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Nitrogen impacts on vascular plants in Britain: an analysis of two national observation networks

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Abstract

Large areas of the United Kingdom currently have nitrogen (N) deposition at rates which exceed the thresholds above which there is risk of damage to sensitive components of the ecosystem (critical loads), and are predicted to continue to do so. Previous studies have shown that this excess N can be very damaging to semi-natural ecosystems. However, such studies have focussed primarily on the relationship of species richness to nitrogen, possibly missing the risk that increased deposition can have on individual plant species. To address this gap in knowledge, we used data from two national observation networks over Great Britain: the vascular plant database and the Botanical Society of the British Isles local change network to examine the response of individual vascular plant species to nitrogen in acid grasslands, calcareous grasslands and heathlands. Presence absence records of individual species, along with mean Ellenberg scores, within 10 km hectads were modelled against N deposition whilst at the same time controlling for the effects of climate, land use and sulphur deposition using generalised additive models. Ellenberg N showed a significant increase with increasing N deposition in almost all habitats across both surveys. Many individual species showed strong relationships with N deposition and clear negative trends in species prevalence to increasing nitrogen were found in all habitats. Species that showed negative relationships to N showed signs of decline at low levels, far below the current critical load levels.

1 Introduction

Atmospheric nitrogen (N) deposition poses a serious threat to sensitive semi-natural habitats in the UK (Hall et al., 2006a; RoTAP, 2011). Estimated levels of nitrogen (N) deposition across the UK are shown in Fig. 1. Large areas of the country exceed the critical loads for nutrient N and critical levels for ammonia, and are predicted to cntinue to do so in 2020 despite reductions in emissions of reactive N gases (Hall et al., 2006b). The critical load is defined as the level below which significant harmful effects on specified sensitive elements of the environment do not occur (Nilsson and Grennfelt, 1988). Therefore, by definition, as N levels surpass the critical load values there is possibility of a significant harmful effect on the environment. There is a growing body of evidence from both experiments and surveillance studies that suggest increases in N have a negative effect on species richness and composition (e.g. Mountford et al., 1993; Wilson et al., 1995; Stevens et al., 2004, 2010a; Maskell et al., 2010; Dupré et al., 2010; Smart et al., 2004; Van den Berg et al., 2010).

A negative relationship between species richness and nitrogen leads us to hypothesise that some individual vascular plant species show a decline in frequency of occurrence with increased nitrogen and are perhaps not found at all in some areas due to high nitrogen deposition levels. However, as some species lose out, decline and potentially become eliminated from the ecosystem, with increased levels of N, some species may flourish. Changes in mean indicator scores based on summarising changes across taxa can reveal strong signals of pollutant impacts. However, plant species respond individualistically so that assessment at an individual species level is required to understand how assemblage-level changes comprise different magnitudes and directions of change among the species present. Expressing habitat change at the species level also allows identification of potential indicators of air pollution and aids interpretation of critical load exceedance scenarios.

There have previously been a number of geographically large-scale studies attempting to determine the impact of N deposition on vegetation in the UK. For example, Stevens et al. (2004) used a large scale spatial survey of acid grasslands to demonstrate declines in species richness, when high N deposition was compared with areas of low N deposition. In the RoTAP report (RoTAP, 2011) results of eleven surveys conducted in the UK are compared. Species richness declined with increasing N deposition in seven of the eleven surveys. Further to this, species richness of vascular plants has been found to decrease in response to N deposition in a number of experimental studies (e.g. Bobbink et al., 1998; Clark and Tilman, 2008; Mountford et al., 1993).

The Countryside Survey has also been used to study the impact of N deposition on semi-natural vegetation communities. This study used data from the 1998 survey to show declines in species richness in both acid grassland and heathland along the UK gradient of N deposition. Trait data was used to propose mechanisms for species loss. These appeared to vary by habitat type; in acid grassland and heathland acidification appeared to be the driving process rather than eutrophication (Maskell et al., 2010). In addition to this large-scale analyses of UK and European data have also detected parallel signals of eutrophication (Dupré et al 2010; Smart et al 2004; RoTAP, 2011). As N deposition increases, plant species and traits associated with higher fertility have become more abundant and stress-tolerant species have declined.

In some studies covering a range of habitats across Europe, Ellenberg values (Ellenberg et al., 1991; Hill et al., 1999) have been used as indicators of N deposition effects (Diekmann and Falkengren-Grerup, 2002; Jones et al., 2004). Ellenberg values describe the realised niche of a plant in relation to its tolerance of certain environmental conditions on a scale of one to nine. The most relevant to N deposition is the N score (nitrogen or nutrients). The Ellenberg N score indicates overall fertility or productivity (Hill and Carey, 1997).

However, none of these previous studies have focussed on relationships that individual species have to N, whilst at the same time accounting for other confounding factors such as climate. As the majority of air pollution policy is focussed on setting appropriate emissions ceilings and the consideration of critical load exceedance, evidence from analysing individual species responses to nitrogen needs to be considered so that critical loads are set at levels to protect the risk of species loss.

The main aim of this paper is to analyse vegetation surveillance datasets on a national scale, in terms of individual species responses and Ellenberg N scores, and collate evidence of possible N deposition impacts/relationships. This is to add to the growing evidence base and provide a sound quantitative foundation for critical load revision that will ensure the protection of species and ecosystem functions, and maintain current conservation commitments and biodiversity targets. These include the aim to maintain or improve the status of wild flora and fauna and their ecosystems and habitats in response to the Convention for Biological Diversity (CBD) Articles 8 and 9.

2 Methods

2.1 Data

Data were taken from two national vegetation datasets to look at relationships with N deposition for three semi-natural habitats: calcareous grassland; acid grassland; and heathland. The databases used were: the Vascular Plant Database, which recorded the presence of all vascular plant species growing within 10 km^2 hectads in the wild between 1987 and 1999 (Preston et al., 2002); and The Botanical Society of the British Isles (BSBI) Local Change Survey which records all vascular plant species growing in the wild in 811 2 × 2 km tetrads located within a regular grid of 10 km^2 hectads across Great Britain. The BSBI survey was conducted in both 1987–1988 and 2003–2004 (Braithwaite et al., 2006), but for this analysis only data from 2003–2004 was used. For the purposes of this assessment, any recorded subspecies were aggregated to the species level, with hybrids and alien species excluded.

Vascular plants were individually assigned to each of the target habitat types using published preference data on habitat affinity and altitudinal ranges (Hill et al., 2004). Only those species selected using the criteria above were further used to generate summary variables. Thus generalist species and those restricted to other non-target habitats were excluded from the calculation of mean Ellenberg values for each recording unit (i.e. tetrad or hectad).

