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Collation of evidence of nitrogen impacts on vegetation in relation to UK biodiversity objectives

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Technical Summary

There is clear evidence, both from other investigations and from this study, that N deposition has an impact on vegetation. Many of these changes have been observed over a range of spatial and temporal scales in both large-scale gradient studies and controlled experiments. In many cases, impacts can be seen below the appropriate critical loads for nitrogen deposition, but continue to occur even at high levels of deposition. A number of sensitive vascular plant, bryophyte and lichen species are at risk of decline in high deposition areas. Fifty eight percent of sensitive semi-natural habitat in the United Kingdom exceeds the critical loads for nutrient nitrogen (Defra, 2010), and is predicted to continue to do so in 2020 despite reductions in emissions of reactive nitrogen (N) gases (RoTAP, In Preparation). This means that there is a threat from reactive N to vegetation in semi-natural habitats. Long-running experiments in a range of habitats have demonstrated a wide range of effects on vegetation species richness, species composition and productivity (Mountford *et al* 1993; Wilson *et al* 1995), soil chemistry (Phoenix *et al* 2003; Pilkington *et al* 2005) and vegetation tissue chemistry (Carroll *et al* 2003; Pilkington *et al* 2005). There have also been a number of geographically large-scale studies attempting to determine the impact of N deposition on vegetation in the UK (Dupré *et al* 2010; Maskell *et al* 2010; Stevens *et al* 2004; Stevens *et al* 2010a).

There have been a considerable number of collations of evidence of impacts of N deposition on vegetation and other biodiversity components (notably NEGTAP, 2001; ROTAP, In Preparation). However, not all surveillance data has been exploited in these reviews, some have never been analysed with respect to N deposition and/or different statistical approaches have complicated comparisons. This project aimed to address this gap by analysing vegetation surveillance datasets, identifying response variables and collating evidence of N deposition impacts.

Methods

This project has used data from eight different national vegetation datasets to look at relationships with N deposition. The datasets used were from the Vascular Plant Database, Botanical Society of the British Isles (BSBI) Local Change Survey, British Bryological Society (BBS) Database, British Lichen Society (BLS) Database, Plantlife Common Plant Survey, Countryside Council for Wales Grassland survey, Scottish Natural Heritage NVC survey, and Natural England Grassland database. These datasets fall into two categories, large-scale tetrad and hectad data and smaller scale quadrat data. Four semi-natural habitats were selected for analysis: acid grasslands, calcareous grasslands, heathlands, and bogs. All four were analysed separately for uplands and lowlands. Spatial analysis investigating the change in drivers across the gradient of deposition in Great Britain was conducted for all datasets. For the Vascular Plant Database and BSBI Local Change temporal analysis was also conducted looking at change in variables along the deposition gradient.

For the tetrad and hectad data we used generalised additive models (GAMs) to assess the impact of N deposition on individual species presence, and on summary variables, taking into consideration other potential drivers including climate, land use and sulphur deposition. Only species with intermediate prevalence could be analysed, since the presence of species that occurred in most, or very few, tetrads or hectads could not be related to explanatory variables. For quadrat data we used canonical correspondence analysis (CCA) to assess the impact of N deposition on individual species. Generalised linear models (GLMs) were used to determine the impact of N deposition on summary variables within the quadrat data.

Key findings

All of the habitats examined showed signs of nutrient enrichment related to nitrogen deposition. A number of vascular plant, bryophyte and lichen species were identified as at risk from nitrogen deposition showing clear negative relationships with nitrogen deposition once other potential environmental controls such as climate had been accounted for. All habitats contained species which showed declines in their probability of presence with increasing N deposition.

Acid grassland

Acid grasslands in the UK have been extensively studied in relation to N deposition demonstrating declines in species richness (Maskell *et al* 2010; Stevens *et al* 2004; Stevens *et al* 2010a), changes in species composition (Carroll *et al* 2003; Gidman *et al* 2006), plant tissue chemistry (Arroniz-Crespo *et al* 2008; Gidman *et al* 2006), reduced soil pH (Stevens *et al* 2006) and increased availability of metals in soils (Stevens *et al* 2009). Temporal analysis of vegetation data collected between 1940 and 2008 showed similar declines in species richness in this habitat (Dupré *et al* 2010).

The results of this project confirmed the sensitivity of acid grasslands to N deposition. Lowland acid grasslands showed increases in their Ellenberg N score in the spatial analysis. In upland acid grasslands there was no significant relationship between Ellenberg N score and N deposition; this was also found in Countryside Survey and a research scale spatial survey (Maskell *et al* 2010; Stevens *et al* 2010b). The Ellenberg N values for bryophytes showed a positive result. Surprisingly there were few datasets indicating effects of soil acidification (Ellenberg R score). This could be due to the restricted number of vascular plant species used in the tetrad and hectad surveys analysed here.

Some species showed clear negative responses to N deposition. In the Vascular Plant Database five out of twelve species for which there was sufficient appropriate data for analysis displayed significant responses showing a very similar negative relationships with increasing N deposition, declining in prevalence to low levels above c.20 kg N ha^{-1} yr^{-1}. Many of these species such as *Cerastium arvense* are rather short-lived species commonest in dry acid grasslands in the south and east of England. In the BBS database a number of species showed both negative and positive responses. Habitat selection for bryophytes was problematic and consequently results must be interpreted with caution, but some species showed very clear results. For example, *Racomitrium lanuginosum* decreased in its probability of presence with increasing N deposition. This species is particularly sensitive to N deposition and experiments and regional surveys and experimental nitrogen additions have both shown strong reductions in relation to N deposition (Baddeley *et al* 1994; Pearce and van der Wal, 2002). Two lichen species showed strong negative responses to N deposition. For example, the probability of presence of *Peltigera didactyla* was reduced to approximately half by 15 kg N ha^{-1} yr^{-1} reaching very low probabilities of presence (once the impact of other variables is accounted for) at high deposition.

Calcareous grassland

Other studies have shown that the relationship between species richness and N deposition in calcareous grasslands is not always as clear as in acid grasslands (Bennie *et al* 2006; Maskell *et al* 2010; RoTAP, In Preparation). This lack of a clear relationship between species richness and N deposition was also found in this report. However, changes in species composition in relation to N deposition have been demonstrated including an increase in grasses and a reduction in forbs (Morecroft *et al* 1994; RoTAP, In Preparation).

As would be expected from grasslands on such highly buffered soils there was no indication of N deposition causing acidification (Ellenberg R score) but there were increases in fertility (Ellenberg N score). Both the Vascular Plant Database and BSBI Local Change spatial analyses showed an increase in the mean Ellenberg N score of approximately one unit between 5 and 35 kg N ha^{-1} yr^{-1} indicating an increase in species of fertile habitats.

In lowland calcareous grasslands a number of species showed negative relationships with N deposition including *Ononis repens* and *Bromopsis erecta* in the BSBI Local Change dataset and *Allium vineale*, *Anacamptis pyramidalis*, and *Spiranthes spiralis* in the Vascular Plant Database. In general, the response curves for these species had shallower slopes than for species showing negative responses in acid grasslands. In upland calcareous grasslands *Melica nutans* was the only species to show a clear negative relationship to N deposition (Vascular Plant Database). It was notable that most species displaying clear negative trends tended to be species restricted to closed lowland calcareous grasslands. Very few species showed clear responses in the temporal analysis.

There were few bryophyte or lichen species associated with calcareous grasslands that showed significant relationships to N deposition. Among those that did show a relationship with N deposition was the lichen *Cladonia foliacea* which showed a negative relationship with N deposition.

Bog

A long-term experiment at Whim bog has demonstrated a range of effects of N deposition on bog vegetation including an increase in the tissue N content and growth of *Calluna vulgaris*, and an increased sensitivity to frost, drought and pathogens (Sheppard *et al* 2008). However, despite the potential for being very sensitive to N addition because they derive their nutrients from rain water, bogs have received relatively little research in relation to N deposition.

There was a paucity of data from lowland bogs which meant that many analyses could not be conducted. In the quadrat data (from Scottish Natural Heritage) lowland bogs showed a reduction in species diversity and richness with increasing N deposition suggesting sensitivity to N inputs. In upland bogs there was no significant relationship between N deposition and species richness but there was a relationship with plant diversity. This indicates that the changes observed are mainly caused by a change in the evenness of species (i.e. the relative area that they cover) rather than richness.

There were sufficient data for analysis of only twelve species in upland and lowland bogs. The only flowering plant displaying a significant temporal trend in relation to N deposition was *Carex limosa* (Upland Bog, Vascular Plant Database). There were both positive and negative relationships with N deposition identified for bryophytes. All the Upland Bog species with negative correlations with N deposition are liverworts. The species with a positive association with N deposition include the moss *Warnstorfia fluitans*, this species is characteristic of degraded bogs and is tolerant of very acidic conditions.

Two lichen species showed significant relationships with N deposition in bogs, *Cladonia arbuscula squarrosa* and *Cladonia portentosa*. *C. portentosa* showed a steep decline in probability of presence between 15 and 25 kg N ha^{-1} yr^{-1} with data becoming too variable to interpret above 30 kg N ha^{-1} yr^{-1}. In heathlands the chemistry of *C. portentosa* has been demonstrated to be very sensitive to N deposition with increases in N and P concentrations of the thallus and enzyme activity affected (Hogan *et al* 2010a; Hogan *et al* 2010b; Hyvarinen and Crittenden, 1998).

Heathland

Heathlands are the community that has received the most research attention in relation to N deposition. In the Netherlands many areas of heathland have been lost due to a combination of N deposition and secondary stresses (Heil and Diemont, 1983). Extensive research evidence has shown that they are sensitive to N deposition with impacts including reduction in species richness (Edmondson, 2007; Maskell *et al* 2010), increased growth, flowering and tissue chemistry of *Calluna vulgaris* (e.g. Britton and Fisher, 2008; Pilkington *et al* 2005; Power *et al* 2006) and increased sensitivity to frost and drought (Britton *et al* 2003; Caporn *et al* 2000).

This report has shown an increase in the fertility of upland and lowland heathlands (Ellenberg N) in spatial and temporal analyses. Lowland heathland was the only community to have shown signs of acidification in the large-scale spatial data for vascular plants, showing a reduction in Ellenberg R score above 15 kg N ha^{-1} yr^{-1}.

As for bog habitats, there were few individual species showing significant relationships with N deposition. However, *Viola canina* displayed a clear negative relationship between probability of presence and N deposition. Two sub-shrubs at the southern limit of their range in Great Britain, *Arctostaphylos uva-ursi* (Vascular Plant Database) and *Vaccinium vitis-idaea* (BSBI Local Change), showed clear negative trends in probability of presence.

A large number of bryophytes were analysed for heathlands with a surprising number of positive relationships. There were also a large number of lichen species showing responses to N deposition, in this case all were negative. Of the more common species several were dramatically reduced in their probability of presence by increasing N deposition. *Cetraria aculeata, Cetraria muricata, Cladonia cervicornis verticillata, Cladonia subulata* and *Cladonia uncialis biuncialis* were all dramatic reductions in their probability of presence by 15 kg N ha^{-1} yr^{-1}. The majority of the species that decline do so from the lowest levels of deposition found in this country.

A summary of the results is presented in Table 1.

Table 1. Summary of results for Ellenberg N score (where at least one data set showed a statistically significant response) and change in the probability of presence for individual species of vascular plants, bryophytes and lichens. Where all species show the same direction of change, the direction is indicated. Data sources are: Vascular Plant Database, BSBI Local Change survey, British Bryological Society database, British Lichen Society database. For the Vascular Plant Database and BSBI Local Change survey spatial and temporal analyses were conducted.

	Acid grassland		**Calcareous grassland**		**Heathland**		**Bog**	
	Lowland	**Upland**	**Lowland**	**Upland**	**Lowland**	**Upland**	**Lowland**	**Upland**
Ellenberg N	+	+	+	+	+	+		+
Vascular plants	Reduction in some species	Change in some species	Change in some species	Change in some species	Change in some species	Change in some species	Change in some species	
Bryophytes		Change in some species		Change in some species		Change in some species		Change in some species
Lichens	Reduction in some species		Change in some species		Reduction in some species		Reduction in some species	

Summary

1. Large areas of the UK exceed the critical loads for nutrient nitrogen (N) and critical levels for ammonia, and are predicted to continue to do so in 2020 despite reductions in emissions of reactive N gases.
2. Previous collations of evidence of impacts of N deposition on vegetation and other biodiversity components have focused on either research in which there is high confidence in the attribution of the impact to deposition, or on indicators for assessing impacts to sites, habitats or species which are considered to be of 'high biodiversity value'. This project attempted to integrate research studies with the broad scale surveillance of biodiversity.
3. The main aim of the project was to analyse vegetation surveillance datasets in relation to N deposition, identify response variables and collate evidence of N deposition impacts.
4. This report focuses on four habitats: acid grassland, calcareous grassland, heathland and ombrotrophic bog. These were considered separately as upland and lowland types where possible.
5. The following datasets were used to analyse the relationship between summary variables (Ellenberg scores, canopy height, specific leaf area), species diversity (species richness, Shannon-Wiener diversity index), individual species occurrence and N deposition: Vascular Plant Database, Botanical Society of the British Isles (BSBI) Local Change Survey, British Lichen Society (BLS) Database, British Bryological Society (BBS) Database, Plantlife Common Plant Survey, Countryside Council for Wales Grassland Survey, Scottish Natural Heritage NVC Survey and Natural England Grassland Database.
6. Spatial analysis was conducted for all datasets, and temporal analysis conducted for the Vascular Plant Database and BSBI Local Change Survey.
7. Large-scale data (hectad and tetrad data) were analysed using generalised additive models (GAMs) while quadrat data were analysed using generalised linear models (GLMs) and canonical correspondence analysis (CCA), to distinguish effects of N deposition from changes in land-use, climate and sulphur deposition.
8. For all of the habitats there was a general trend for increasing Ellenberg N scores with N deposition in the spatial analysis indicating an increase in fertility in the large-scale analyses. Results were clearest for lowland acid grassland; for other communities changes were significant in some of the datasets analysed but not in others.
9. Ellenberg R, a score related to soil pH, showed few significant responses to N deposition within the datasets analysed.
10. Specific leaf area and canopy height were not as sensitive a measure as Ellenberg N scores, and sometimes returned non-significant results when Ellenberg N score returned significant ones.
11. Analysis of species diversity and richness could only be conducted on quadrat data, and was perhaps subject to the NVC sampling bias because NVC methodology requires that sampled vegetation is homogenous and representative of NVC types. Although some significant results were detected, few of these showed clear trends.
12. Some vascular plant species showed clear declines in the spatial analysis of response to N deposition. Very few species showed positive responses to N. Temporal analysis showed some species increasing and others decreasing on the N deposition gradient, although changes were of a small magnitude.
13. Canonical correspondence analysis identified species positively and negatively associated with N deposition in the quadrat data.
14. In spatial analysis some bryophytes were identified as clearly declining in relation to N deposition, but others increased, showing that bryophyte species vary in their response to N.

15. In spatial analysis lichens gave very clear results with some species showing dramatic declines with increasing N deposition.
16. Changes in the abundance of individual species and in species assemblages in relation to the N deposition gradient have been clearly demonstrated in this study, over a range of spatial and temporal scales in large-scale gradient studies.
17. The spatial and temporal analyses in this study, combined with previous evidence from surveys and experiments, provide clear evidence of species-level impacts of N deposition in all four of the habitats investigated.
18. This exercise has clearly reinforced the evidence base that nitrogen deposition is having a profound effect on a range of species. This in turn is having an adverse effect on the structure and function of many ecosystems. These impacts on biodiversity and the links to UK biodiversity objectives are discussed in detail in the second report for this project (Emmett *et al* 2011).

Contents

1 Introduction

Atmospheric nitrogen (N) deposition poses a serious threat to sensitive semi-natural habitats in the UK (Hall *et al* 2006a; NEGTAP, 2001). Large areas of the country exceed the critical loads for nutrient N and critical levels for ammonia, and are predicted to continue to do so in 2020 despite reductions in emissions of reactive N gases (Hall *et al* 2006b). N deposition in the UK is shown in Figure 1.1. Long-running experiments in a range of habitats have demonstrated a wide range of effects on vegetation species richness, species composition and productivity (Mountford *et al* 1993; Wilson *et al* 1995), soil chemistry (Phoenix *et al* 2003; Pilkington *et al* 2005b) and vegetation tissue chemistry (Carroll *et al* 2003; Pilkington *et al* 2005b). Experiments demonstrate the potential for damage to ecosystems; previously, in order to show that these changes are actually occurring in the UK, two approaches or a combination of them has been used: monitoring over time and large-scale surveys.

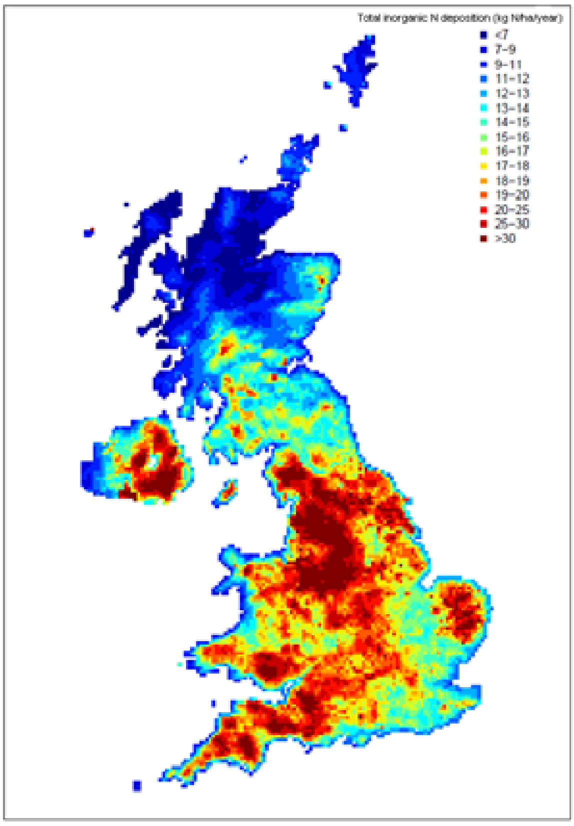


Figure 1.1. Total inorganic N deposition (kg N ha^{-1} yr^{-1}) to heathland and rough grazing land in the UK. CBED deposition data for 1996 – 98 as used in this project. Data from CEH Edinburgh.

There have previously been a number of geographically large-scale studies attempting to determine the impact of N deposition on vegetation in the UK. Stevens *et al* used a large scale spatial survey of acid grasslands to demonstrate declines in species richness (Stevens *et al* 2004), changes in species composition, reduced soil pH (Stevens *et al* 2006) and increased availability of metals in soils (Stevens *et al* 2009b) when high N deposition was compared with areas of low N deposition. The ESF-funded BEGIN project (Biodiversity of European Grasslands – Impact of Nitrogen Deposition) has built on this with an international survey of acid and calcareous grasslands in the Atlantic biogeographic region of Europe. This large transect study confirmed earlier findings demonstrating a loss of species richness with greatest losses at high levels of deposition (Stevens *et al* 2010a). Temporal analysis of vegetation data collected between 1940 and 2008 showed similar declines in species richness in this habitat (Dupré *et al* 2010). In calcareous grassland, results are more complicated with climatic gradients being a primary influence on species composition, but changes in species composition related to N deposition were observed as a secondary influence (Alard *et al* in press). 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. The species richness of calcareous grassland did not show a relationship with N deposition but in this habitat N deposition was correlated with climatic variables so it was not possible to separate them. Other responses such as change in Ellenberg N values were observed (Maskell *et al* 2010). There are further investigations currently underway including work being conducted as part of the Defra Terrestrial Umbrella programme and surveys conducted by The University of York which will build this evidence base.

There have been a considerable number of collations of evidence of impacts of N deposition on vegetation and other biodiversity components (notably NEGTAP, 2001; RoTAP, in preparation). However, there has tended to be a focus on either research scale studies in which there is high confidence in the attribution of the impact to deposition, or a focus on indicators with a view to assessing impacts to sites, habitats or species which are considered to be of 'high biodiversity value'. This means that until now we have lacked a collation that attempts to integrate the research studies with the broad scale surveillance of biodiversity.

Much of air pollution policy is focussed on setting appropriate emissions ceilings and the consideration of critical load exceedance. To support policy, evidence from surveillance needs to be used to 'add weight' to the nutrient N critical loads exceedance maps (i.e. provide stronger evidence of biodiversity changes linked to predictions based on critical load exceedance). In addition, policy requires that this pressure is linked to biodiversity objectives, and this can be considered both broadly in the wider countryside and narrowly on sites, habitats and species for which specific biodiversity targets have been set. Whilst there remain policy/legislative obligations, and thus evidence needs, for the latter (i.e. Habitats Directive Favourable Conservation Status and BAP), convincing evidence of broad impacts, particularly if linked with changes to the provision of ecosystem services, is also increasingly required.

A workshop held by JNCC in 2009 (background paper and minutes are available at http://www.jncc.gov.uk/page-4424) identified that there is scope for further analysis of the results of some of the broad scale surveillance schemes in order to provide stronger evidence of the effects of N deposition on vegetation at all spatial scales. It concluded that a consistent message shown from a consistent analysis across broad scale surveillance datasets would be very valuable to help demonstrate how N deposition is impacting on vegetation across the countryside. Therefore, the purpose of this project was to provide an analysis of broad scale vegetation surveillance datasets in order to correlate spatial and temporal vegetation trends to N deposition. We have collated these results, those from Countryside Survey, and research scale survey and experiments to provide evidence of N impacts in relation to biodiversity objectives.

The main aim of the project was to analyse vegetation surveillance datasets, identify response variables and collate evidence of N deposition impacts. To address this aim the following objectives have been met:

a The identification of a set of relevant response variables which can be analysed from the various broad scale vegetation surveillance datasets in relation to N deposition.

b A full spatial and temporal analysis of the surveillance datasets against N deposition data, whilst accounting for other factors (such as climate, sulphur deposition), focussed on particular habitats.

c Collation and summary of the results of the surveillance analyses undertaken under part (b) and the use this output, together with results from Countryside Survey and research scale survey and experiments, to provide evidence of the effects of N deposition on vegetation.

d Agreement with habitat specialists on the relevance of parameters (including species composition and structure, and biogeochemical measures) which have shown a response to N deposition in the surveillance analysis, and/or from research scale evidence, to 'conservation value' and agreement on what extent of change in these variables is of concern in respect of objectives or targets for habitats/species. These response variables may subsequently feed into the design of surveillance schemes, analysis of data and assessment of implications, and dynamic modelling.

A workshop was held in Peterborough in June 2010 as part of objective d of the project. The outcomes of this workshop are reported in the second report from this project (Emmett *et al* 2001).

This report focuses on objectives a to c, beginning with a brief review of previous research into the impacts of N deposition on vegetation (section 1.1). In section 2 we have then provided an outline of the methodology used in this study and in section 3 report the results of the analysis conducted. Finally we discuss the results for each habitat and compare them with findings from previous research (section 4).

1.1 Vegetation responses to nitrogen deposition

Nitrogen deposition impacts upon vegetation communities in a number of different ways. Species richness of vascular plants and bryophytes has been found to decrease in response to N deposition in a number of experimental studies (Bobbink *et al* 1998; Clark and Tilman, 2008; Mountford *et al* 1993). In the RoTAP report (in preparation) results of eleven surveys conducted in the UK are compared. Species richness declined with increasing N deposition in seven of the eleven surveys, although calcareous grassland showed an initial increase then decline. Surveys which did not show a decline in species richness were in *Racomitrium* heaths, woodland epiphytes and Scottish montane habitats. Table 1.1 is taken from ROTAP and shows a summary of the results found in surveys.

In acid grassland the main component of species richness loss was forb species, which declined in both cover and richness (Stevens *et al* 2004). Of the six studies reviewed in RoTAP (in preparation) that recorded forb richness, four showed declines in richness, one (calcareous grassland) showed an initial increase followed by a decrease, and only one showed an increase (*Racomitrium* heaths).

Table 1.1. Summary of key ecosystem responses in regional or national surveys. Arrows indicate direction of response, circles indicate no response and shaded boxes indicate response not measured. Taken from ROTAP (in preparation). AGS=Acid Grassland Survey: 68 acid grasslands (NVC type U4) sampled across Great Britain over 2002 and 2003 (Stevens, 2004; Stevens *et al* 2006), CGS = Calcareous Grassland Survey: calcareous grasslands (mainly NVC CG1 and 2) sampled across Great Britain in 2006/7 (Ashmore, in prep). CMS= Calluna Moorland Survey: 36 Calluna heather moorlands sampled across northern Great Britain over 2005-6 (Edmondson, 2007). RHS=Racomitrium Heath survey: 22 Racomitrium heathland sampled across northern Great Britain in 2007-08 (Armitage *et al* in prep). SDS = Sand Dune Survey: 11 coastal dune grasslands sampled in England and Wales in 2002 (Jones *et al* 2004). WES = Woodland epiphyte survey: 7 Atlantic Oak woodlands sampled in Scotland and the north of England for epiphytic moss, liverwort and lichen 8 communities, measured in 2002 (Mitchell *et al* 2005). SMont = Scottish Montane survey: sites sampled across Scotland in 2006 (Britton *et al* in prep); SMoor=Scottish Moorland survey: sites sampled across Scotland in 2006 (Britton *et al* in prep). CS-Grass=Countryside Survey mixed grasslands: about 2000 plots sampled across Great Britain in 1998 and 2007; CS-H/B=Countryside Survey heath and bog: about 2000 plots sampled across Great Britain in 1998 and 2007; CS-Wood=Countryside Survey broadleaved woodland: about 800 plots sampled across Great Britain in 1998 and 2007.

	AGS	CGS	CMS	RHS	SDS	WES	SMont	SMoor	CS-Grass	CS-H/B	CS-Wood
N-dep	5-35	5-35	6-31	?	7-29	10-53	8-22	5-20	?	?	?
Species richness	↓	↑, then ↓	↓	o	↓	O	o	↓	↓	↓	↓
Forb cover	↓			↑			o	o	o	↑	↑
Forb richness	↓	↑, then ↓	↓	↑			↓	↓			
Bryophyte cover	o			↓	o	o	↑	o	o	↑	o
Bryophyte richness	o	o	↓	o		O	↑	o			
Lichen cover				o		o	o	↓			
Lichen richness		o	o	o		o	o	↓			
Ericoid cover				↑			↓	o		↑	
Ericoid richness				↑			↓	↓			
Graminoid cover	o			↑	↑		↑	o	↑	↑	↓
Graminoid richness	↓	o		↓			o	↓			

Some species are particularly sensitive to N deposition. Stevens *et al* (2009b) identified a number of species positively or negatively associated with N deposition in acid grassland, heathland and bog. One problem with the use of individual species as an indicator of N impacts at a site specific level is that there are many potential reasons that a plant may be absent from a site. Using relatively common species or identifying lists of several species can be used to overcome this problem. The GBMOVE plant species niche models (Smart *et al* in press) could potentially be used to identify species that are vulnerable on particular sites, where they are close to their abiotic thresholds.

Stevens *et al* (2009b) recommended grass:forb ratio (based on cover) as an indicator of N deposition impact in acid grassland. This indicator was selected as one appropriate for use in rapid assessment monitoring schemes such as Common Standards Monitoring (CSM) because it is relatively quick and easy to assess even without specialist botanical knowledge, has a good relationship with N deposition inputs, and shows community response to N deposition. However, grass:forb ratio is also strongly affected by management and a high grass:forb ratio may be due to e.g. fertiliser or herbicide application, or inappropriate grazing.

Survey data generally support conclusions from experiments that non-vascular plants, especially lichens, appear to be particularly sensitive to N deposition. In a regional survey Mitchell *et al* (2005) examined epiphytic moss, liverwort and lichen communities in Atlantic Oak woodlands in Scotland and the north of England. They were able to identify a number of species that were either positively or negatively correlated with N deposition. Species associated with low N deposition were *Isothecium myosuroides* and *Frullania tamarisci*. Species associated with the higher N deposition site were *Hypnum andoi*, *Cladonia coniocraea*, *Hypotrachyna laevigata*, and *Hypogymnia physodes*. However, the highest levels of deposition considered in this study were relatively low compared to some parts of the UK.

Ellenberg values (Ellenberg *et al* 1991; Hill *et al* 1999) have been used in a range of habitats throughout Europe 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 are the N score (nitrogen or nutrients) and R (reaction – soil pH). The indicators have been used successfully in a number of studies but there is some debate about the value of using Ellenberg scores as an indicator of N deposition. The Ellenberg N score was originally described as a nitrogen score but it has also been argued that it in fact indicates overall fertility or productivity (Hill and Carey, 1997), which changes interpretation.

CSR scores (Grime *et al* 2007) are derived from vegetation surveys, knowledge of plant functional traits and field and mesocosm experiments conducted by the Unit of Comparative Plant Ecology at Sheffield University. Within a triangular graph they give plants a score according to how competitive they are (C), how tolerant they are of stress (S) and whether they have the characteristics of a ruderal species (R). If eutrophication is apparent in a habitat we might expect stress tolerators to decline and competitors to increase. CSR scores have been little used in N deposition research but in acid grassland Stevens *et al* (2010b) found no relationship between N deposition and C or S scores.

Given the wide range of potential changes in species diversity and composition that can result from N deposition, this project uses national species and vegetation databases to determine the impact of N deposition on vegetation across Great Britain.

2 Methods

This project has used data from eight different national vegetation datasets to look at relationships with N deposition for four semi-natural habitats in the uplands and lowlands. These datasets fall into two categories, large-scale tetrad and hectad data and smaller scale quadrat data. For the tetrad and hectad data we used generalised additive models to assess the impact of N deposition on individual species and summary variables taking into consideration other potential drivers including climate, land use and S deposition. For quadrat data we used canonical correspondence analysis to assess the impact of N deposition on individual species. Generalised linear models were used to determine the impact of N deposition on summary variables within the quadrat data.

The methods section begins with a justification of the habitats investigated in this project, followed by a summary of the datasets used and the response variables investigated. This is followed by a description of the driver variables included in the analysis and a description of how habitats were allocated to either upland or lowland. Finally there is a detailed description of the modelling and analysis methods used.

2.1 Habitats investigated in this project

This report focuses on four habitats: acid grassland, calcareous grassland, heathland and ombrotrophic bog. The communities have been selected for different reasons. There is considerable survey (e.g. Stevens *et al* 2004, submitted) and experimental (e.g. Carroll *et al* 2000) evidence that acid grasslands are sensitive to N deposition due to the prevalence of species adapted to low nutrient conditions and soils susceptible to acidification. Their occurrence in areas of high deposition in the UK such as the Peak District, means that they are also vulnerable to N deposition. Lowland dry acid grassland is a UK BAP priority habitat. Calcareous grasslands also have a large number of species adapted to low nutrient conditions and although their soils are well buffered against pH change so they are less sensitive to acidification, they frequently have high biodiversity. Both lowland and upland calcareous grassland habitats are listed under Annex I of the Habitats Directive and are UK BAP priority habitats. Heathland is the community that has received the most research attention in relation to N deposition. In the Netherlands many areas of heathland have been lost due to a combination of N deposition and secondary stresses (Heil and Diemont, 1983). Extensive research evidence has shown that they are sensitive to N deposition (e.g. Pilkington *et al* 2005a; Power *et al* 1995). Both lowland and upland heathland habitats are listed under Annex I of the Habitats Directive and are UK BAP priority habitats. Ombrotrophic bogs receive all of their nutrients from rainwater. Consequently the plants found in this community are adapted to very low nutrient conditions. This makes them potentially very sensitive to N deposition and experimental evidence has confirmed this (e.g. Hogg *et al* 1995; Pitcairn *et al* 1995). Several bog habitats are listed under Annex I of the Habitats Directive and are UK BAP priority habitats including blanket bog and lowland raised bog. All habitats investigated were considered as upland and lowland types individually where possible.

2.2 Datasets

In order to meet the overall aim of this project we have investigated relationships with N deposition in eight different datasets. These are divided into two main types, those that record species presence at a large spatial scale (e.g. 10-km squares) and those that record vegetation cover or presence in small quadrats (e.g. 2-m squares). Some of the datasets also have a temporal element, i.e. the survey has been repeated. The following datasets were analysed:

2.2.1 Vascular Plant Database

The Vascular Plant Database records the presence of all vascular plant species growing in the wild within 10-km squares (hectads). All of the UK is covered. For analysis, subspecies were aggregated to the species level, with hybrids and alien species excluded. The data analysed have been divided into two time periods: 1930 to 1969 and 1987 to 1999. For the spatial analysis all available hectads were used. For the temporal analysis only hectads in both surveys were used. Data have been published in two atlases (Perring and Walters, 1962; Preston *et al* 2002).

2.2.2 British Bryological Society Database

The British Bryological Society Database records the presence of all bryophyte species growing within 10-km squares (hectads). All of the UK is covered. Records used in the analysis span the last 50 years.

2.2.3 Botanical Society of the British Isles (BSBI) Local Change Survey

The BSBI Local Change Survey records all vascular plant species growing in the wild in 811 2-km squares (tetrads). The tetrads are in a regular grid across Great Britain. For analysis, subspecies were aggregated to the species level, with hybrids and alien species excluded. The first survey was conducted in 1987-88 and this was repeated in 2003-04. For the spatial analysis all available tetrads were used. For the temporal analysis only tetrads recorded in both surveys were used. Data have been published in a book analysing change between the two surveys (Braithwaite *et al* 2006).

2.2.4 British Lichen Society (BLS) Database

The BLS Database records the presence of all lichen species growing within 10-km squares (hectads). All of the UK is covered although data is more thoroughly collected in some areas than others. Records used in the analysis span the last 50 years.

2.2.5 Plantlife Common Plant Survey

The Common Plant Survey looks at the presence and percentage cover of 65 common species in two plots: a 5 x 5m 'centre' plot and a 1 x 20m linear plot which is taken on a linear feature. Surveyors can also record in optional habitats plots if they feel there is a habitat of particular interest. These can be either square or linear. There are up to three visits per year, and maximum cover is recorded. The survey has been conducted annually since 2000 at as many of the sites as possible. Because the survey is conducted by volunteers the coverage is variable. Data are held for a total of 3863 plots.

2.2.6 Countryside Council for Wales Grassland Survey

This survey gives data from Welsh lowland grasslands with a varying number of 2 x 2m quadrats per site. Data were collected according to National Vegetation Classification protocols (Rodwell, 1992). All species were identified and percentage cover was recorded. Sites were visited once during the survey period and data were collected over a number of years. The survey covers all protected grasslands in Wales. The resultant dataset contains data from 397 calcareous and 940 acid grassland quadrats.

2.2.7 Scottish Natural Heritage NVC Survey

This survey gives data from Scottish heathlands, mires, acid grasslands and calcareous grasslands. Data were collected according to National Vegetation Classification protocols (Rodwell, 1992). Bryophytes and lichens may not have been consistently recorded so have been removed from this database. Data were collected over a number of years and do not cover the whole of Scotland, only selected sites. The resultant dataset contains data from 2,775 bog locations (NVC M communities), 1,100 heathland locations (NVC H communities), 275 calcareous (NVC CG communities) and 1,189 acid grassland locations (NVC U communities).

2.2.8 Natural England Grassland Database

This survey gives data from English grasslands with a varying number of 2 x 2m quadrats per site. Data were collected according to National Vegetation Classification protocols (Rodwell, 1992). Bryophytes and lichens may not have been consistently recorded so have been removed from this database. Data were collected over a number of years and only cover selected sites. The resultant dataset contains data from 5,332 calcareous and 149 acid grasslands. Site level presence/absence data was used for this dataset due to quadrats on a site not being individually labelled.

2.3 Response variables used in this study

This study has investigated a range of response variables within the datasets described above. For datasets that record species presence at a large spatial scale we have investigated relationships between atmospheric N deposition and:

- Individual species responses (both current distribution and change in distribution)
- Ellenberg R and N scores (Hill *et al* 1999; Hill *et al* 2007)
- Specific leaf area (SLA, see below)
- Plant canopy height.

The large-scale datasets used in this investigation are somewhat limited in the analysis that can be applied to them. They record the presence of species within a given area so presence of individual species is an important response to consider. This allowed us to identify species that are especially vulnerable to N deposition and which are not found in areas of high deposition. Average Ellenberg R and N scores were calculated based on the presence of species in each habitat. Ellenberg scores define a species' realised niche. N scores are on a scale of one to nine, where one represents the most infertile habitats and nine represents fertile habitats. R scores are also on a scale of one to nine where one is a highly acid habitat and nine is a calcareous habitat. We also examined average values for functional traits that are thought to be related to competition and competitive ability: plant canopy height and SLA. More competitive plants typical of nutrient rich situations would be expected to have higher canopy height and SLA. SLA is a measure of leaf area divided by dry mass. Fast-growing, competitive species which are able to take advantage of additional nutrients have a low SLAs whereas stress-tolerant, slow-growing species typically have high SLA.

Ellenberg values and plant height were taken from PLANTATT (Hill *et al* 2004). SLA data were taken from the LEDA database and from data compiled by the Unit of Comparative Plant Ecology at Sheffield University.

For datasets where we have quadrat level data, variables based on plant cover and scores for individual sites can also be used. For these datasets we investigated all of the above response variables together with:

- species richness; and
- species diversity.

Species richness is an important component of diversity and has been shown to respond to N deposition in a range of habitats. Species diversity was measured using the Shannon-Weiner diversity index which takes into account both species richness and evenness. The Shannon-Weiner diversity index was calculated as follows:

$$H = -\sum P_i(\ln P_i)$$

where P_i is the proportion of each species in the sample. In the quadrat data, Domin cover values were divided by 10 to transform them into numbers between 0 and 1. A higher index indicates more species with a more even distribution of cover between them. Note that no analyses were possible for the Natural England datasets because of duplicated species entries relating to the same quadrat ID code. In analyses where no cover data were used, these data were reduced to unique lists for each ID but this reduction step was unsafe where cover data were concerned because of different cover scores assigned to duplicate species entries.

2.4 Driver variables

Data were assembled for three types of ecological driver: land-use, atmospheric pollutant deposition and climate as follows:

2.4.1 Land-use

Intensity of land-use in each grid square was measured as the proportion of arable plus improved grassland. Extent was based on the remotely sensed Land Cover Map 2000.

2.4.2 Climate

Long-term annual average data were available at the 5-km square scale based on interpolated estimates provided by the Met Office (www.metoffice.gov.uk). Three variables were selected: minimum January temperature, maximum July temperature and annual rainfall. For the temporal analyses the climatic explanatory variables were calculated as the slope coefficient of a linear regression of annual values against time starting in 1980 and ending in 2005. Where spatial differences across Britain in the most recent surveys were being analysed, the explanatory variable was the annual average value from 1980 to 2005.

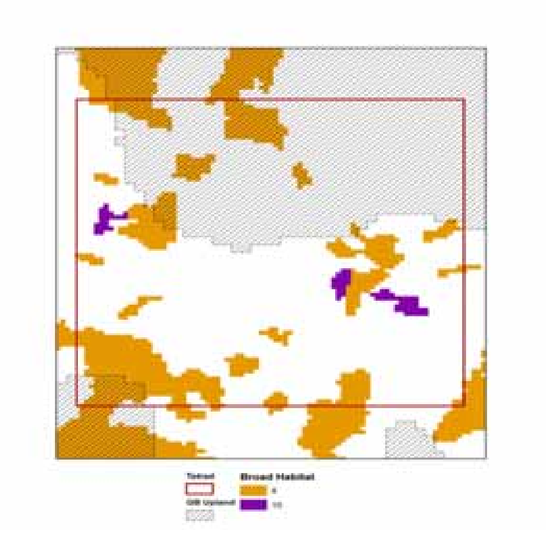
2.4.3 Atmospheric pollutant deposition

Cumulative N deposition data were not available so current N deposition was used as a proxy for cumulative deposition. If cumulative data were based on back-casting from current deposition patterns (as in Dupre *et al* 2010) we would expect to see very similar results. However, if cumulative deposition data based on emission changes over time were available this may show different results. We used estimates of total N deposition at the 5-km square scale provided by CEH Edinburgh (NEGTAP, 2001; Smith *et al* 2000), calculated as the mean of the estimates for 1996, ’97 and ’98 from the CBED model for deposition to moorland. Because deposition of nitrate and ammonium are correlated with each other we did not analyse them separately but only considered total N deposition. Sulphur (S) deposition and reductions in S deposition since the early seventies were based on FRAME model (Fine Resolution Ammonia Exchange) (Fournier *et al* 2000) model estimates calculated for 2005 and 1971. The explanatory variable was the difference between the two estimates for each 5-km square.

GIS and database querying were used to spatially match botanical data with driver datasets. Where the resolution of the botanical records was greater than that of the driver variable data, the driver data were averaged and therefore up-scaled to cover the size of the botanical recording unit. For example, climate and deposition data were available at 5-km square scale and intensive land use was available for each 1-km square, whilst some species records were at the hectad (10-km square) level. Therefore for analyses of hectad data, species records for the grid square were matched with the average of the driver variables taken across the smaller grid squares coinciding with the larger hectad.
All of the driver datasets gave information at a larger scale than the quadrat data were collected. This means that variability in the driver data at a smaller scale than the resolution at which data is available is not known so there may be errors in the estimates provided.

2.4.4 Allocation of upland and lowland

Hectads (10-km squares) and Tetrads (2-km squares) 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 25m raster coverage. The upland mask is composed of the upland delineation for England based on English Natural Areas, a Welsh upland mask provided by CCW, and the combined upland and montane masks from SNH. This is the same upland mask that was used in Countryside Survey analysis of Priority Habitats in Scotland (http://www.snh.org.uk/data/boards_and_committees/scientific_advisory_papers/ 2009-Jan/CountrysideSurvey2007-ScotlandResults.pdf). An example tetrad is shown below (Figure 2.1).



Orange = Acid grassland
Purple = Dwarf Shrub Heath

Figure 2.1. An example tetrad, NY38J, situated in the Scottish borders.

The Scottish mask is at 50m resolution so some tetrads were internally subdivided, for example acid grassland in the example above. Where a target Broad Habitat only occurs in lowland or upland sectors then the grid square record for species assigned to that habitat will only be included in the relevant sector. Here for example, the square would contribute lowland records to the heathland analysis. We do not know if a species assigned to Dwarf Shrub Heath and recorded in the tetrad was actually located in lowland Dwarf Shrub Heath.

