetation Classification dataset (Averis *et al.* 2004). Applying the regression equations to the N deposition trajectories for each 10 × 10-km cell containing a specific habitat allowed us to predict change in species richness due to N deposition over time (WebFigure 1). We expressed the output as a percentage relative to the maximum species richness in the absence of N deposition (ie the y intercept) and summed results across habitats and grid cells to assess impacts across GB (see WebPanel 1 for full detail).

Results

We find that, across habitats and regardless of the response scenario chosen, modeled species richness for 2015 is approximately two-thirds of the species richness that would occur in the absence of N deposition (range: 65–68%; Figure 2). The largest loss, with species richness around 25% of 1900 levels, is in the south of GB, coinciding with the highest levels of N deposition. Of the five selected habitat types, acid grassland and upland heathland were associated with the highest losses, whereas bogs were associated with the lowest losses (WebFigure 2).

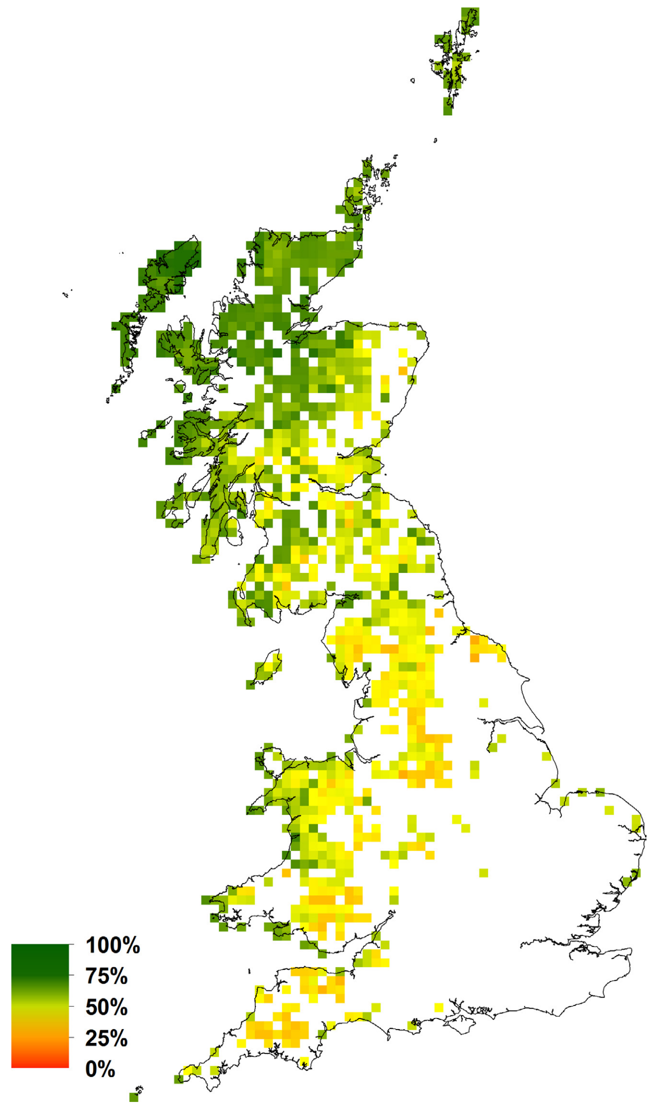

Figure 2. *Projected species richness in 2015 for five widely distributed habitats across the island of Great Britain. Figure based on the 30-year lagged response scenario. The map shows mean species richness of all habitats in each cell, scaled to 100% species richness in the absence of N deposition. Note that there are no data for southeast England due to a low abundance of N-sensitive semi-natural habitats: this region is dominated by agricultural systems and/or habitats on calcareous soils.*

All models demonstrate declines in species richness due to N deposition from 1900 through the late 20th century (Figure 3). The instant response scenario shows species richness at the start of the 20th century to be around three-quarters of the "no-N-deposition" baseline (due to existing industrial emissions) followed by a steady decline to the 1990s and then some degree of recovery. Models based on cumulative N response, by contrast, show species