Hectads (10 × 10 km squares) and tetrads (2 × 2 km square) were processed to determine upland and lowland strata and to locate focal Broad Habitats. Broad Habitat occurrence was derived from the Land Cover Map 2000 25 m raster coverage. The upland mask is composed of the upland delineation for England based on English Natural Areas, a Welsh upland mask provided by Countryside Council for Wales (CCW), and the combined upland and montane masks from Scottish Natural Heritage (SNH).

To understand fully the potential effects of Nitrogen on vascular plants we investigated relationships between atmospheric N deposition and: individual species' responses (presence/absence in each recording unit based on current distribution); and Ellenberg N scores (Hill et al., 1999, 2007). This allowed us to identify species that are especially vulnerable to N deposition and those which are not found in areas of high deposition, whilst Ellenberg N scores allow us to assess the extent to which these different species patterns reflected prior knowledge of their association with different levels of fertility. Thus we calculated average Ellenberg N scores based on the presence of species within each habitat. N scores are on a scale of one to nine, where one represents the most infertile habitats and nine represents fertile habitats.

2.2 Driver variables

Ecological drivers known to affect species occurrence were included in the model so that the effects could be partialled out before looking into the relationship with N deposition. Additional variables included were: intensity of land-use in each grid square; minimum January temperature; maximum July temperature; total annual rainfall; and sulphur (S) deposition. Intensity of land use was measured as the proportion of arable plus improved grassland in the grid square as calculated from Land Cover Map 2000. Climate data was based on long term averages from the Met Office covering the period from 1980 to 2005. S deposition was the difference in model estimates for 1971 and 2005 as based on the FRAME model (Fine Resolution Ammonia Exchange) (Fournier et al., 2000). For N deposition we used estimates at the 5 km^2 scale provided by CEH Edinburgh (NEGTAP, 2001; Smith et al., 2000), calculated as the mean of the estimates for 1996, 1997 and 1998 from the CBED model for deposition to moorland. Whenever the resolution of the botanical records was greater than that of the driver variable data, the driver data were averaged over the size of the botanical recording unit.

2.3 Modelling of response variables

We used a generalised additive model (GAM) (Hastie and Tibshirani, 1990) based approach to model both species presence/absence and Ellenberg N scores. This allowed the effects of other covariates of interest to be modelled and accounted for before looking at the relationship between the response variable and N. The flexible, non-linear, smooth terms used in the GAM framework allow for the possibility that a species may be unaffected beneath a certain level of N but showing signs of change beyond this threshold, thus conforming to the critical loads definition.

Any spatial structure in the model residuals was accounted for in the GAM by including an additional two-dimensional smooth term, i.e. a planar surface, in the model. This term is defined as an interaction between the two coordinate axes. Therefore any spatial dependence between hectads, missing spatial covariates or spatially structured recording effort is accounted for as much as is possible. This, rather broad scale way of handling residual spatial structure was assessed by repeating a subset of models in a Bayesian framework allowing for a complex, localised, fine scale dependence structure to be specified. Results from such analyses confirmed that the broader scale dependence method of the GAMs performed equally as well. Furthermore, for the BSBI tetrad data a random effect term for hectad was also included to account for differing levels of variability to data from within the same hectad to data from differing hectads.

Finally, to maintain an element of consistency across the analyses, all models were started with the same set of terms and driver variables, which were included in the model in the same order.

2.4 Model inference

For both the hectad and tetrad models, regression parameters for any fixed linear terms and parameters for each of the smooth terms were estimated, together with standard errors, by either approximating the true likelihood or using quasi likelihood methods. Having fit the model with all terms, individual terms were selected based on F-tests, the

AIC score (Akaike, 1969) and the generalised cross validation score. Non significant terms were only removed if the AIC and GCV scores improved upon their removal. The covariate corresponding to N was always included in the model whether it was significant or not, as it was this relationship that ultimately we were interested in. The final model was checked by examining plots of residuals and quantile-quantile plots of the observed and predicted values.

To formally assess the impact of N, the p-value from the F-test associated with the N covariate was returned along with a graphical plot of the estimated smooth term in the GAM for N deposition. Both the p-value and the plots together provide a full assessment of the modelled relationship, including predicted strength, direction and change points, that N has in relation to the vegetation response variable.

Because of the complex modelling framework and the number of driver variables used in building the model, data sets with a small number of observations could not be analysed and were therefore removed. Also species with less than 10 % and greater than 90 % of presences in the data set were also removed as convergence in the model was difficult to achieve.

3 Results

Results are presented separately for the analysis of the individual species' presence/absence and the calculated Ellenberg N score. Furthermore, each of the three habitats: calcareous grassland, acid grassland and heathland are listed individually for the species response analysis. The number of hectads within each of the three habitats for the two recording schemes is shown in Table 1. Histograms showing the ranges of N deposition covered within each habitat for which data were analysed are given in Appendix A.

It is important to note that the low sample sizes for analysis are not solely because of too few records in either recording scheme. It is the combination of sampling units coinciding with grid cells with identifiable and hence larger areas of the focal habitat i.e. the presence records for species in cells where Land Cover Map did not pick up the habitat of interest were not included.

3.1 Individual species response

Removing the very rare and very common species from the analysis (those with an overall presence of less than 10 % and greater than 90 % respectively) the presence/absence of the remaining species occurring in the sampling units according to Table 1, was modelled as outlined above. P-values obtained from testing the null hypothesis of no association between presence/absence and N deposition, having accounted for other driver variables, are given in Appendix B for all species analysed. For species where a significant association with N deposition was found, the relationships are plotted as probability of presence against increasing total inorganic N deposition ($\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$). The critical load is also included in these plots.

3.1.1 Calcareous grassland

In the Vascular Plant Database the presence/absence of 40 species in lowland calcareous grassland were modelled. Of these, 17 showed significant relationships with N deposition (Appendix B). Nine species showed negative relationships (Fig. 2a) with N deposition: *Allium vineale, Anacamptis pyramidalis, Carlina vulgaris, Cynoglossum officinale, Echium vulgare, Geranium columbinum, Ononis repens, Rosa micrantha* and *Spiranthes spiralis*. All of these species showed changes in their probability of presence even at low levels of N deposition well below the critical load of 20 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$. Four species showed positive relationships (Fig. 2b) with N deposition: *Carex spicata, Knautia arvensis, Lathyrus nissolia* and *Stachys officinalis.* All of which appeared to increase to around 25 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ and then stabilise. There were also four species (*Centaurium erthraea, Epipactis helleborine, Linum bienne* and *Pastinaca sativa*) that showed hump-backed distributions (Fig. 2c) with the peak occurring around the critical load level. For upland calcareous grasslands there was only sufficient data to analyse seven species. Two species showed significant relationships with N deposition (Fig. 2d). *Alchemilla xanthochlora* showed a significant increase with N deposition, whereas *Melica nutans* showed a generally declining probability of presence with increasing N deposition. The slight increase at low levels of deposition is due to the wide variation in the data at this point.