It could occur in both sectors in this example: *Deschampsia flexuosa* could occur in acid grassland only in the upland polygons but in heathland in the lowland polygons. Given that species were selected with consideration to their preference for upland or lowland habitats this is unlikely to be a serious limitation of the dataset.

Quadrat data were allocated to upland or lowland using the same masks based on their location.

2.5 Allocation of habitat

Vascular plants and bryophytes were individually assigned to each of the target habitat types using published preference data on habitat affinity. Preference indices for Broad Habitat were taken from PLANTATT (Hill *et al* 2004) for vascular plants. For bryophytes preference for EUNIS categories were used in the absence of Broad Habitat data. This information was taken from BRYOATT (Hill *et al* 2007) where a score of 3 is used to indicate a normal habitat for the species. Hence species associated with D1 Raised and blanket bogs, F4 Dry temperate shrub heathland and E1 Dry grasslands were selected. This is slightly different to the habitat classification provided in PLANTATT and results in generalist species being reported in more than one habitat rather than species being allocated to the habitat they are most strongly associated with. Splitting E1 species into acidophilous and calcareous groups was achieved using the Ellenberg-style R values also published in BRYOATT. Scores 1 to 4 were allocated to acid grasslands and 8 and 9 calcareous grasslands. Species which occurred in less than 10% or more than 90% of hectads were removed from the analysis.

Only those species selected using the criteria above were used to generate summary variables for each grid square. Thus generalist species and those restricted to other non-target habitats were excluded from the calculation of mean Ellenberg values, mean canopy height and mean SLA per grid square.

Lichen species were selected based on expert opinion (Janet Simkin and others, British Lichen Society). The selected lichen taxa were associated with, and largely limited to, the target habitats (therefore terricolous, excluding montane and coastal species), not too scarce or regionally distributed, and accurately represented in the BLS database, without the patchiness that can result from intensive recording of some areas and neglect of others.

Quadrat data were allocated to habitats based on their recorded classification in the datasets. For acid grasslands all NVC U habitats were selected, for calcareous grasslands all CG habitats were selected, for heathlands all H habitats were selected and for bogs all M habitats were selected. The reliability of this allocation is likely to depend on the surveyor. This selection means that there are likely to be some habitats included that do not strictly fall under the generic headings given, however, not all of the datasets gave full NVC classifications and hence a more precise allocation was not possible.

2.6 Modelling of response variables

As the aim of the study was to assess the marginal effect of N on vegetation having taken account of confounding factors that are known to, or thought to, have a significant impact on vegetation, a model-based approach to the analysis was adopted. A model based approach allowed the effects of other covariates of interest to be modelled out and accounted for before looking at the relationship that the residuals have to N. To ensure that this was the case, in every model formula the final term was N, hence any strong effects of the other covariates were accounted for first.

The vegetation variable often being assessed was presence or absence of a particular species within the surveyed tetrad or hectad. However, presence / absence data is clearly not normally distributed, which many commonly used statistical modelling techniques assume from the outset. A non-normal response variable, such as species presence/absence or species richness, requires the model to be flexible enough to handle different error distributions. Generalised linear models (GLMs) (McCullagh and Nelder, 1989) are a class of models with such properties and were therefore adopted as the framework upon which analyses were based. In GLMs the linear modelling is performed on a link scale, a log link scale is a commonly used example, and error distributions such as binomial (corresponding to presence/absence data) and Poisson (corresponding to count data such as species richness) can be handled. Using this model framework ensured that the estimated uncertainty associated with the vegetation response variable was based on the correct distributional assumption.

2.6.1 Hectad data

In order to provide a full, robust assessment of the relationship between N and vegetation, the strong spatial aspect of the hectad data needed to be taken into account in the model. This is so that the assumption of independent observations made by the GLMs was not violated. Spatial dependence in the hectad data could be down to genuine dependence such as competition or coexistence between the vegetation in neighbouring hectads, a missing covariate from the model with a definite spatial component or a feature of the spatial grid design. For example, a patch of a particular species may, simply by chance, cross the intersection of four hectads, hence making presence/absence information from these four hectads non-independent. This spatial dependence structure could be handled by fitting a smooth, purely spatial surface to the model residuals. If the adopted model could fit a smooth non-linear spatial trend surface then it would also be able to fit smooth functions for the relationship between the response and each of the driver variables. A method allowing this flexibility, where non-linear terms could be fitted, was thus considered.

Generalised additive models (GAMs) (Hastie and Tibshirani, 1990) are a class of models extended from the generalised linear model framework by allowing the fixed linear terms to be flexible smoothly varying functions instead. Essentially a number of cubic polynomials are pieced together in such a way as to form a continuous fit through the data. The final smooth function is the one that best fits the scatterplot of the response variable versus the current covariate of interest having taken account of other covariates in the model. An example is shown below in Figure 2.2. Here the smooth function follows the underlying relationship between the response variable and the driver variable present in the data. It is important to note that the trend fitted is regarded as a mean trend and hence the confidence intervals plotted are confidence intervals around the mean (i.e. confidence of where the mean is), not individual observations. This explains why many observations lie outside of the interval.

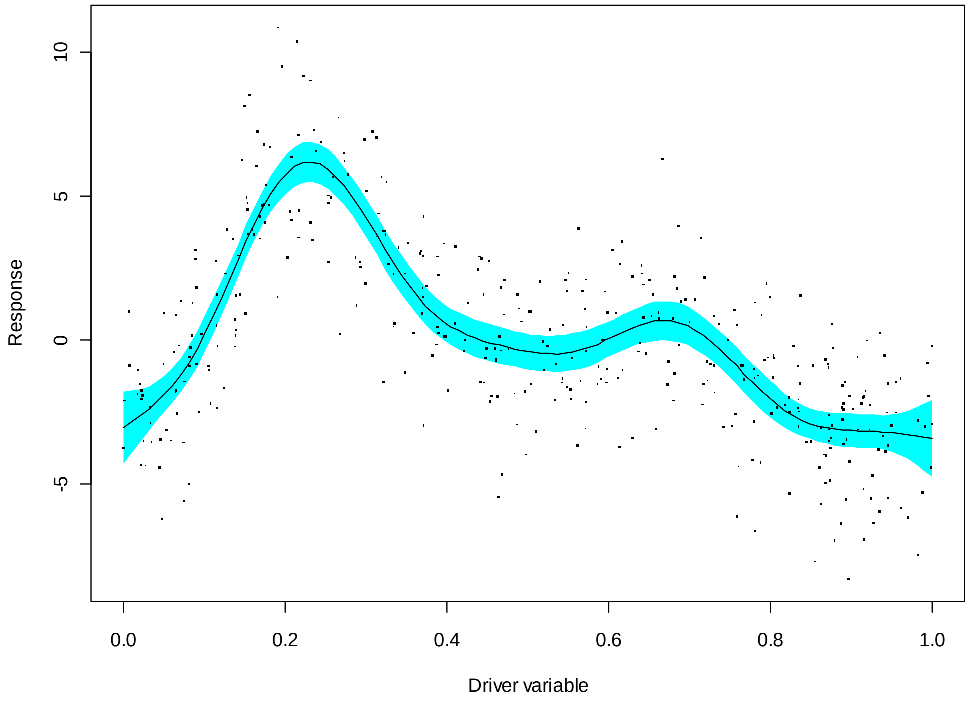


Figure 2.2. Example of a fitted smooth function between the response variable and a driver variable in the GAM.

Spatial dependence between the hectads 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 structure that would be present in the model residuals is mopped up by its inclusion. So rather than this dependence being inherited in the estimates of the standard errors, as it would be if the dependence was ignored, it is accounted for directly in the model. This method accounts for broad scale rather than fine scale variation and it can often be an important step/ consideration to decide on the scale at which local dependence is present. To assess this, a number of models were also set up in a Bayesian framework allowing for a localised, fine-scale dependence structure to be specified. In this model setup the value in a hectad is modelled conditional on the values in all connected hectads. An example of this structure is shown in Figure 2.3, where adjoined hectads are taken to have some inherent dependence. Results from such analyses confirmed that the broader scale dependence method of the GAMs performed equally as well as the full Bayesian model. Due to the vast amount of data to model, model complexities in the Bayesian approach, computational effort required, time to run the models and time taken to set the models up, the GAMs were deemed the most appropriate choice for the remainder of the data to be analysed.

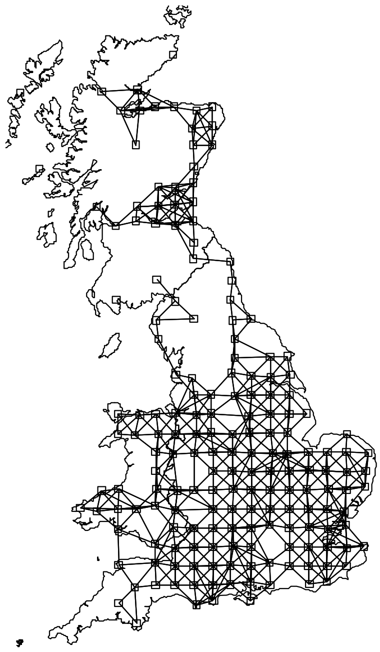


Figure 2.3. Example of fine scale, local dependence accounted for in the more complex Bayesian models. Hectads connected via a line are modelled as having a dependence structure.

2.6.2 Tetrad data

Because the tetrads are sub-samples from within a wider hectad, the tetrad data have the same spatial dependence between hectads as exhibited in the purely hectad datasets. Therefore, this needed to be modelled out in the same way as outlined above. Further to this spatial dependence, however, the tetrad data are more than likely to violate a further assumption of the models - that being of equal variability. This is because it is likely that the vegetation response from two tetrads within the same hectad are more likely to be more similar than observations from tetrads in two different hectads. Looking at a map of the tetrad/hectad layout in Figure 2.4, it is easy to imagine that variability within a hectad is likely to be less than the variability between the different hectads. Therefore, our model for the tetrad data had to also compensate for the expected differing levels of variation present in the data.

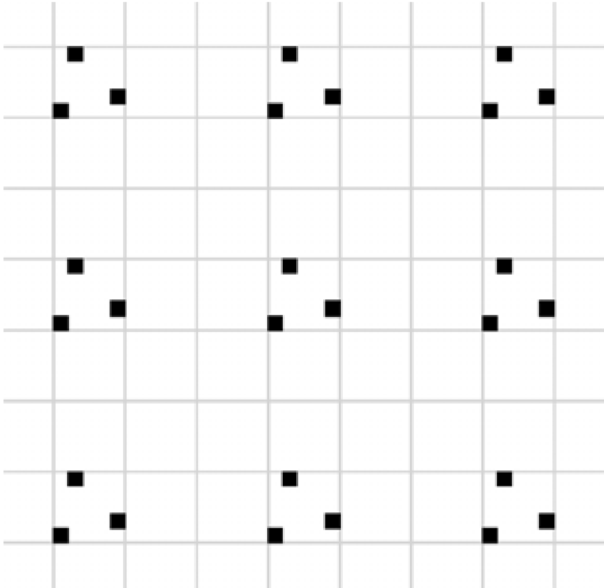


Figure 2.4. Example layout of tetrads within hectads. Black squares represent tetrads.

Generalised additive mixed models (Lin and Zhang, 1999) extend the framework of the standard GAM to include extra random components in the model in the same way that generalised linear mixed models do for the standard GLM. The random components included in the mixed model are to account for unobserved effects that could influence the outcome of the response variable. In this context they were used to allow for an unobserved effect within hectads. That is to say that although we did not measure anything directly, we allowed data observed from within different hectads to have different distributions. Hence the variation within a hectad and the variation between hectads were separated out using a random effects component for hectad in the mixed model.

2.6.3 Model inference

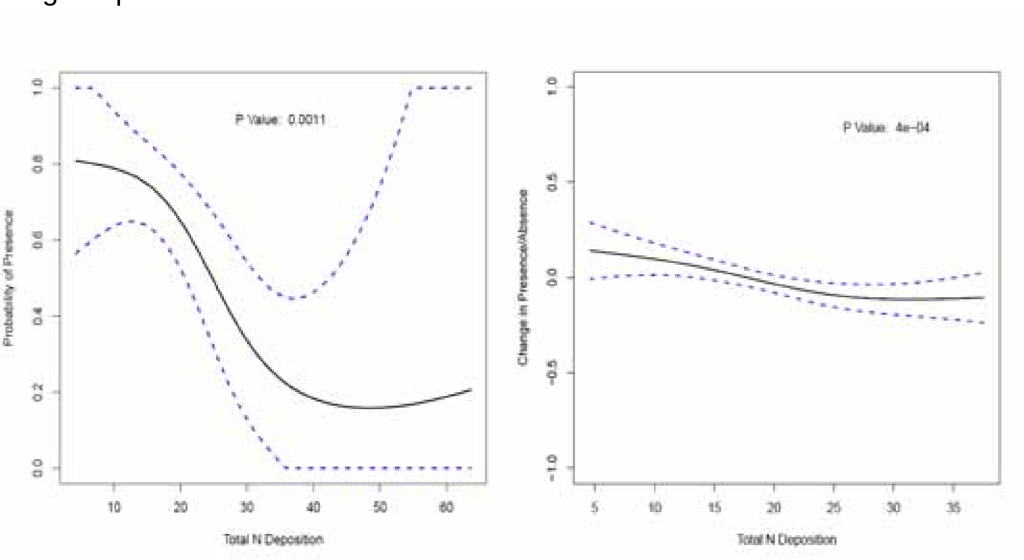
For both the hectad and tetrad models, regression parameters for any fixed linear terms and parameters for each of the smooth terms were estimated, together with standard errors, by either approximating the true likelihood or using quasi-likelihood methods.

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, similar to that shown in Figure 2.2. This also included upper and lower confidence intervals around the mean trend. 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.

2.6.4 Model output interpretation

The output from the model of the fitted smooth and estimated p-value requires some clarification and guidance before they are formally presented in the results section (section 3). The output produced from the models is displayed, as previously mentioned, as a smooth plot of the fitted mean trend of the relationship between the response variable and N deposition together with estimated confidence intervals. Two examples of such model outputs are shown below and both highlight aspects that need to be considered when interpreting the plots.



(a) **(b)**

Figure 2.5. Typical graphical output from the models used in the analysis

In Figure 2.5a, it is important to note the very wide confidence intervals at the upper end of the N scale. This is due to the lack of data above a value of 35. Although the mean trend shows a slight rise at about 50 on the N scale, we cannot read anything into that because our confidence intervals tell us that we really do not have a clear understanding of what the relationship looks like at such high ranges of the data. Using evidence from this plot, we would probably find it very hard to reject any null hypothesis about the mean trend between N and the probability of species occurrence at N values greater than 40. The p-value shows this relationship to be significant despite the very wide confidence intervals at this upper end. This highlights the strength of the relationship at the lower end of the N scale, which is itself an important point to draw out from the plots.

In Figure 2.5b, the scaling of the y-axis is crucial. Here it ranges from -1 to 1. The value -1 represents change from species presence to species absence, 0 represents no change and 1 represent a change of species absence to species presence. The scale of the y-axis in all plots should be viewed closely. Related to the y-axis scaling is another feature of some plots which is highlighted in Figure 2.5b. From the p-value we can see that the relationship is highly significant. However, if we were to look solely at this plot, we may not reach the same conclusion as it may appear that there is not much effect. This is simply because of the scale. If the scale on the y-axis was from -0.3 to 0.3, the negative relationship would look much steeper, the plot would look much stronger and we would be in no doubt as to its significance. For ecologically meaningful interpretation, the scale was always maintained at 0 to 1 for presence/absence data and -1 to 1 for presence/absence change data. So it is very possible to have statistically significant results that appear to have little effect when plotted on an ecologically meaningful scale. This is why we believe it is important to use both the p-value and the plot to obtain full results and gain a full understanding of the relationships present in the data.

Because the smooth terms in the GAM are attempting to fit a trend that follows the data as closely as possible, overfitting can be a problem. What is meant by this is that if we allow the smooth terms in the model to be too flexible, it is possible that they essentially just join up the data points on the scatter plot. This is shown in Figure 2.6 below, which is the same data and model from Figure 2.2, but the smooth function is now too flexible and has become very spiky and volatile rather than smoothly varying. It is clear that the better outcome of the model in terms of interpretability, predictive power and underlying true relationship assessment is Figure 2.2 rather than Figure 2.6. To overcome this and to be sure that the general trends and patterns are captured as opposed to every nuance in the data, restrictions were placed on the fitted smooth functions such that the maximum number of turning points allowed was pre-specified.

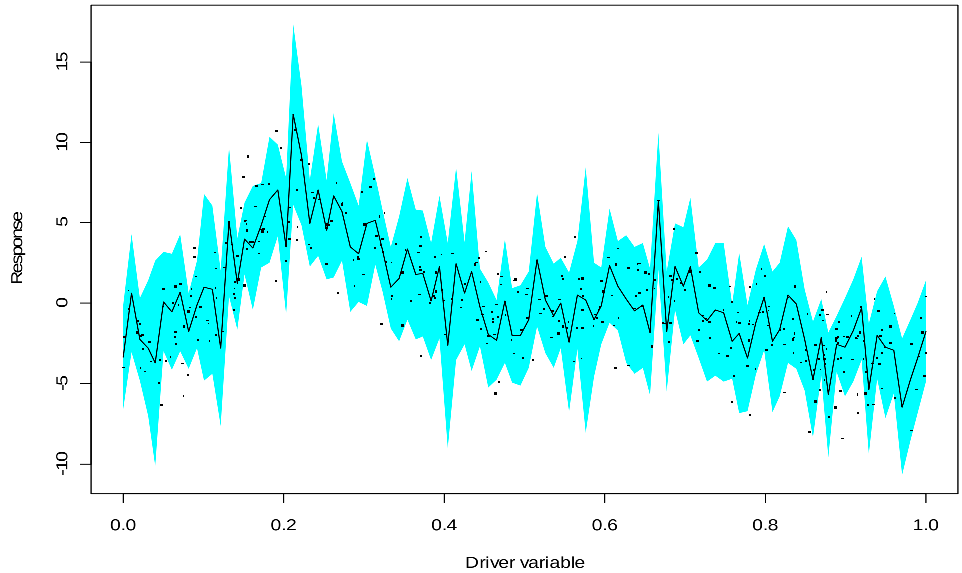


Figure 2.6. Data and model as in Figure 2.2 but the smooth function has been allowed to be too flexible.

Because of the complex modelling framework and the number of driver variables used in building the model, datasets with a small number of observations could not be analysed. This was often because the number of parameters that needed to be estimated in the model was greater than the number of observations in the dataset. Also, for some datasets we may have been able to construct the model, but full model convergence was not reached. This means that estimated parameters and modelled relationships are very unreliable and should not be used. To achieve successful model convergence it is necessary for the response variable and the covariate data to have sufficient coverage across the sample space. What is meant by this is that enough data are required at each level of the driver variables and response variables to accurately estimate the effect at each level. This is particularly true with presence/absence data where very rare species may not have enough observations of presence to estimate that aspect of the model accurately or very common species that do not have enough absences. Because of this it was decided that an initial filter would be put in place to exclude species with less than 10% (5% in the temporal analysis) and greater than 90% of presences in the dataset. This avoided many convergence problems and model error problems. Similarly, covariates that have very uneven distributions, where at the extreme ends of the range very few data were sampled, may lead to relationships that cannot be clearly defined and hence affect model convergence. At low deposition there are few sites so species may have a high probability of presence at low deposition as a consequence.

Both of these issues of variable coverage and dataset sample size could lead to non-convergence, errors or failures in the model. Datasets with insufficient data and analyses where model convergence was not reached were excluded from the results. This is rather than compromising the results and consistency by subjectively altering the model formula. It is important to stress that 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.

Relationships shown in the plots may not necessarily comply with what one observes with a simple correlation between N deposition and the response. This is because the approach taken in this project was to account for any available additional covariates as well as a spatial term before analysing for the relationship with N deposition.

Differences will be magnified when the covariates are correlated, as with N deposition and the spatial term. In some circumstances the spatial term may soak up the effect that one would expect to see N deposition have. This is because the spatial term may describe the broad scale changes that are actually more correlated with space generally than the more subtle, finer scale changes in N deposition. Hence, an expected signal between the response and N deposition may not appear in the marginal N deposition plots displayed and the spatial signal cannot be seen.

It is also important to note that p values are rounded so where graphs say $p=0$ in reality this is $p<0.0001$.

2.7 Analysis of quadrat data

2.7.1 Generalised linear models

Quadrat datasets were only available for one time point and so modelling focussed on detecting spatial associations between N deposition and response variables. The response variables calculated were mean Ellenberg R and N (indicators of soil pH and substrate productivity respectively), mean plant canopy height, mean SLA (an indicator of aboveground Net Primary Production (Garnier *et al* 2004)), species count per plot and the Shannon-Weiner diversity index. Ellenberg values and plant height were taken from PLANTATT (Hill *et al* 2004). SLA data were taken from the LEDA database[1] and from data compiled by the Unit of Comparative Plant Ecology at Sheffield University. All data recorded in each quadrat were used to calculate summary variables.

Generalised linear models (GLMs) were used to test whether total N deposition was able to explain a significant amount of the spatial variation in each response variable, having already fitted covariates relating to climate, sulphur deposition and intensive land use. A normal error distribution was applied for all variables except species count where Poisson error and a log link were specified with over-dispersion incorporated by a flexible scale parameter. Where plots could be nested within an identifiable site then site ID was used as a random class variable in a Generalised linear mixed model. Degrees of freedom were down-weighted according to the approximation of Satterthwaite (1946). All analyses of quadrat data were carried out in SAS using proc mixed, proc glimmix and proc genmod (Little *et al* 2000; Singer, 1998).

[1] http://www.leda-traitbase.org/LEDAportal/

2.7.2 Canonical correspondence analysis

Canonical correspondence analysis (CCA) was used to determine the response of species in the quadrat data. CCA is a multivariate ordination technique for direct gradient analysis. Species composition is directly related to measured environmental variables. The technique assumes species have unimodal distributions along environmental gradients. The resultant ordination diagram conveys large amounts of information regarding the environmental variables and their relations to species. CCA distributes individual species in this ordination diagram in a position that reflects their net tolerance to environmental factors. For all the datasets examined using CCA, an analysis was run initially to see if there were significant associates between the species composition and environmental variables using forward selection with a Monte Carlo permutation test. N deposition was then used as an environmental variable and all other significant variables were used as co-variables. CCA was carried out using CANOCO 4.5 (ter Braak and Smilauer, 2002).

3 Results

Results are presented individually for each of the datasets examined. The discussion section draws the results together examining them for each habitat. For all datasets, the individual species examined are listed in an Appendix. Key results (those that are statistically significant and not of a very small magnitude) are provided in this results section of the report. All other significant results are provided in the Electronic Appendices. Note that there is some overlap between this results document and the Electronic Appendices in order to ensure that the Electronic Appendices provide a complete set of significant results.

When interpreting the graphs, note that if a species shows a significant negative relationship this means that the species is negatively associated with N deposition when all other conditions are constant. The decline in probability of presence shown is entirely due to N deposition so the species is at risk from nitrogen deposition. If a species shows a significant positive relationship with N deposition this indicates that when all other conditions are constant the species is positively associated with N deposition. If all other conditions are optimal this species could potentially increase in its occurrence at high deposition.

3.1 Vascular Plant Database

Appendix 1 provides a list of the species investigated for the Vascular Plant Database and Electronic Appendix 1 gives the full set of significant results for species. Two types of analysis have been conducted using this data; spatial and temporal analysis. Spatial analysis investigates the relationship with N deposition based on the gradient of deposition in GB. Temporal analysis looks at change between two data collection periods (1930 to 1969 and 1987 to 1999) in relation to recent N deposition levels in the grid square. The data have been analysed for Ellenberg scores (spatial and temporal), plant canopy height (spatial), SLA (spatial) and the probability of presence of individual species (spatial and temporal). Care must be taken in interpreting the graphs above 40 kg N ha^{-1} yr^{-1} as there are very few areas where deposition is this high.

3.1.1 Nitrogen deposition

The number of hectads in Great Britain for each habitat is given in Table 3.1.1. Ranges of deposition for each habitat for which data were analysed are given in Figure 3.1.1.

Table 3.1.1. Number of hectads for each habitat.

Habitat	Lowland	Upland
Acid grassland	1143	1203
Calcareous grassland	1546	662
Bog	102	741
Heathland	855	1284

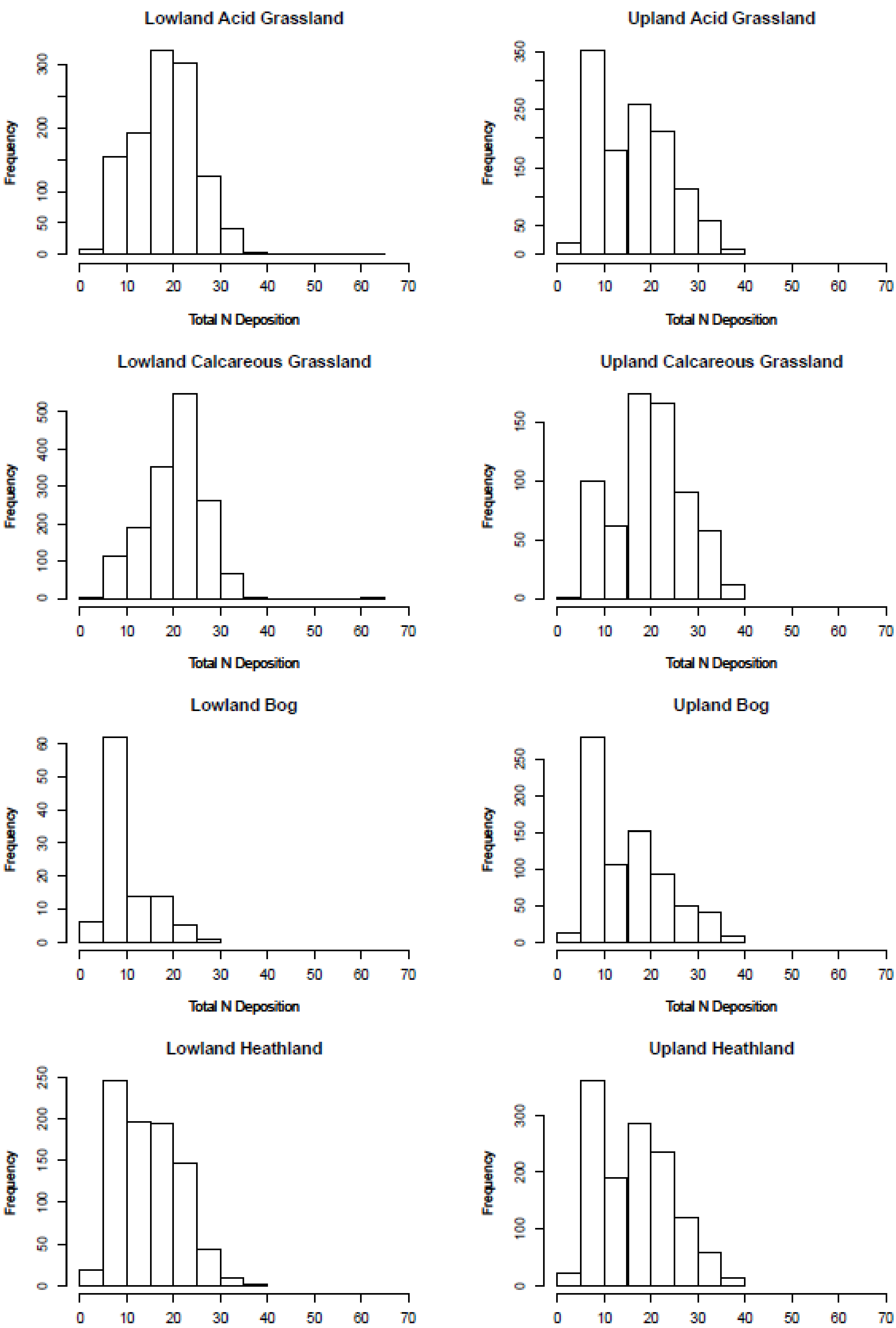


Figure 3.1.1. Frequency histograms of N deposition (kg N ha^{-1} yr^{-1}) for each of the habitats for which data were analysed.

3.1.2 Ellenberg N

i Acid grassland

Average Ellenberg N score showed a clear increase with increasing N deposition in the spatial analysis (indicating an increase in fertility) for lowland acid grassland (Figure 3.1.2). For upland acid grassland there was no significant relationship between Ellenberg N and N deposition. In the temporal analysis of lowland acid grassland there was an increase in Ellenberg N score between the two survey periods; in areas of high deposition this increase was much greater than in areas of low deposition (Figure 3.1.3). As with the spatial analysis there was no significant response in upland acid grassland.

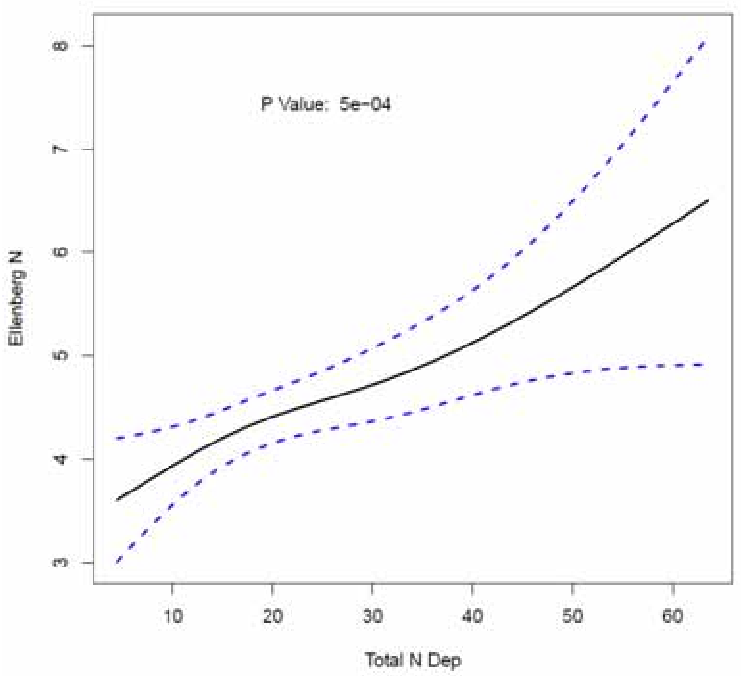


Figure 3.1.2. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from Vascular Plant Database.

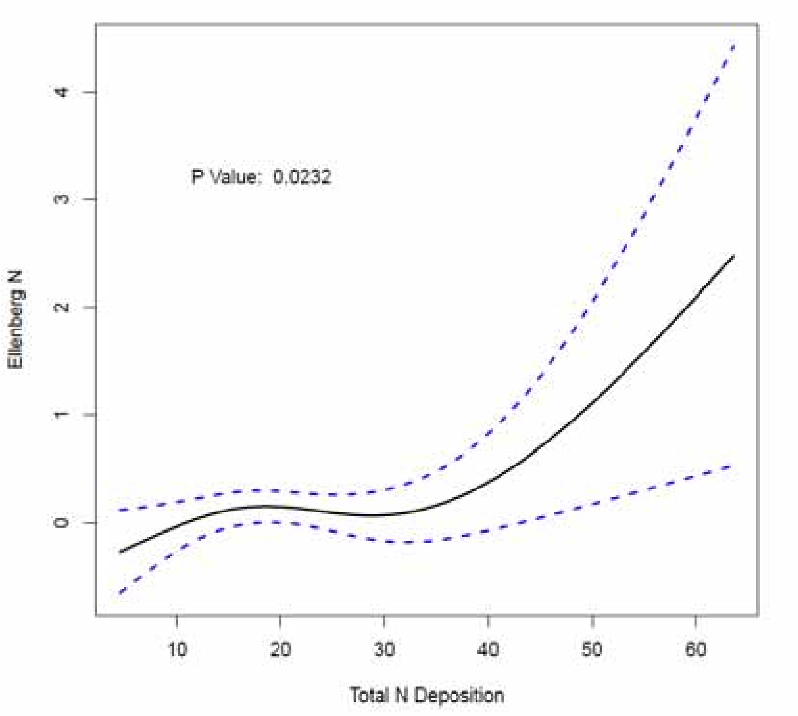


Figure 3.1.3. Temporal change in mean Ellenberg N score between survey periods (1930-1969, and 1987-1999) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in lowland acid grassland. Data from Vascular Plant Database.

ii Calcareous grassland

There were significant results for both lowland and upland calcareous grassland in the spatial analysis of Ellenberg N scores but the two communities showed slightly different results. Upland calcareous grassland showed an increase in Ellenberg N score with N deposition as seen in other habitats (Figure 3.1.4) but lowland calcareous grassland showed a humpbacked response with mean Ellenberg N score increasing up to 30 kg N ha^{-1} yr^{-1}, before levelling out and declining at highest levels of deposition where there are very few sites and a lot of variability in the data (Figure 3.1.5).

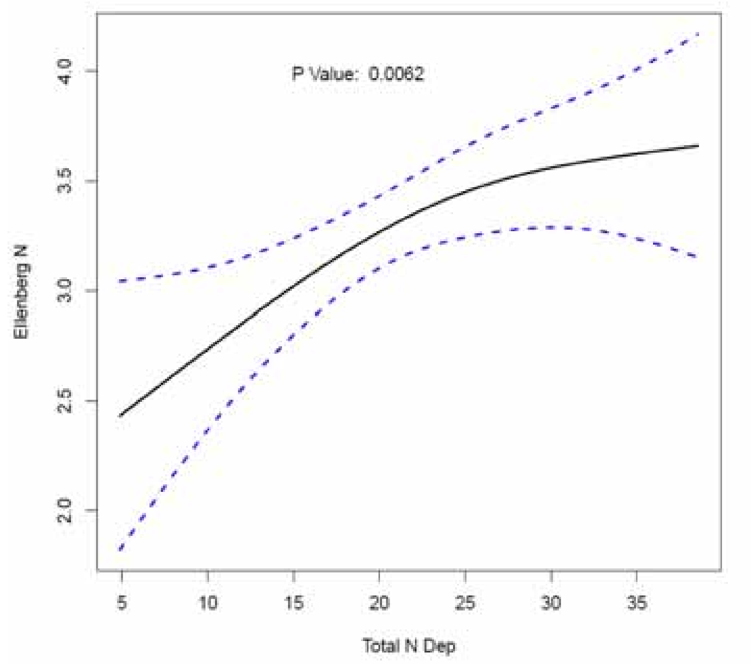


Figure 3.1.4. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland calcareous grassland. Data from Vascular Plant Database.

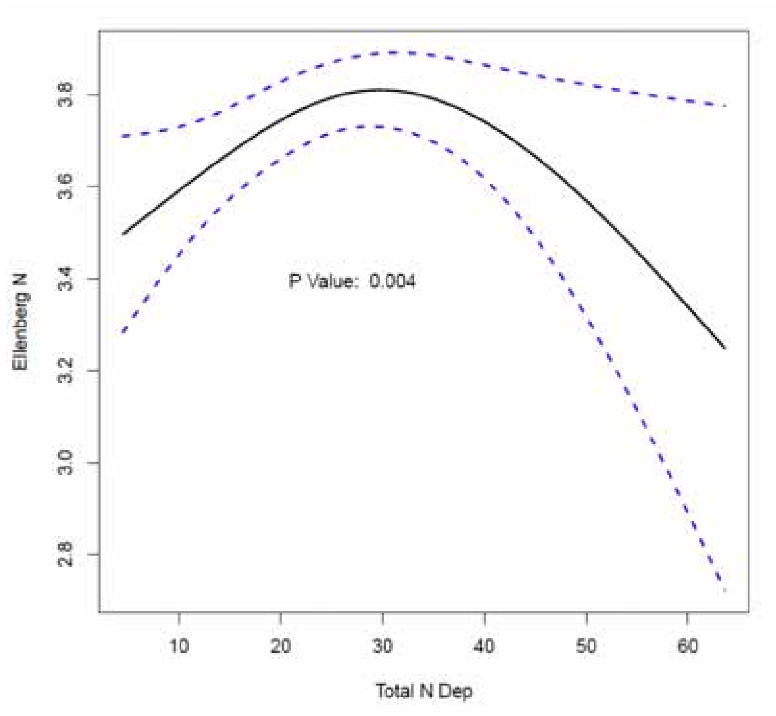


Figure 3.1.5. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland calcareous grassland. Data from Vascular Plant Database.

There was no significant relationship between change in the Ellenberg N score between survey periods and recent N deposition for either lowland or upland calcareous grassland (lowland p=0.11; upland p=0.73).

iii Bog

There were insufficient data for spatial analysis of Ellenberg N in lowland bog, but upland bog showed a clear increase in Ellenberg N score with increasing N deposition (Figure 3.1.6).

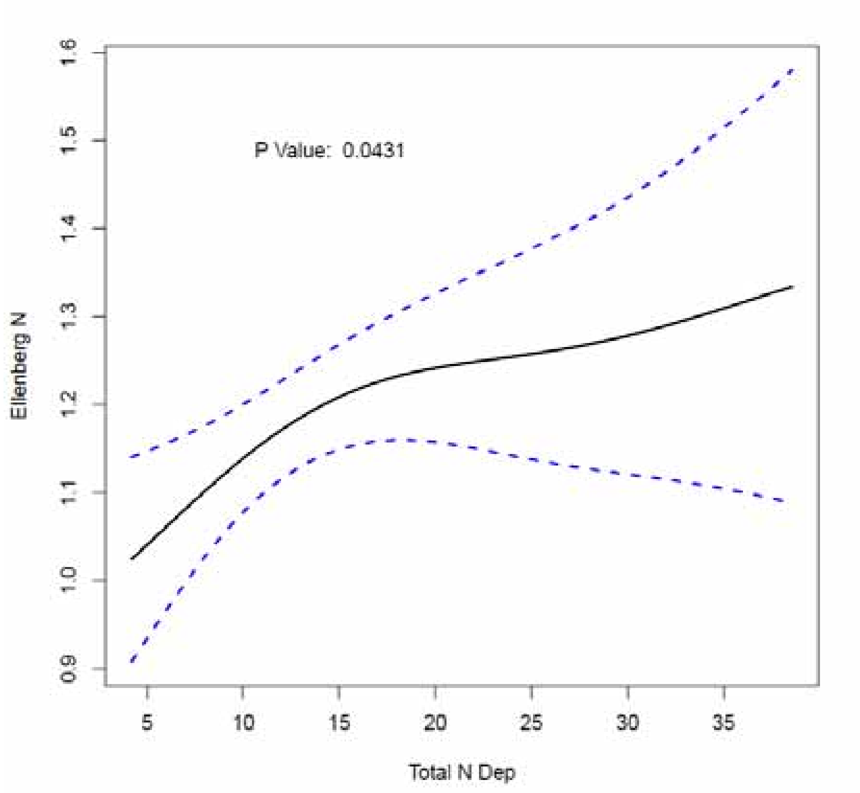


Figure 3.1.6. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland bog. Data from Vascular Plant Database.

It was also only possible to investigate temporal change in Ellenberg N score in upland bog, but there was no significant relationship between change in the Ellenberg N score between survey periods and recent N deposition (p=0.95).

iv Heathland

Both upland and lowland heathland showed a significant increase in Ellenberg N score and N deposition in the spatial analysis (Figures 3.1.7 and 3.1.8). In the temporal analysis there was no significant relationship between change in the Ellenberg N score and N deposition for lowland heathland. Upland heathland did show a significant positive relationship but it was of a very small magnitude (<0.1) and so unlikely to be ecologically relevant.

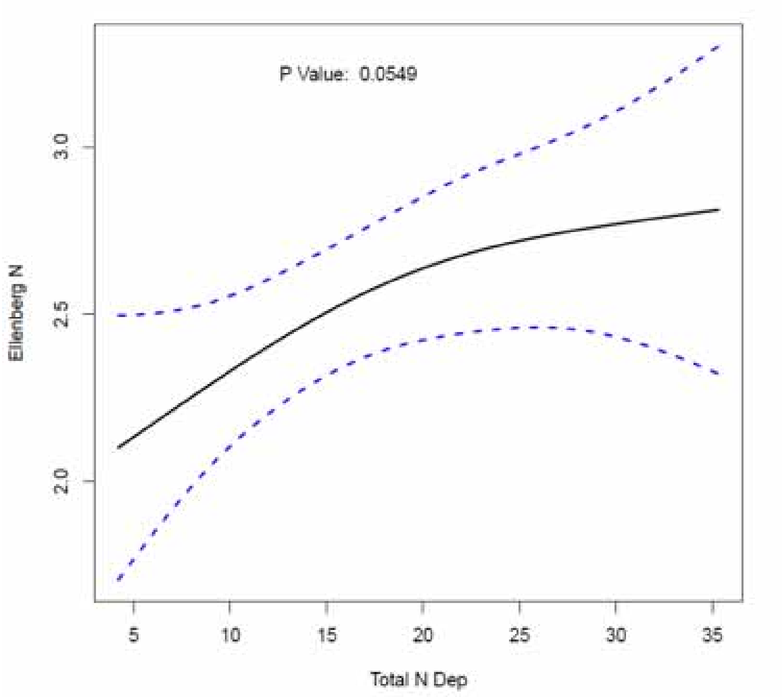


Figure 3.1.7. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland heathland. Data from Vascular Plant Database.