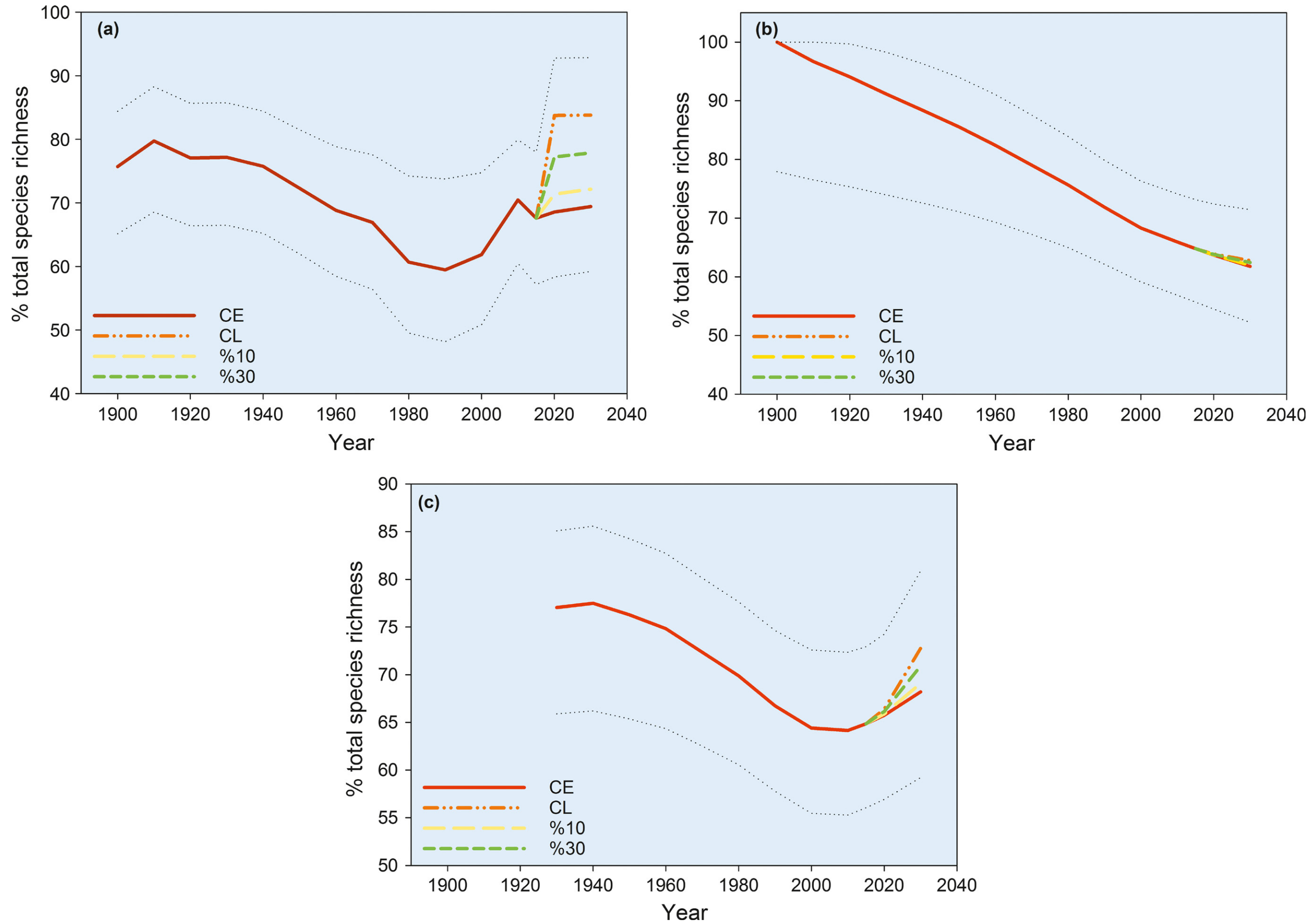

Figure 3. *Projections of change in overall mean species richness due to N deposition across the five habitats for 1900–2030 on the basis of (a) instant, (b) cumulative, and (c) lagged response scenarios. Results show projections and estimated uncertainties based on 95% confidence bands (dotted envelopes around lines) of the underlying regressions, with four scenarios for future N deposition: currently expected (CE), 10% or 30% reduction above expectations (10%, 30%), and reduction to the critical load (CL).*

richness gradually declining as N accumulates in the system over time, with no recovery. Results from models based on 30-year cumulative N deposition impacts (where, by definition, responses cannot be modeled until 1930) are between these extremes. Under all response scenarios, the decline in species richness through the 20th century is greater than the uncertainties inherent in the underlying relationships based on 95% confidence intervals of the regressions. The timing and extent of recovery differs among the various scenarios: assuming an instant ecosystem response to N deposition, recovery begins at the end of the 20th century as N deposition declines; assuming a 30-year lagged response to N deposition, impacts increase to the end of the 20th century and then stabilize; and assuming the response is to cumulative N deposition, species richness continues to decline through 2030 (Table 1; Figure 3; WebFigure 3; WebVideo 1).