In the BSBI local change survey there were sufficient data for analysis of 17 species within lowland calcareous grasslands. Eight showed a significant relationship with N deposition (Fig. 3a): *Bromopsis erecta, Campanula glomerata, Carex spicata, Centaurea scabiosa, Daucus carota, Ononis repens, Sanguisorba minor* and *Viola odorata*. Of these, a number of species show changes of a small magnitude or complex responses but there are clear, steep declines for a number of species including *B. erecta, C. glomerata, C. spicata* and *O. repens*. There were 12 species analysed in upland calcareous grasslands of which three species showed significant correlations with N deposition: *Persicaria vivipara, Rubus saxatilis* and *Thalictrum alpinum.* All of these species showed hump-backed relationships with N deposition (Fig. 3b).

3.1.2 Acid grassland

In the Vascular Plant Database there were sufficient data to test probability of presence for eleven species (between 10 and 90 % of hectads occupied) for lowland acid grassland. Five of these species showed a significant relationship with N deposition: *Cerastium arvense, Cerastium semidecandrum, Trifolium arvense, Vicia lathyroides* and *Viola canina*. All five species showed similar trends (Fig. 4), with the probability of presence declining rapidly with increasing deposition, including at levels below the critical load of 15 kg N $\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$, and then tailing off. Only one species was investigated for upland acid grassland but did not show a significant response to N deposition.

In the BSBI data for lowland acid grasslands there was sufficient data on only one species in the data set (Appendix B), *Senecio sylvaticus*, which did not show a significant relationship with N deposition. For upland acid grassland again only one species had sufficient data for analysis: *Agrostis vinealis*. *A. vinealis* showed a significant hump-backed response to N deposition, increasing to 25 kg N ha^{-1} yr^{-1} then declining.

3.1.3 Heathland

Within the Vascular Plant Database there was sufficient data for analysis of four species in lowland heathland. Two species showed a significant relationship with N deposition (Fig. 5a). *Platanthera bifolia* had a positive relationship with N deposition, with probability of presence increasing steadily as N deposition increased. *Viola canina* has a negative relationship with N deposition declining considerably in its probability of presence between 10 and 25 kg N ha^{-1} yr^{-1}. In upland heathlands it was possible to analyse ten species (Appendix B). Two species showed significant relationships with N deposition. *Arctostaphylos uva-ursi* had a negative relationship with N deposition declining in probability of presence up to 15 kg N ha^{-1} yr^{-1} and then remaining at very low levels (Fig. 5b). *Trientalis europaea* showed a hump-backed distribution peaking at approximately 18 kg N ha^{-1} yr^{-1}.

In the BSBI Local Change data there were insufficient data to perform analysis on any of the 16 potential lowland heathland species in the data set. However, in upland heathland there were seven species for which analysis could be performed (Appendix B). Of these, three showed significant relationships with N deposition: *A. vinealis*, *Listera cordata* and *Vaccinium vitis-idaea* (Fig. 6). *A. vinealis* and *L. cordata* showed similar hump-backed responses with peak probability of presence at around 20 kg N ha^{-1} yr^{-1}, whereas *V. vitis-idaea* showed a clear decline in response to N deposition.

3.2 Ellenberg N

Plots of modelled relationships between Ellenberg N score and total inorganic N deposition for all habitats are shown in Fig. 7a for the Vascular Plant database and Fig. 7b for the BSBI database.

Using data from the Vascular Plant Database, average Ellenberg N scores showed a clear increase with increasing N deposition (indicating an increase in fertility) for lowland acid grasslands ($p = 0.0005$). For upland acid grasslands, however, there was no significant ($p = 0.32$) relationship between Ellenberg N and N deposition. This result was echoed in the analysis of the BSBI Local Change data, showing a clear increase in the lowlands ($p = 0.01$), but no significant result in the upland acid grasslands ($p = 0.42$).

There were significant results for both lowland ($p = 0.004$) and upland ($p = 0.0062$) calcareous grasslands in the analysis of Ellenberg N scores from the Vascular Plant Database with both communities showing a significant increase in mean Ellenberg N with increasing N deposition. Results from the BSBI Local Change data in upland calcareous grasslands showed no significant relationship between N deposition and mean Ellenberg N score ($p = 0.72$), whereas lowland calcareous grassland showed a significant ($p = 0.0074$) increase. Unlike the acid grasslands analysis however this relationship is non-linear.

Analysis of the vascular plant database for both upland and lowland heathlands showed a significant ($p = 0.0059$ and $p = 0.0549$, respectively) increase in Ellenberg N score. The analysis of BSBI Local Change data for heathlands showed mixed results between upland and lowland communities with no significant response for the analysis of upland heathland ($p = 0.98$) but a clear, significant ($p = 0.0015$) increase in Ellenberg N with increasing deposition for lowland heathland.

4 Discussion

4.1 Individual species response

4.1.1 Acid grassland

For lowland acid grassland, consistent trends were found in the Vascular Plant Database with five species displaying significant responses showing a very similar negative relationship, declining in occupancy to low levels before stabilising ca. 25 kg N ha^{-1} yr^{-1}. With the exception *of Viola canina*, which the BSBI Local Change survey suggested was declining due to its vulnerability to eutrophication, all are small, low-growing or prostrate species most typical of dry acid grassland in the south and east of England. All have low Ellenberg N-values and thus are typical of infertile environments. Unfortunately, there were no species with suitable coverage (between 10 and 90 % occupancy) in the BSBI Local Change dataset to test the effects of N deposition and to enable us to confirm whether there were consistent trends among species within tetrads that contained lowland acid grassland. It is difficult to draw conclusions for upland acid grassland as only *Agrostis vinealis* displayed a significant (hump-backed) response reaching an optimum in occupancy at ca. 25 kg N ha^{-1} yr^{-1} in the BSBI Local Change dataset.

4.1.2 Calcareous grassland

Overall, the results for lowland calcareous grassland were broadly similar for the Vascular Plant and BSBI Local Change datasets with around half the species which displayed significant responses showing negative trends in occupancy in relation to increasing N deposition. However, only one species, the legume *Ononis repens*, showed this significant negative response in both datasets.