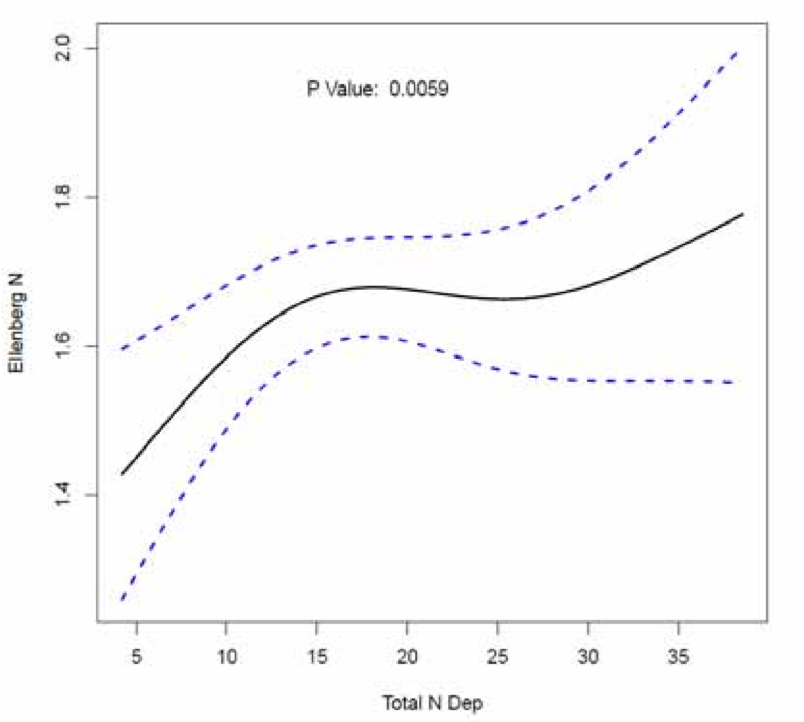


Figure 3.1.8. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland heathland. Data from Vascular Plant Database.

3.1.3 Ellenberg R

i Acid grassland

Ellenberg R scores showed no significant relationship with N deposition in either upland or lowland acid grassland in the spatial (lowland p=0.39; upland p=0.19) or temporal analysis (lowland p=0.59; upland p=0.57) although in all cases the trend was towards lower scores or a greater degree of acidification at high deposition.

ii Calcareous grassland

Calcareous grassland also failed to show any significant relationships between Ellenberg R and N deposition in the spatial analysis (lowland p=0.06; upland p=0.8), although again trends were towards lower R scores at high N deposition and results were quite close to being significant. Temporal analysis failed to show any significant relationship between Ellenberg R change and N deposition (lowland p=0.32; upland p=0.27) and changes in Ellenberg R scores were of a very small magnitude.

iii Bog

Ellenberg R scores showed no significant relationship with N deposition in either upland or lowland bog in the spatial (lowland p=0.67; upland p=0.89) or temporal analysis (lowland p=0.91; upland p=0.87).

iv Heathland

Heathland also failed to show many significant changes in Ellenberg R scores with no significant relationship between Ellenberg R score and N deposition in the spatial analysis (lowland p=0.11; upland p=0.06). In the temporal analysis there was no significant relationship between change in Ellenberg R score and N deposition in upland heathland (p=0.79) but in lowland heathlands there was a significant trend with increasing Ellenberg R score above 20 kg N ha^{-1} yr^{-1} (Figure 3.1.9).

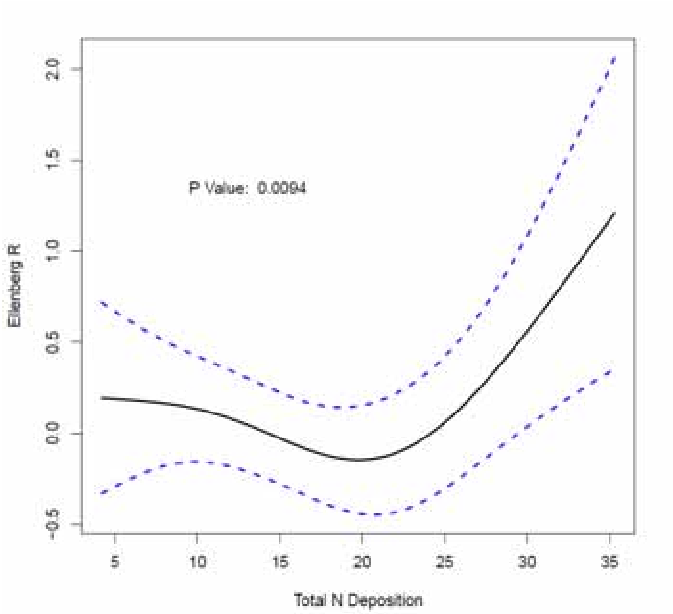


Figure 3.1.9. Temporal change in mean Ellenberg R score between survey periods (1930-1969, and 1987-1999) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in lowland heathland. Data from Vascular Plant Database.

3.1.4 Plant canopy height

i Acid grassland

Results for plant height in lowland acid grassland were similar to Ellenberg N scores showing a significant increase in canopy height with increasing N deposition (Figure 3.1.10). For upland acid grassland the results were not significant but there was a trend for increasing plant height (p=0.15).

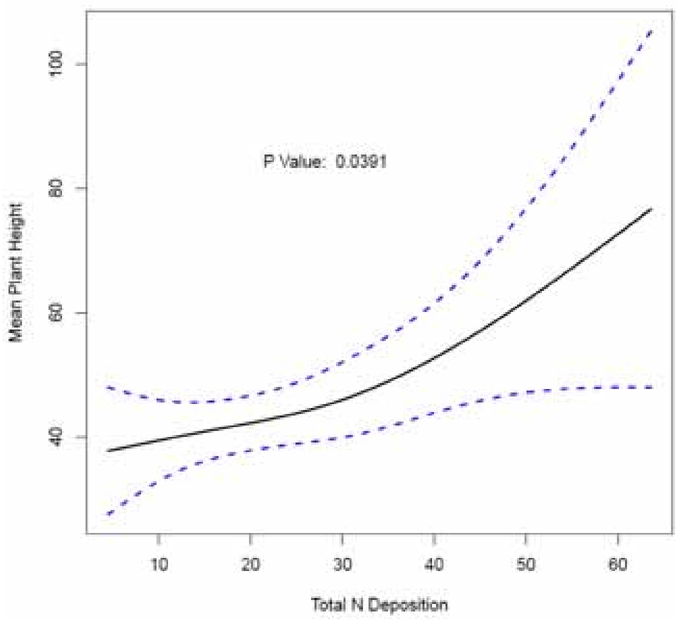


Figure 3.1.10. Spatial analysis of mean plant canopy height against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from Vascular Plant Database.

ii Calcareous grassland

For calcareous grassland there was no significant relationship between mean plant canopy height and N deposition in lowland grassland. In upland calcareous grassland there was a clear increase in plant height up to approximately 20kg ha^{-1} yr^{-1} after which there is little change (Figure 3.1.11).

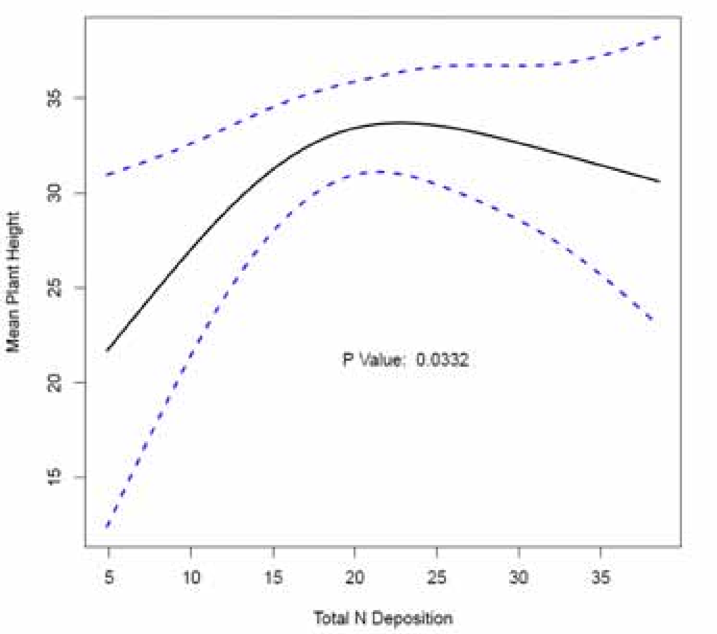


Figure 3.1.11. Spatial analysis of mean plant height against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland calcareous grassland. Data from Vascular Plant Database.

iii Bog

In bog there were no significant relationships between plant height and N deposition (lowland p=0.25; upland p=0.73).

iv Heathland

Mean canopy height in lowland heathland showed a similar relationship to N deposition as seen in calcareous grassland, with an increase in plant height up to approximately 20kg ha^{-1} yr^{-1} after which there is little change (Figure 3.1.12). There was no significant relationships between plant height and N deposition in upland heathland (p=0.92).

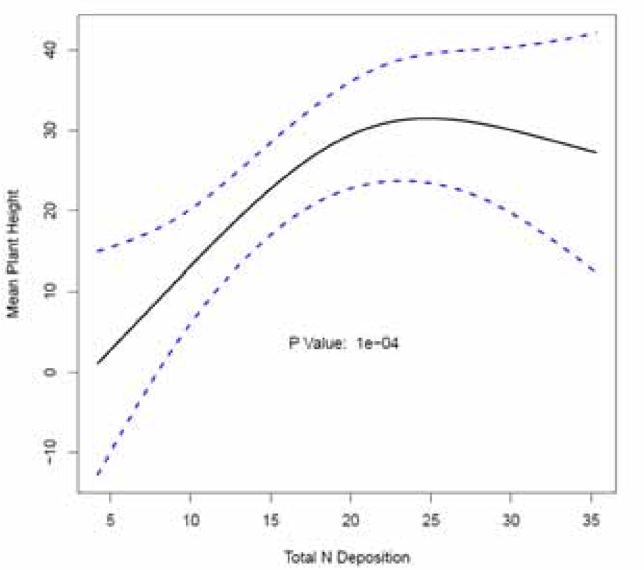


Figure 3.1.12. Spatial analysis of mean plant canopy height against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland heathland. Data from Vascular Plant Database.

3.1.5 Specific leaf area

i Acid grassland

Lowland acid grassland showed no significant relationship between N deposition and SLA (p=0.98) but in upland acid grassland there was a significant positive relationship with SLA peaking at approximately 20 kg N ha^{-1} yr^{-1} and then showing no further increase (Figure 3.1.13).

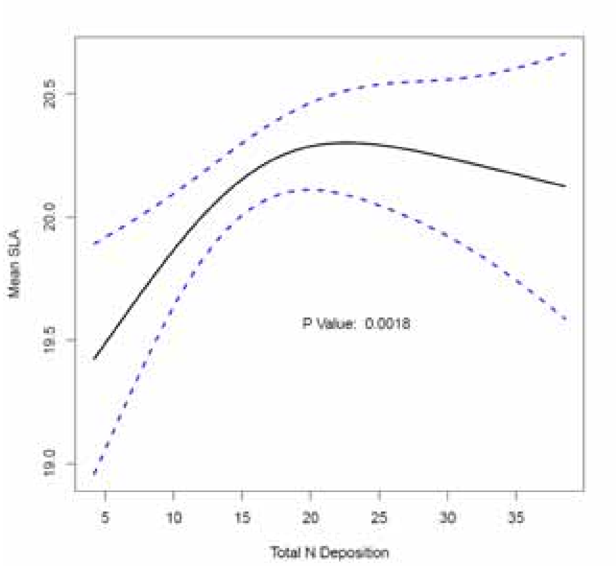


Figure 3.1.13. Spatial analysis of mean SLA against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland acid grassland. Data from Vascular Plant Database.

ii Calcareous grassland

Calcareous grassland showed no significant relationship in upland grassland (p=0.13) but in lowland grassland there was a significant relationship. Mean SLA showed a similar relationship to lowland acid grassland, increasing to approximately 20 kg N ha^{-1} yr^{-1} and then showing no further increase (Figure 3.1.14).

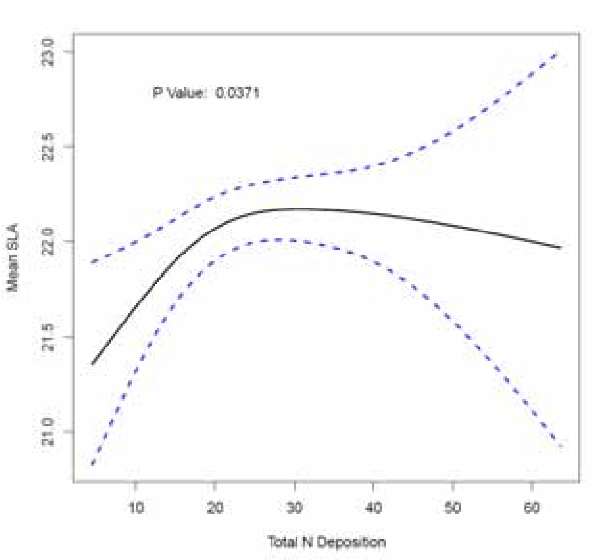


Figure 3.1.14. Spatial analysis of mean SLA against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland calcareous grassland. Data from Vascular Plant Database.

iii Heathland and Bog

Neither heathland nor bog showed any significant relationship between N deposition and SLA in either upland or lowland communities (bog: lowland p=0.05, upland p=0.82); heathland: lowland p=0.79, upland p=0.36).

3.1.6 Individual species responses

i Spatial analysis of individual species

a Acid grassland

Of 44 potential species there were sufficient data to test probability of presence for twelve species (between 10 and 90% of hectads occupied) for lowland acid grassland (Appendix 1). 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 tends, declining in the probability of presence rapidly with increasing deposition and then tailing off (Figures 3.1.15 to 3.1.19). Four species were investigated for upland acid grassland with sufficient data for analysis of one (Appendix 1). This did not show a significant response to N deposition.

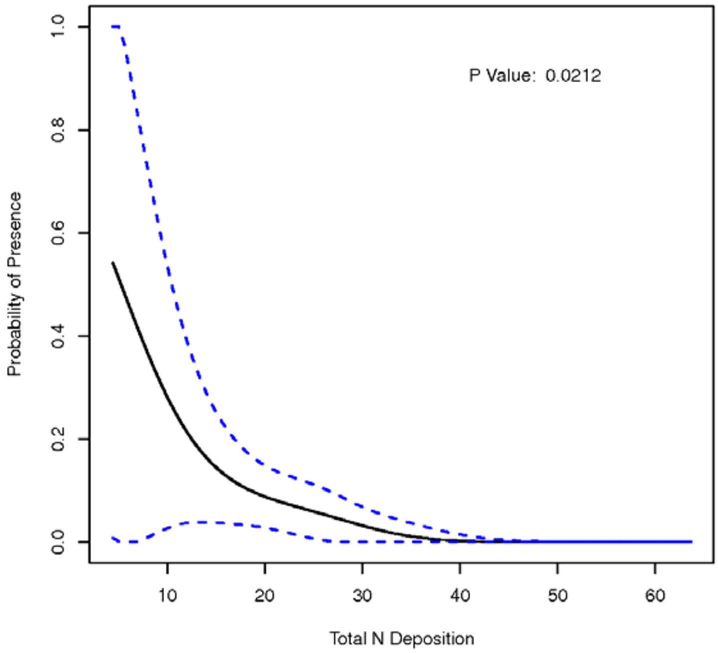


Figure 3.1.15. Spatial change in the probability of presence of *Cerastium arvense* in lowland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

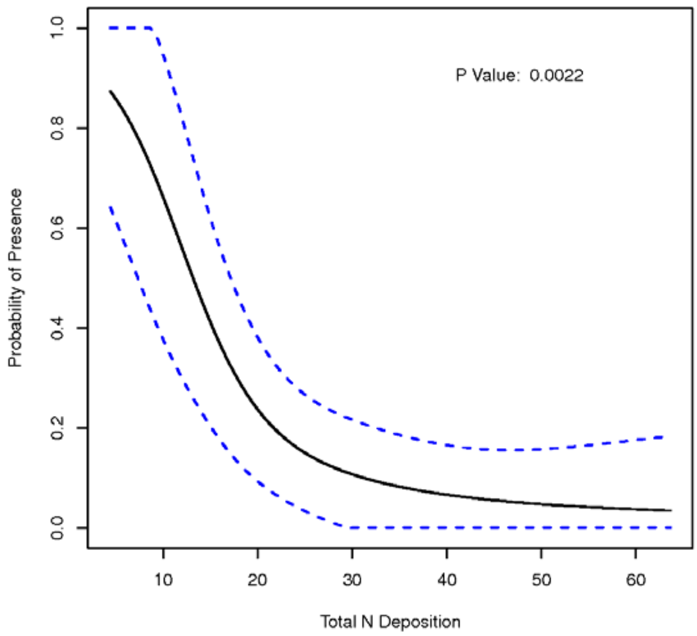


Figure 3.1.16. Spatial change in the probability of presence of *Cerastium semidecandrum* in lowland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

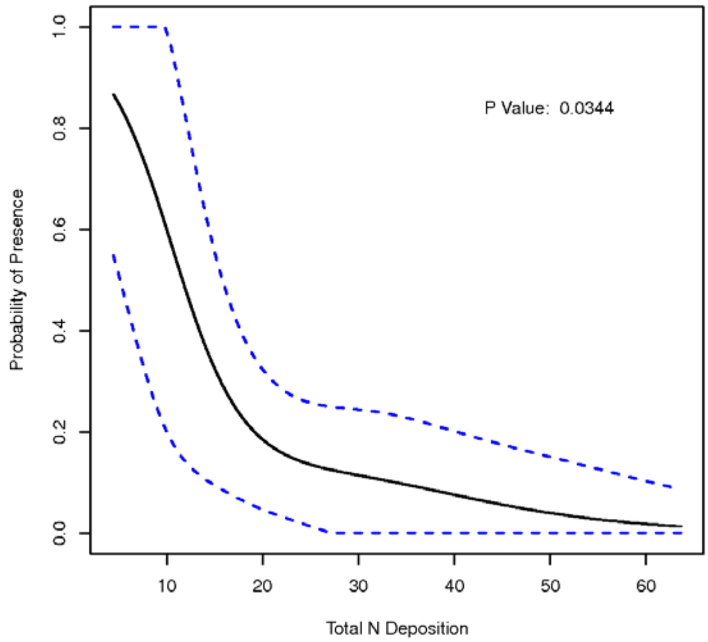


Figure 3.1.17. Spatial change in the probability of presence of *Trifolium arvense* in lowland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

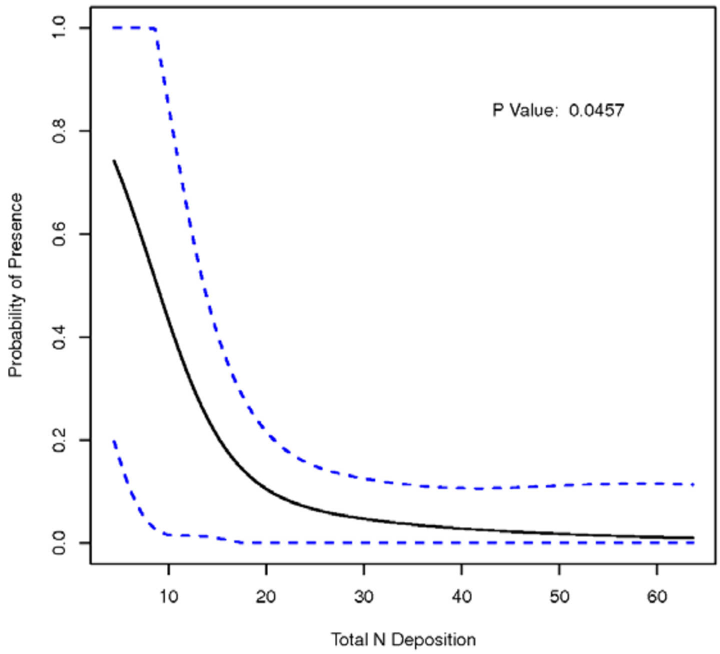


Figure 3.1.18. Spatial change in the probability of presence of *Vicia lathyroides* in lowland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

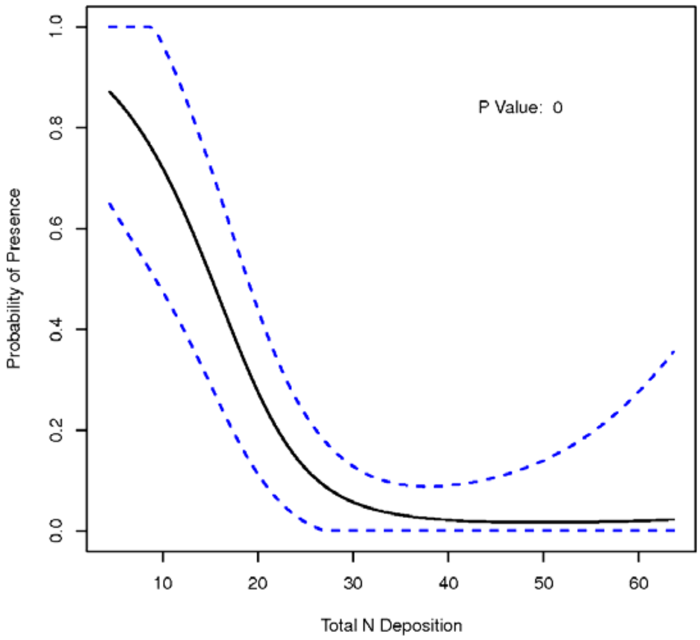


Figure 3.1.19. Spatial change in the probability of presence of *Viola canina* in lowland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

b Calcareous grassland

Of 91 species in the dataset there were sufficient data (between 10 and 90% of hectads occupied) for analysis of 40 species in lowland calcareous grassland. Of these, 17 showed significant relationships with N deposition (Appendix 1). Nine species showed negative relationships 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 large changes in their probability of presence, even at low levels of N deposition (Figures 3.1.20 to 3.1.27), with the exception of *Rosa micrantha* which only occurred at relatively low probability of presence in the analysis.

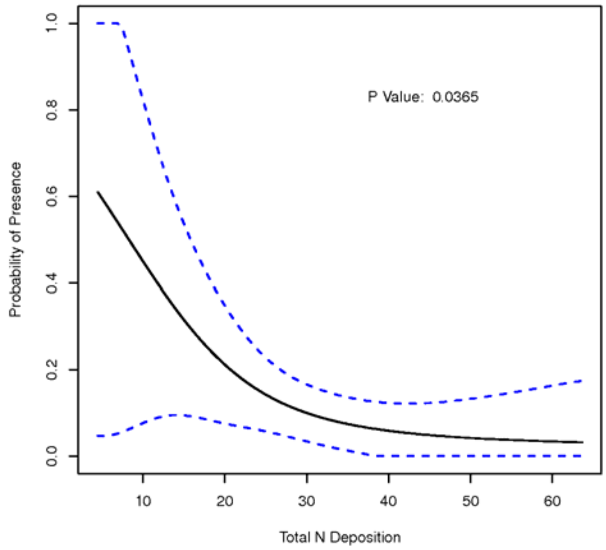


Figure 3.1.20. Spatial change in the probability of presence of *Allium vineale* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

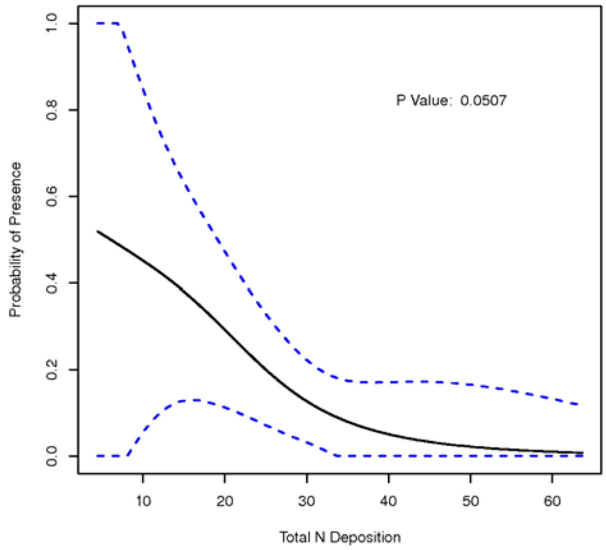


Figure 3.1.21. Spatial change in the probability of presence of *Anacamptis pyramidalis* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

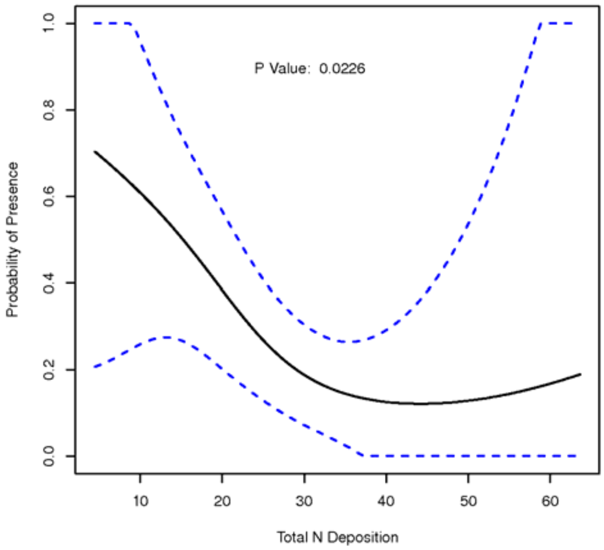


Figure 3.1.22. Spatial change in the probability of presence of *Carlina vulgaris* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

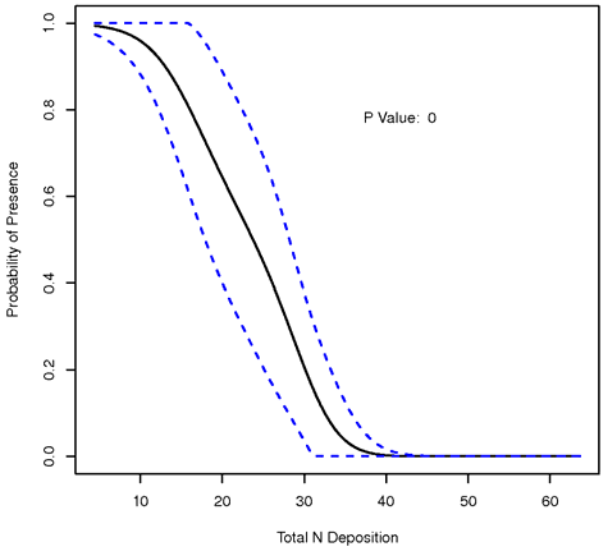


Figure 3.1.23. Spatial change in the probability of presence of *Cynoglossum officinale* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

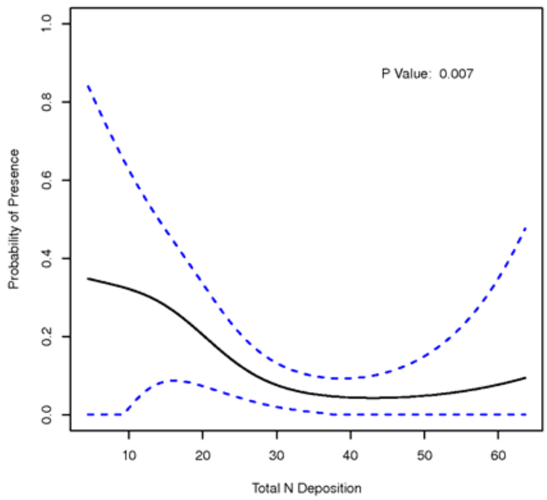


Figure 3.1.24. Spatial change in the probability of presence of *Echium vulgare* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

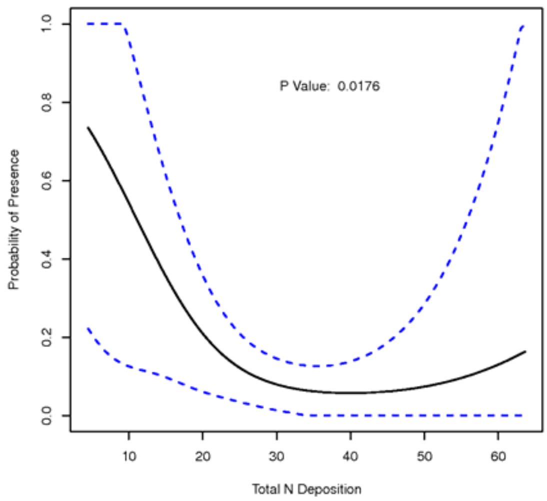


Figure 3.1.25. Spatial change in the probability of presence of *Geranium columbinum* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

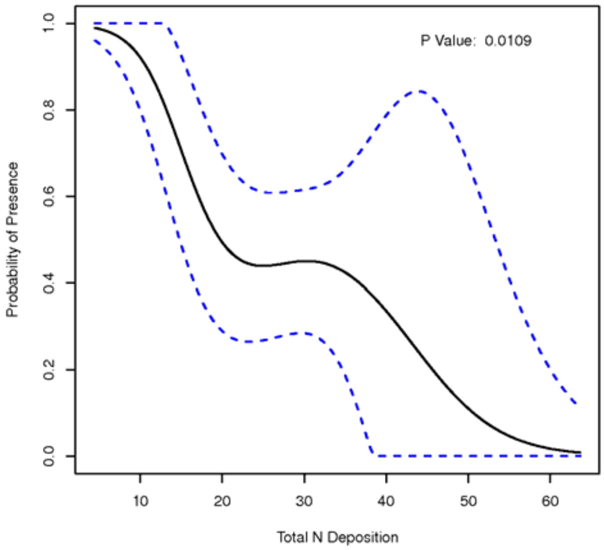


Figure 3.1.26. Spatial change in the probability of presence of *Ononis repens* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

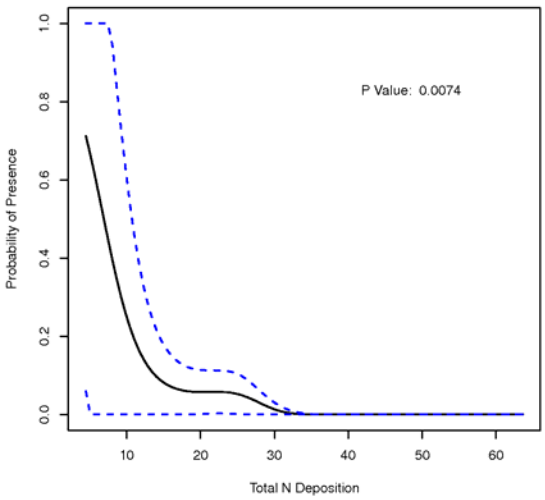


Figure 3.1.27. Spatial change in the probability of presence of *Spiranthes spiralis* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

In lowland calcareous grassland there were also two species which showed positive relationships with N deposition: *Lathyrus nissolia*, which showed an increase in probability of presence with N deposition (Figure 3.1.28), and *Stachys officinalis,* which increased to about 30 kg N ha^{-1} yr^{-1} and then declined slightly, but in both cases there was a large variability in the data at high deposition (Figure 3.1.29). There were also three species (*Carex spicata, Epipactis helleborine and Knautia arvensis*) which showed hump-backed distributions (Electronic Appendix 1).

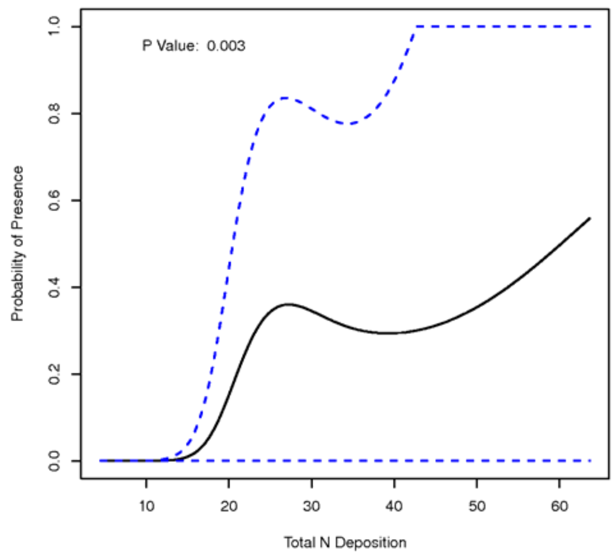


Figure 3.1.28. Spatial change in the probability of presence of *Lathyrus nissolia* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

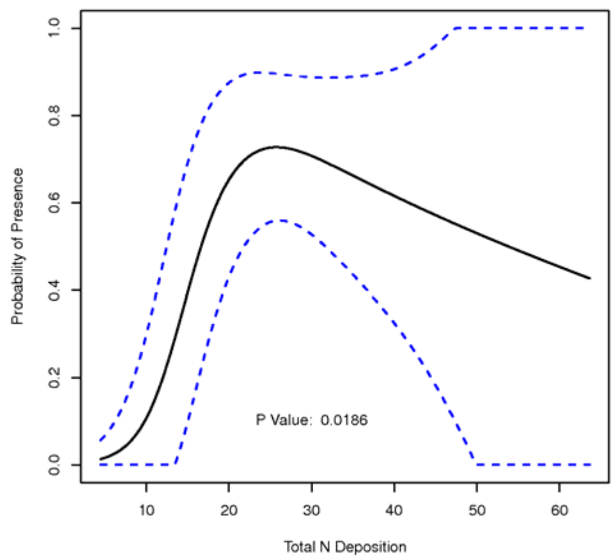


Figure 3.1.29. Spatial change in the probability of presence of *Stachys officinalis* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

For upland calcareous grassland 35 species were examined but there were only sufficient data for analysis of nine of these species. Two species showed significant relationships with N deposition. *Alchemilla xanthochlora* showed a significant increase with N deposition (Figure 3.1.30) whereas *Melica nutans* showed a generally declining probability of presence with increasing N deposition (Figure 3.1.31). The slight decrease at low levels of deposition is due to the wide variation in the data at this point.

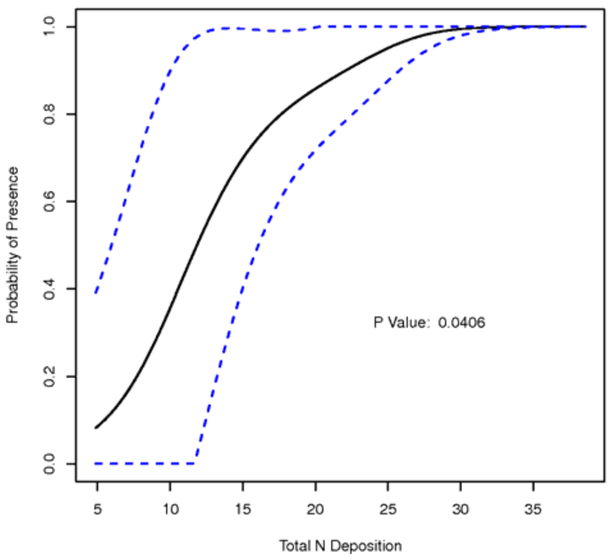


Figure 3.1.30. Spatial change in the probability of presence of *Alchemilla xanthochlora* in upland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

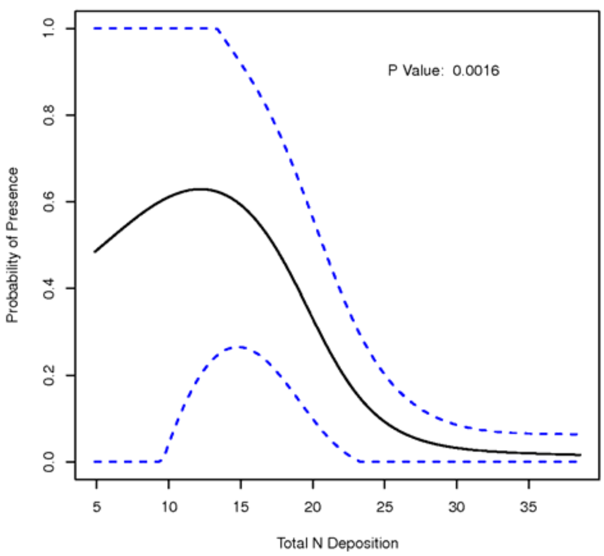


Figure 3.1.31. Spatial change in the probability of presence of *Melica nutans* in upland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

c Bog

Only one of the seven potential lowland bog species in the dataset had sufficient data for analysis (Appendix 1). This was *Drosera intermedia* which did not show a significant relationship with N deposition (p=0.53).

In upland bog there were sufficient data for analysis of five out of the six possible species (Appendix 1) but none of the species showed significant relationships with N deposition.

d Heathland

Of 19 lowland heathland species in the dataset there were sufficient data for analysis of four species. Only two species showed a significant relationship with N deposition. *Platanthera bifolia* had a positive relationship with N deposition, with probability of presence increasing steadily as N deposition increased (Figure 3.1.32). *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} (Figure 3.1.33).

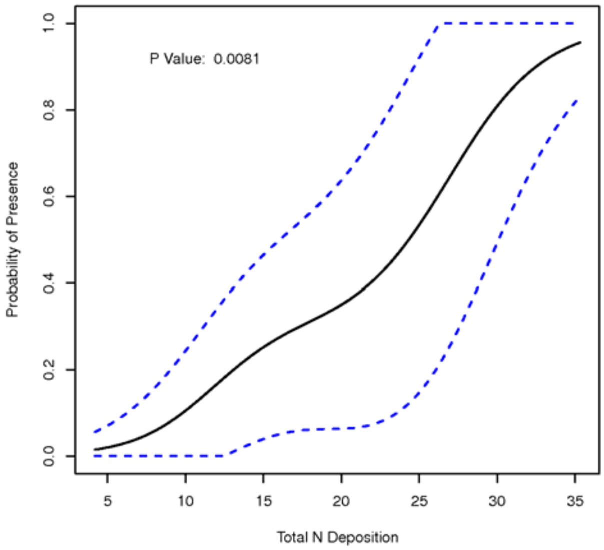


Figure 3.1.32. Spatial change in the probability of presence of *Platanthera bifolia* in lowland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

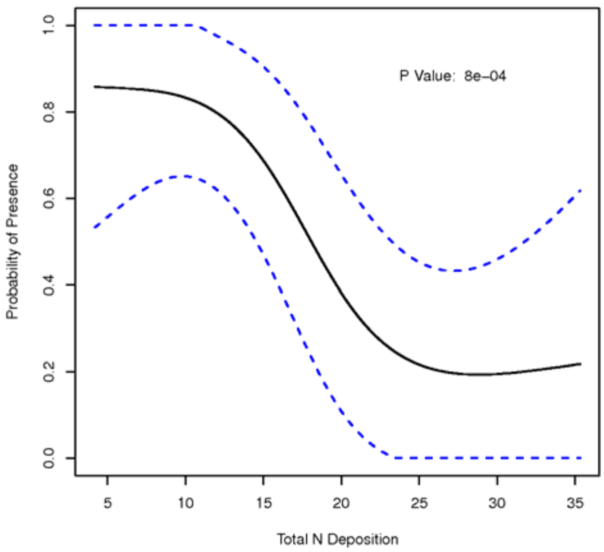


Figure 3.1.33. Spatial change in the probability of *Viola canina* presence of in lowland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

In upland heathland it was possible to analyse ten of 15 potential species (Appendix 2). Two species showed significant relationships with N deposition. *Arctostaphylos uva-ursi* had negative relationships with N deposition declining in probability of presence up to

15 kg N ha^{-1} yr^{-1} and then remaining at very low levels (Figure 3.1.34). *Trientalis europaea* showed a hump-backed distribution peaking at approximately 15 kg N ha^{-1} yr^{-1}.

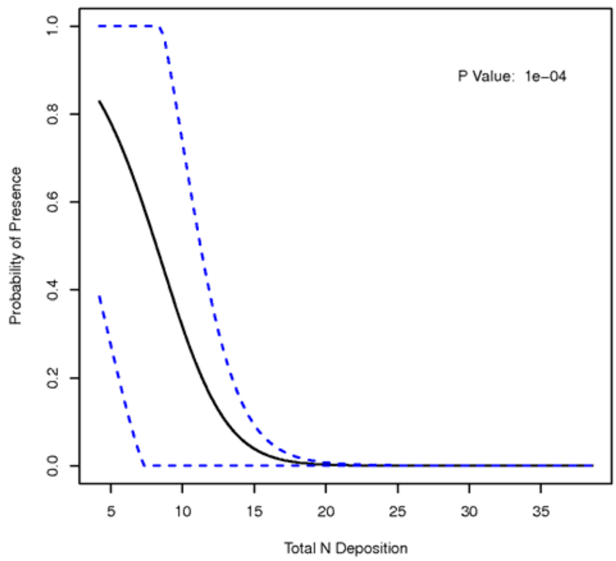


Figure 3.1.34. Spatial change in the probability of presence of *Arctostaphylos uva-ursi* in upland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

ii Temporal analysis of individual species

The need for sufficient data in both the (1930 to 1969 and 1987 to 1999) data collection periods means that there were some different species analysed for change than were analysed for probability of presence in the later data collection period. Species for which there were sufficient data for analysis are listed in Appendix 1.

a Acid grassland

For lowland acid grassland 43 species were examined (Appendix 1). Of these species, eight showed a significant relationship with N deposition. A number of the changes were of a small magnitude (see Electronic Appendix 1). Although these gave a statistically significant response to N deposition this indicates that the change in the probability of presence/absence is very small. For many species this is a consequence of the majority of the observations from the hectads remaining constant, while only a small proportion of the hectads change. This means that species which have a restricted distribution are more likely to show a change than those that are widespread.

There were a number of species that did show changes of a sufficiently large magnitude to be of interest; six species showed a negative relationship with N deposition. This means that they either increased less or decreased more in their probability of presence at high deposition than they did at low deposition (based on current deposition). These species were: *Cerastium semidecandum, Myosotis ramosissima, Ornithopus perpusillus, Senecio sylvaticus, Trifolium arvense* and *Trifolium micranthum*. Two of these species, *Ornithopus perpusillus,* and *Trifolium arvense* showed particularly clear relationships (Figures 3.1.35 to 3.1.36, other species are presented in Electronic Appendix 1). No species showed positive changes with N deposition. None of the three species examined for upland acid grassland (Appendix 1) showed a significant relationship with N deposition.

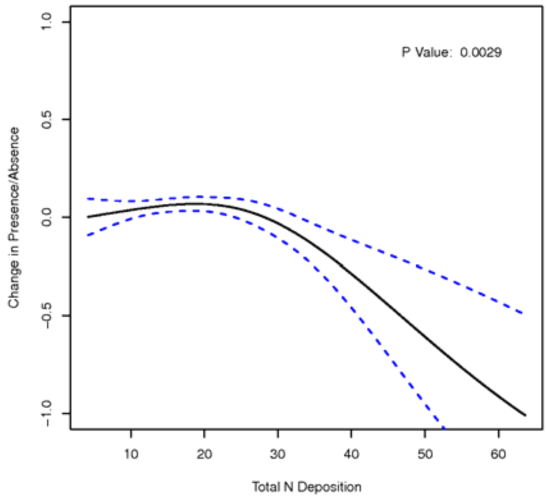


Figure 3.1.35. Temporal change in the probability of presence of *Ornithopus perpusillus* between survey periods (1930-1969, and 1987-1999) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in lowland acid grassland. Data from Vascular Plant Database.