Discussion

If, as expected, these five habitats are representative of N-sensitive ecosystems, and if biodiversity is defined simply as total plant species richness, then only under the most extreme assumption of cumulative N deposition will the UK fail to meet the SDG target to *halt* biodiversity loss due to N deposition. Other developed countries are likely to follow similar trajectories by reducing N emissions. All models agree that currently expected N emission reductions will not lead to species richness returning to levels of the early 20th century by 2030 (Table 1). The scale of further deposition cuts that would be required to achieve levels of species richness last seen in the early 20th century (1900–1940 mean) ranges from very large (27.3% reduction for the optimistic instant impact/instant recovery scenario) to vast (92% reduction for the 30-year lagged impact/lagged recovery). Given the non-linear relationship between N emission and N deposition, achieving such large deposition reductions might require even larger emission reductions (RoTAP 2012). Clearly it is highly unlikely that this degree of deposition reduction will be achieved, and therefore the loss of species richness is unlikely to be substantially reversed. The most pessimistic possibility is that no extent of N deposition

Table 1. Predictions of mean species richness (as a percentage of expected species richness in the absence of N deposition) across five selected habitats on the island of Great Britain for 2030, using three response scenarios and four N deposition scenarios

	Predicted mean % species richness for 2030 (and uncertainty) based on:			
Response to N deposition	*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)

Notes: Values in parentheses show uncertainties in predictions based on 95% confidence bands of the underlying regressions.

cuts will lead to the recovery of habitats that have undergone fundamental regime shifts, as shown by the cumulative impact/no recovery scenario. However, the most likely outcome is probably only a very modest improvement in GB-wide species richness in the five habitats by 2030 (eg 3% average increase in species richness with currently expected emissions reductions and the 30-year lagged response scenario). Similarly, a limited recovery is likely to occur in other countries where deposition has peaked. N effects, however, are expected to extend into previously unaffected regions of the world, partly due to the export of industrial and agricultural N emissions from the developed world with imported goods. Achieving the SDG target for N deposition is likely to be extremely challenging.

The main policy tool used to control air pollution in Europe, and increasingly around the rest of the world, is the concept of the critical load (CL): a level of pollution loading below which negative consequences for a specified habitat type are not known to occur (Bobbink and Hettelingh 2011). CLs are assigned on the basis of experimental studies and expert opinion, but both the existence of an "impact floor" and the ranking of ecosystem sensitivity have recently been questioned for some habitats (Payne *et al.* 2013; Armitage *et al.* 2014; Field *et al.* 2014). In our models, one unexpected finding is that comprehensive cuts in N deposition across the UK achieve a higher GB-wide recovery of species richness than the same overall reduction of N deposition based on the lowest CL for each grid cell (WebTable 1). This is because the survey data that underlie our models do not support the ranking of habitat sensitivity used by CLs (Field *et al.* 2014). Our results suggest that more widespread use of critical loads should be conducted with caution. However, it should be noted that CLs are not used solely for the preservation of plant biodiversity and that there are other applications (eg ecosystem biogeochemical changes) for which targeted reduction in N deposition on the basis of CLs may be more effective (Table 1).

Large reductions in N deposition are achievable. For instance, the Netherlands has halved NH_3 emissions since 1990, primarily by requiring enhancements to agricultural technology (Sutton *et al.* 2015). In the UK, measures such as improvements in manure spreading, manure storage, and livestock management have the potential to make a substantial difference in exchange for a comparatively modest investment (Dragosits *et al.* 2015). Similarly, there may be a role for active habitat management to remove accumulated N (eg burning, grazing, turf cutting) and thereby accelerate recovery (Storkey *et al.* 2015; Jones *et al.* 2017). Enforcing such options would require considerable political will and funding. Our results demonstrate the large-scale nature of the N deposition problem, which has accumulated over many years and over extensive regions, and show that positive biodiversity outcomes from reductions in N deposition are unlikely to be achieved quickly.

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Supporting Information

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