It was notable that most species displaying clear negative trends (in either dataset) tended to be specialists of grazed nutrient-poor calcareous grassland in the UK generally showing declines in the BSBI Local Change survey (e.g. *Bromopsis erecta, Campanula glomerata, Carlina vulgaris, Spiranthes spiralis*). These were typically species with low Ellenberg N-values. Species displaying more complex (hump-backed) or positive trends in the Vascular Plant Database dataset are generally more typical of taller mesotrophic swards, often subject to some shade (e.g. *Epipactis helleborine, Knautia arvensis, Lathyrus nissolia, Stachys officinalis*). Increased biomass production following increased N deposition would therefore favour the latter species and may partly account for the reported declines of some of the rarer species dependent on shorter swards. *Carex spicata*, which also showed a positive relationship to N deposition, was found to have increased in the BSBI Local Change Survey. They suggested that increases were potentially a result of increased availability in gaps of drought-prone grasslands and verges.

In upland calcareous grassland, *Melica nutans* was the only species to show a clear negative relationship with N, whereas *Alchemilla xanthochlora* had greatest probability of occurrence at the highest N deposition levels. *Melica nutans* was shown to decline in the Local Change survey, thought to be a result of suffering from competition. *A. xanthochlora* was also shown to decline in the local change survey thought to be as a result of eutrophication. It is typically a species of unimproved hay meadows, although it does appear capable of surviving in tall-herb communities on roadsides and therefore may be increasing in unmanaged habitats. Three species displayed a hump-backed relationship to N deposition in the BSBI Local Change dataset, with an optimum in occupancy between 10–20 $\text{kg N ha}^{-1}\,\text{yr}^{-1}$ (*Persicaria vivipara, Rubus saxatilis, Thalictrum alpinum*). Again these results are difficult to interpret but may represent the localised distribution of these species to a narrow altitudinal and geographical range in the uplands, and therefore a highly restricted N deposition gradient, or a potential unmodelled interaction between N deposition and another covariate in the model.

4.1.3 Heathland

In the Vascular Plant Database, only two species displayed significant trends for lowland heath, *Viola canina* declining and *Platanthera bifolia* increasing significantly in probability of presence with increasing N deposition. *V. canina* is a species with a low Ellenberg N score and its low stature means it does not compete well with competitive species. The latter result is very surprising as *P. bifolia* is an uncommon plant of unimproved pastures and wet heathlands shown to be declining in the Local Change survey thought to be caused by a long term response to management of moorland for grouse. Having applied the habitat masks, there were no species in lowland heathland recorded in the BSBI Local Change dataset that had sufficient coverage (between 10 and 90 % occupancy) to allow testing of the spatial effects of N deposition.

The results for upland heathland showed two sub-shrubs *Arctostaphylos uva-ursi* (Vascular Plant Database) and *Vaccinium vitis-idaea* (BSBI Local Change) displaying clear negative trends in occupancy with increasing N deposition. Both of these species have low Ellenberg values. Two species associated with more humid upland heathlands, *Trientalis europaeus* and *Listera cordata*, displayed distinct optima at around 20 kg N ha^{-1} yr^{-1}, possibly reflecting their restricted distributions along the N deposition gradient. Both are elusive species. An alternative hypothesis for *Listera cordata* might be its dependence on aerial deposition of nutrients for growth in nutrient-poor habitats. This species typically roots within *Sphagnum* tussocks and therefore attains most of its nutrients from decaying matter or rainwater.

4.2 Ellenberg N

There was a general trend for increasing Ellenberg N scores across many habitats indicating an increase in fertility. The most prominent changes occurred in lowland acid grasslands, where Ellenberg N showed an increase in both data sets. This gives a very clear signal that mean Ellenberg N is higher at high deposition, indicating increased fertility. However, the magnitude of these changes were generally quite small – an increase of approximately one unit on the Ellenberg N scale between deposition of 5 and 30 kg N ha^{-1} yr^{-1}. It is somewhat surprising that lowland grasslands appear to show more change than upland ones. Due to their tendency to have soils with a lower nutrient status, we might expect upland grasslands to be more sensitive. Although this is dependent on the species present being capable of exploiting any excess N. For upland acid grasslands the lack of a convincing Ellenberg N score response to N deposition is not entirely surprising as this has also been found in research scale spatial surveys which have suggested acidification from N deposition may be the main driver of reductions in species richness rather than eutrophication (Maskell et al., 2010; Stevens et al., 2010).

The two datasets generally show consistent results between the habitats with only slight differences in the shape of the response, whilst the general pattern and modelled scores are broadly aligned.

4.3 General comments

This study set out to evaluate the response of individual vascular plant species to N deposition and assess how significant relationships found relate to current critical load levels. After accounting for a number of additional explanatory variables, we have found evidence that a number of species show clear responses to Nitrogen even at low levels. Although the models allow for the possibility of no change up to a threshold after which we see a decline, there are few instances where this is indeed the case. Where we do see significant relationships to N deposition, there are many changes that occur well below the critical load, with Ellenberg values increasing from the lowest N levels and some species showing strong responses at low deposition. This indicates that current critical loads are not protecting all species and that conservation and biodiversity targets are at risk of not being delivered. Ongoing effects are also found above critical load values indicating there may be benefits from reductions in deposition however small and at any level. Within all three habitats, there are a number of species with low Ellenberg values, which may have been expected to respond negatively to N deposition but do not show a significant relationship with N deposition here. This may be for a number of reasons as this analysis is based on data using large recording units, there may be interactions with climate not detected and presence absence data may be too coarse and insensitive to change. Abundance of individual species would be more sensitive to change but targeted surveys are needed to collect such data. The main benefits of using a large scale study with comprehensive nationwide coverage, as done here, are that we have good coverage over the N deposition gradient with which to build our models, any inference drawn is not spatially restricted and there is no chance that we only model an unusual niche of a given species.

However, using large scale data and large recording units meant that the assignment of species to a habitat was at a coarse scale and may not be as accurate as smaller scale data and smaller recording units such as quadrats, which contain species data from known habitat types. It is also important to note that the analysis presented did not extend to species which were too rare or too abundant. We were therefore only working with the middle range of species and all our conclusions are based on modelling these species. It may be, however, that the rare or abundant species show more sensitive changes or differing relationships to those presented here.

To ensure that relationships seen here did not reflect a potential correlation between N deposition and habitat area, the theory being that the larger the habitat area the more likely we are to find a record, some selected species were re-modelled with habitat area included as an additional covariate in the model. However, no differences to the original analysis were found and the plotted relationships remained unchanged.