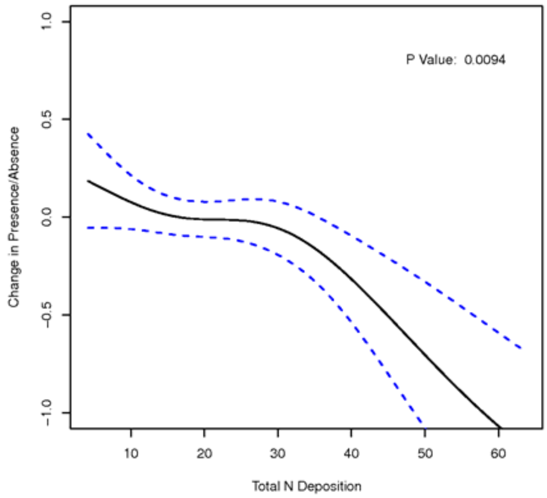


Figure 3.1.36. Temporal change in the probability of presence of *Trifolium arvense* between survey periods (1930-1969, and 1987-1999) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in lowland acid grassland. Data from Vascular Plant Database.

b Calcareous grassland

For lowland calcareous grassland 82 species were analysed (Appendix 1). Six species showed significant relationships with N deposition: *Anacamptis pyramidalis, Carex spicata, Centaurea scabiosa, Convallaria majalis, Orchis morio* and *Rosa rubiginosa*. Almost all of the species showed changes of a small magnitude (see Appendix 1) with the exception of *Carex spicata*. This species showed a decline this was only at the very highest levels of N deposition (greater than 30 kg N ha^{-1} yr^{-1}) so this may not be a real effect.

Thirty-two species were examined for upland calcareous grassland with four species showing significant relationships with N deposition (Appendix 1). All of these were of a small magnitude or were not clear.

c Bog

Five species were examined for lowland bog (Appendix 1) but none showed significant changes in their probability of presence in relation to recent N deposition. In upland bog only one species of the six examined showed a significant relationship. *Carex limosa* changed from a positive change in presence at low deposition (i.e. an increase) to a negative change (i.e. a decrease) at high deposition (Figure 3.1.37).

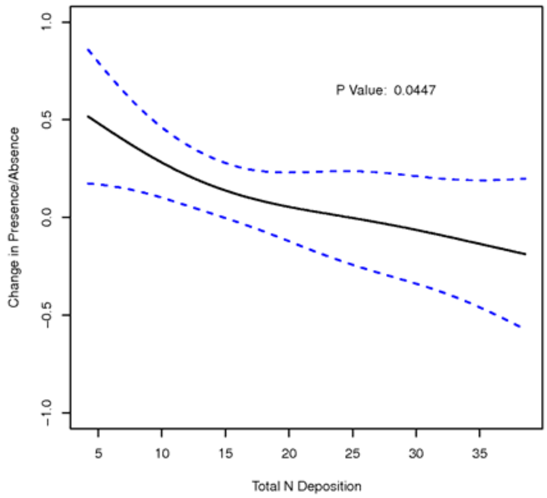


Figure 3.1.37. Temporal change in the probability of presence of *Carex limosa* between survey periods (1930-1969, and 1987-1999) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in lowland acid grassland. Data from Vascular Plant Database.

d Heathland

Eighteen species were examined in lowland heathland but none of the species with sufficient data showed significant relationships with N deposition relationship with N deposition (Appendix 1).

Sixteen species were analysed for upland heathland (Appendix 1) with seven species showing significant relationships with N deposition. However, for the majority of these changes were of a very small magnitude.

3.2 Botanical Society of the British Isles (BSBI) Local Change Survey

Appendix 2 provides a list of the species investigated for the BSBI Local Change survey and Electronic Appendix 2 gives the full set of significant results for individual species. Two types of analysis have been conducted using this data, spatial and temporal analysis. The data have been analysed for Ellenberg scores (spatial and temporal), plant height (spatial), SLA (spatial) and the probability of presence of individual species (spatial and temporal). Temporal analysis was conducted between the two BSBI Local Change surveys in 1987-88 and 2003-04.

3.2.1 Nitrogen deposition

The number of tetrads for each habitat is given in Table 3.2.1. Ranges of deposition for each habitat for which data were analysed are given in Figure 3.1.1.

Table 3.2.1. Number of tetrads for each habitat.

Habitat	Lowland	Upland
Acid grassland	164	158
Calcareous grassland	377	209
Heathland	43	231
Bog	1	59

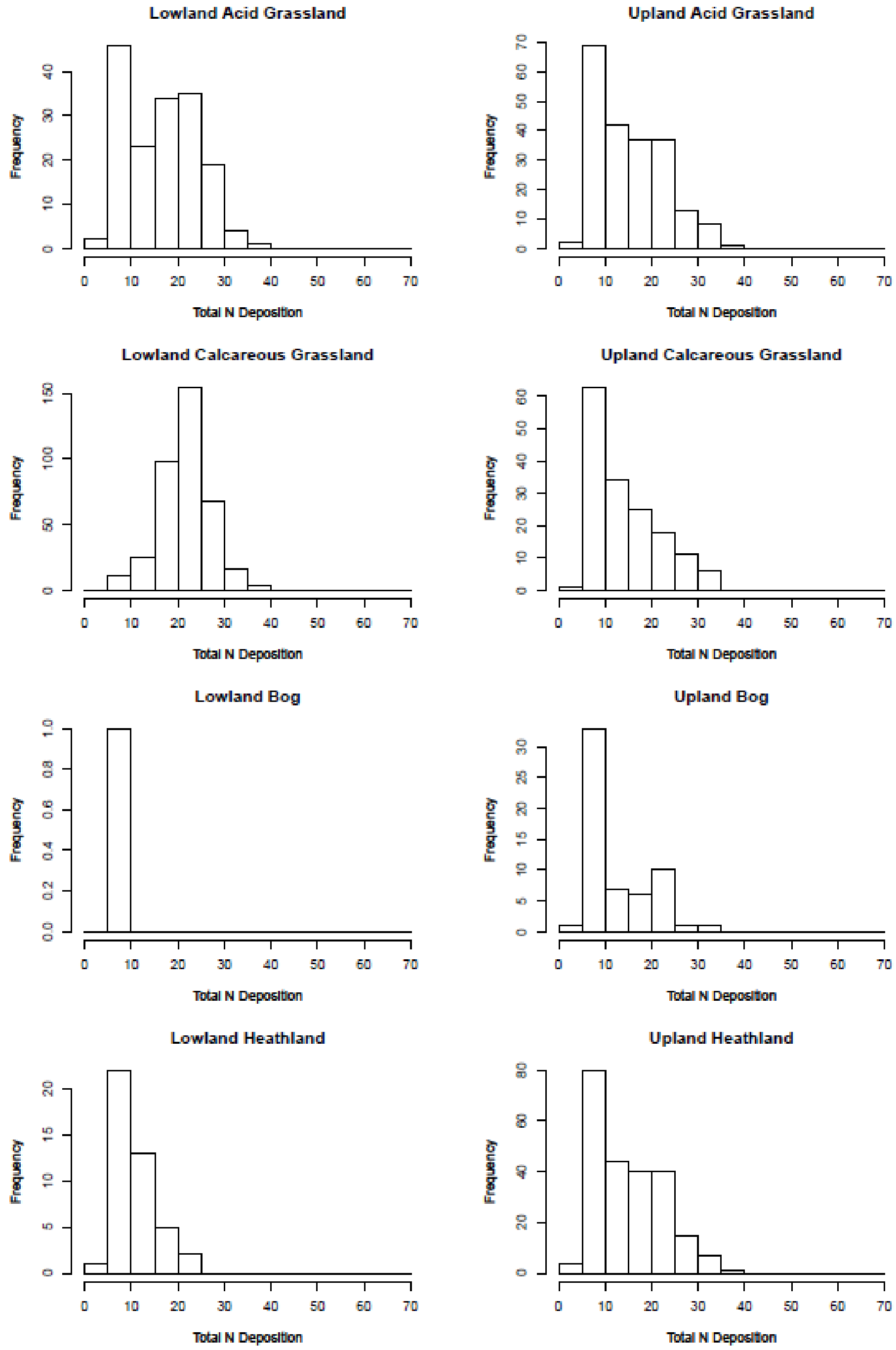


Figure 3.2.1. Frequency histograms of N deposition (kg N ha^{-1} yr^{-1}) for each of the habitats for which data were analysed.

3.2.2 Ellenberg N

i Acid grassland

Average Ellenberg N showed some clear spatial trends. For lowland acid grassland Ellenberg N showed a clear linear increase with increasing N deposition (Figure 3.2.2). For upland acid grassland, although there was a trend for increasing Ellenberg N at the highest levels of deposition, this result was not significant (p=0.42). There were insufficient data for temporal analysis of upland acid grassland for this dataset but lowland acid grassland showed a significant negative relationship between change in Ellenberg N and N deposition (Figure 3.2.3).

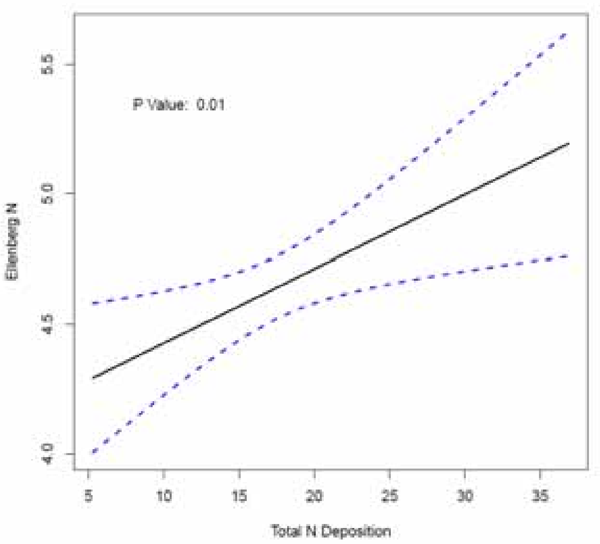


Figure 3.2.2. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from BSBI Local Change Survey.

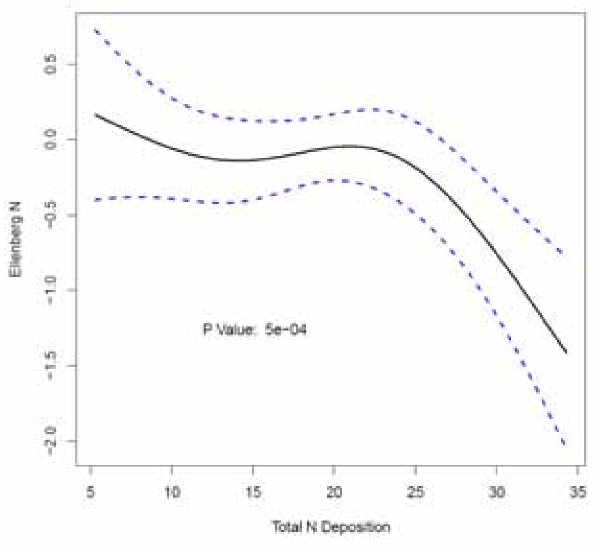


Figure 3.2.3. Temporal change in the mean Ellenberg N score between survey periods (1987-1988, and 2003-2004) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in lowland acid grassland. Data from BSBI Local Change Survey.

ii Calcareous grassland

For the spatial analysis of upland calcareous grassland there was no significant relationship between N deposition and mean Ellenberg N score (p=0.72) but lowland calcareous grassland showed a significant increase in mean Ellenberg N with increasing N deposition. Unlike acid grassland this relationship is not linear (Figure 3.2.4). Temporal analysis of lowland calcareous grassland showed no significant relationship between change in Ellenberg N between the two surveys (p=0.31) but temporal analysis of upland calcareous grassland showed a negative change in Ellenberg N over the survey period at low deposition, moving to a positive change in Ellenberg N over the survey period at high deposition (Figure 3.2.5).

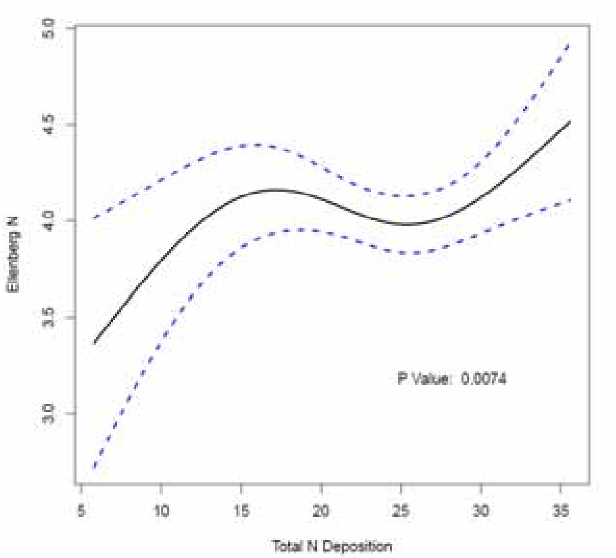


Figure 3.2.4. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland calcareous grassland. Data from BSBI Local Change Survey.

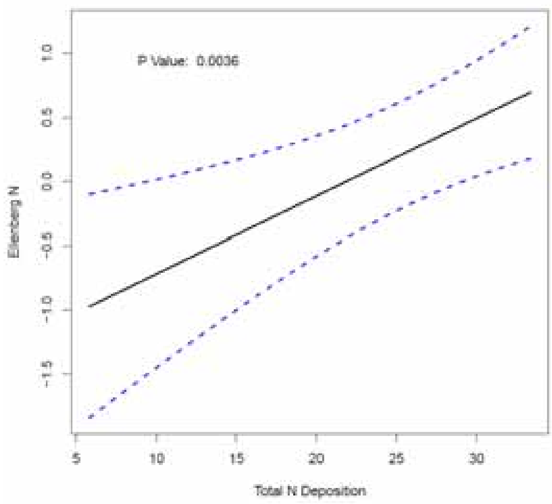


Figure 3.2.5. Temporal change in the mean Ellenberg N score between survey periods (1987-1988, and 2003-2004) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in upland calcareous grassland. Data from BSBI Local Change Survey.

iii Bog

For bog there were only sufficient data for analysis for spatial change in upland bog; here there was no significant response in mean Ellenberg N (p=0.10).

iv Heathland

Heathland also showed mixed results between upland and lowland communities with no significant response for the spatial analysis of upland heathland (p=0.98) but a clear increase in Ellenberg N with increasing deposition for lowland heathland (Figure 3.2.6). There were insufficient data to examine temporal change in upland heathland Ellenberg N but lowland heathland showed a very small increase in Ellenberg N up to 17 kg N ha^{-1} yr^{-1} then a reduction in Ellenberg N at high levels of N deposition (Figure 3.2.7).

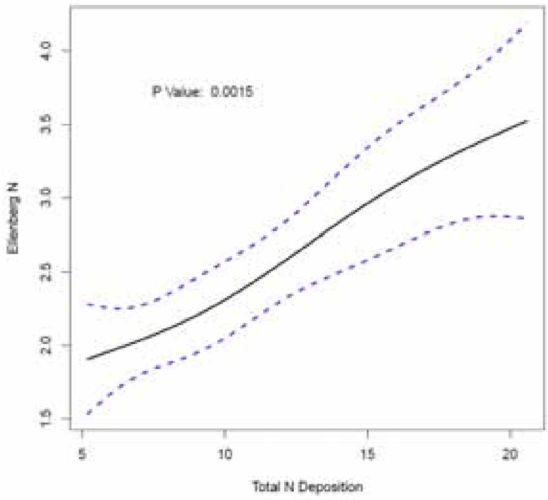


Figure 3.2.6. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland heathland. Data from BSBI Local Change Survey.

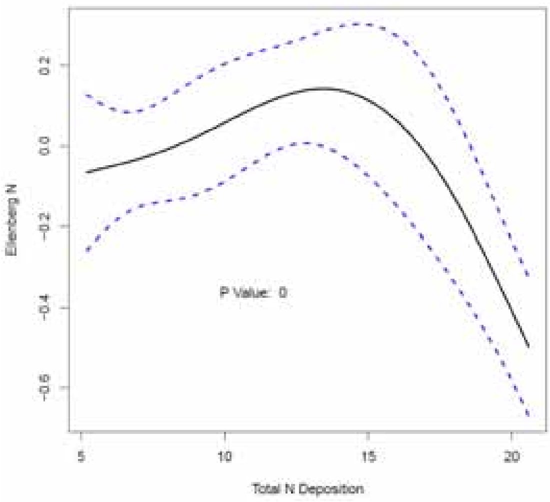


Figure 3.2.7. Temporal change in the mean Ellenberg N score between survey periods (1987-1988, and 2003-2004) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in lowland heathland. Data from BSBI Local Change Survey.

3.2.3 Ellenberg R

i Acid grassland

In acid grassland, spatial analysis of Ellenberg R scores showed no significant results (lowland p=0.21, upland p=0.30). The same was true of temporal analysis (lowland p=0.56, upland p=0.70).

ii Calcareous grassland

Calcareous grassland also showed no significant results in the spatial analysis (lowland p=0.39, upland p=0.92). Temporal analysis showed reductions between the survey periods in Ellenberg R for upland calcareous grassland across the deposition gradient but the magnitude of these reductions were much smaller where N deposition was higher (Figure 3.2.8). In lowland calcareous grassland there were small reductions in mean Ellenberg R score at low deposition increasing to small increases at high deposition (Figure 3.2.9).

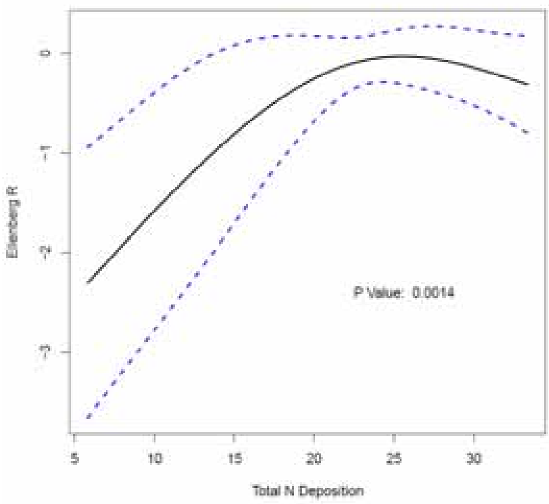


Figure 3.2.8. Temporal change in the mean Ellenberg R score between survey periods (1987-1988, and 2003-2004) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in upland calcareous grassland. Data from BSBI Local Change Survey.

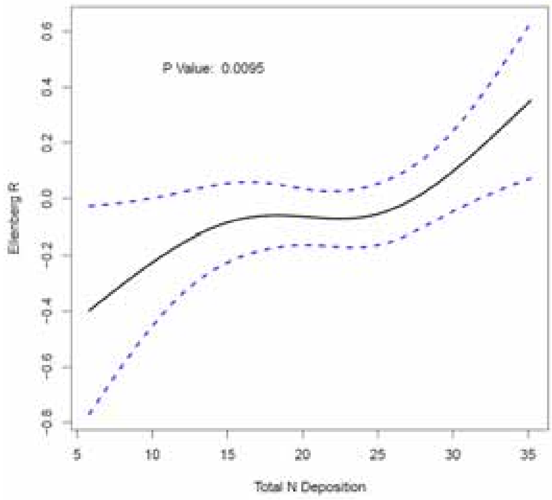


Figure 3.2.9. Temporal change in the mean Ellenberg R score between survey periods (1987-1988, and 2003-2004) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in lowland calcareous grassland. Data from BSBI Local Change Survey.

iii Heathland and bog

There were insufficient data for spatial or temporal analysis of lowland bog but upland bog showed no significant relationship between Ellenberg R and N deposition in the spatial analysis (p=0.10). Temporal analysis showed an increase in Ellenberg R at low deposition but a reduction in Ellenberg R at high deposition giving an overall negative trend with increasing N deposition (Figure 3.2.10).

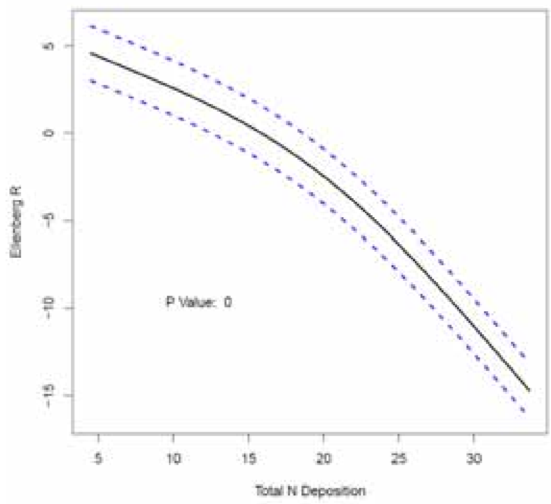


Figure 3.2.10. Temporal change in the mean Ellenberg R score between survey periods (1987-1988, and 2003-2004) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in upland bog. Data from BSBI Local Change Survey.

There was no significant relationship between N deposition and Ellenberg R for upland heath (p=0.92) in spatial analysis but lowland heath showed a decline in Ellenberg R above approximately 14 kg N ha^{-1} yr^{-1} indicating acidification (Figure 3.2.11). Temporal analysis showed no significant relationships between change in Ellenberg R and N deposition for lowland heathland but upland heathland showed both increases and decreases although there is high variability in the data at higher levels of deposition. Although this relationship is statistically significant it may not be ecologically significant because the changes are of a very small magnitude (Figure 3.2.12).

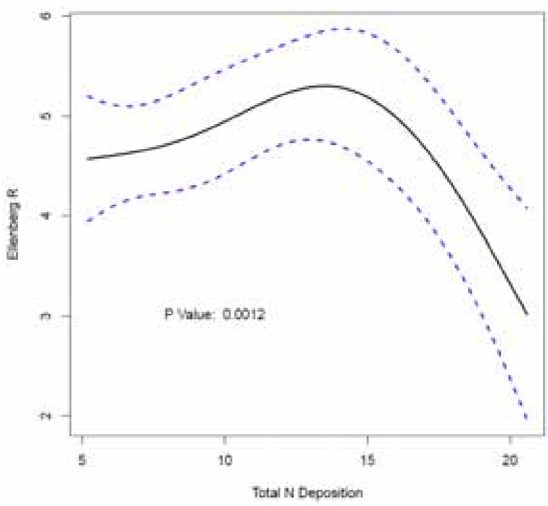


Figure 3.2.11. Spatial analysis of mean Ellenberg R score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland heathland. Data from BSBI Local Change Survey.

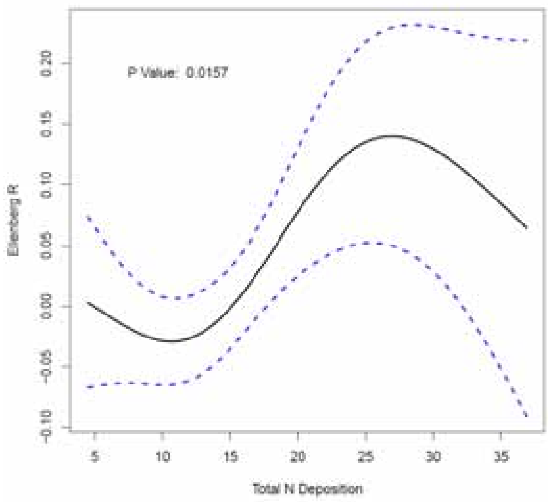


Figure 3.2.12. Temporal change in the mean Ellenberg R score between survey periods (1987-1988, and 2003-2004) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in upland heathland. Data from BSBI Local Change Survey.

3.2.4 Plant canopy height

Canopy height was examined spatially for each of the four habitats. Neither upland nor lowland acid grassland showed a significant relationship between mean plant height and N deposition (lowland p=0.78, upland p=0.10). Calcareous grassland also failed to show a significant relationship between mean plant height and N deposition (lowland p=0.92, upland p=0.09). There were insufficient data to analyse mean plant height for lowland bog, but as with acid and calcareous grassland, upland bog did not show a significant relationship between plant height and N deposition (p=0.62). Lowland heathland did show a significant relationship between mean plant height and N deposition with a reduction in mean height between 0 and 10 kg N ha^{-1} yr^{-1} (Figure 3.2.13). Upland heathland showed no significant relationship (p=0.23).

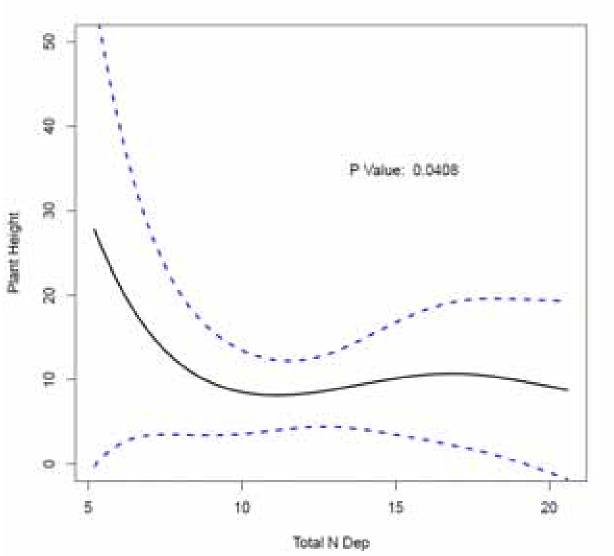


Figure 3.2.13. Spatial analysis of mean plant height against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland heathland. Data from BSBI Local Change Survey.

3.2.5 Specific leaf area

There were sufficient data for analysis of mean SLA and N deposition for upland and lowland acid grassland, calcareous grassland and heathland but none showed significant relationships with N deposition (acid grassland: lowland p=0.83, upland p=0.09; calcareous grassland lowland p=0.21, upland p=0.11; heathland lowland p=0.64, upland p=0.87).

3.2.6 Individual species responses

i Spatial analysis of individual species

ii Acid grassland

For lowland acid grassland there were sufficient data on only one of the possible 33 species in the dataset (Appendix 2), *Senecio sylvaticus*, which did not show a significant relationship with N deposition.

For upland acid grassland one of the four possible species had sufficient data for analysis: *Agrostis vinealis*. *Agrostis vinealis* showed a significant relationship with N deposition with a hump-backed response to N deposition, increasing to 25 kg N ha^{-1} yr^{-1} then declining but with very high variability in the data at high deposition (Figure 3.2.14).

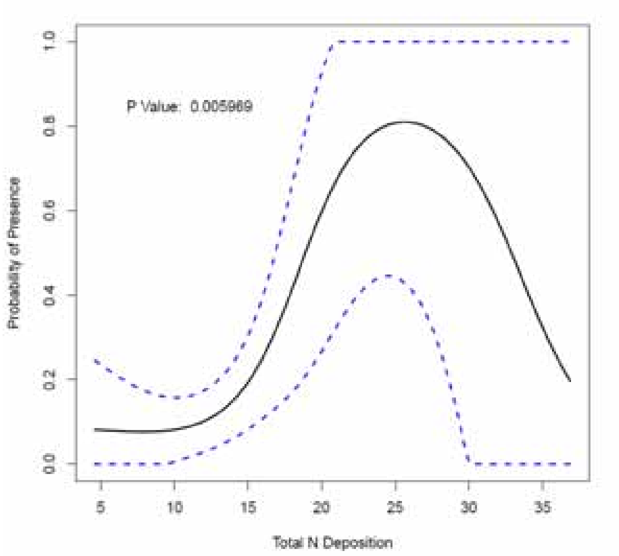


Figure 3.2.14. Spatial change in the probability of presence of *Agrostis vinealis* in upland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BSBI Local Change Survey.

iii Calcareous grassland

Lowland calcareous grasslands are typically very species rich, consequently there were 74 species for potential analysis. Of these there were sufficient data for analysis of 17 species. Eight showed a significant relationship with N deposition: *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 declines for a number of species including *Bromopsis erectus, Campanula glomerata, Carex spicata* and *Ononis repens* (Figures 3.2.15 to 3.2.18).

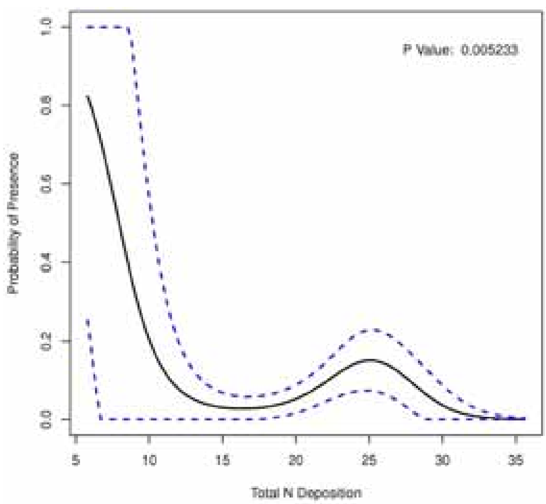


Figure 3.2.15. Spatial change in the probability of presence of *Bromopsis erecta* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BSBI Local Change Survey.

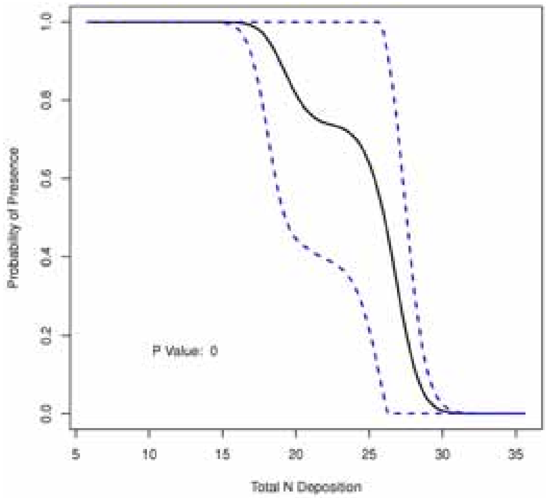


Figure 3.2.16. Spatial change in the probability of presence of *Campanula glomerata* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BSBI Local Change Survey.

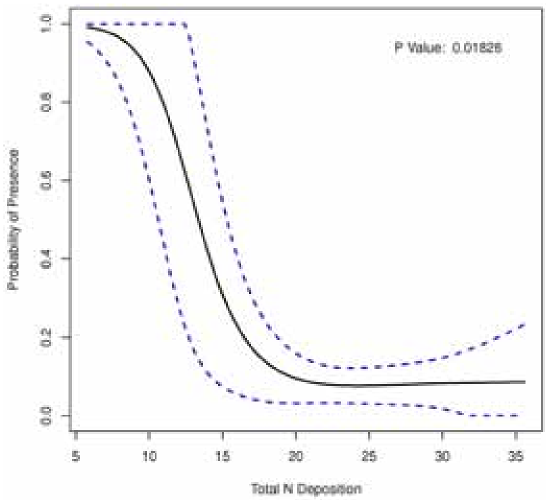


Figure 3.2.17. Spatial change in the probability of presence of *Carex spicata* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BSBI Local Change Survey.

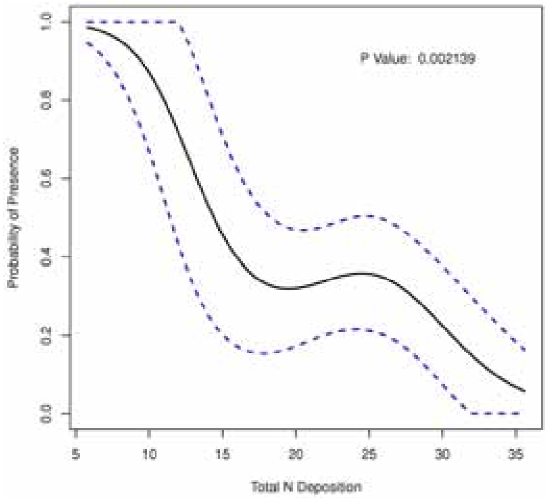


Figure 3.2.18. Spatial change in the probability of presence of *Ononis repens* in lowland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BSBI Local Change Survey.

There were 23 upland calcareous grassland species in the dataset of which 12 had sufficient data for analysis. Of these, 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 (Electronic Appendix 2).

iv Heathland

There were insufficient data to perform analysis on any of the 16 potential lowland heathland species in the dataset. However, for the 13 upland heathland species there were seven species for which analysis could be performed (Appendix 2). Of these, three showed significant relationships with N deposition: *Agrostis vinealis*, *Listera cordata* and *Vaccinium vitis-idaea*. Of these species two showed ecologically interesting results, *Listera cordata* showed a hump-backed response with peak probability of presence at 20 kg N ha^{-1} yr^{-1} (Figure 3.2.19) and *Vaccinium vitis-idaea* showed a clear decline in response to N deposition (Figure 3.2.20).

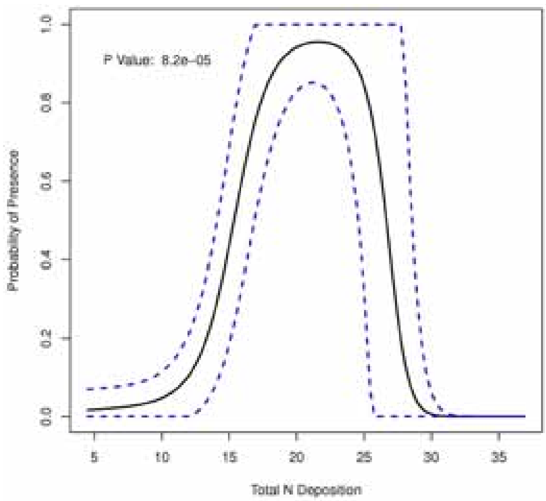


Figure 3.2.19. Spatial change in the probability of presence of *Listera cordata* in upland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BSBI Local Change Survey.

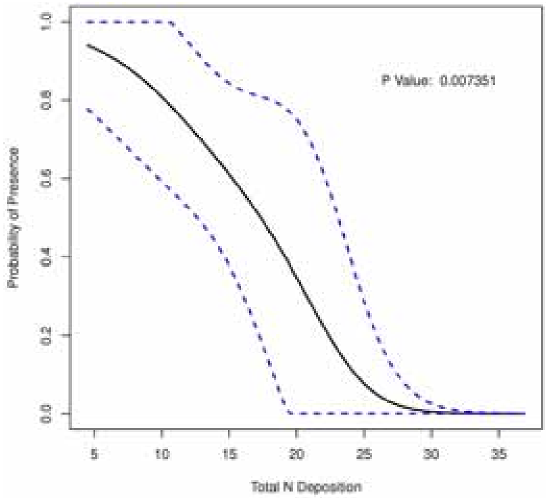


Figure 3.2.20. Spatial change in the probability of presence of *Vaccinium vitis-idaea* in upland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BSBI Local Change Survey.

i Temporal analysis of individual species

The need for sufficient data in both the 1987-88 and 2003-04 surveys means that there are different species analysed for temporal change than were analysed for probability of presence in 2003-04. Species for which there were sufficient data for analysis are listed in Appendix 2.

a Acid grassland

For acid grassland there were no species with either sufficient data or change in their distribution for analysis to be completed.

b Calcareous grassland

For calcareous grassland there were no species with either sufficient data or change in their distribution for analysis to be completed.

c Heathland

In lowland heathland there were sufficient data for analysis of thirteen species (Appendix 2). Of these, two species showed a significant response: *Scleranthus annuus* and *Viola lactea*. *Scilla autumnalis* showed virtually no change whereas *Scleranthus annuus* showed greatest losses at high deposition (Figure 3.2.21). *Viola lactea* showed a very slight increase at high deposition but the magnitude of this change was very small.

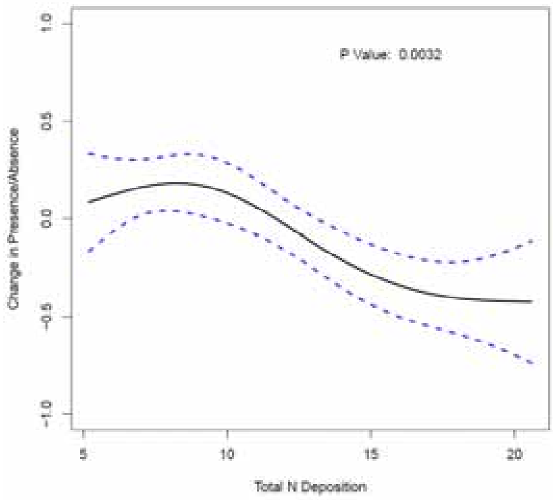


Figure 3.2.21. Temporal change in the probability of presence of *Scleranthus annuus* between survey periods (1987-1988, and 2003-2004) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in lowland heathland. Data from BSBI Local Change Survey.

Upland heathland had 13 species for which there were sufficient data for analysis but only two showed a significant relationship with N deposition: *Lycopodium annotinum* and *Trientalis europaea*. *Lycopodium annotinum* showed a positive change in presence/absence at low deposition (i.e. an increase in range) but a negative change at high deposition (i.e. a reduction in range) resulting in a negative relationship with N deposition although there was little change in the middle deposition values (Figure 3.2.22). *Trientalis europaea* shows a very similar response.

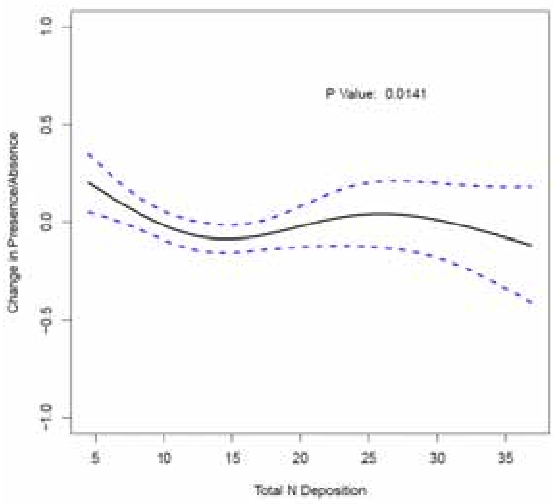


Figure 3.2.22. Temporal change in the probability of presence of *Lycopodium annotinum* between survey periods (1987-1988, and 2003-2004) against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for hectads in lowland heathland. Data from BSBI Local Change Survey.

3.3 British Lichen Society (BLS) Database

Appendix 3 provides a list of lichen species investigated in this report together with their habitat preferences. Preferences for upland and lowland were not known for all lichen species so habitats were not divided for this analysis. Care must be taken when interpreting the data because records were collated over a long period of time (1960 to 2009 inclusive), consequently species that have declined since 1960 will still be recorded as present. Due to the nature of the data only data on individual species occurrences were analysed.

3.3.1 N deposition

The number of hectads for each habitat is given in Table 3.3.1. Ranges of deposition for each habitat for which data were analysed are given in Figure 3.3.1.

Table 3.3.1. Number of hectads for each habitat.

Habitat	Lowland
Acid grassland	1484
Calcareous grassland	1082
Bog	925
Heathland	1704

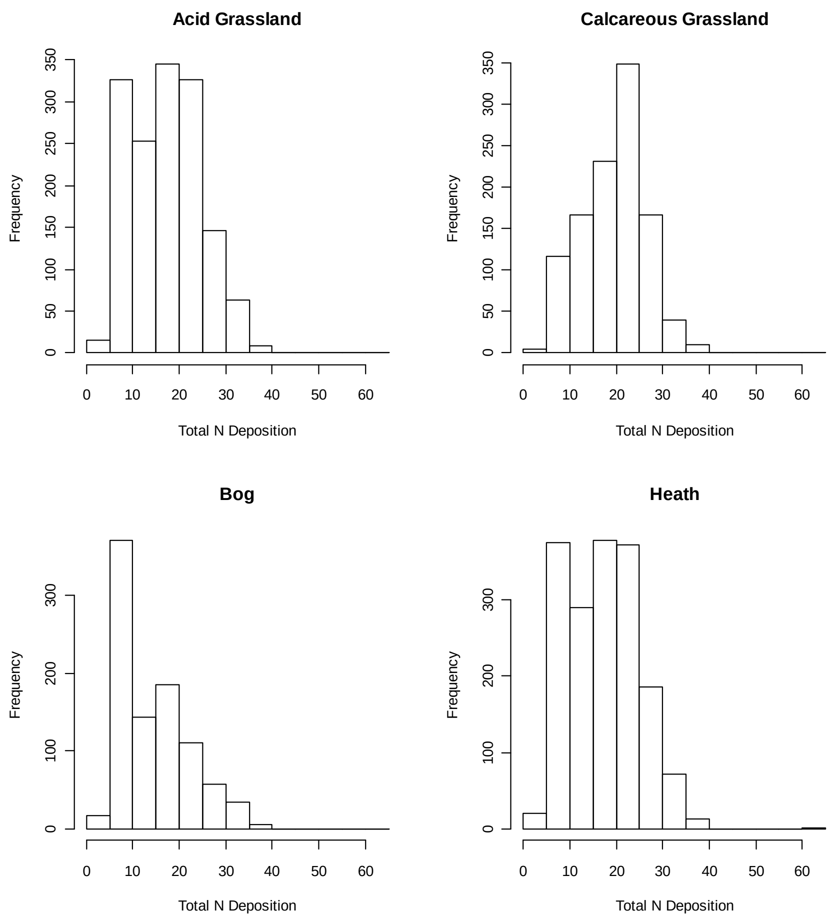


Figure 3.3.1. Frequency histograms of N deposition (kg N ha^{-1} yr^{-1}) for each of the habitats for which data were analysed.

3.3.2 Individual species

i Acid grassland

Of seven acid grassland lichen species that were investigated for their response to N deposition, three showed a significant response to N deposition: *Catapyreneum lachneum, Cetraria aculeata* and *Peltigera didactyla*. Due to the low occurrence of *Catapyreneum lachneum* in acid grassland hectads only the later two species showed an ecologically relevant change in their distribution. The probability of presence of *Cetraria aculeata* is reduced with increasing N deposition reaching very low levels at 20 kg N ha^{-1} yr^{-1} (Figure 3.3.2). *Peltigera didactyla* shows a consistent decline in probability of presence as N deposition increases (Figure 3.3.3). Responses of all three species can be seen in Electronic Appendix 3 and two are shown below.