Our work has sought to separate out the effect of N deposition from other variables known to affect the response of interest. To this end we included in the model all extra variables we thought ecologically meaningful and for which data was available. We also included a generic spatial surface and used a flexible class of models. All of the which mean we have made less assumptions, are less open to bias and have accounted for more possible confounding issues than any other similar study. We therefore see this as a key contributor to a growing body of scientific evidence suggesting species level impacts in all three habitats investigated and potential effects at low deposition values beneath current critical load levels.

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Table 1. The number of sampling units (hectads or tetrads) across Great Britain containing each of the three studied habitats from each of the two surveys.

	Habitat	Lowland	Upland
Vascular Plant Database	Acid grassland	1143	1203
	Calcareous grassland	1546	662
	Heathland	855	1284
BSBI Local Change	Acid grasslands	164	158
	Calcareous grasslands	377	209
	Heathland	43	231

Table B1. Full table of results showing the p-values testing the null hypothesis that there is no relationship between species occurrence and N deposition. Significant results are highlighted in bold.

Vascular Plant Database			
Habitat	Species	P-Value	Change
Upland Acid Grassland			
	Viola lutea	0.4131	
Upland Calcareous Grassland			
	Alchemilla xanthochlora	**0.0406**	**Positive**
	Galium boreale	0.2170	
	Melica nutans	**0.0016**	**Negative**
	Persicaria vivipara	0.3801	
	Rubus saxatilis	0.4809	
	Thalictrum alpinum	0.9106	
	Viola lutea	0.3051	
Upland Heath			
	Arctostaphylos uva-ursi	**0.0001**	**Negative**
	Cornus suecica	0.3167	
	Cryptogramma crispa	0.5060	
	Diphasiastrum complanatum	0.9520	
	Empetrum nigrum	0.2198	
	Lycopodium clavatum	0.3648	
	Rubus chamaemorus	0.7752	
	Trichophorum cespitosum	0.6715	
	Trientalis europaea	**0.0237**	**Hump-Back**
	Vaccinium vitis-idaea	0.0919	
Lowland Acid Grassland			
	Anthriscus caucalis	0.7252	
	Aphanes australis	0.2999	
	Cerastium arvense	**0.0212**	**Negative**
	Cerastium semidecandrum	**0.0022**	**Negative**
	Myosotis ramosissima	0.0990	
	Ornithopus perpusillus	0.6780	
	Scleranthus annuus	0.2995	
	Senecio sylvaticus	0.9415	
	Trifolium arvense	**0.0344**	**Negative**
	Vicia lathyroides	**0.0457**	**Negative**
	Viola canina	**0.0000**	**Negative**

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Table B1. Continued.

Lowland Calcareous Grassland			
	Allium vineale	**0.0365**	**Negative**
	Anacamptis pyramidalis	0.0507	
	Blackstonia perfoliata	0.0571	
	Brachypodium pinnatum	0.2820	
	Bromopsis erecta	0.8306	
	Carex spicata	**0.0478**	**Positive**
	Carlina vulgaris	**0.0226**	**Negative**
	Catapodium rigidum	0.7550	
	Centaurium erythraea	**0.0087**	**Hump-Back**
	Centaurea scabiosa	0.8592	
	Cirsium acaule	0.5282	
	Cirsium eriophorum	0.0905	
	Clinopodium vulgare	0.2215	
	Cynoglossum officinale	**0.0000**	**Negative**
	Daucus carota	0.2341	
	Echium vulgare	**0.0070**	**Negative**
	Epipactis helleborine	**0.0280**	**Hump-Back**
	Filago vulgaris	0.1019	
	Geranium columbinum	**0.0176**	**Negative**
	Geranium sanguineum	0.1388	
	Hypericum hirsutum	0.1314	
	Inula conyzae	0.0880	
	Knautia arvensis	**0.0014**	**Positive**
	Lathyrus nissolia	**0.0030**	**Positive**
	Linum bienne	**0.0306**	**Hump-Back**
	Ononis repens	**0.0109**	**Negative**
	Ononis spinosa	0.6074	
	Ophrys apifera	0.1344	
	Orchis morio	0.2136	
	Origanum vulgare	0.2222	
	Pastinaca sativa	**0.0154**	**Hump-Back**
	Picris hieracioides	0.4054	
	Poa angustifolia	0.9579	
	Rosa micrantha	**0.0105**	**Negative**
	Rosa rubiginosa	0.3157	
	Sanguisorba minor	0.1927	
	Sherardia arvensis	0.3197	
	Spiranthes spiralis	**0.0074**	**Negative**
	Stachys officinalis	**0.0186**	**Positive**
	Viola odorata	0.3596	
Lowland Heath			
	Platanthera bifolia	**0.0081**	**Positive**
	Radiola linoides	0.0527	
	Scleranthus annuus	0.6258	
	Viola canina	**0.0008**	**Negative**

Table B1. Continued.

BSBI Local Change Survey Database			
Habitat	Species	P-Value	Change
Upland Acid Grassland			
	Agrostis vinealis	**0.0060**	**Hump-Back**
Lowland Acid Grassland			
	Senecio sylvaticus	0.1240	
Lowland Calcareous Grassland			
	Brachypodium pinnatum	0.4144	
	Bromopsis erecta	**0.0052**	**Negative**
	Campanula glomerata	**0.0000**	**Negative**
	Carex spicata	**0.0183**	**Negative**
	Catapodium rigidum	0.1609	
	Centaurea scabiosa	0.1047	
	Centaurium erythraea	**0.0000**	**Negative**
	Crepis capillaris	0.2595	
	Daucus carota	**0.0218**	**Negative**
	Knautia arvensis	0.1527	
	Ononis repens	**0.0021**	**Negative**
	Origanum vulgare	0.5387	
	Pastinaca sativa	0.9980	
	Salvia verbenaca	0.4535	
	Sanguisorba minor	**0.0000**	**Negative**
	Stachys officinalis	0.0962	
	Viola odorata	**0.0251**	**Hump-Back**
Upland Calcareous Grassland			
	Alchemilla alpina	0.2052	
	Galium boreale	0.7008	
	Persicaria vivipara	**0.0001**	**Hump-Back**
	Rubus saxatilis	**0.0321**	**Hump-Back**
	Saxifraga aizoides	0.2127	
	Saxifraga oppositifolia	0.1236	
	Selaginella selaginoides	0.0605	
	Thalictrum alpinum	**0.0231**	**Hump-Back**
Upland Heath			
	Agrostis vinealis	**0.0206**	**Hump-Back**
	Arctostaphylos uva-ursi	0.1448	
	Listera cordata	**0.0001**	**Hump-Back**
	Lycopodium clavatum	0.0880	
	Rubus chamaemorus	0.0707	
	Trichophorum cespitosum	0.0701	
	Vaccinium vitis-idaea	**0.0074**	**Negative**

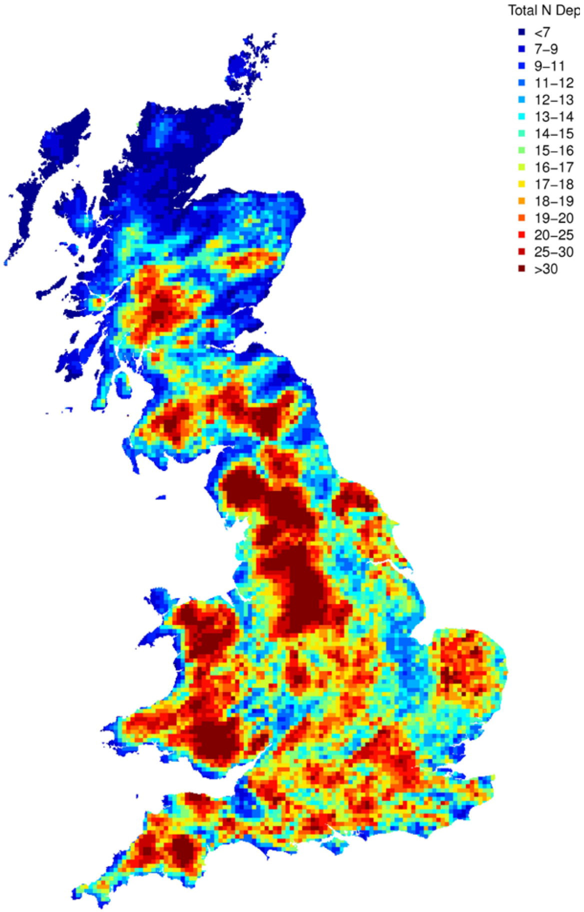

Fig. 1. Total inorganic N deposition (kg N ha^{-1} yr^{-1}) to heathland and rough grazing land in the UK. CBED deposition data for 1996–1998.

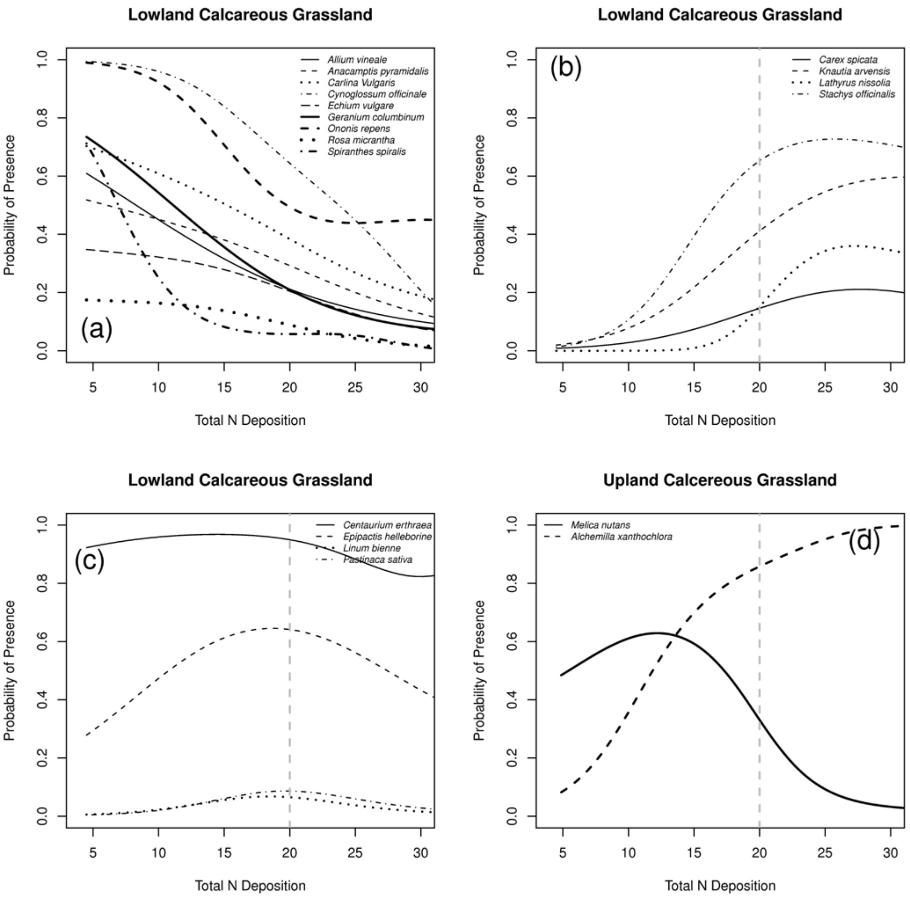

Fig. 2. Change in probability of presence for species with significant relationship to N deposition in calcareous grasslands in the Vascular Plant database against increasing total inorganic N deposition (kg N ha^{-1} yr^{-1}).

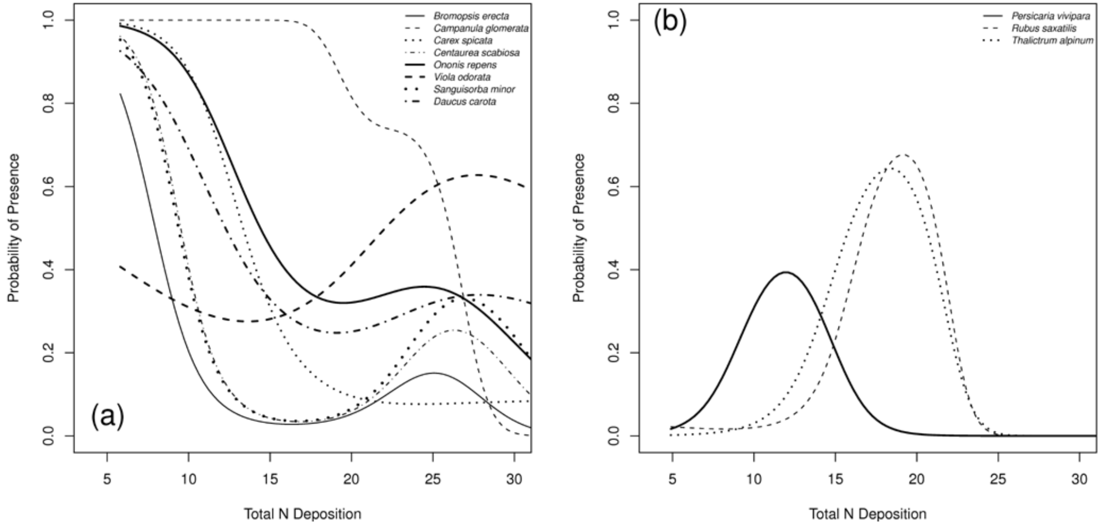

Fig. 3. Change in probability of presence for species with significant relationship to N deposition in calcareous grasslands in the BSBI local change survey database against increasing total inorganic N deposition (kg N ha^{-1} yr^{-1}).