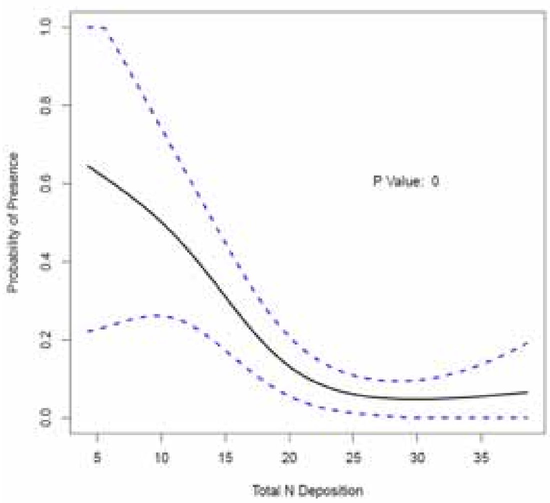


Figure 3.3.2. Spatial change in the probability of presence of *Cetraria aculeata* in acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

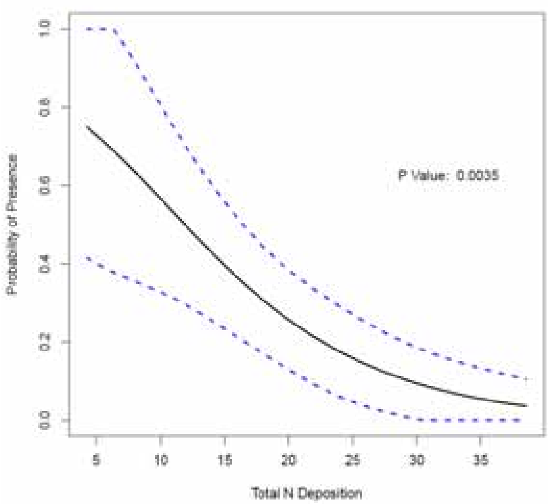


Figure 3.3.3. Spatial change in the probability of presence of *Peltigera didactyla* in acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

ii Calcareous grassland

Sixteen species were examined for calcareous grassland and two showed a significant response to N deposition, *Diploschistes muscorum* and *Cladonia foliacea*. *Cladonia foliacea* showed a reduced probability of occurrence above 20 kg N ha^{-1} yr^{-1} (Figure 3.3.4) and *Diploschistes muscorum* showed a decrease followed by an increase (Electronic Appendix 3). This response does not look realistic and is likely to be due to patchy recording or a different driver influencing the data; variability at both low and high deposition is very high.

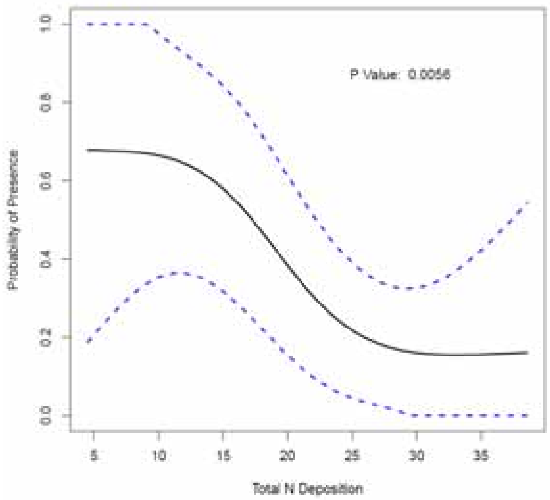


Figure 3.3.4. Spatial change in the probability of presence of *Cladonia foliacea* in calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

iii Bog

Six species were examined for bogs and two of these showed significant relationships with N deposition, *Cladonia arbuscula squarrosa* and *Cladonia portentosa*. *Cladonia arbuscula squarrosa* shows a humpback response to N deposition initially increasing in its probability of occurrence, peaking around 15 kg N ha^{-1} yr^{-1} and then declining (see Electronic Appendix 3). *Cladonia portentosa* shows a reduction in the chance of occurrence between 10 and 25 kg N ha^{-1} yr^{-1} but then shows an increase at the highest deposition levels (Figure 3.3.5). This increase is likely to be an artefact of few records at high deposition as variability in the data is very high.

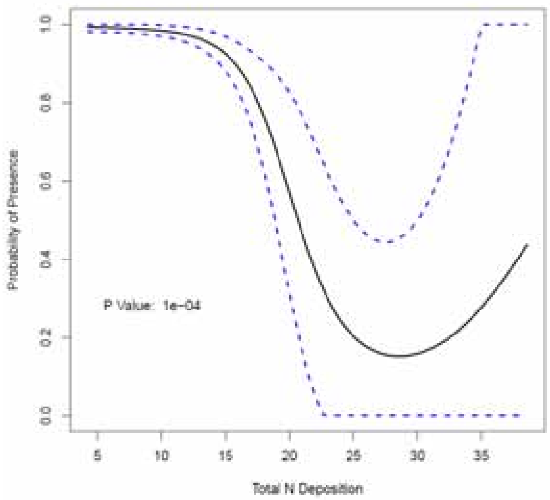


Figure 3.3.5. Spatial change in the probability of presence of *Cladonia portentosa* in bog with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

iv Heathland

In heathland 26 species were investigated and 17 showed a significant relationship with N deposition (*Cetraria aculeata, Cetraria muricata, Cladonia arbuscula squarrosa, Cladonia cervicornis cervicornis, Cladonia cervicornis verticillata, Cladonia floerkeana, Cladonia glauca, Cladonia portentosa, Cladonia strepsilis, Cladonia subulata, Cladonia uncialis biuncialis, Dibaeis baeomyces, Diploschistes muscorum, Lichenomphalia hudsoniana, Lichenomphalia umbellifera, Peltigera hymenina,* and *Placynthiella uliginosa*). Of these, several species showed changes of a small magnitude, U shaped or inconsistent changes (see Appendix 3 and Electronic Appendix 3). *Cetraria aculeata, Cetraria muricata, Cladonia cervicornis cervicornis, Cladonia cervicornis verticillata, Cladonia portentosa, Cladonia subulata, Cladonia uncialis biuncialis,* and *Peltigera hymenina* all showed strong negative responses (Figures 3.3.6 to 3.3.13) although both *Peltigera hymenina* and *Cladonia portentosa* have large errors at the very lowest levels of deposition. *Cladonia glauca*, *Cladonia strepsilis, Dibaeis baeomyces, Lichenomphalia hudsoniana* and *Lichenomphalia umbellifera* all showed negative responses but due to the relative rarity of the species in the analyses, the changes are all of a small magnitude. It is interesting to note that many of the species have reached a very low probability of presence by 20 kg N ha^{-1} yr^{-1}.

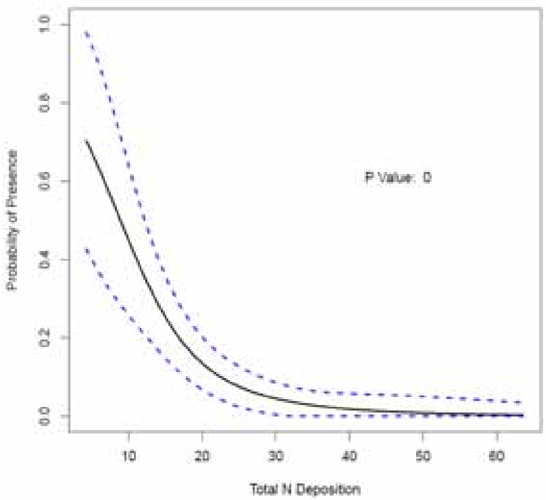


Figure 3.3.6. Spatial change in the probability of presence of *Cetraria aculeata* in heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

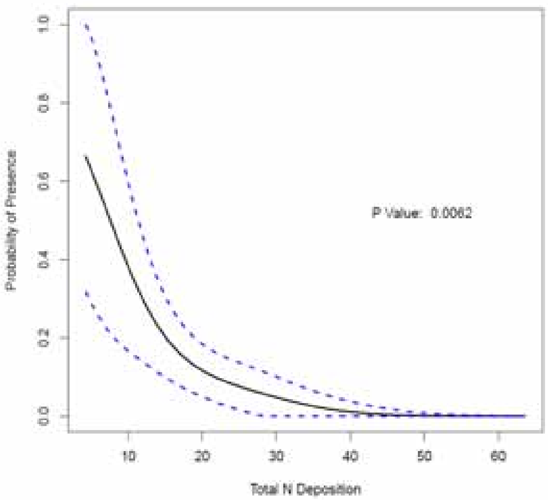


Figure 3.3.7. Spatial change in the probability of presence of *Cetraria muricata* in heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

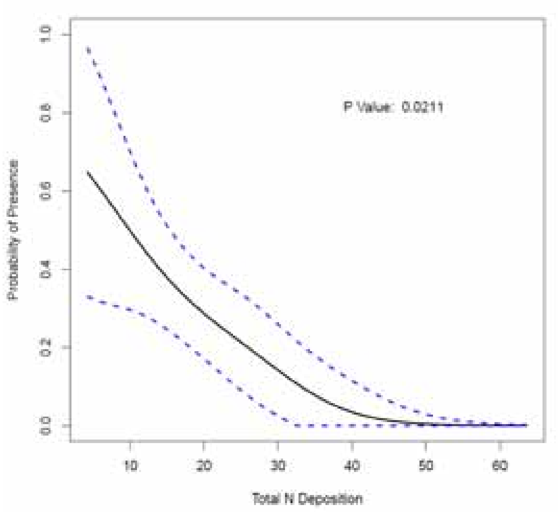


Figure 3.3.8. Spatial change in the probability of presence of *Cladonia cervicornis verticillata* in heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

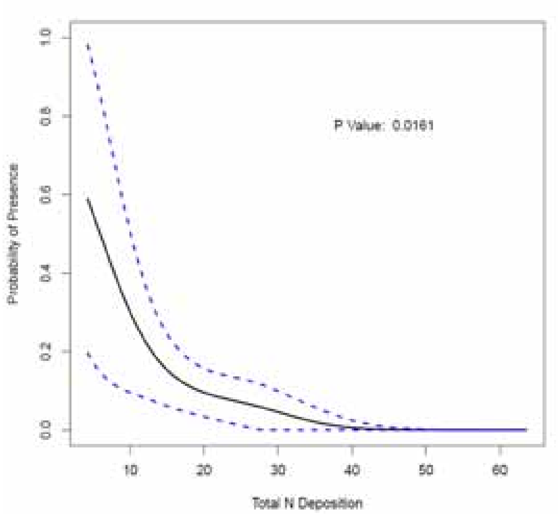


Figure 3.3.9. Spatial change in the probability of presence of *Cladonia cervicornis cervicornis* in heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

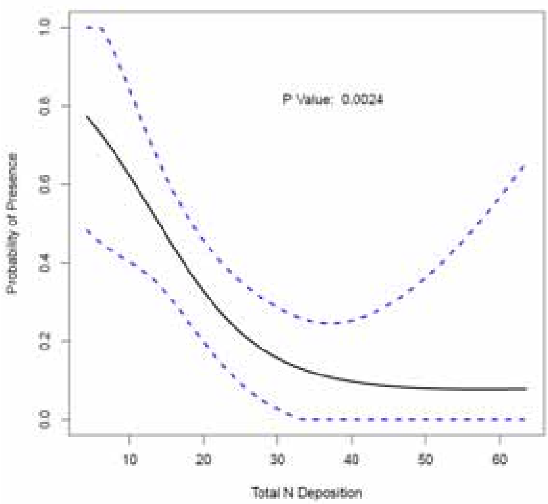


Figure 3.3.10. Spatial change in the probability of presence of *Cladonia portentosa* in heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

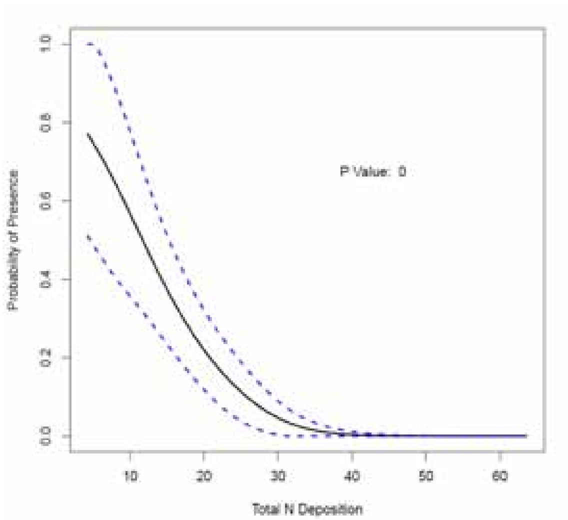


Figure 3.3.11. Spatial change in the probability of presence of *Cladonia subulata* in heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

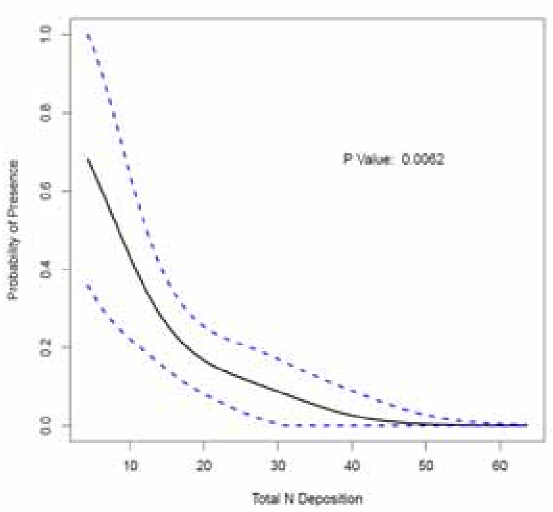


Figure 3.3.12. Spatial change in the probability of presence of *Cladonia uncialis biuncialis* in heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

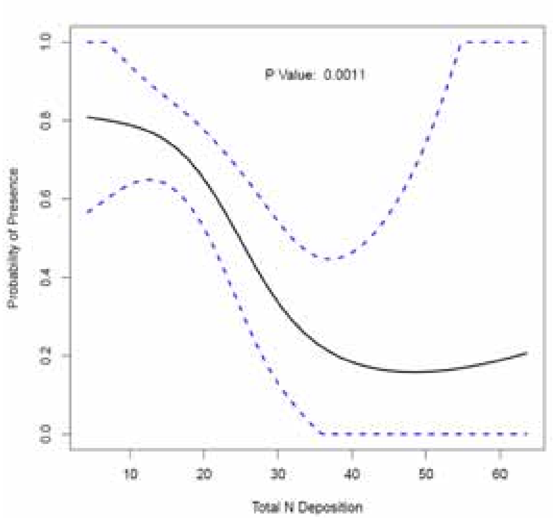


Figure 3.3.13. Spatial change in the probability of presence of *Peltigera hymenina* in heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS Database.

3.4 British Bryological Society Database

Spatial analysis was conducted on the British Bryological Society data (Appendix 4 and Electronic Appendix 4) to investigate changes in Ellenberg scores. Spatial analysis of the relationship between individual species and N deposition was also conducted. Care must be taken in interpreting this data as it spans the period 1960 to 2009 so there may have been changes in the distribution of individual species that have occurred within this time.

3.4.1 N deposition

The number of hectads for each habitat is given in Table 3.4.1. Ranges of deposition for each habitat for which data were analysed are given in Figure 3.4.1.

Table 3.4.1. Number of hectads for each habitat.

Habitat	Upland	Lowland
Acid grassland	1250	1411
Calcareous grassland	840	1608
Bog	723	1469
Heathland	1274	363

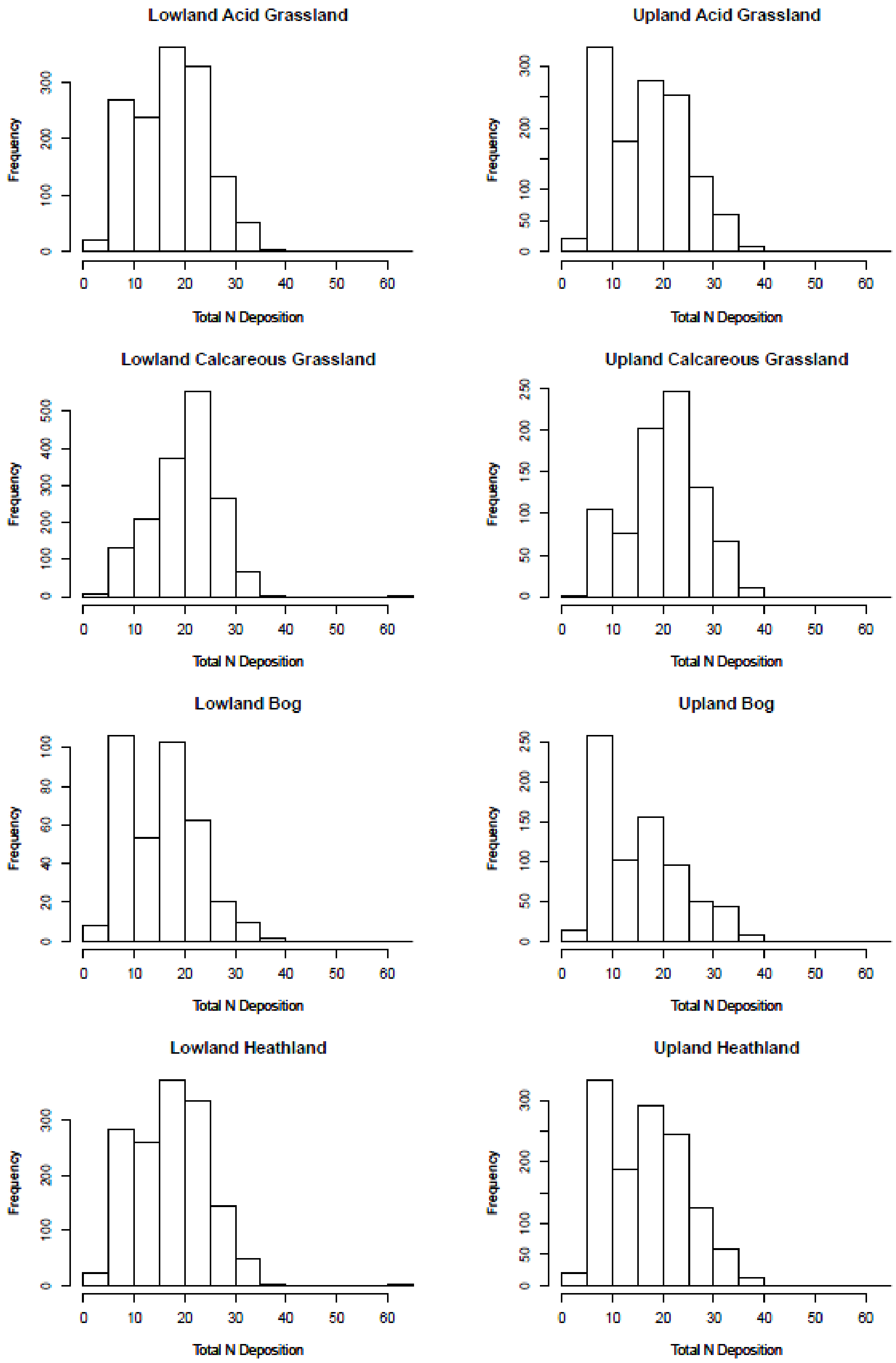


Figure 3.4.1. Frequency histograms of N deposition (kg N ha^{-1} yr^{-1}) for each of the habitats for which data were analysed.

3.4.2 Ellenberg N

i Acid grassland

Lowland acid grassland showed no significant change in mean Ellenberg N score with increasing N deposition (p=0.83) but in upland acid grassland there was a significant increase in Ellenberg N score. In upland acid grassland mean Ellenberg N increased (indicating higher fertility) to approximately 18 kg N ha^{-1} yr^{-1} and then showed little further change (Figure 3.4.1).

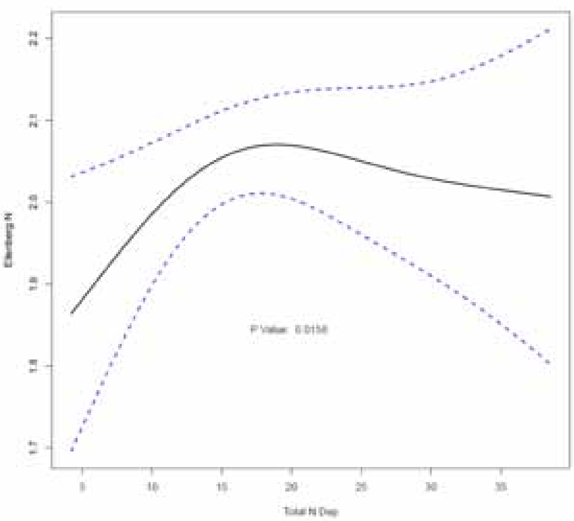


Figure 3.4.1. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland acid grassland. Data from BBS Database.

ii Calcareous grassland

Neither upland nor lowland calcareous grassland showed significant changes in mean Ellenberg N score in relation to N deposition (lowland p=0.09; upland p=0.15).

iii Bog

There were insufficient data for analysis of lowland bog but upland bog showed a significant change in Ellenberg N score with a similar pattern to the acid grassland. Mean Ellenberg N score increased up to approximately 23 kg N ha^{-1} yr^{-1} and then showed little further change (Figure 3.4.2). Although the graph shows a slight decline at high deposition there is also a lot more variability in the data at this point.

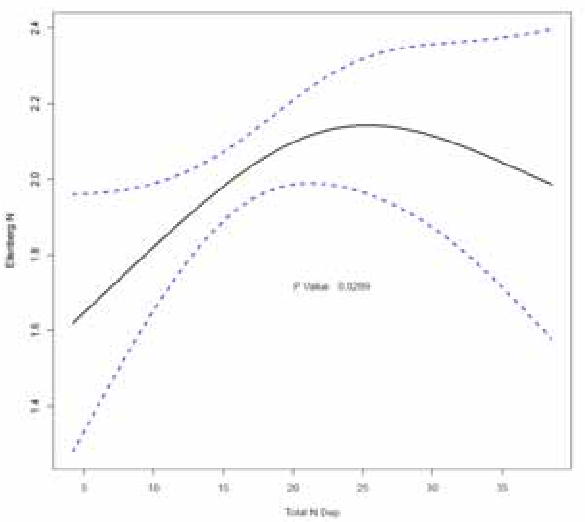


Figure 3.4.2. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland bog. Data from BBS Database.

iv Heathland

As with lowland acid grassland, lowland heathland Ellenberg N was not significantly related to N deposition (p=0.61) but there was a significant relationship for upland heathland where mean Ellenberg N peaks at approximately 15 kg N ha^{-1} yr^{-1} (Figure 3.4.3). Ellenberg N appears to fall after this point but variability in the data set also increases.

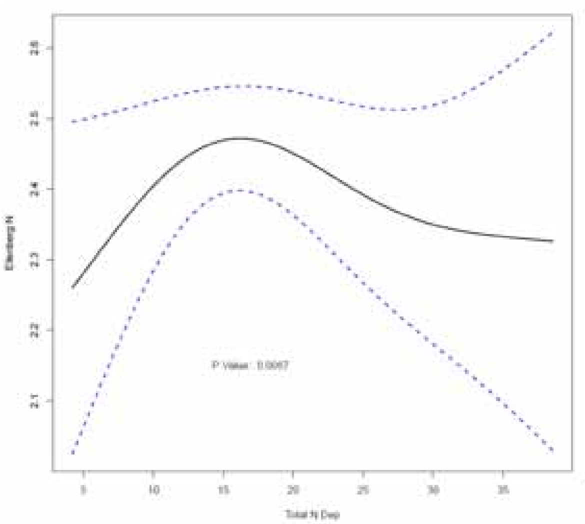


Figure 3.4.3. Spatial analysis of mean Ellenberg N score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland heathland. Data from BBS Database.

3.4.3 Ellenberg R

Only one habitat showed significant changes in Ellenberg R scores. Both upland and lowland acid and calcareous grassland showed no significant relationship between Ellenberg R score and N deposition (acid: lowland p=0.06, upland p=0.14; calcareous: lowland p=0.19, upland p=0.20). There were insufficient data for analysis of lowland bog but upland bog showed a small increase in mean Ellenberg R score with increasing N deposition (Figure 3.4.4). Heathland also showed no significant relationship between mean Ellenberg R score and N deposition (lowland p=0.58; upland p=0.27).

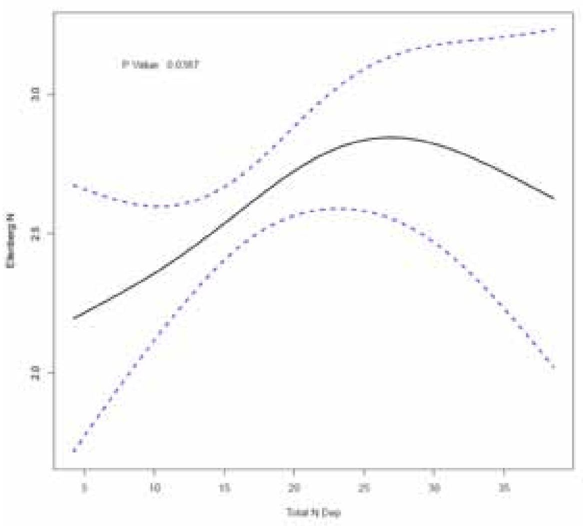


Figure 3.4.4. Spatial analysis of mean Ellenberg R score against total current inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland bog. Data from BBS Database.

3.4.4 Individual species

i Acid grassland

Lowland acid grassland had no species with sufficient levels of presence for analysis.

Forty-six species were analysed for upland acid grassland (Appendix 4) with twelve showing a significant relationship between probability of presence and N deposition. Of these species, three showed negative relationships with N deposition (*Frullania tamarisci*, *Racomitrium lanuginosum* and *Scapania gracilis*) (Figures 3.4.5 to 3.4.7). Declines in probability of presence were particularly apparent for *Frullania tamarisci* and *Scapania gracilis* which declined across the gradient of deposition, whereas *Racomitrium lanuginosum* declined to approximately 18 kg N ha^{-1} yr^{-1} and then increased slightly to a relatively high, probability of presence.

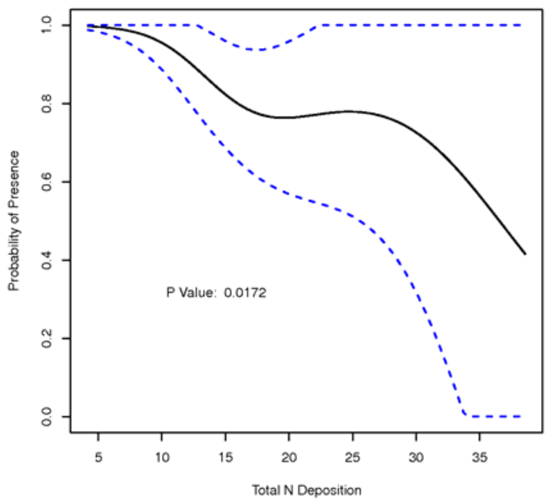


Figure 3.4.5. Spatial change in the probability of presence of *Frullania tamarisci* in upland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

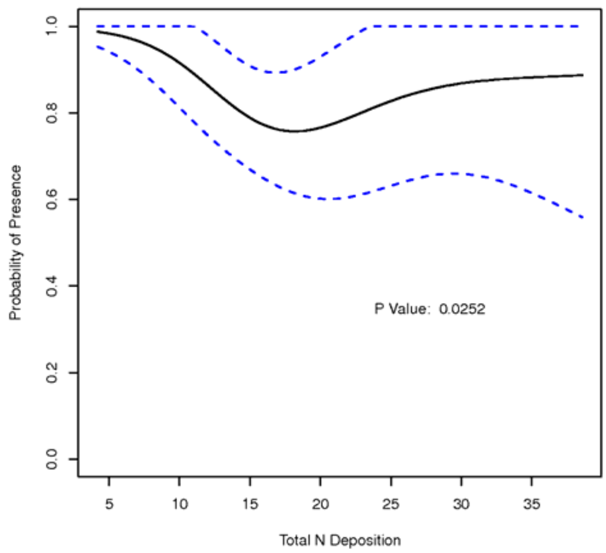


Figure 3.4.6. Spatial change in the probability of presence of *Racomitrium lanuginosum* in upland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

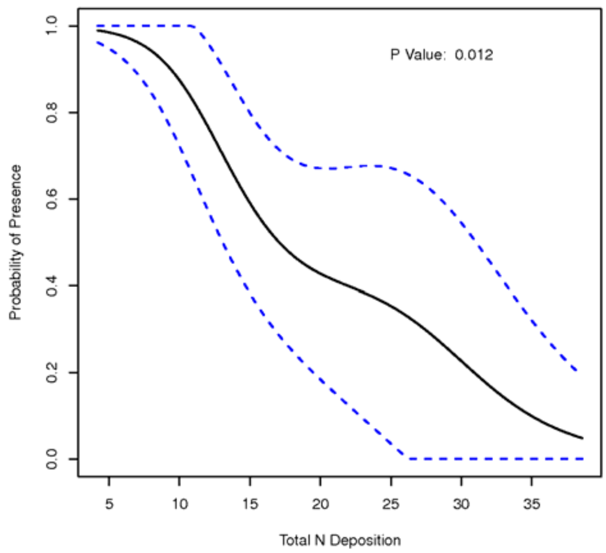


Figure 3.4.7. Spatial change in the probability of presence of *Scapania gracilis* in upland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

Six species showed a positive relationship with N deposition, increasing in their probability of presence as N deposition increased. These species were: *Archidium alternifolium, Gymnocolea inflata, Leptodontium flexifolium, Lophozia ventricosa, Racomitrium ericoides* and *Sanionia uncinata*. *Lophozia ventricosa* showed changes of a small magnitude and *Leptodontium flexifolium* had a large variability in the data at low deposition, but the other four species showed clear increases across the deposition gradient (Figures 3.4.8 to 3.4.11).

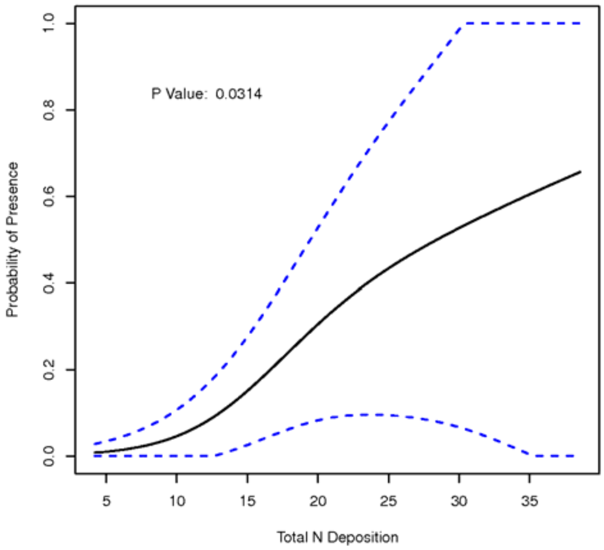


Figure 3.4.8. Spatial change in the probability of presence of *Archidium alternifolium* in upland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

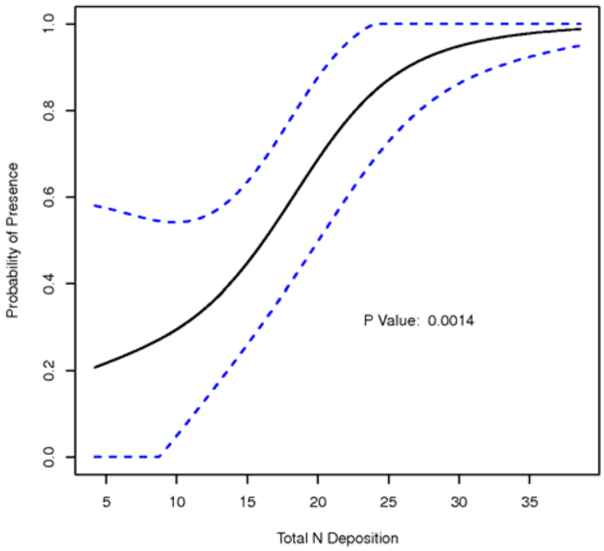


Figure 3.4.9. Spatial change in the probability of presence of *Gymnocolea inflata* in upland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

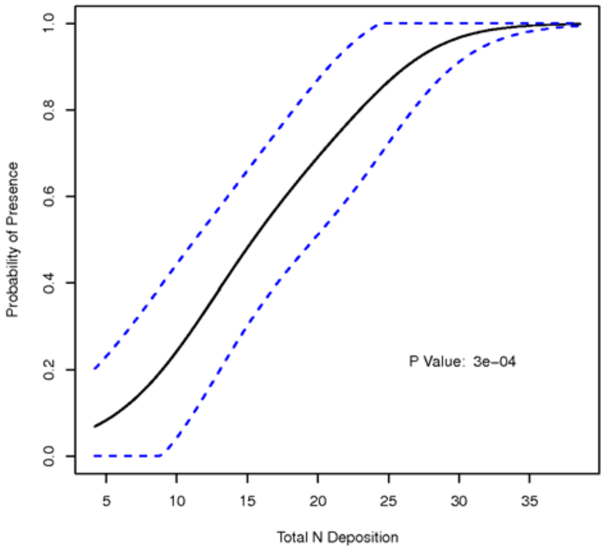


Figure 3.4.10. Spatial change in the probability of presence of *Racomitrium ericoides* in upland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

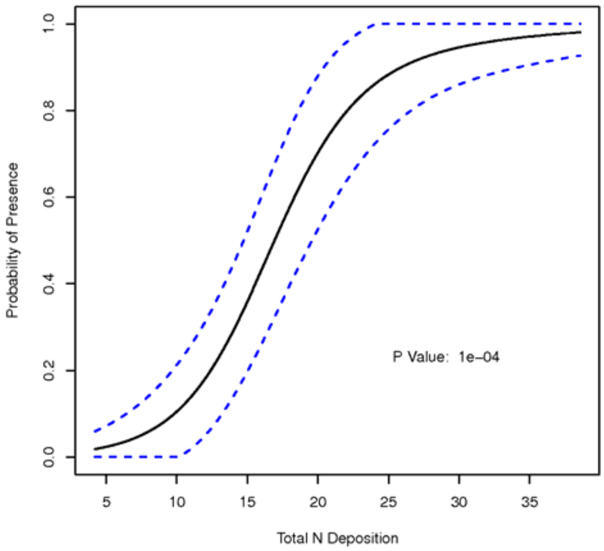


Figure 3.4.11. Spatial change in the probability of presence of *Sanionia uncinata* in upland acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

ii Calcareous grassland

There was no species in the dataset with an appropriate proportion of presences (between 10 and 90%) in lowland calcareous grassland for analysis.

In upland calcareous grassland ten species were tested (Appendix 4). Two species showed a significant relationship between probability of presence and N deposition, *Didymodon vinealis* and *Leiocolea turbinata* (Figures 3.4.12 and 3.4.13). Both of these species showed positive relationships, increasing in their probability of presence with increasing N deposition.

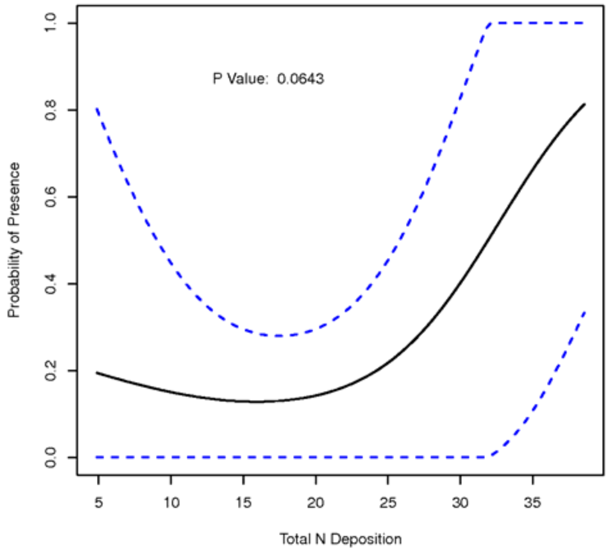


Figure 3.4.12. Spatial change in the probability of presence of *Didymodon vinealis* in upland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

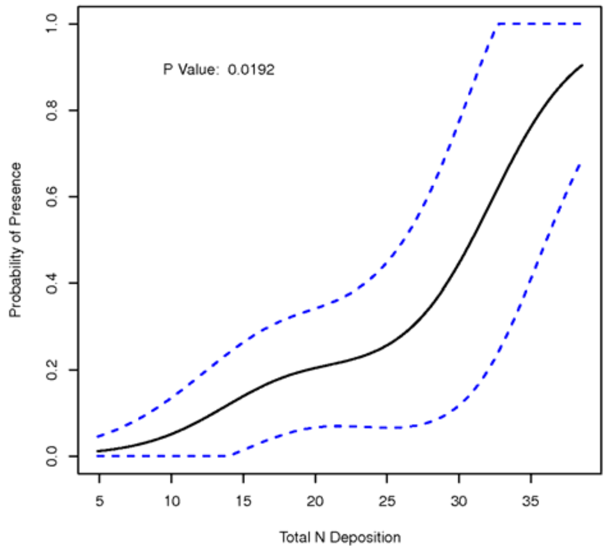


Figure 3.4.13. Spatial change in the probability of presence of *Leiocolea turbinata* in upland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

iii Bog

There was no species in the dataset with an appropriate proportion of presences (between 10 and 90%) in lowland bog for analysis.

Seventy-two species were analysed for upland bog (Appendix 4) but only 17 of these showed significant relationships with N deposition. Four species showed negative relationships with N deposition: *Anastrophyllum minutum, Calypogeia sphagnicola, Odontoschisma denudatum* and *Scapania umbrosa* (Figures 3.4.14 to 3.4.17). All of the species that had negative relationships with N deposition reached very low probabilities of presence by 20 to 25 kg N ha^{-1} yr^{-1}.

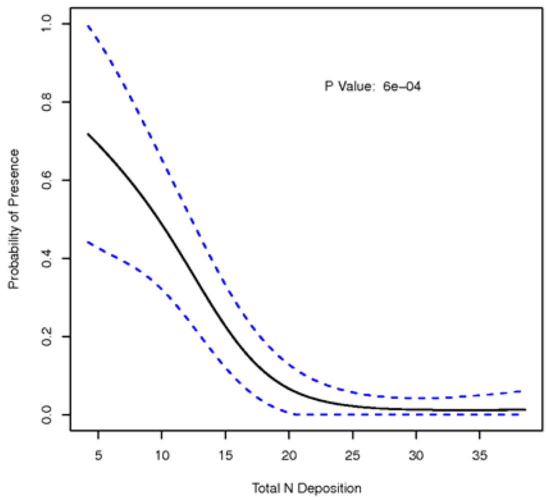


Figure 3.4.14. Spatial change in the probability of presence of *Anastrophyllum minutum* in upland bog with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

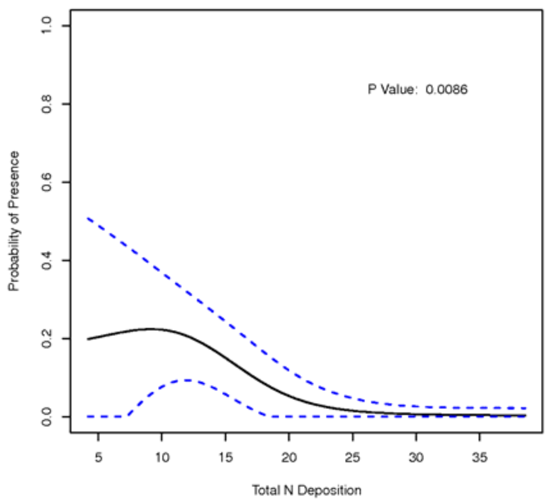


Figure 3.4.15. Spatial change in the probability of presence of *Calypogeia sphagnicola* in upland bog with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

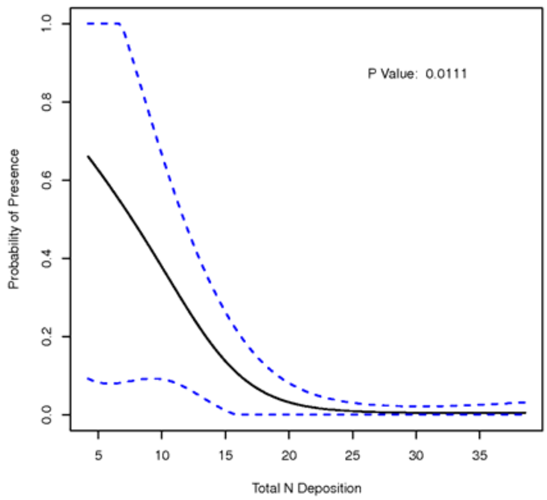


Figure 3.4.16. Spatial change in the probability of presence of *Odontoschisma denudatum* in upland bog with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

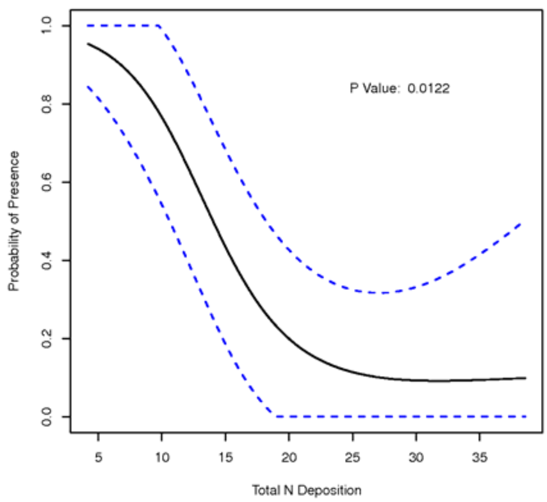


Figure 3.4.17. Spatial change in the probability of presence of *Scapania umbrosa* in upland bog with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

Six species showed positive relationships with N deposition: *Calypogeia neesiana, Dicranum bonjeanii, Gymnocolea inflata, Lophozia incisa, Pleurozia purpurea* and *Warnstorfia fluitans*. The majority of these species showed steady increases across the deposition gradient (see 3.4.18 for example). The very high probability of presence of *Warnstorfia fluitans* at high deposition may be a result of there being few upland bog hectads at high deposition.

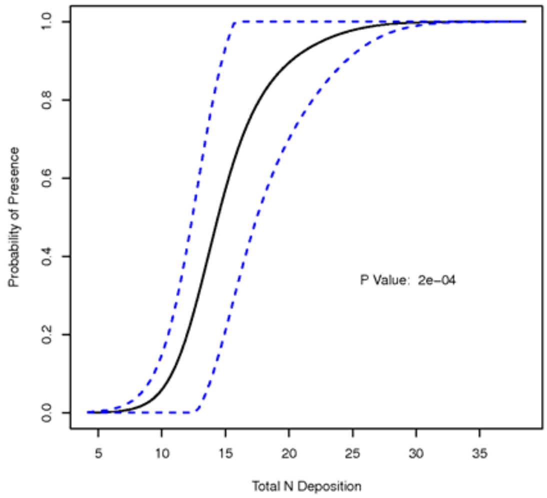


Figure 3.4.18. Spatial change in the probability of presence of *Warnstorfia fluitans* in upland bog with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

iv Heathland

There was no species in the dataset with sufficient presences for analysis in lowland heathland.

For upland heathland 127 species were analysed with 33 showing significant responses to N deposition (Appendix 4). Five species showed a negative response to N deposition (*Anastrophyllum minutum, Fossombronia wondraczekii, Lepidozia pearsonii, Leucobryum glaucum* and *Microlejeunea ulicina*). *Anastrophyllum minutum, Lepidozia pearsonii* and *Microlejeunea ulicina* all decline to low levels at high deposition with *Microlejeunea ulicina* reaching a very low probability of presence at under 20 kg N ha^{-1} yr^{-1} (Figures 3.4.19 to 3.4.23).

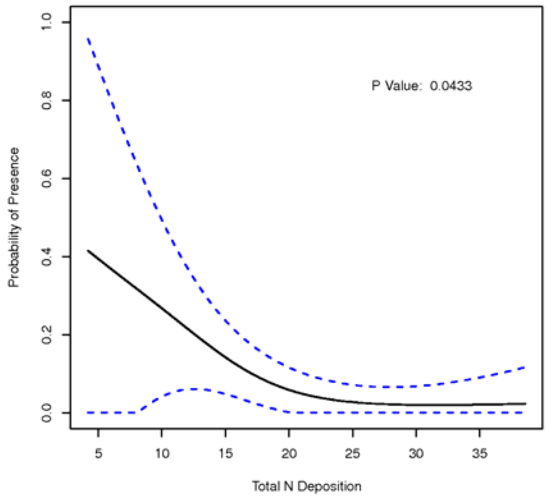


Figure 3.4.19. Spatial change in the probability of presence of *Anastrophyllum minutum* in upland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

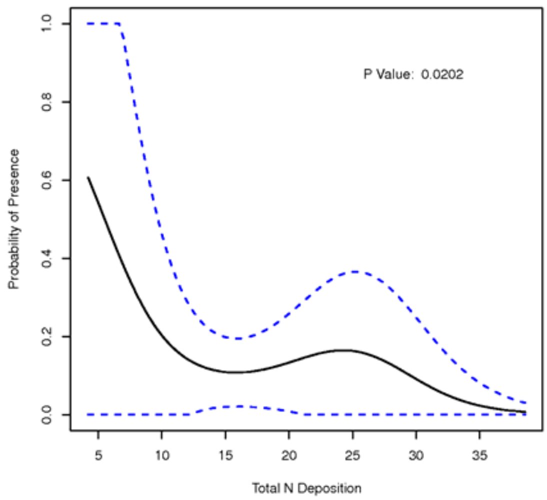


Figure 3.4.20. Spatial change in the probability of presence of *Fossombronia wondraczekii* in upland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

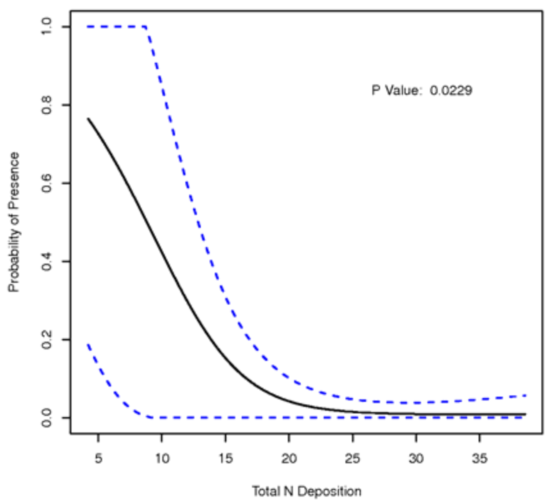


Figure 3.4.21. Spatial change in the probability of presence of *Lepidozia pearsonii* in upland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

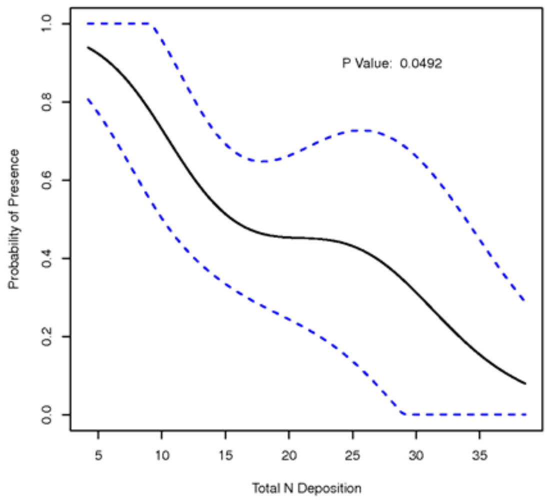


Figure 3.4.22. Spatial change in the probability of presence of *Leucobryum glaucum* in upland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

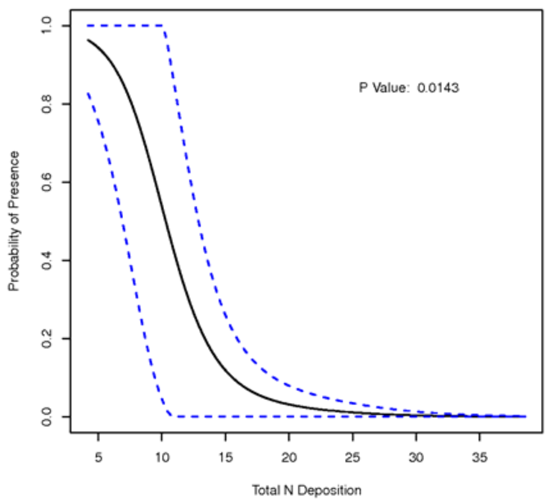


Figure 3.4.23. Spatial change in the probability of presence of *Microlejeunea ulicina* in upland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

The most common response for individual bryophyte species in upland heathland was a positive one (i.e. an increase in the probability of presence with increasing N deposition). Twenty species showed a positive response to N deposition: *Aulacomnium palustre, Barbilophozia hatcheri*, *Calypogeia arguta, Cephalozia connivens, Dicranella schreberiana, Fissidens bryoides s.l., Gymnocolea inflata, Hylocomium splendens, Mylia anomala, Odontoschisma sphagni, Polytrichum commune, Racomitrium ericoides, Scapania irrigua, Sphagnum denticulatum, Sphagnum fallax, Sphagnum russowii, Sphagnum squarrosum, Sphagnum subnitens, Sphagnum tenellum* and *Warnstorfia fluitans*. Figures for all these species (together with all other significant results) are given in Electronic Appendix 4. Figures 3.4.24 and 3.4.25 show *Dicranella schreberiana* and *Fissidens bryoides s.l*. as examples.

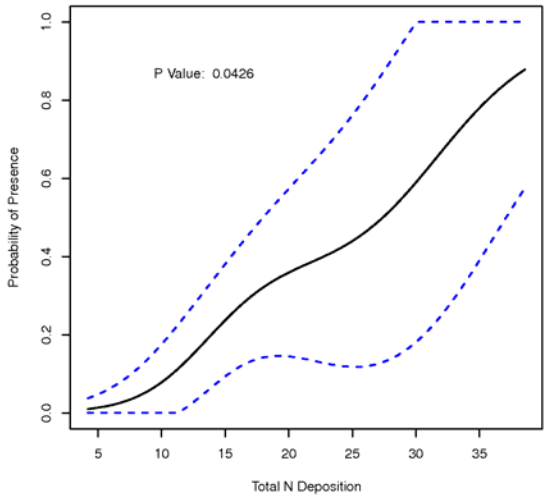


Figure 3.4.24. Spatial change in the probability of presence of *Dicranella schreberiana* in upland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

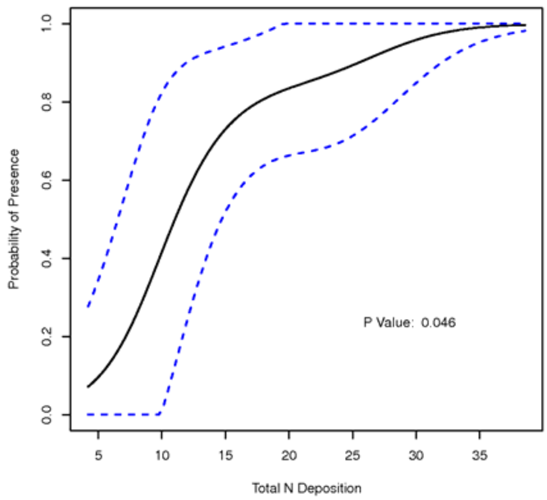


Figure 3.4.25. Spatial change in the probability of presence of *Fissidens bryoides s.l.* in upland heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BBS Database.

3.5 Countryside Council for Wales Grassland Survey

3.5.1 N deposition

The number of quadrats for each habitat is given in Table 3.5.1.

Table 3.5.1. Number of quadrats for each habitat.

Habitat	Lowland	Upland
Acid grassland	891	49
Calcareous grassland	397	

For lowland acid grassland a correlation matrix shows that N deposition tends to be higher where the largest reductions in SOy occurred and in the cooler and wetter areas sampled.

Most quadrats were located in areas above the upper empirical critical load (15 kg N ha^{-1} yr^{-1}) but below 30 kg N ha^{-1} yr^{-1}(Figure 3.5.1).

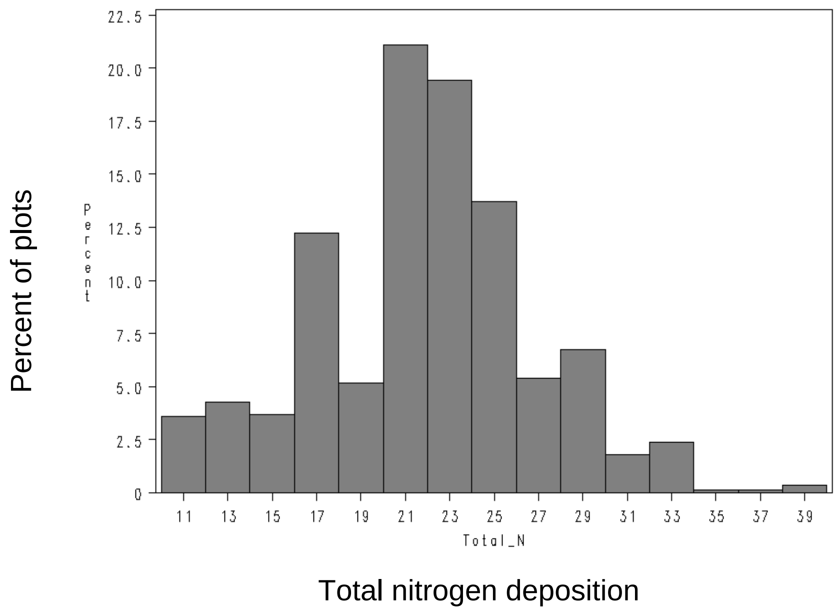


Figure 3.5.1. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the CCW lowland acid grassland dataset.

The upland acid grassland dataset was a relatively small dataset of just 49 quadrats, compared to 891 in lowland acid grasslands. No significant correlations were apparent between N deposition and other covariates.

Nitrogen deposition values were clustered mainly above the upper Critical Load limit[2] of 15 kg N ha^{-1} yr^{-1} but with few values at the highest deposition levels (Figure 3.5.2).

[2] Empirical Critical Loads are based on Table 11.1 in Bobbink *et al* (2010) Empirical N critical loads for natural and semi-natural ecosystems: 2010 update and review. The cross-reference from EUNIS code to UK Priority Habitats is based on Table 1.1 in Hall *et al* (2004) Update to: The Status of UK Critical Loads, Critical Loads Methods & Maps. UK National Focal Centre, CEH Monks Wood.

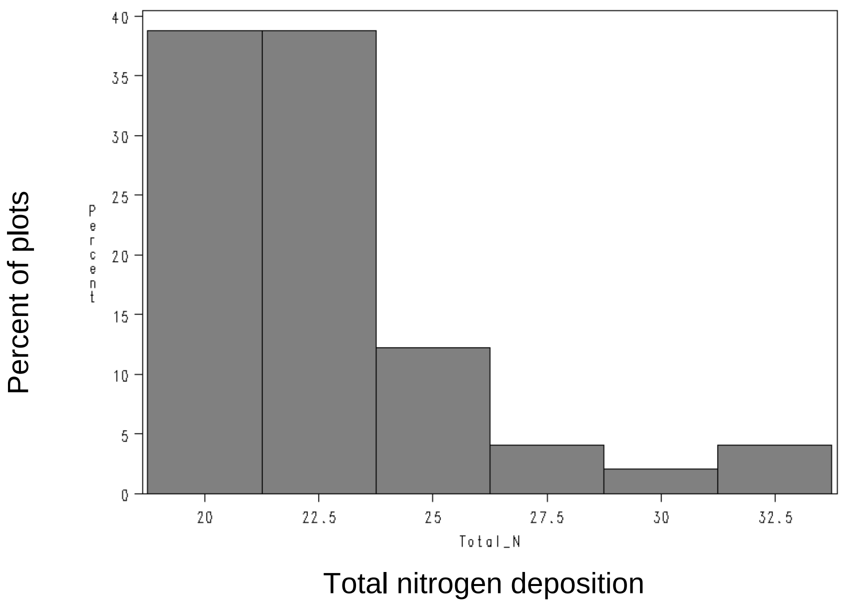


Figure 3.5.2. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the CCW upland acid grassland dataset.

Lowland calcareous grassland showed positive and strongly negative correlations between total N deposition and rainfall and minimum January temperature respectively. Hence, highest N deposition coincided with the coolest and wettest areas sampled.

The dataset was approximately evenly split either side of the mid-point 20 kg N ha^{-1} yr^{-1} empirical critical load (upper and lower limits, 25-15 kg N ha^{-1} yr^{-1}) for calcareous grassland but with most plots at the lower end of the deposition gradient (Figure 3.5.3).

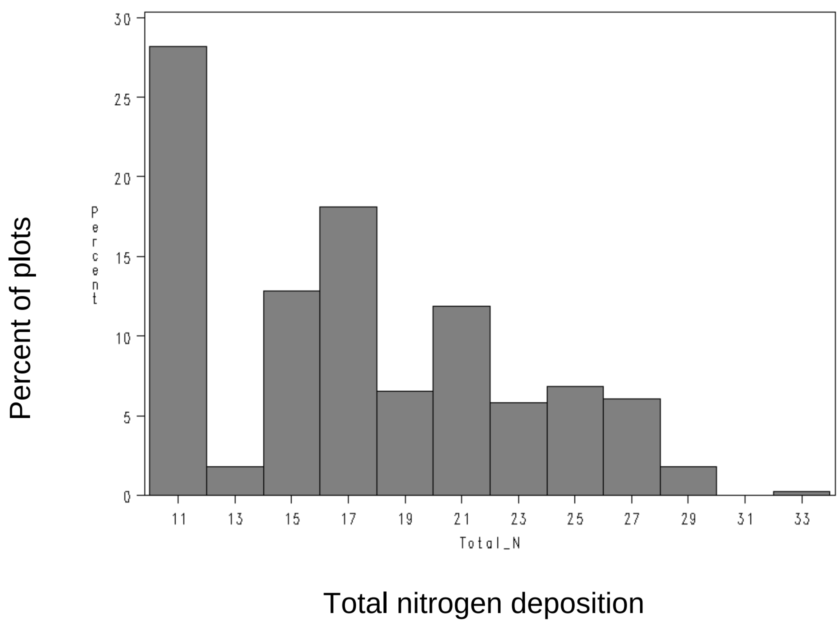


Figure 3.5.3. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the CCW calcareous grassland dataset.

3.5.2 Ellenberg N

For lowland acid grassland no significant relationship of mean Ellenberg N with N deposition was detected. A quadratic model was significant (p=0.033) for upland acid grassland with low mean Ellenberg N values in plots with the highest deposition (Figure 3.5.4).

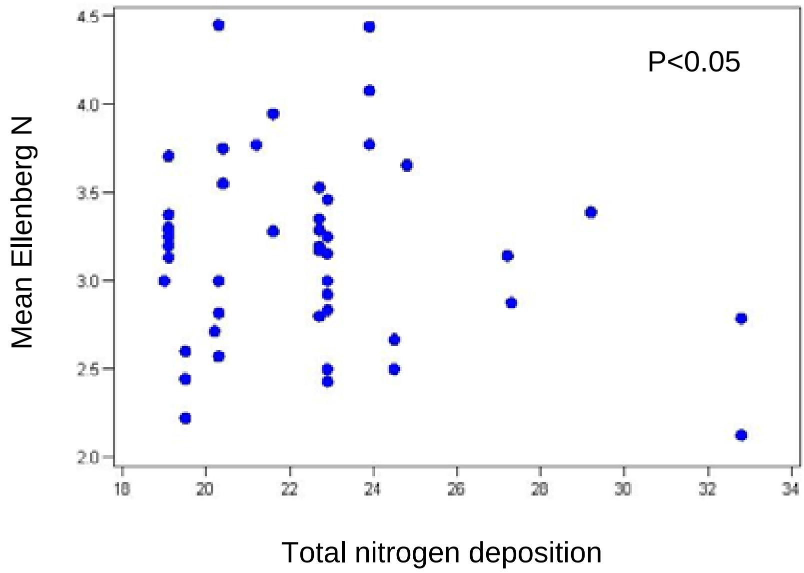


Figure 3.5.4. Scatterplot of mean Ellenberg N versus total inorganic N deposition (kg ha^{-1} yr^{-1}) for upland acid grassland. Data from CCW Grassland Survey.

Lowland calcareous grassland showed no significant effects of N deposition, either as a linear or quadratic model (p=0.16).

3.5.3 Ellenberg R

There was no significant relationship between Ellenberg R score and N deposition in lowland acid grassland (p=0.34). Upland acid grassland had a significant quadratic model (p=0.006) between N deposition and mean Ellenberg R suggesting an initial increase and then decrease along the deposition gradient. Again a plot of the data shows a poor fit (Figure 3.5.5).

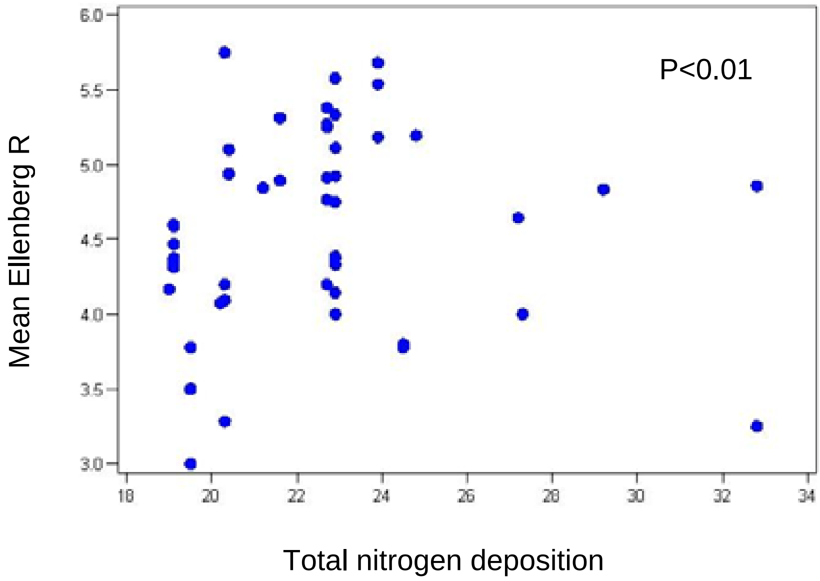


Figure 3.5.5. Scatterplot of mean Ellenberg R versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for the upland acid grassland. Data from CCW Grassland Survey.

For calcareous grassland a quadratic relationship between mean Ellenberg R and N deposition was found (p<0.001) but a plot of the relationship shows marked scatter and an unconvincing fit (Figure 3.5.6). The direction of the quadratic suggests an initial increase in score and then a decline. A significant negative correlation (p<0.01) with change in SOy deposition indicates that the lowest scores are associated with areas that experienced the least reduction in sulphur deposition.

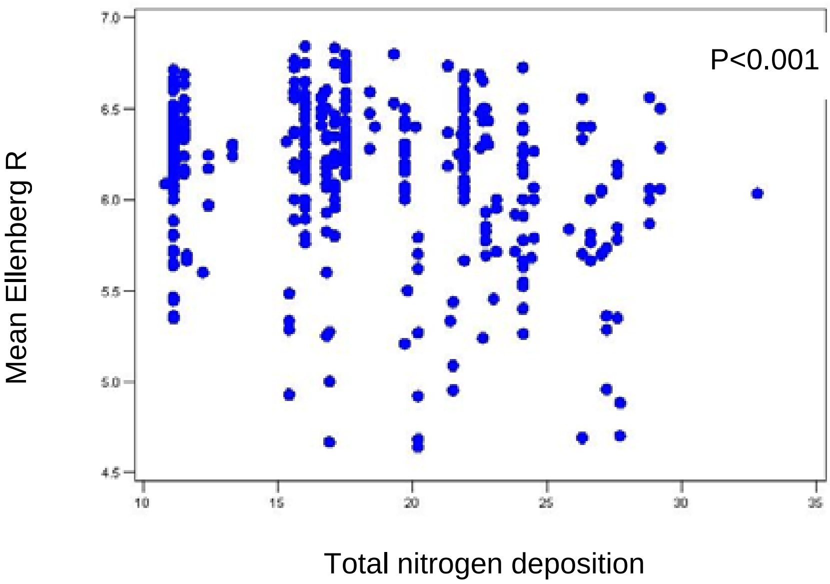


Figure 3.5.6. Scatterplot of mean Ellenberg R versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland calcareous grassland. Data from CCW Grassland Survey.

3.5.4 Plant canopy

Lowland acid grassland showed a weakly significant quadratic model best fitted the relationship between mean canopy height and total N deposition with taller vegetation at the middle of the deposition range (Figure 3.5.7). Upland acid grassland showed no significant relationship between N deposition and mean plant height (p=0.15).

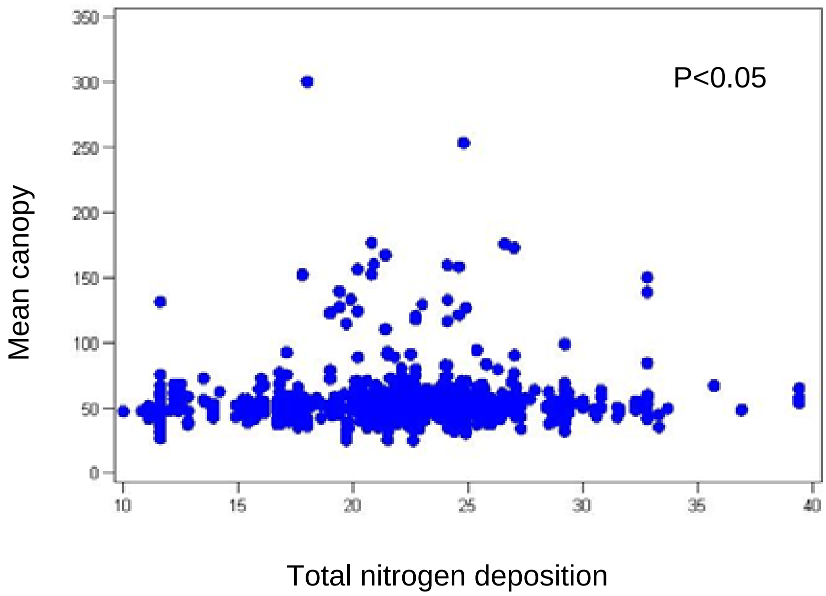


Figure 3.5.7. Scatterplot of mean canopy height (mm) versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from CCW Grassland Survey.

For lowland calcareous grassland a significant quadratic model best fitted the relationship between mean canopy height and N deposition with taller vegetation at middle deposition values but there was much scatter evident (Figure 3.5.8).

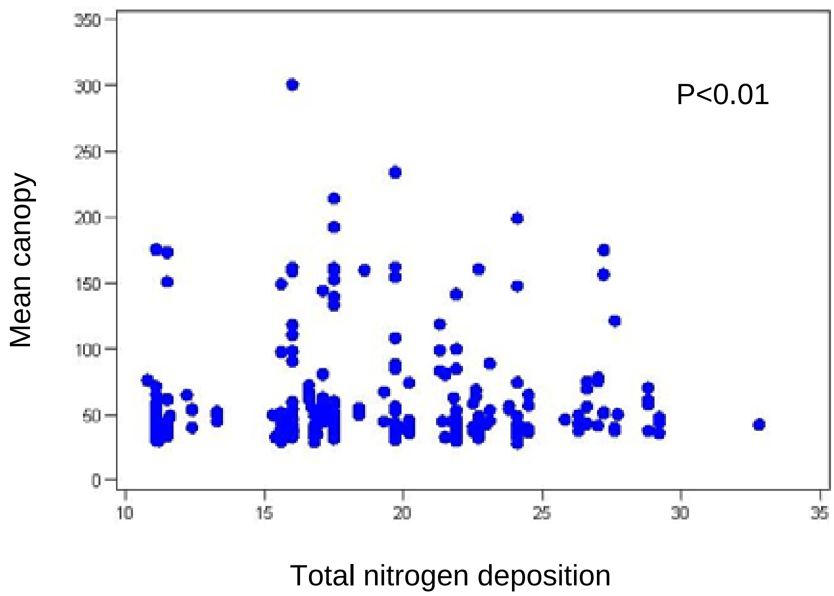


Figure 3.5.8. Scatterplot of mean canopy height (mm) versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland calcareous grassland. Data from CCW Grassland Survey.

3.5.5 Specific leaf area

Mean SLA showed no significant relationship with N deposition for lowland or upland acid grassland.

For lowland calcareous grassland there was a weakly significant quadratic model fit between mean SLA and N deposition. The scatterplot suggests that lower mean SLA values become less common at higher N deposition but much scatter is evident (Figure 3.5.9).

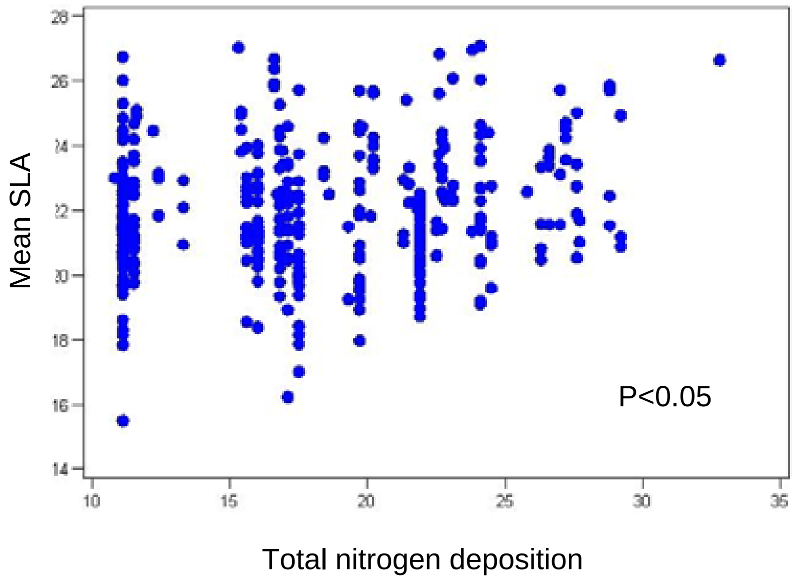


Figure 3.5.9. Scatterplot of mean SLA versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland calcareous grassland. Data from CCW Grassland Survey.

3.5.6 Species diversity

In lowland acid grassland there was a significant negative linear relationship between N deposition and species richness although there is a large degree of variability in the data evident (Figure 3.5.10). There was no significant linear or quadratic relationship between species richness and N deposition in upland acid grassland, however, this was a very small dataset of only 49 quadrats.

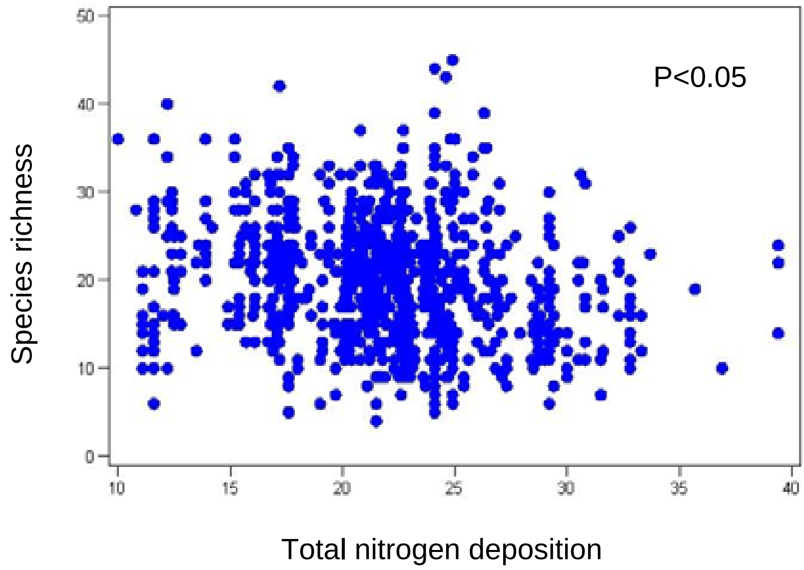


Figure 3.5.10. Scatterplot of species richness versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from CCW Grassland Survey.

Species diversity gave a strongly significant negative linear relationship with N deposition in lowland acid grassland indicating a less even distribution of species and less species at high deposition (Figure 3.5.11).

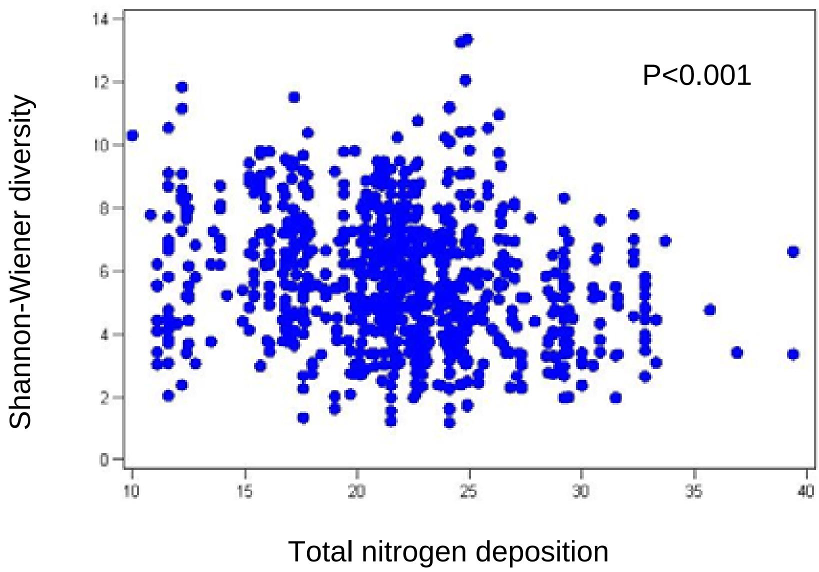


Figure 3.5.11. Scatterplot of Shannon diversity index versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from CCW Grassland Survey.

Upland acid grassland also gave a negative linear relationship between N deposition and species diversity (Figure 3.5.12).

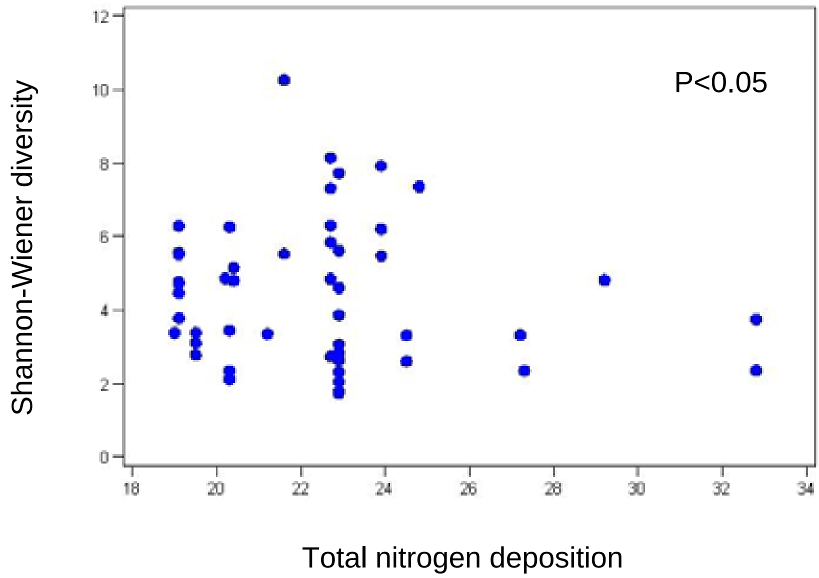


Figure 3.5.12. Scatterplot of Shannon diversity index versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland acid grassland. Data from CCW Grassland Survey.

Lowland calcareous grassland did not show any significant linear or quadratic relationships between species richness or diversity and N deposition.

3.5.7 Individual species responses

i Acid grassland

For lowland acid grassland CCA with forward selection showed that rainfall, minimum January temperature, maximum July temperature, N deposition and SOy deposition all had a significant effect on species composition. N deposition was used as an environmental variable in the analysis and other variables were included as co-variables in the analysis. Only species which occurred in more than 10% of quadrats are considered here although all species were included in the analysis. CCA identified a number of species positively and negatively associated with N deposition. *Poa pratensis, Rumex acetosa* and *Veronica chamaedrys* were all associated with low deposition whilst *Molinea caerulea, Nardus stricta, Calluna vulgaris, Cirsium palustre, Lathyrus linifolius* and *Stachys officinalis* were all associated with higher deposition (Figure 3.5.13).

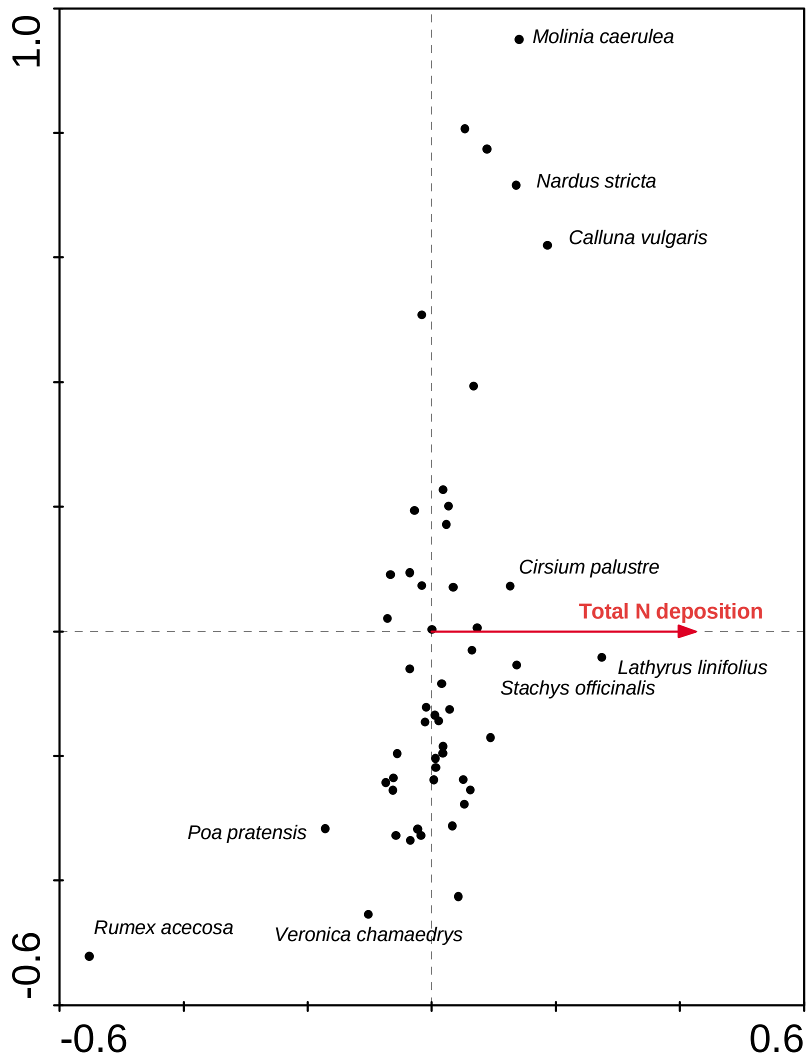


Figure 3.5.13. CCA ordination for lowland acid grassland showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from CCW Grassland Survey.

In upland acid grassland rainfall, area of intensive land use, N deposition and SOy deposition all had a significant effect on species composition. N deposition was used as an environmental variable in the analysis and other variables were included as co-variables in the analysis. Species associated with high deposition were *Agrostis capillaris, Dianthus deltoides* and *Koeleria macrantha*. Species associated with low deposition were *Ajuga reptans, Rumex acetosa, Genista anglica* and *Arenaria serpyllifolia* (Figure 3.5.14).

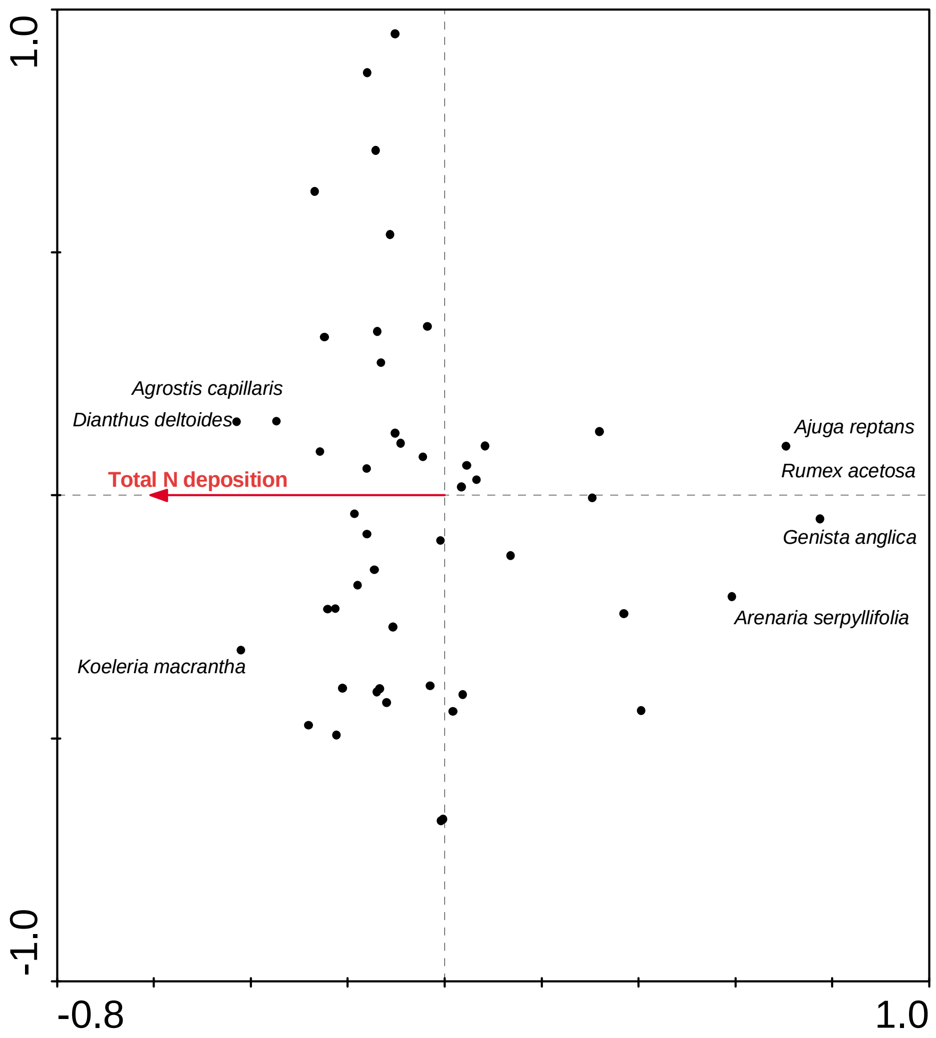


Figure 3.5.14. CCA ordination for upland acid grassland showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from CCW Grassland Survey.

ii Calcareous grassland

There were only sufficient data to examine lowland calcareous grassland in this dataset. Rainfall, minimum January temperature, maximum July temperature, area of intensive land use, N deposition and SOy deposition all had a significant effect on species composition. N deposition was used as an environmental variable in the analysis and other variables were included as co-variables. Species which increased in their occurrence/cover at high deposition were *Centaurea nigra, Bellis perennis* and *Helictotrichon pubescens*. *Pimpinella saxifraga* and *Polygala vulgaris* were associated with low deposition (Figure 3.5.15).