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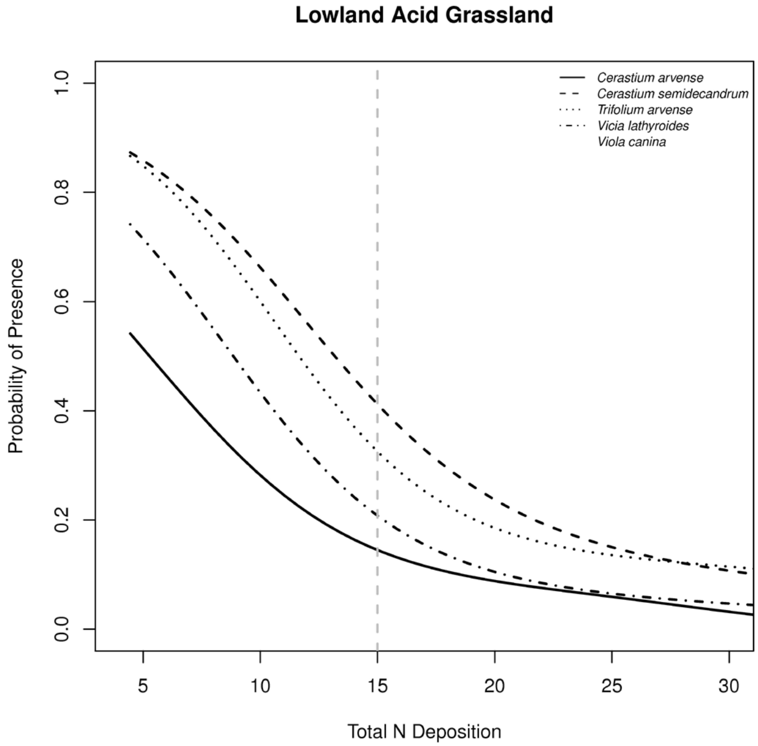

Fig. 4. Change in probability of presence for species with significant relationship to N deposition in acid grasslands in the Vascular Plant database against increasing total inorganic N deposition (kg N ha^{-1} yr^{-1}).

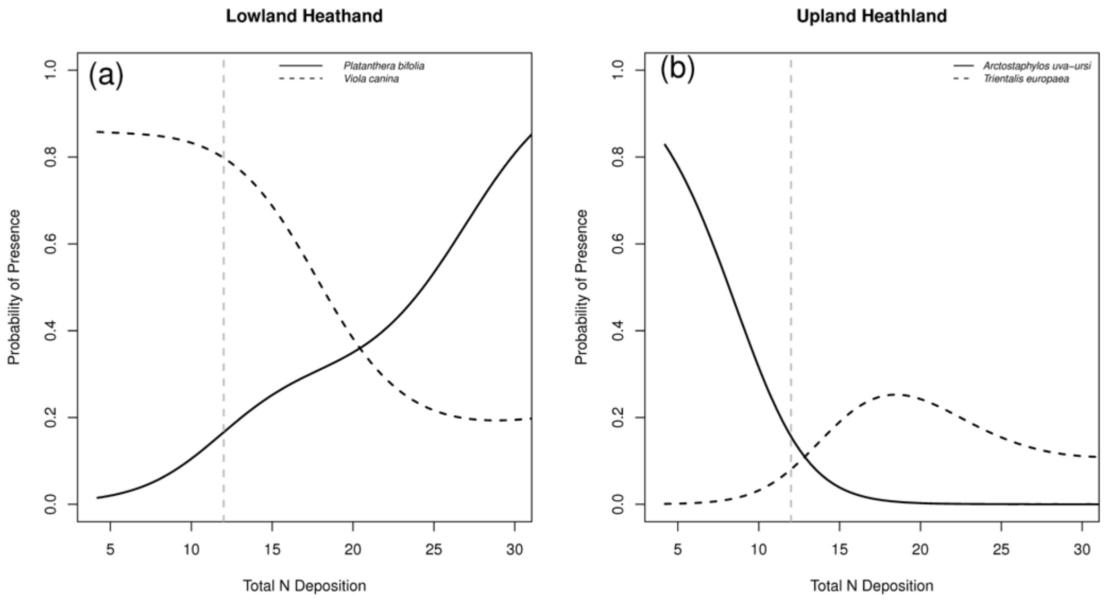

Fig. 5. Change in probability of presence for species with significant relationship to N deposition in heathland in the Vascular Plant database against increasing total inorganic N deposition ($\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$).

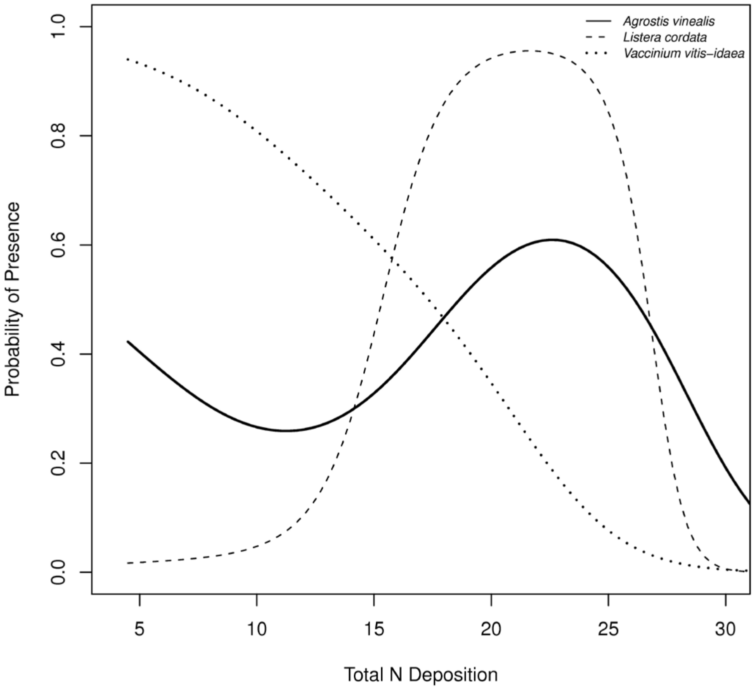

Fig. 6. Change in probability of presence for species with significant relationship to N deposition in heathland in the BSBI local change survey database against increasing total inorganic N deposition (kg N ha^{-1} yr^{-1}).