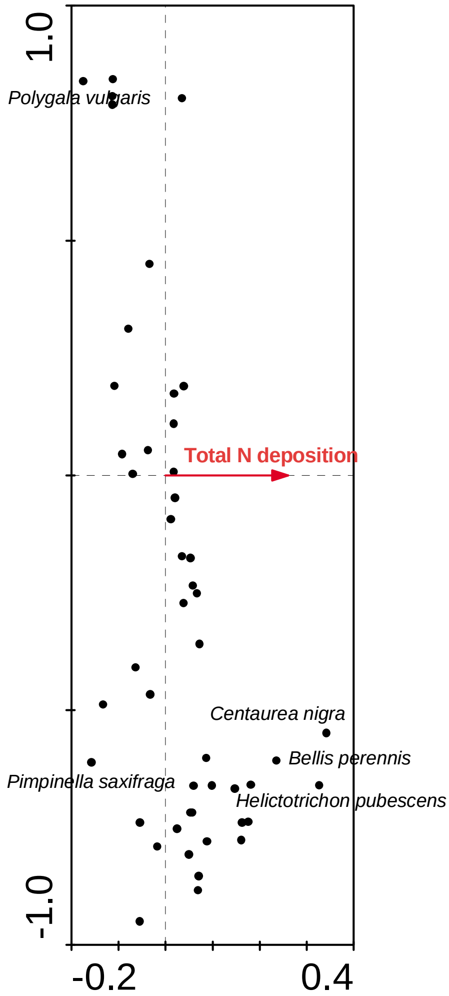


Figure 3.5.15. CCA ordination for lowland calcareous grassland showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from CCW Grassland Survey.

3.6 Scottish Natural Heritage NVC Survey

3.6.1 Nitrogen deposition

The number of quadrats for each habitat is given in Table 3.6.1.

Table 3.6.1. Number of quadrats for each habitat.

Habitat	Lowland	Upland
Acid grassland	105	1084
Calcareous grassland		275
Bog	307	2187
Heathland	61	1039

The lowland acid grassland dataset was a small dataset with the strongest intercorrelation being positive and between total N deposition and maximum July temperature indicating higher N deposition in locations with the warmest summers.

Plots covered the range below and above the empirical critical load for acid grassland of between 10 and 15 kg N ha^{-1} yr^{-1} (Figure 3.6.1).

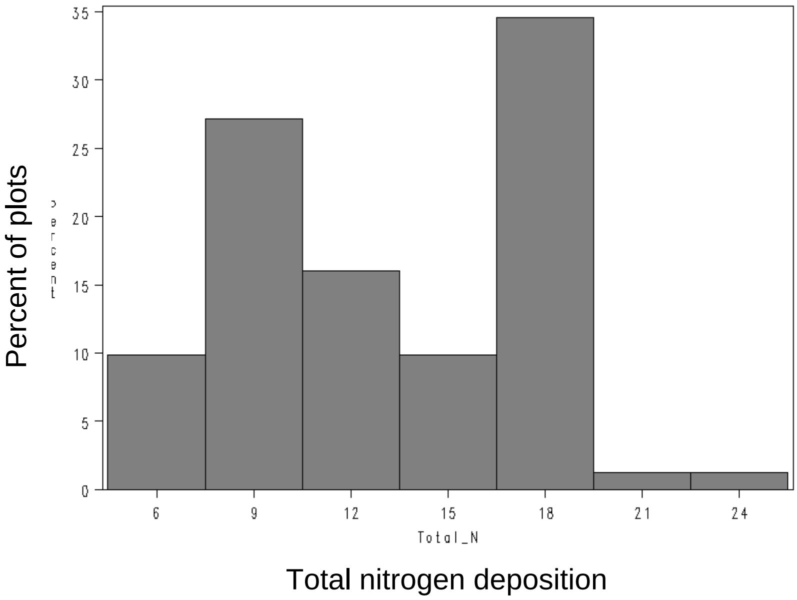


Figure 3.6.1. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the SNH lowland acid grassland dataset.

Minimum January temperature and total N deposition were moderately negatively correlated such that locations with the coolest winters had the highest N deposition for upland acid grassland. Plots covered the range below and above the empirical critical load for acid grassland of between 10 and 15 kg N ha^{-1} yr^{-1} (Figure 3.6.2).

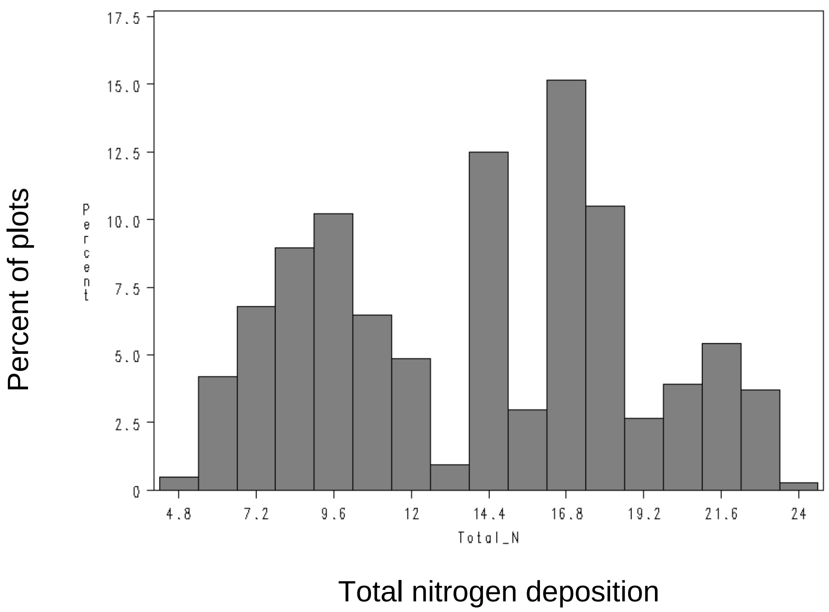


Figure 3.6.2. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the SNH upland acid grassland dataset.

For upland calcareous grassland the strongest correlation was between N deposition and change in SOy deposition. SOy had reduced in areas with the highest contemporary N deposition hence possibly confounding historical acidification impacts with N-induced acidification. Correlation results also highlighted that the sampled locations with the warmest winters had the lowest N deposition.

Over 90% of plots coincided with estimated N deposition below the upper empirical N critical load of 25 kg N ha^{-1} yr^{-1} for calcareous grassland and with most plots at the lower end of the deposition gradient (Fig 3.6.3).

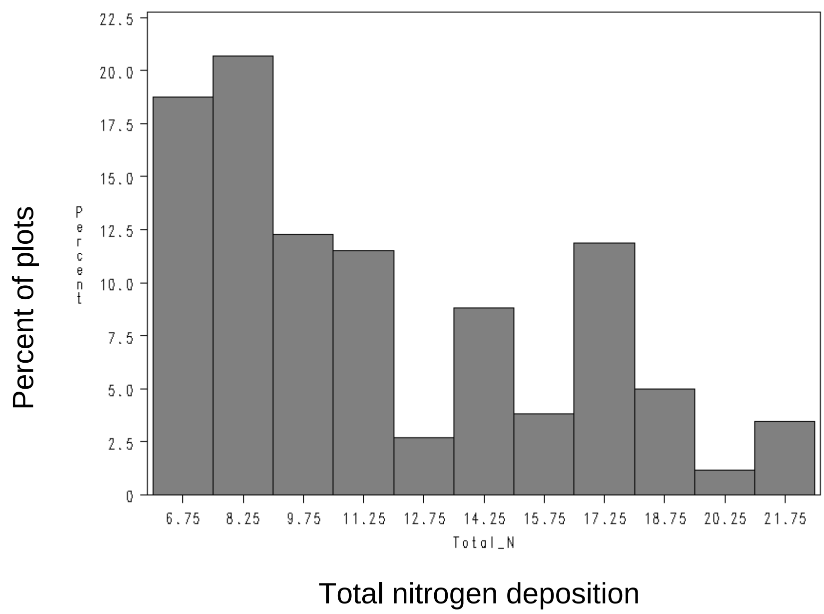


Figure 3.6.3. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the SNH upland calcareous grassland dataset.

Although a small dataset (n=61 plots), for lowland heathland a reasonably large range of each covariate were sampled. SOy change was negatively correlated with total N deposition such that the largest reductions in sulphur were estimated for areas with the highest contemporary N deposition. This could mean possible confounding of historical SOy-related acidification with N-related acidification impacts. This dataset covers the range below and between the empirical critical load interval for dry and northern wet heathlands (10 - 20 kg N ha^{-1} yr^{-1}). (Figure 3.6.4).

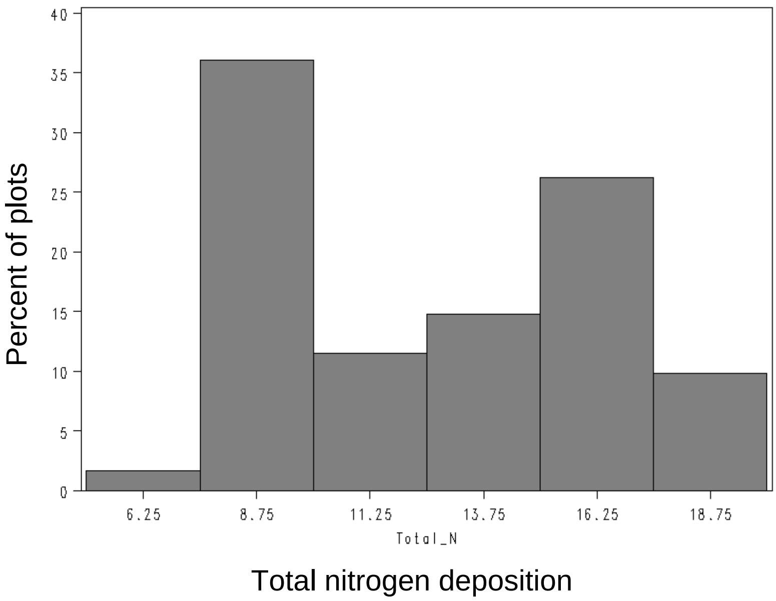


Figure 3.6.4. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the SNH lowland heathland dataset.

As with lowland heathland, for upland heathland SOy change was negatively correlated with total N deposition such that the largest reductions in sulphur were estimated for areas with the highest contemporary N deposition. This could mean possible confounding of historical SOy-related acidification with N-related acidification impacts. While just over 50% of plots were located in areas below the lower empirical CL limit (10 kg N ha^{-1} yr^{-1}) plots did cover the range but with very few above the upper limit of 20 kg N ha^{-1} yr^{-1} (Figure 3.6.5).

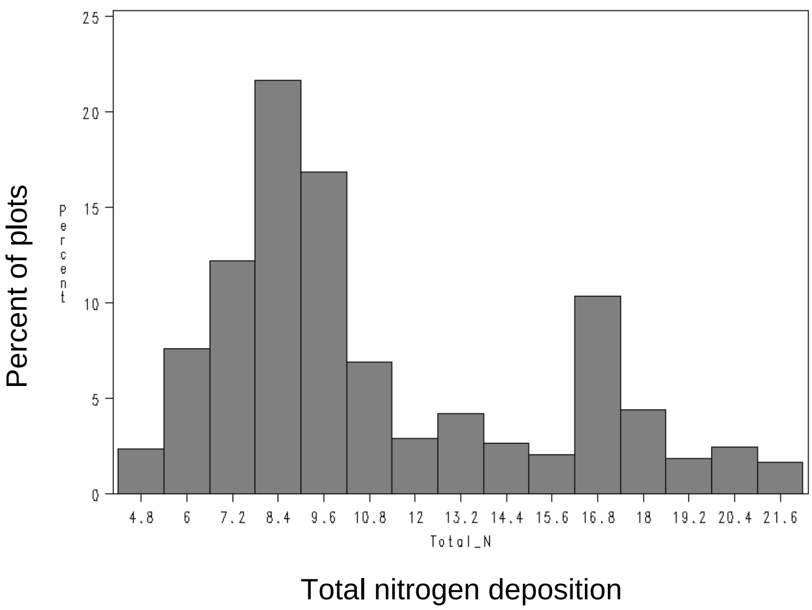


Figure 3.6.5. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the SNH upland heathland dataset.

In lowland bog SOy change was negatively correlated with total N deposition such that the largest reductions in sulphur were estimated for areas with the highest contemporary N deposition. This could mean possible confounding of historical SOy-related acidification with N-related acidification impacts. However, areas with the highest SOy reduction were not sampled presumably simply reflecting the absence of lowland bog in these areas in Scotland. Weak intercorrelations were found between N deposition and other covariates.

A total of 307 plots were available from lowland bog in Scotland. Coverage along the N deposition gradient was somewhat uneven with most plots clustering around 10 and 16 kg N ha^{-1} yr^{-1}. However, the lower empirical CL limit is 5 so the dataset adequately covers a range of deposition expected to impact the ecosystem but there are very few sites at less than 5 kg N ha^{-1} yr^{-1} (Figure 3.6.6).

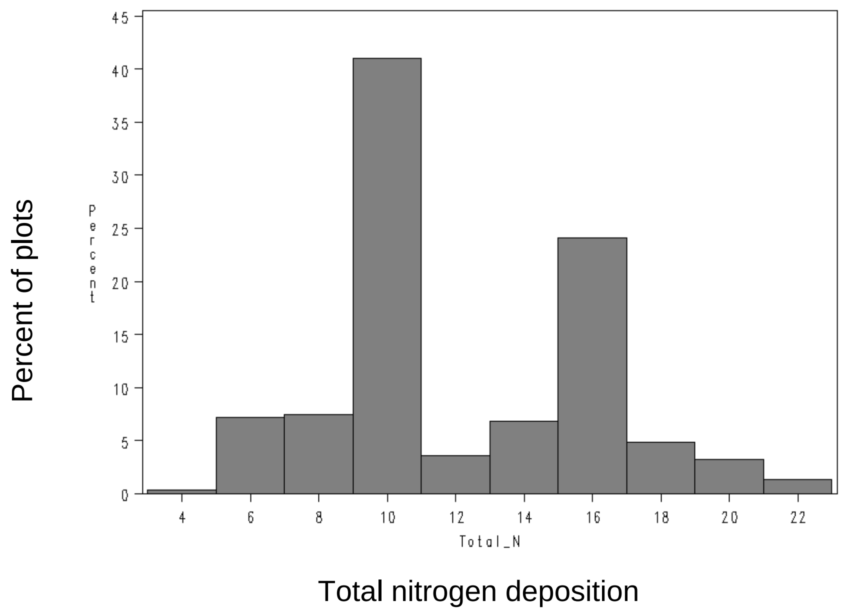


Figure 3.6.6. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the SNH lowland bog dataset.

In upland bog the strongest correlation was the same as most of the other datasets; SOy change was negatively correlated with total N deposition such that the largest reductions in sulphur were estimated for areas with the highest contemporary N deposition. This could mean possible confounding of historical SOy-related acidification with N-related acidification impacts. Albeit with much scatter, correlations were also evident between total N and average climate data for the period 1980 to 2005. The strongest of these was the negative correlation between total N and minimum January temperature hence the coolest locations for upland bog had the highest N deposition. Again though, much scatter was apparent, usefully reducing collinearity and increasing the power of isolating the unique signal of N deposition.

This was a large dataset of 2,187 plots covering a long deposition gradient and also adequately spanning the empirical critical load limits from 5 to 10 kg N ha^{-1} yr^{-1} and above (Figure 3.6.7).

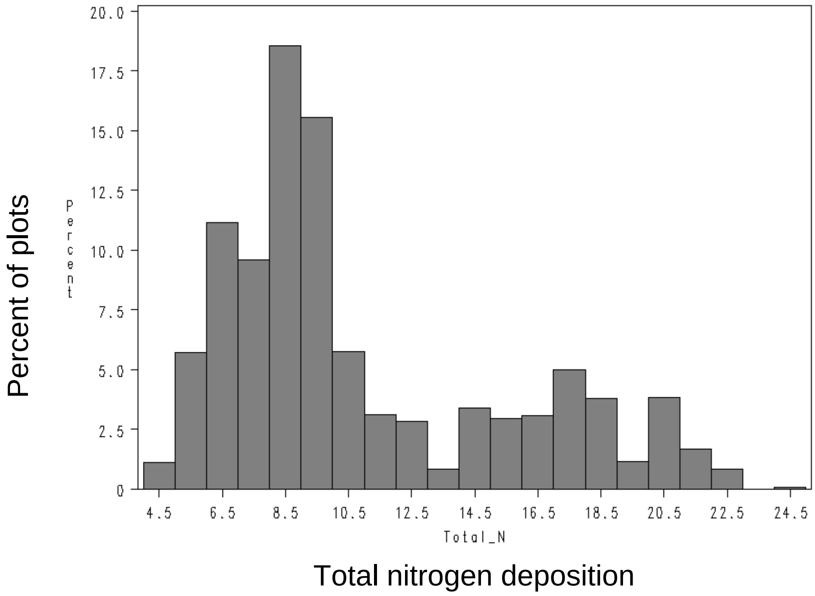


Figure 3.6.7. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the Scottish upland bog dataset.

3.6.2 Ellenberg N

For lowland acid grassland a significant quadratic rather than linear model best fitted the data but this was still a poor fit given the amount of scatter evident (Figure 3.6.8).

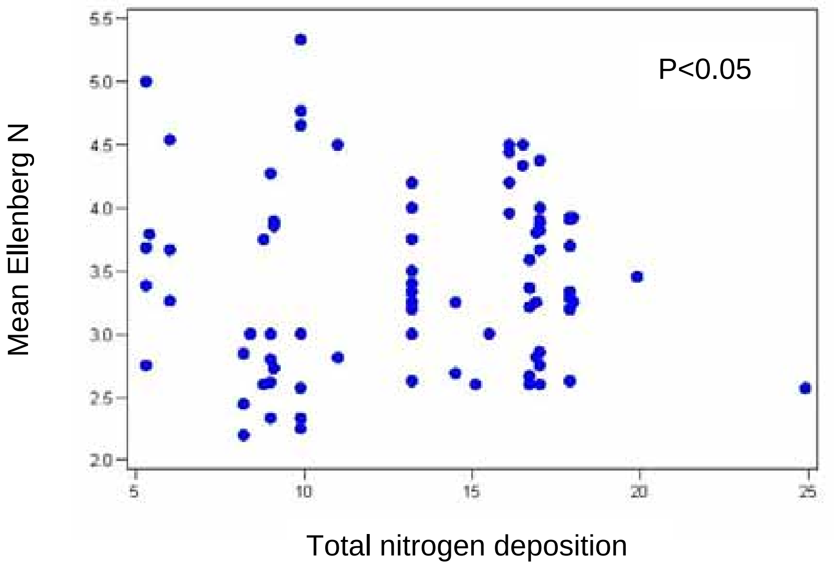


Figure 3.6.8. Mean Ellenberg N plotted against total N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from SNH NVC Survey.

A statistically significant ($P<0.01$) negative linear model best fitted the relationship between mean Ellenberg N and total N deposition in upland acid grassland data but this was a very poor fit given the amount of scatter evident.

In calcareous grassland a positive and highly statistically significant linear relationship was found between mean Ellenberg N and total N deposition (Figure 3.6.9).

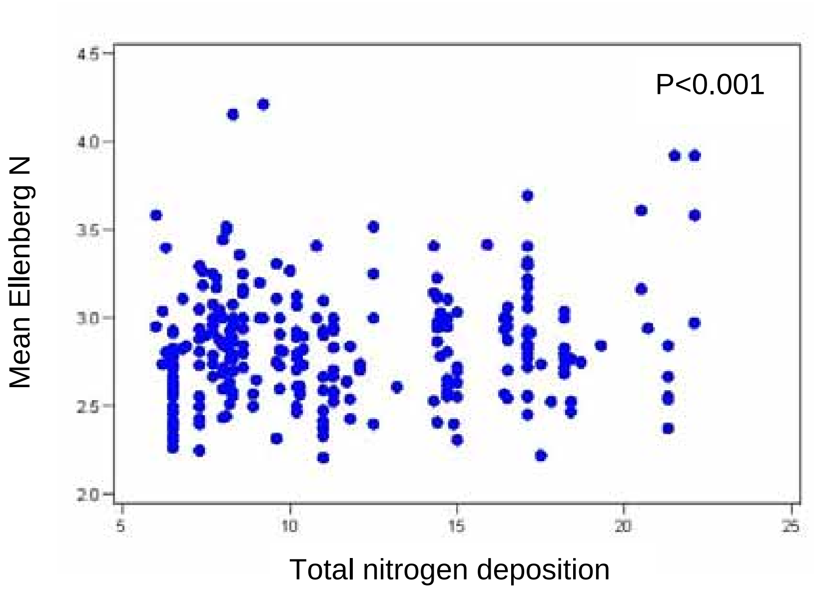


Figure 3.6.9. Mean Ellenberg N plotted against total N deposition (kg N ha^{-1} yr^{-1}) for upland calcareous grassland. Data from SNH NVC Survey.

For lowland heathland a statistically significant negative linear model best fitted the relationship between mean Ellenberg N and total N deposition data but this was a poor fit given the amount of scatter evident. There was no significant relationship detected for upland heathland.

Lowland bog showed a statistically significant positive linear relationship between mean Ellenberg N and total N deposition data but this was a very poor fit given the amount of scatter evident. A statistically significant quadratic model best fitted the relationship between mean Ellenberg N and total N deposition data but this was also a very poor fit with a large amount of scatter evident.

3.6.3 Ellenberg R

A quadratic rather than linear model best fitted the lowland acid grassland data giving a significant result but this was still a poor fit given the amount of scatter evident (Figure 3.6.10).

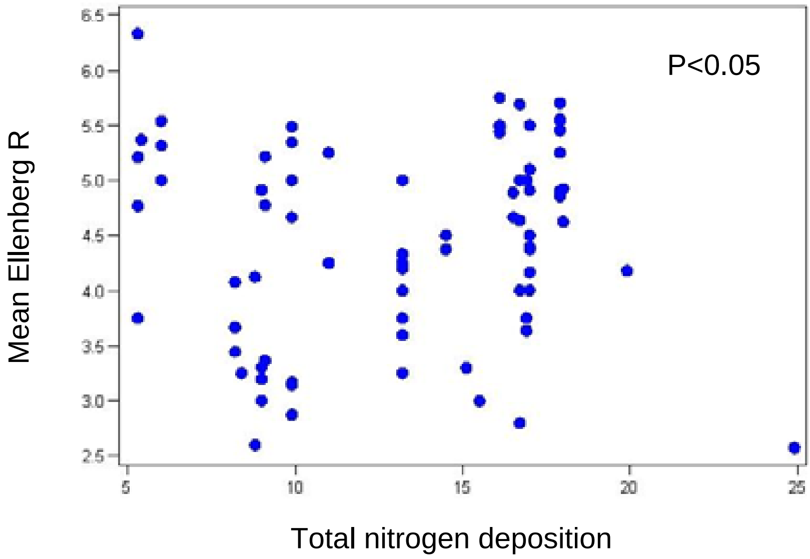


Figure 3.6.10. Mean Ellenberg R plotted against total N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from SNH NVC Survey.

A statistically significant negative linear model best fitted the relationship between mean Ellenberg R and total N deposition for upland acid grassland data but, as with the Ellenberg R score for this community, this was an extremely poor fit given the amount of scatter evident.

In upland calcareous grassland there was no significant relationship between N deposition and Ellenberg R score. This was also true of lowland heathland. Upland heathland had a statistically significant negative linear model between mean Ellenberg R and total N deposition data but as with many analyses in this dataset this was a very poor fit given the amount of scatter evident.

Lowland bog had no significant relationships between N deposition and Ellenberg R score and although there was a statistically significant quadratic relationship between mean Ellenberg R and total N deposition this was a very poor fit with a large amount of scatter evident.

3.6.4 Plant canopy height

There were no significant relationships between N deposition and canopy height for lowland or upland acid grassland, calcareous grassland, and lowland heathland. In upland heathland a statistically significant negative linear model best fitted the relationship between mean plant canopy height and total N deposition (Figure 3.6.11).

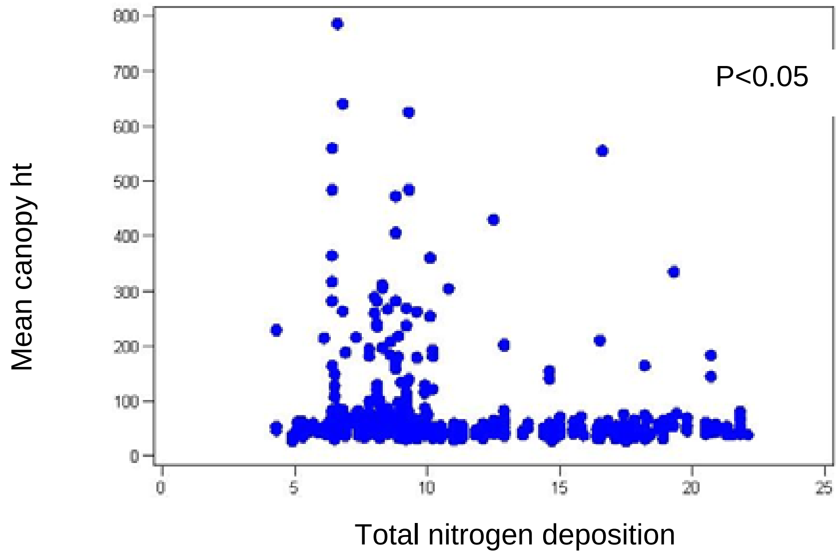


Figure 3.6.11. Mean plant canopy height (mm) plotted against total N deposition (kg N ha^{-1} yr^{-1}) for upland heathland. Data from SNH NVC Survey.

Lowland bog showed no significant relationship between canopy height and N deposition but upland bog had a statistically significant negative linear relationship between mean plant canopy height and total N deposition (Fig 3.6.12).

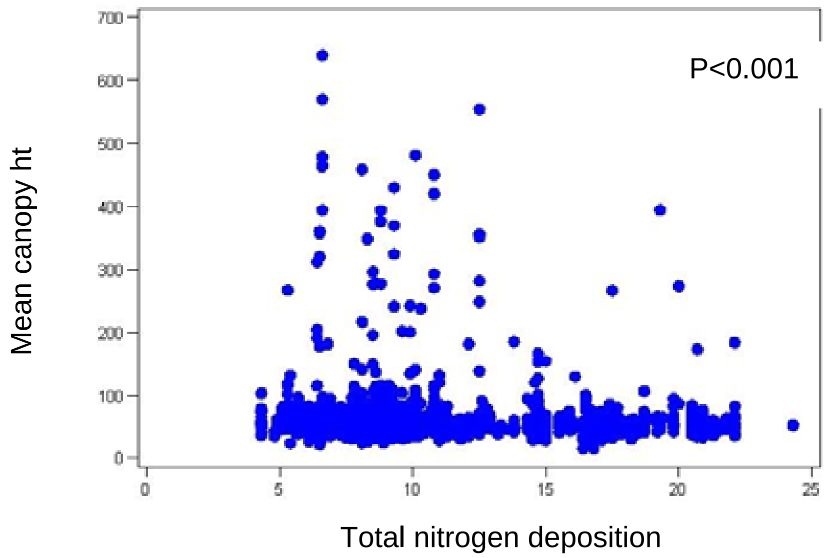


Figure 3.6.12. Mean plant canopy height (mm) plotted against total N deposition (kg N ha^{-1} yr^{-1}) for Scottish upland bog. Data from SNH NVC Survey.

3.6.5 Specific leaf area

A weakly significant quadratic model best fitted the data for lowland acid grassland. A linear model was not significant. Results were possibly influenced by two outliers at high N deposition and results may be different with these omitted (Figure 3.6.13).

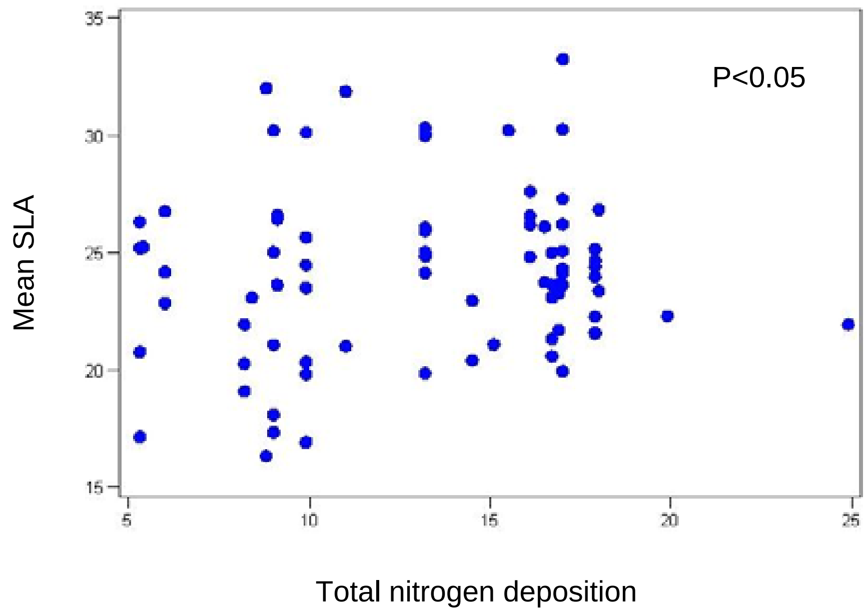


Figure 3.6.13. Mean Specific Leaf Area (SLA) plotted against total N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from SNH NVC Survey.

Upland acid grassland showed a strongly significant negative linear relationship with total N deposition but although the relationship is somewhat clearer than for other communities there is a lot of scatter evident and therefore low explanatory power (Figure 3.6.14).

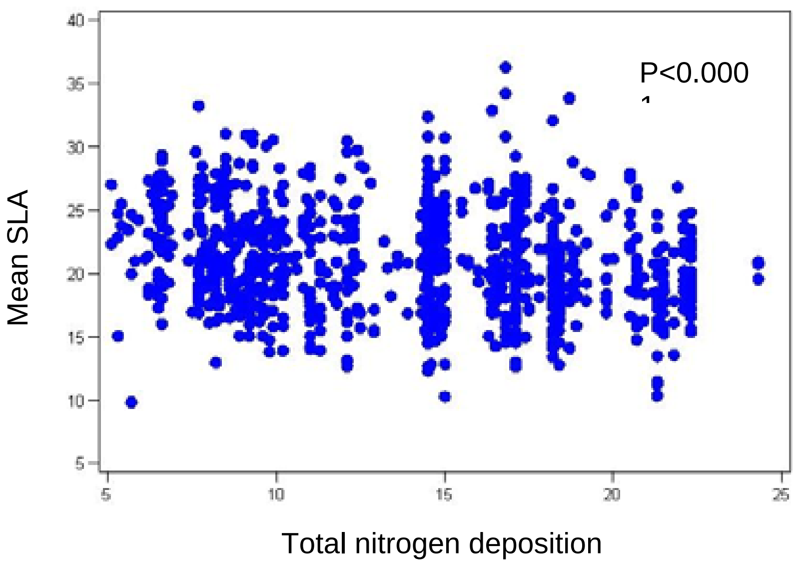


Figure 3.6.14. Mean Specific Leaf Area (SLA) plotted against total N deposition (kg N ha^{-1} yr^{-1}) for upland acid grassland. Data from SNH NVC Survey.

In upland calcareous grassland a significant positive linear relationship was found between mean SLA and total N deposition. Much scatter was evident and the fit was a poor one (Figure 3.6.15).

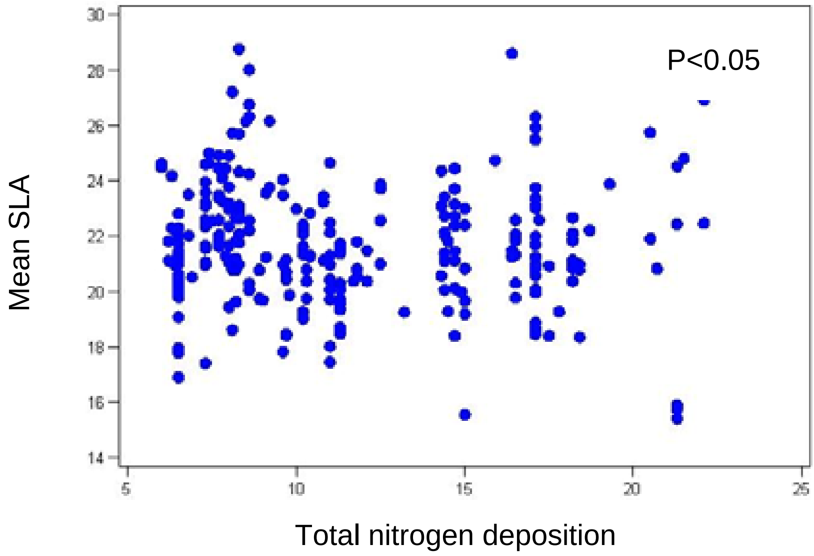


Figure 3.6.15. Mean Specific Leaf Area (SLA) plotted against total N deposition (kg N ha^{-1} yr^{-1}) for upland calcareous grassland. Data from SNH NVC Survey.

In lowland heathland only a linear model was significant indicating declining mean SLA with increasing total N deposition. However, much scatter was evident and the relationship was largely driven by an outlier so the model must be considered a poor fit. In upland heathland a significant hump-shaped quadratic model best fitted the relationship between mean SLA and total N deposition but again much scatter was evident and a poor overall fit to the data.

In lowland bog there was a weakly significant quadratic (U-shaped) relationship with total N deposition. Much scatter is evident and the relationship is unconvincing (Fig 3.6.16).

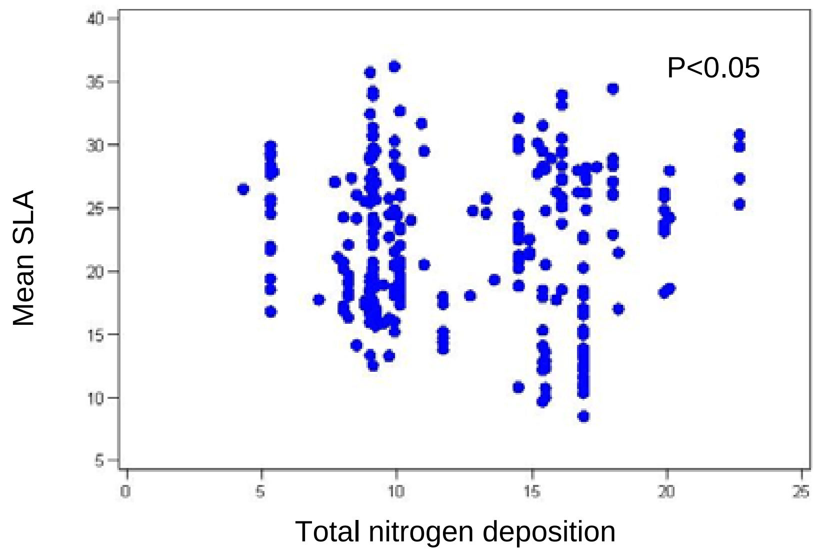


Figure 3.6.16. Mean Specific Leaf Area (SLA) plotted against total N deposition (kg N ha^{-1} yr^{-1}) for Scottish lowland bog. Data from SNH NVC Survey.

A strongly significant (hump-shaped) quadratic relationship best fitted the relationship between mean SLA and total N deposition in upland bog. Much scatter was evident though.

3.6.6 Species diversity

In lowland acid grassland species richness showed a significant positive linear relationship with N deposition but the fit for the relationship is very unsatisfactory and there is a large amount of scatter in the data (Figure 3.6.17). Species diversity showed a very similar relationship, which although significant is not convincing. Upland acid grassland showed no significant relationships for species richness or diversity with N deposition.

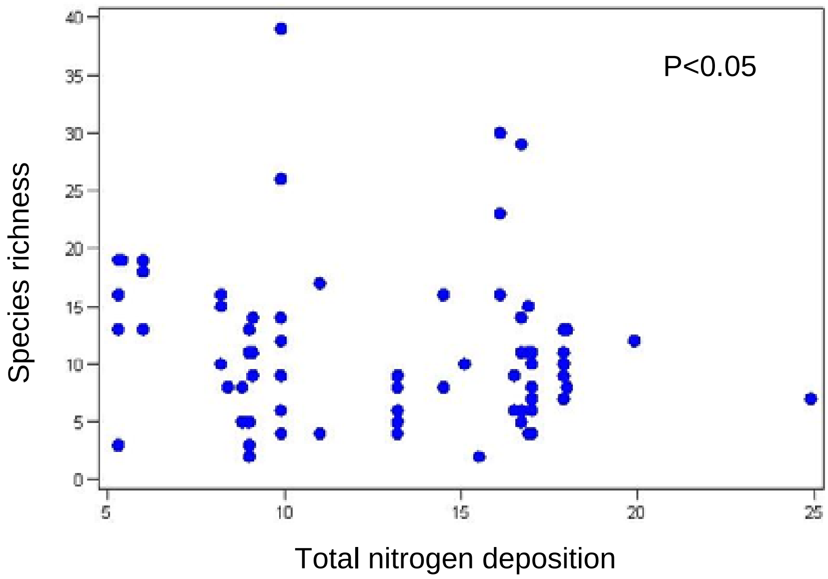


Figure 3.6.17. Scatterplot of species richness versus total N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from SNH NVC Survey.

Neither species richness nor diversity of upland calcareous grassland showed significant relationships with N deposition.

Species richness of lowland heathland showed no significant relationship with N deposition but species diversity gave a strongly significant negative linear relationship indicating a less even distribution of cover among the species present and less species at higher N deposition (Figure 3.6.18).

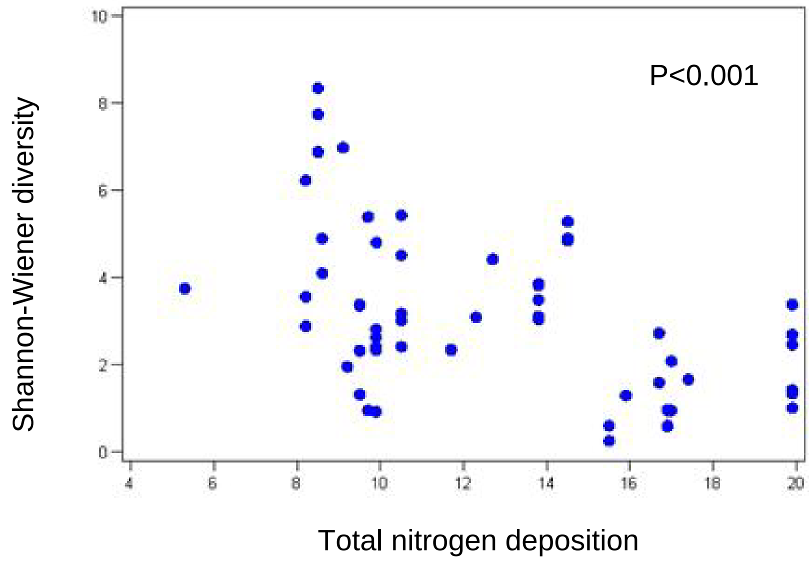


Figure 3.6.18. Scatterplot of Shannon diversity index (H1) versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland acid grassland. Data from SNH NVC Survey.

Upland heathland showed a significant hump-backed quadratic model best fitted the species richness data although the very large amount of scatter in the data suggests that this is not an ecologically relevant relationship (Figure 3.6.19). Species diversity showed a very similar relationship which although significant is not convincing.

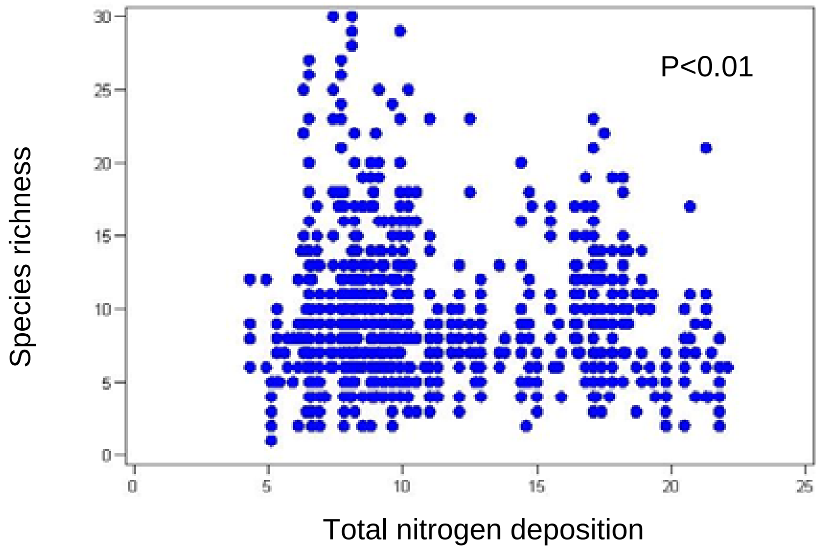


Figure 3.6.19. Scatterplot of species richness versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for upland heathland. Data from SNH NVC Survey.

Lowland bog showed a highly significant negative linear decline in species richness (Figure 3.6.20) and species diversity but there was no significant relationship between species richness and N deposition in upland bog. For species diversity of upland bog a hump-backed quadratic model best fitted the data, although with a large amount of scatter evident along the deposition gradient.

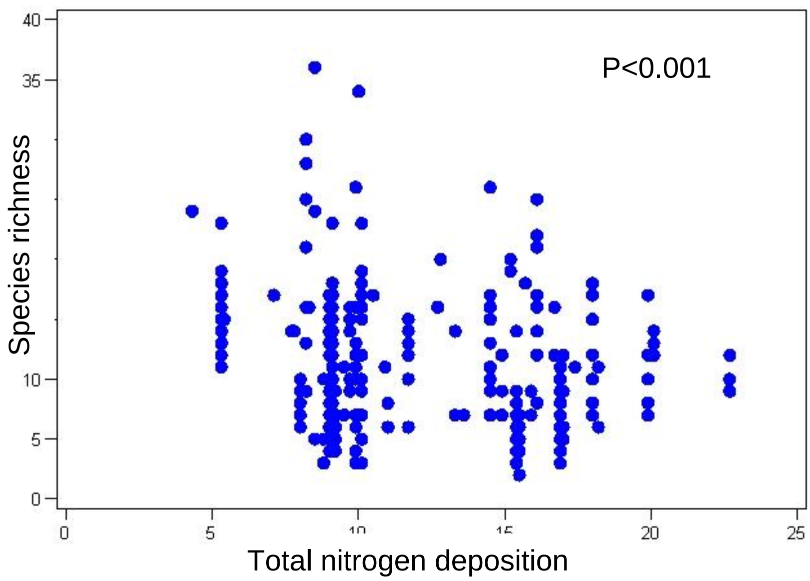


Figure 3.6.20. Scatterplot of species richness versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland bog. Data from SNH NVC Survey.