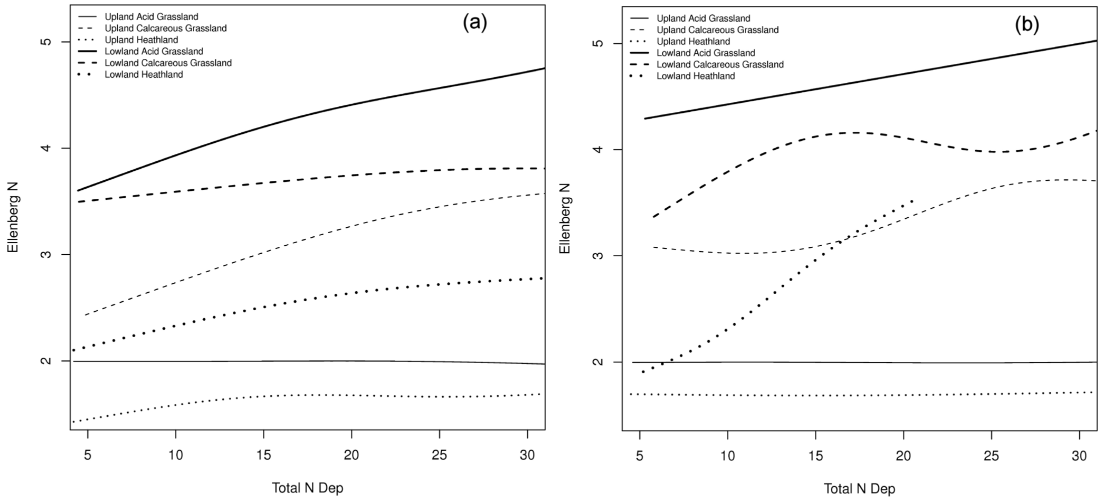

Fig. 7. Modelled response of Ellenberg N scores against total inorganic N deposition (kg N ha^{-1} yr^{-1}) using data from **(a)** the Vascular Plant database and **(b)** the BSBI local change survey.

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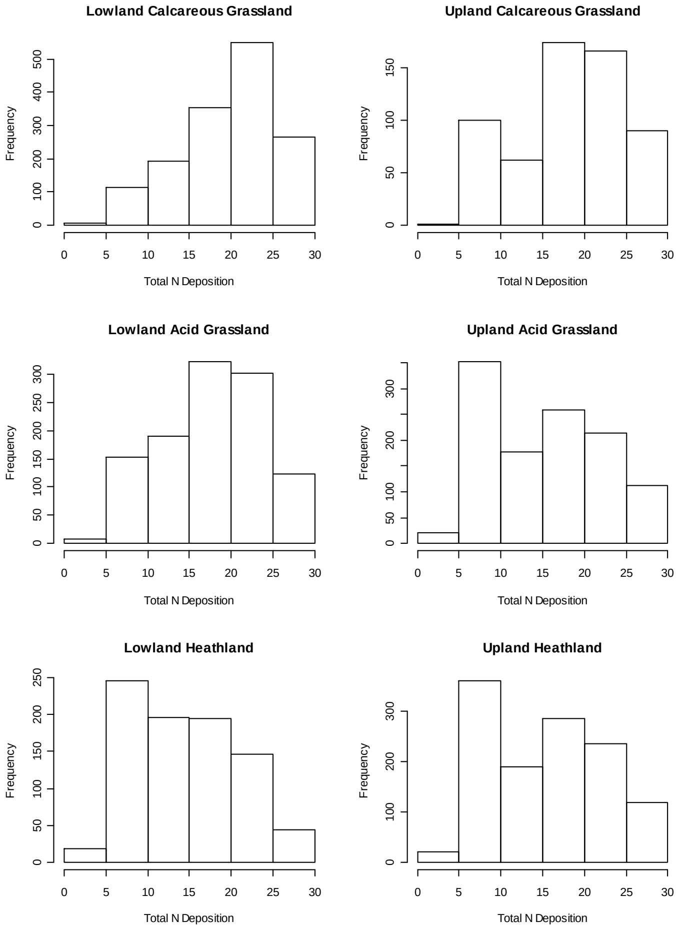

Fig. A1. Histograms showing the distribution of N deposition in the Vascular plant database between 0–30 kg N ha^{-1} yr^{-1}.

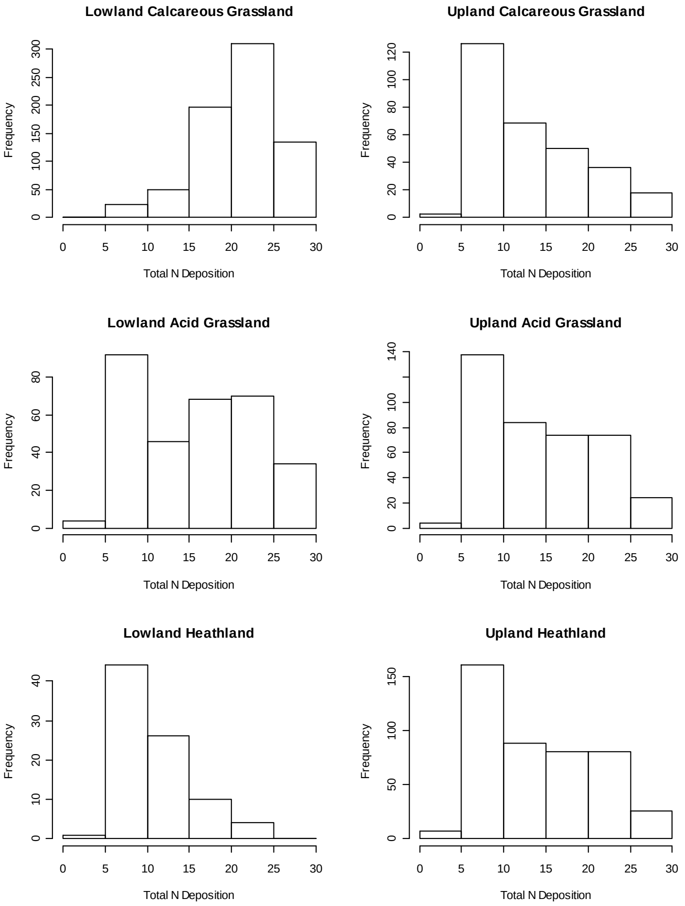

Fig. A2. Histograms showing the distribution of N deposition in the BSBI local change database between 0–30 kg N ha^{-1} yr^{-1}.