3.6.7 Individual species responses

i Acid grassland

Both upland and lowland acid grassland were analysed in the SNH data. Lowland acid grassland species composition showed significant relationships with rainfall, minimum January temperature, maximum July temperature, area of intensive land use, N deposition and SOy deposition. N deposition was used as an environmental variable in the analysis and all others were used as co-variables. Once these variables were taken into account the resulting ordination diagram shows that there is very little variation on the second axis, this is why the diagram is long and thin (Figure 3.6.21). Species occurring on over 10% of quadrats which were associated with high N deposition were *Senecio sylvaticus, Stellaria holostea, Galium aparine* and *Anemone nemorosa*. Species associated with low deposition included *Geranium robertianum, Epilobium montanum* and *Hypericum androsaemum*.

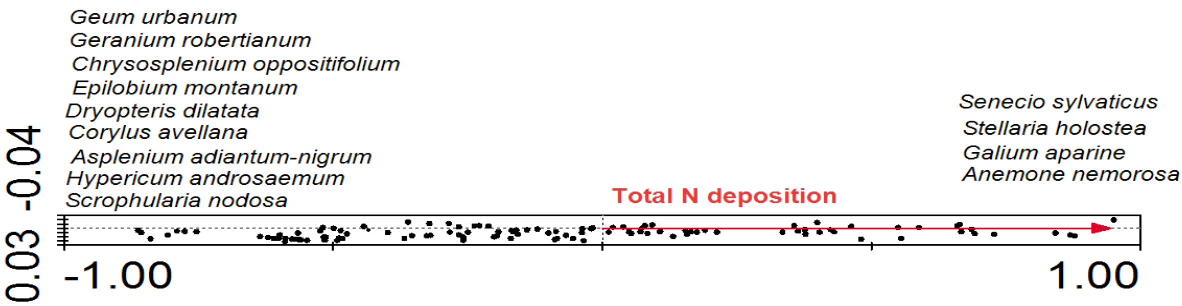


Figure 3.6.21. CCA ordination for lowland acid grassland showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from SNH NVC Survey.

Upland acid grassland showed less variation in the dataset explained by N deposition (represented by the length of the arrow in the diagram) (Figure 3.6.22). As with lowland acid grassland species composition showed significant relationships with rainfall, minimum January temperature, maximum July temperature, area of intensive land use, N deposition and SOy deposition. N deposition was used as an environmental variable in the analysis and all others were used as co-variables. Species associated with high deposition (and occurring in more than 10% of quadrats) included *Poa nemoralis, Sedum acre, Equisetum arvense,* and *Vaccinium oxycoccos*. The species most strongly associated with low deposition were *Betula pendula, Corylus avellana* and *Salix cinerea*. It is interesting that these are all tree species and may actually represent less intensive management in low deposition areas.

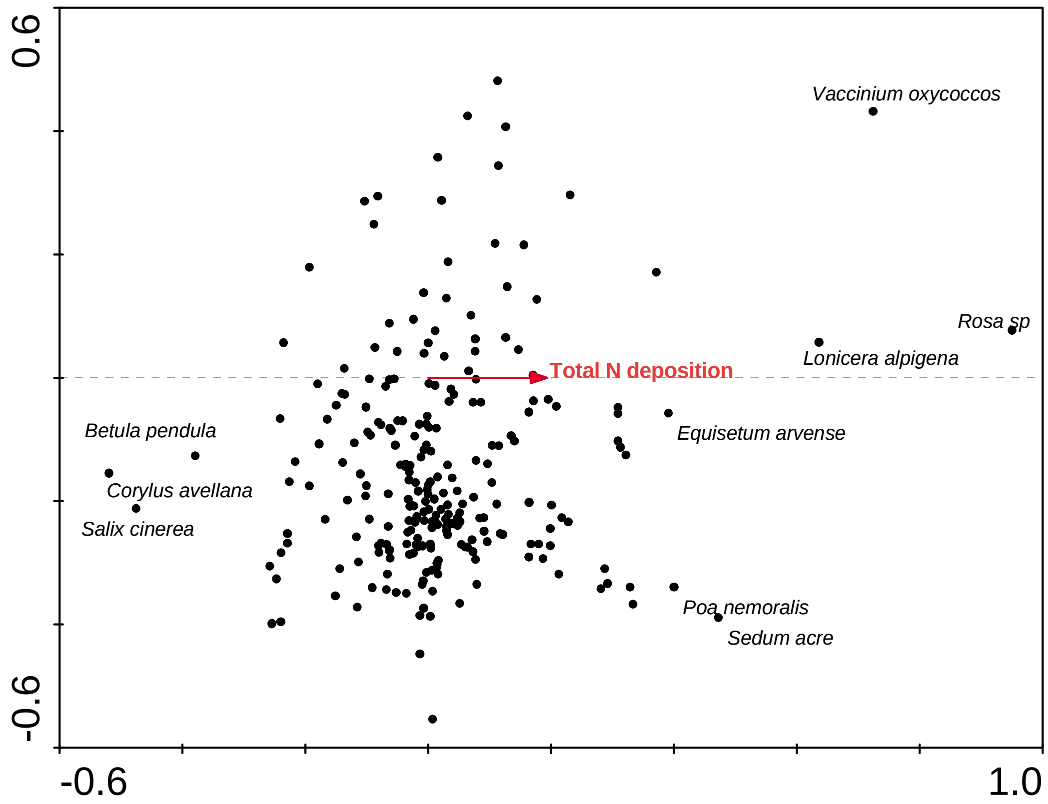


Figure 3.6.22. CCA ordination for upland acid grassland showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from SNH NVC Survey.

ii Calcareous grassland

There were only sufficient quadrats from upland calcareous grassland for analysis. Species composition showed significant relationships with rainfall, minimum January temperature, maximum July temperature, N deposition and SOy deposition. N deposition was used as an environmental variable in the analysis and other variables were used as co-variables. N deposition only explained a small amount of variation in the dataset shown by the short arrow length in Figure 3.7.23. Species which occurred in more than 10% of quadrats and associated with highest levels of deposition were *Chrysosplenium oppositifolium, Epilobium anagallidifolium* and *Rubus idaeus*. Species associated with low deposition were *Digitalis purpurea, Triglochin palustre, Ranunculus flammula, Potentilla anserina* and *Arcostaphylos uva-ursi*.

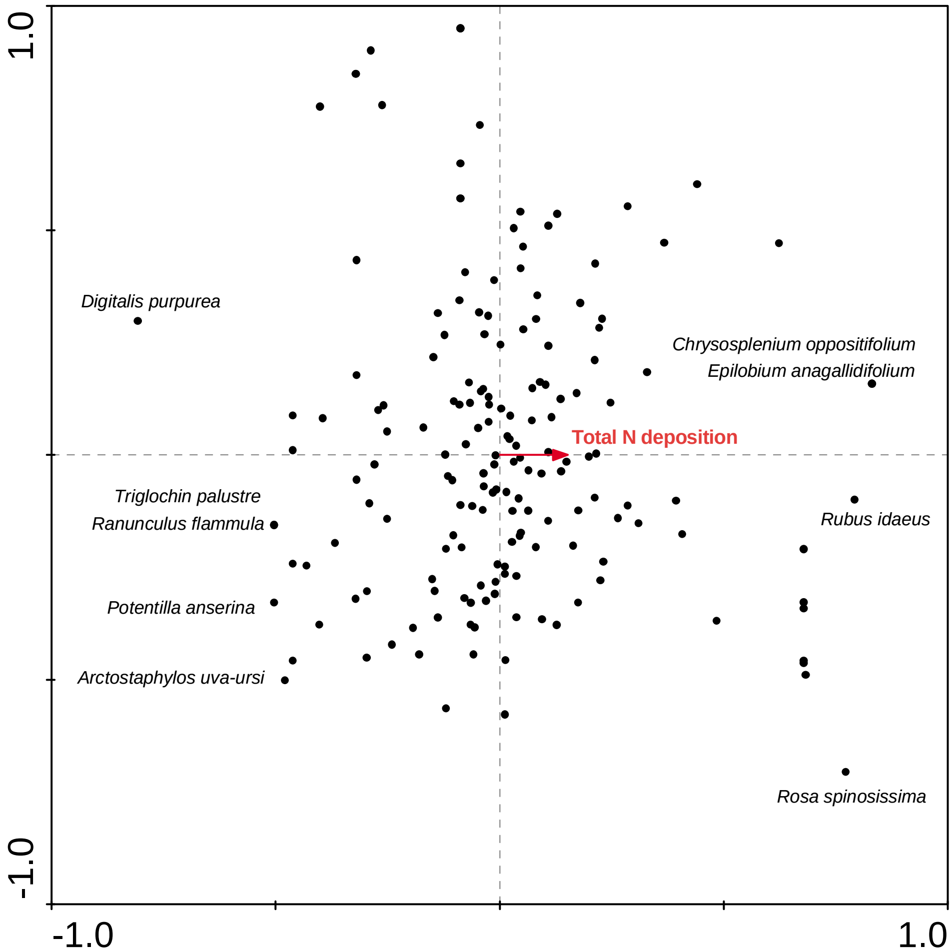


Figure 3.6.23. CCA ordination for upland calcareous grassland showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from SNH NVC Survey.

iii Bog

Lowland bog species composition was significantly correlated with rainfall, minimum January temperature, maximum July temperature, N deposition and SOy deposition. N deposition was used as an environmental variable in the analysis and other variables were used as co-variables. Species that were associated with the highest levels of N deposition were *Lychnis flos-cuculi* and *Hypericum pulchrum*. Species associated with low deposition were *Stellaria holostea, Carex bigelowii, Myosotis* sp. and *Carex limosa* (Figure 3.6.24).

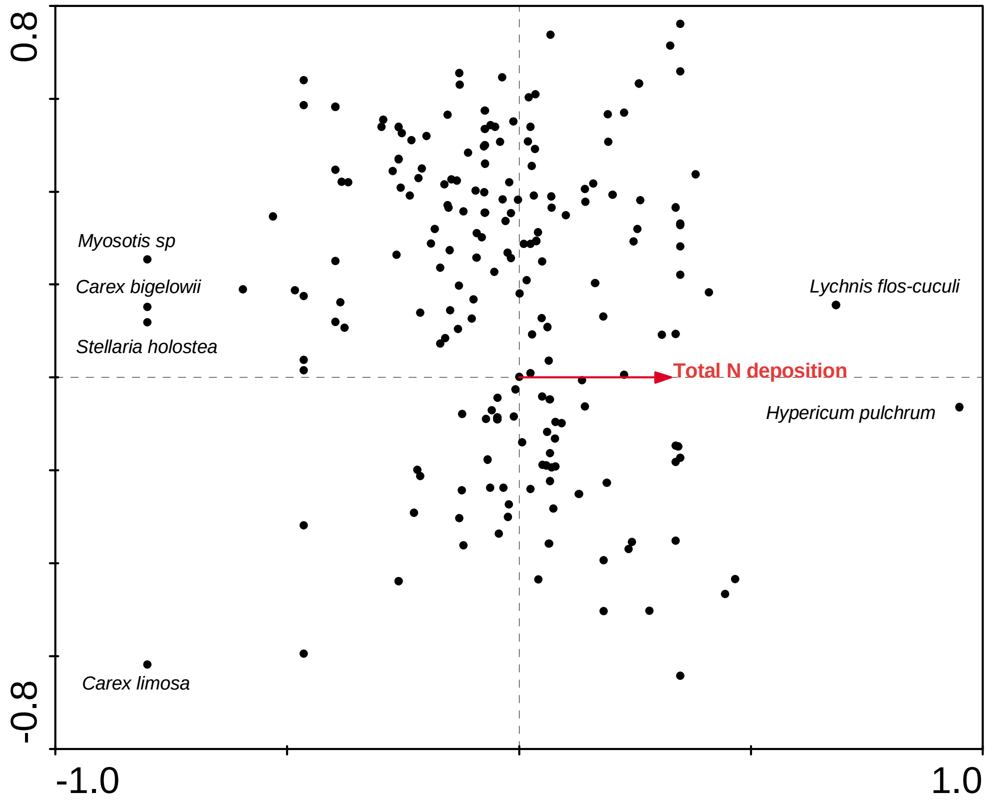


Figure 3.6.24. CCA ordination for lowland bog showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from SNH NVC Survey.

Upland bog showed a large amount of variation that was not accounted for in the analysis shown by the strong spread of points on the y axis of Figure 3.6.25. Species composition was significantly correlated with rainfall, minimum January temperature, maximum July temperature, area of intensive land use, N deposition and SOy deposition. N deposition was used as an environmental variable in the analysis and other variables were used as co-variables. Species that were associated with high deposition were *Ilex aquifolium, Quercus robur, Scutellaria galericulata* and *Lycopus europaeus*. Species associated with low deposition were *Cicuta virosa, Stellaria graminea, Carex chordorrhiza* and *Festuca arundinacea*.

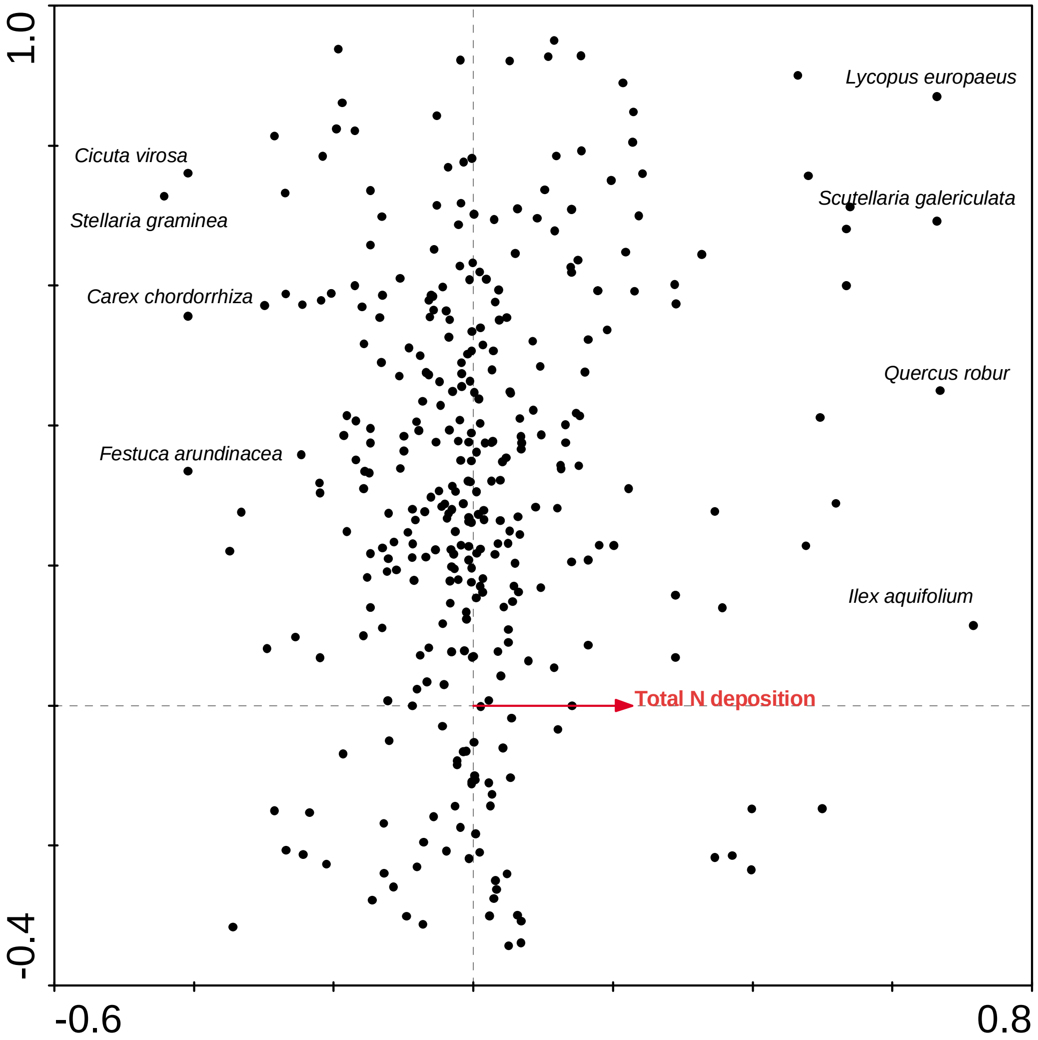


Figure 3.6.25. CCA ordination for upland bog showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from SNH NVC Survey.

iv Heathland

Lowland heathland was a relatively small dataset and few of the variables explained significant variability in the species composition; only N deposition and rainfall. N deposition was used as an environmental variable in the analysis and rainfall was used as a co-variable. Species particularly associated with high deposition were *Salix aurita, Myrica gale, Narthecium ossifragum, Carex nigra, Trichophorum cespitosum* and *Sorbus aucuparia*. Species associated with low deposition were *Holcus mollis, Jasione montana* and *Rumex acetosa* (Figure 3.6.26).

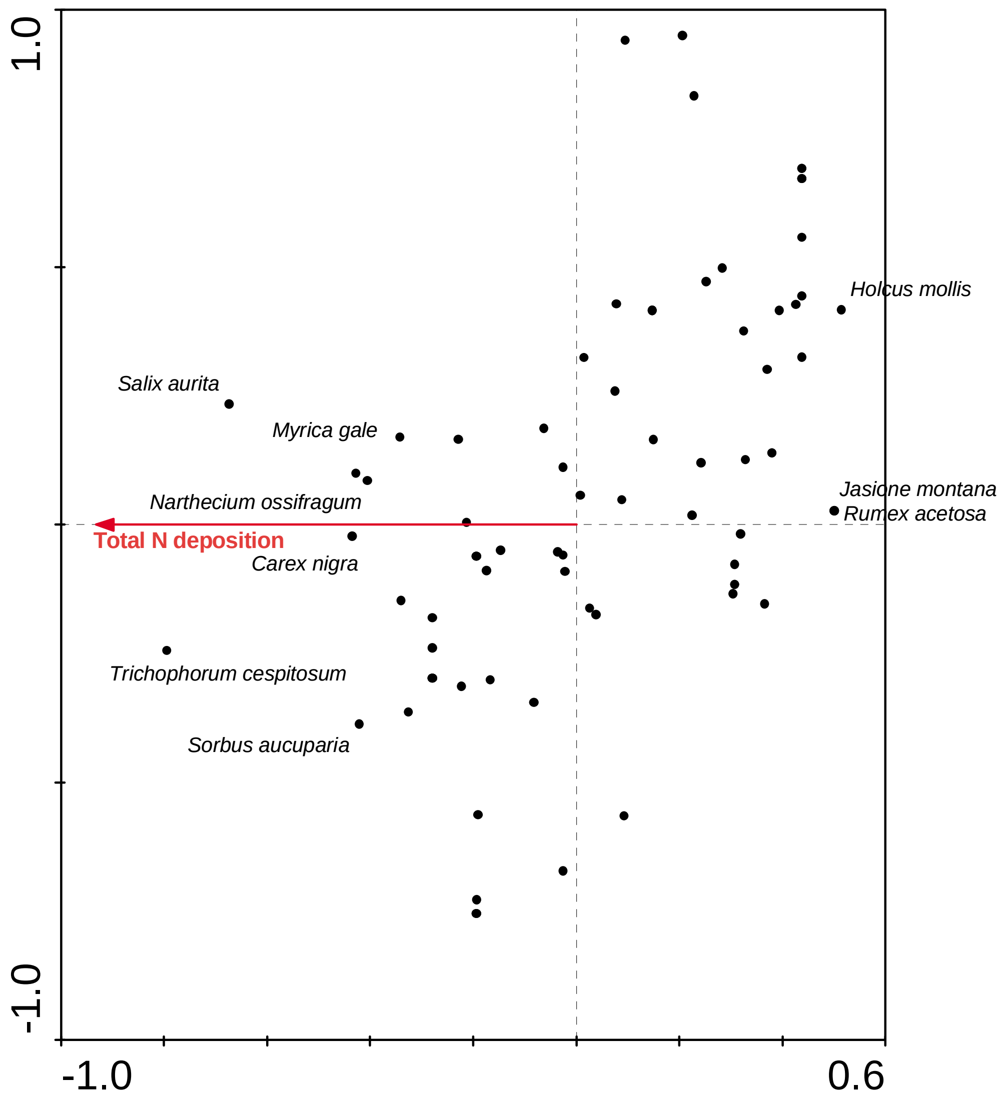


Figure 3.6.26. CCA ordination for lowland heathland showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from SNH NVC Survey.

In upland heathland, rainfall, minimum January temperature, maximum July temperature, area of intensive land use, N deposition and SOy deposition all explained significant variation in species composition. N deposition was used as an environmental variable in the analysis and other variables were used as co-variables. Species associated with high deposition were *Myrica gale, Euphrasia nemorosa* and *Sagina procumbens*. Species associated with low deposition were *Saussurea alpina, Ajuga reptans, Juncus bulbosus, Euphrasia sp., Anagallis tenella* and *Helianthemum nummularium* (Figure 3.6.27).

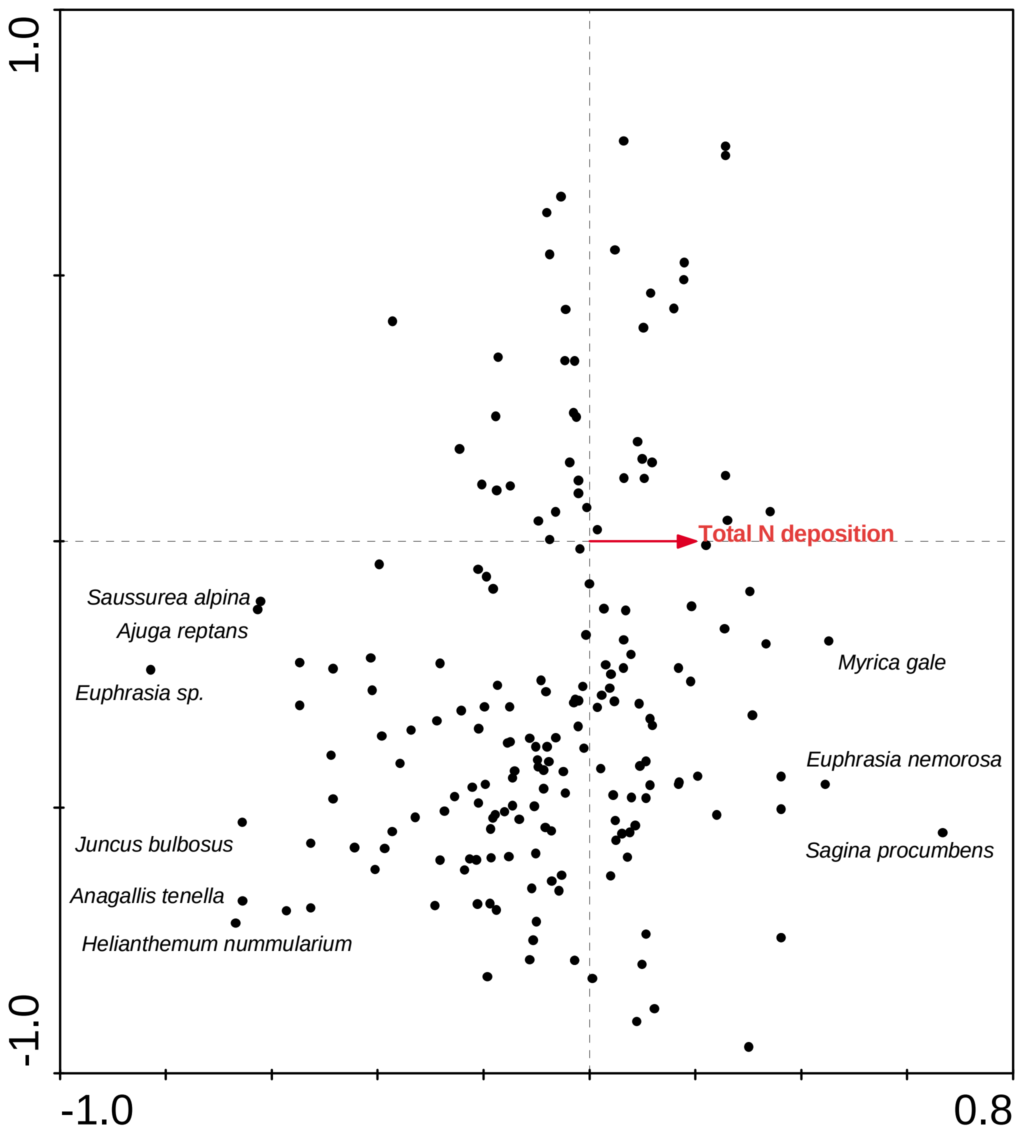


Figure 3.6.27. CCA ordination for upland heathland showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from SNH NVC Survey.

3.7 Natural England Grassland Database

3.7.1 Nitrogen deposition

The number of quadrats for each habitat is given in Table 3.7.1.

Table 3.7.1. Number of quadrats for each habitat.

Habitat	Lowland
Acid grassland	149
Calcareous grassland	5332

A weak but significant correlation was found between N deposition and SOy deposition change for lowland acid grassland indicating that the lowest N deposition values tended to coincide with areas that experienced the largest reduction in sulphur deposition since the early seventies.

Nitrogen deposition values were clustered largely clustered above the empirical N Critical Load (Figure 3.7.1).

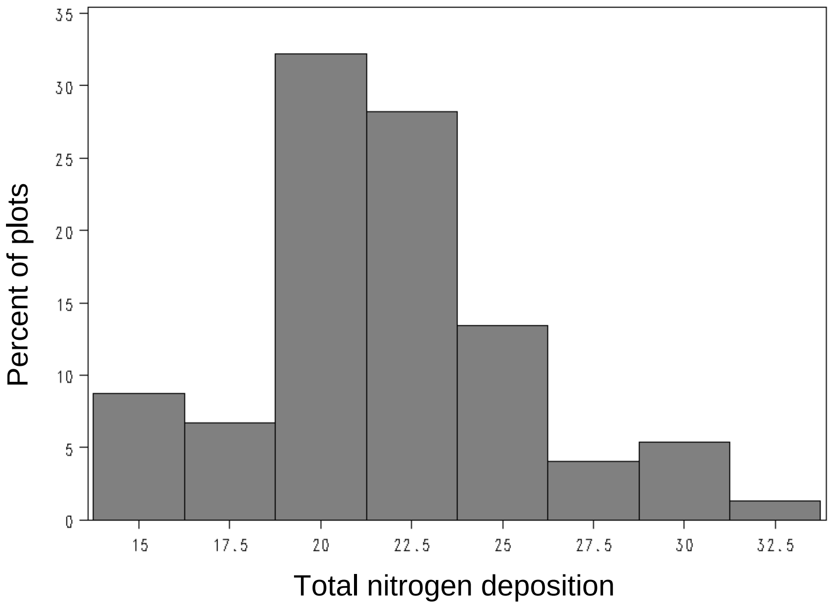


Figure 3.7.1. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the Natural England lowland acid grassland dataset.

For lowland calcareous grassland correlation coefficients between variables were all highly significant. This was not surprising given the very large number of samples in the dataset (n=5332). Particularly large values of coefficients involving N deposition (>0.5 <-0.5) were found for SOy change (negative, indicating that high N deposition areas were associated with the largest reductions in S deposition) and mean minimum January temperatures (negative, indicating that highest N deposition was associated with the coolest and highest rainfall areas).

Plots were mainly clustered in the interval from the lower to upper empirical Critical Load for calcareous grassland (15-25 kg N ha^{-1} yr^{-1}) (Figure 3.7.2).

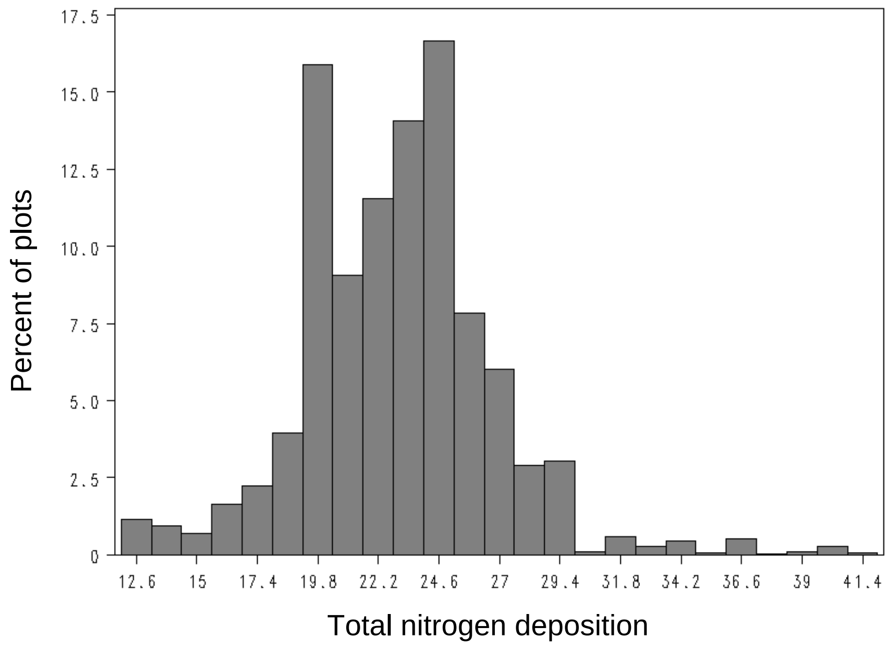


Figure 3.7.2. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the Natural England lowland calcareous grassland dataset.

3.7.2 Ellenberg N

There was no significant relationship between mean Ellenberg N score and N deposition for lowland acid grassland (p=0.62). There was a significant relationship between mean Ellenberg N score and N deposition for calcareous grassland. Despite the wedge-shaped appearance of the mass of points (Figure 3.7.3), a negative linear model was the best fit to total N deposition (p=0.015).

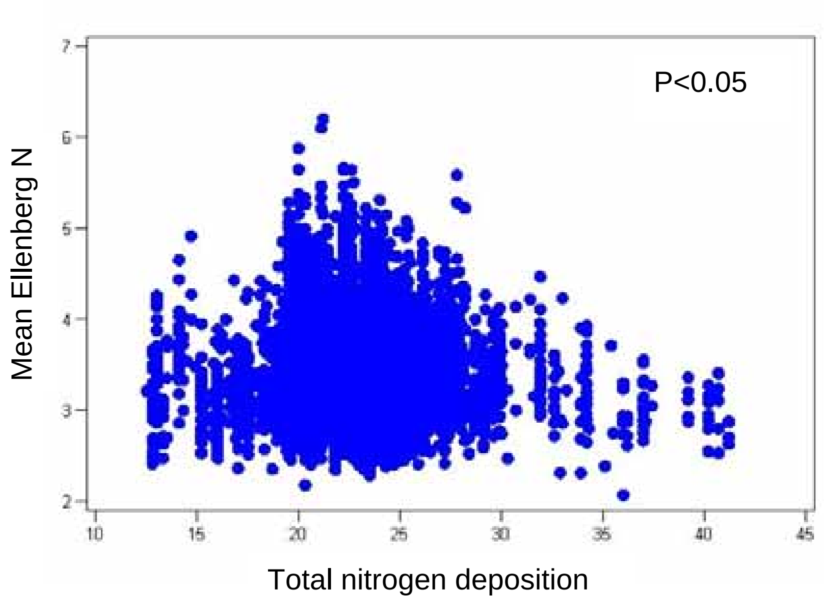


Figure 3.7.3. Scatterplot of mean Ellenberg N versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland calcareous grassland. Data from Natural England Grassland Database.

3.7.3 Ellenberg R

There was no significant relationship between mean Ellenberg R score and N deposition for lowland acid grassland (p=0.64). For lowland calcareous grassland both quadratic and linear models were a statistically significant fit but the linear model was the more highly significant fit (p<0.0001) indicating that mean Ellenberg R scores tended to decline at the higher end of the deposition gradient (Figure 3.7.4).

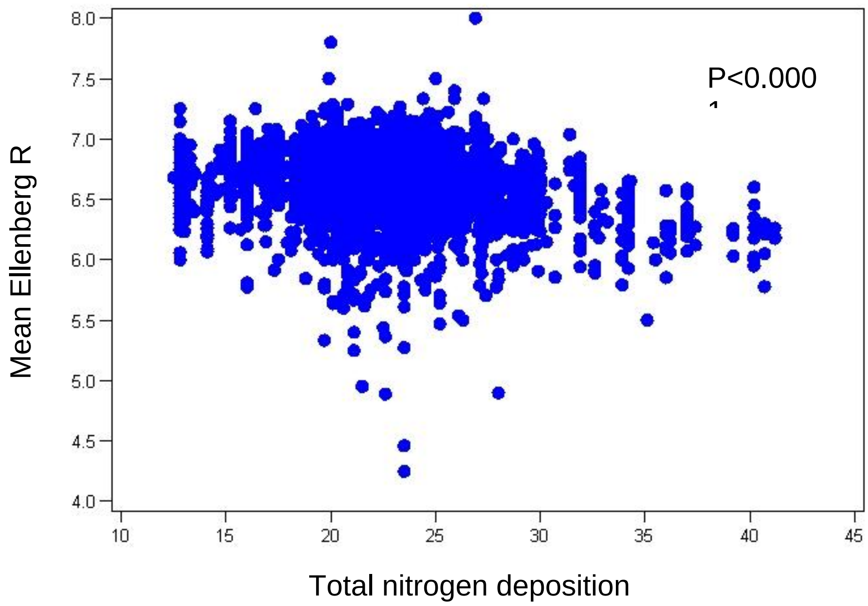


Figure 3.7.4. Scatterplot of mean Ellenberg R versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland calcareous grassland. Data from Natural England Grassland Database.

3.7.4 Plant canopy height

Neither lowland acid nor calcareous grassland showed a significant relationship between mean plant height and N deposition (acid: p=0.71; calcareous: p=0.48).

3.7.5 Specific leaf area

There was no significant relationship between mean SLA and N deposition for lowland acid grassland (p=0.93). For lowland calcareous grassland a highly significant linear model best fitted the relationship between mean SLA and N deposition. A quadratic term was not significant. The direction of the N deposition parameter indicates declining SLA with increasing deposition (Figure 3.7.5).

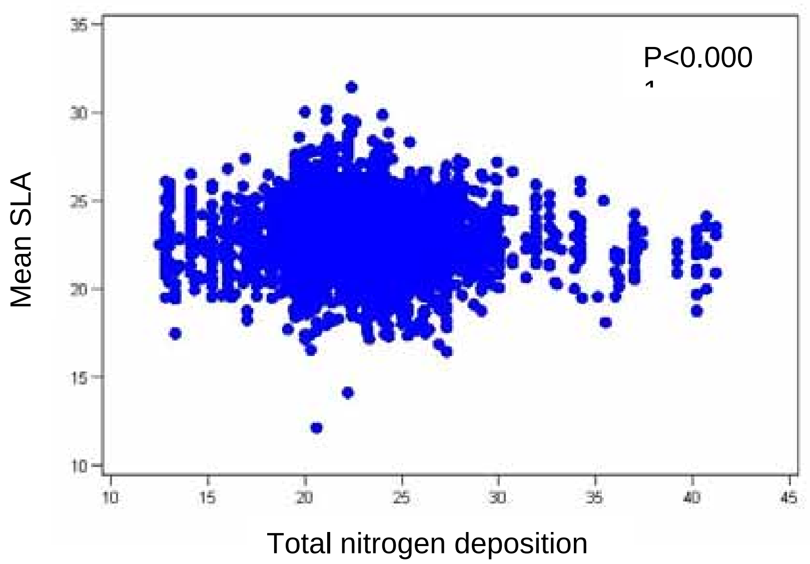


Figure 3.7.5. Scatterplot of mean SLA versus total inorganic N deposition (kg N ha^{-1} yr^{-1}) for lowland calcareous grassland. Data from Natural England Grassland Database .

3.7.6 Species diversity

There were no significant linear or quadratic relationships between N deposition and species richness in either lowland acid or calcareous grassland.

3.7.7 Individual species responses

i Acid grassland

For lowland acid grassland CCA with forward selection showed that rainfall, minimum January temperature, maximum July temperature, area of intensive land use, N deposition and SOy deposition all had a significant effect on species composition. N deposition was used as an environmental variable in the analysis and other variables were included as co-variables. Only species which occurred in more than 10% of quadrats are considered in the interpretation of the data although all species were included in the analysis. CCA identified a number of species positively and negatively associated with N deposition. Species positively associated with N deposition were *Hypochaeris radicata, Pteridium aquilinum, Carex hirta, Calluna vulgaris* and *Deschampsia flexuosa*. Species associated with low deposition were *Agrostis stolonifera, Veronica chamaedrys, Ranunculus acris* and *Koeleria macrantha* (Figure 3.7.6).

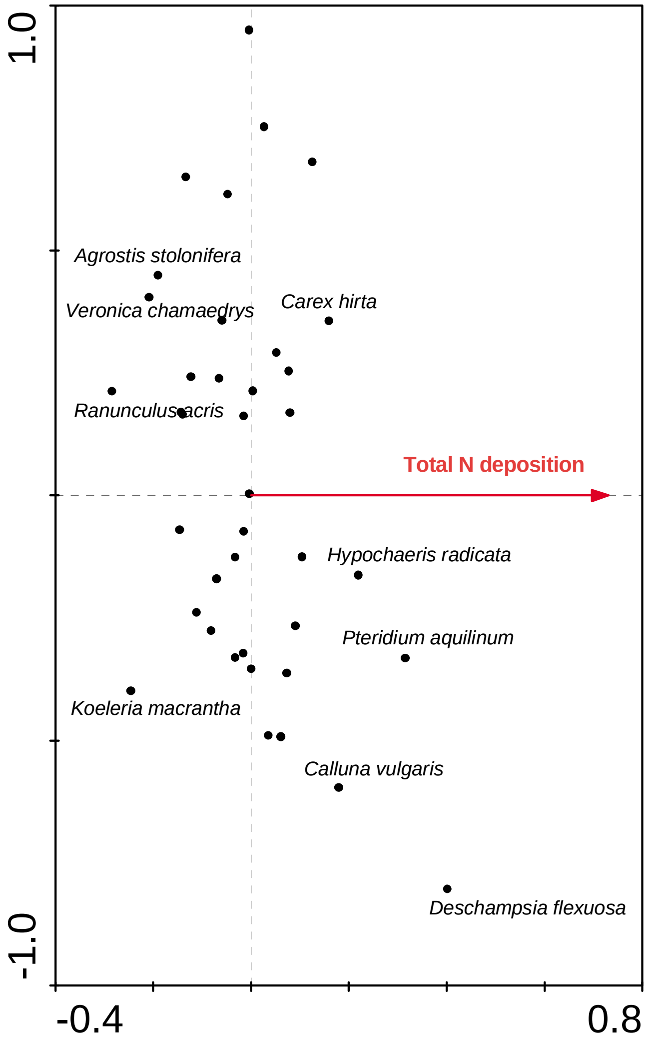


Figure 3.7.6. CCA ordination for lowland acid grassland showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from Natural England Grassland Database.

ii Calcareous grassland

In lowland calcareous grassland rainfall, minimum January temperature, maximum July temperature, area of intensive land use, N deposition and SOy deposition all had a significant effect on species composition. N deposition was used as an environmental variable in the analysis and other variables were included as co-variables. Species most strongly associated with low N deposition were *Poa pratensis, Crataegus monogyna* and *Filipendula vulgaris*. Species associated with high deposition were *Anthoxanthum odoratum, Agrostis capillaris, Cynosurus cristatus* and *Polygala calcarea* (Figure 3.7.7).

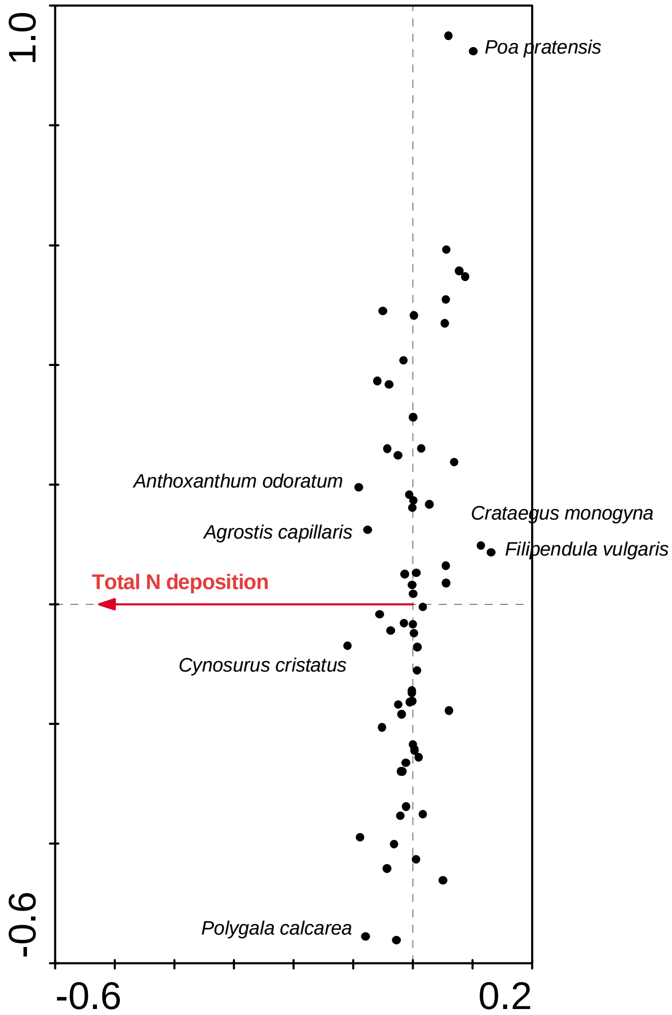


Figure 3.5.7. CCA ordination for lowland calcareous grassland showing markers for species which occur in more than 10% of quadrats. Labelled species are those most strongly positively or negatively associated with N deposition. Data from Natural England Grassland Database.

3.8 Plantlife Common Plant Survey

Due to the small amount of data in the common plants survey, once habitats had been selected it was not possible to statistically analyse the data so the data have been presented on graphs. Data were taken from 27 calcareous grassland sites and 10 heathland sites.

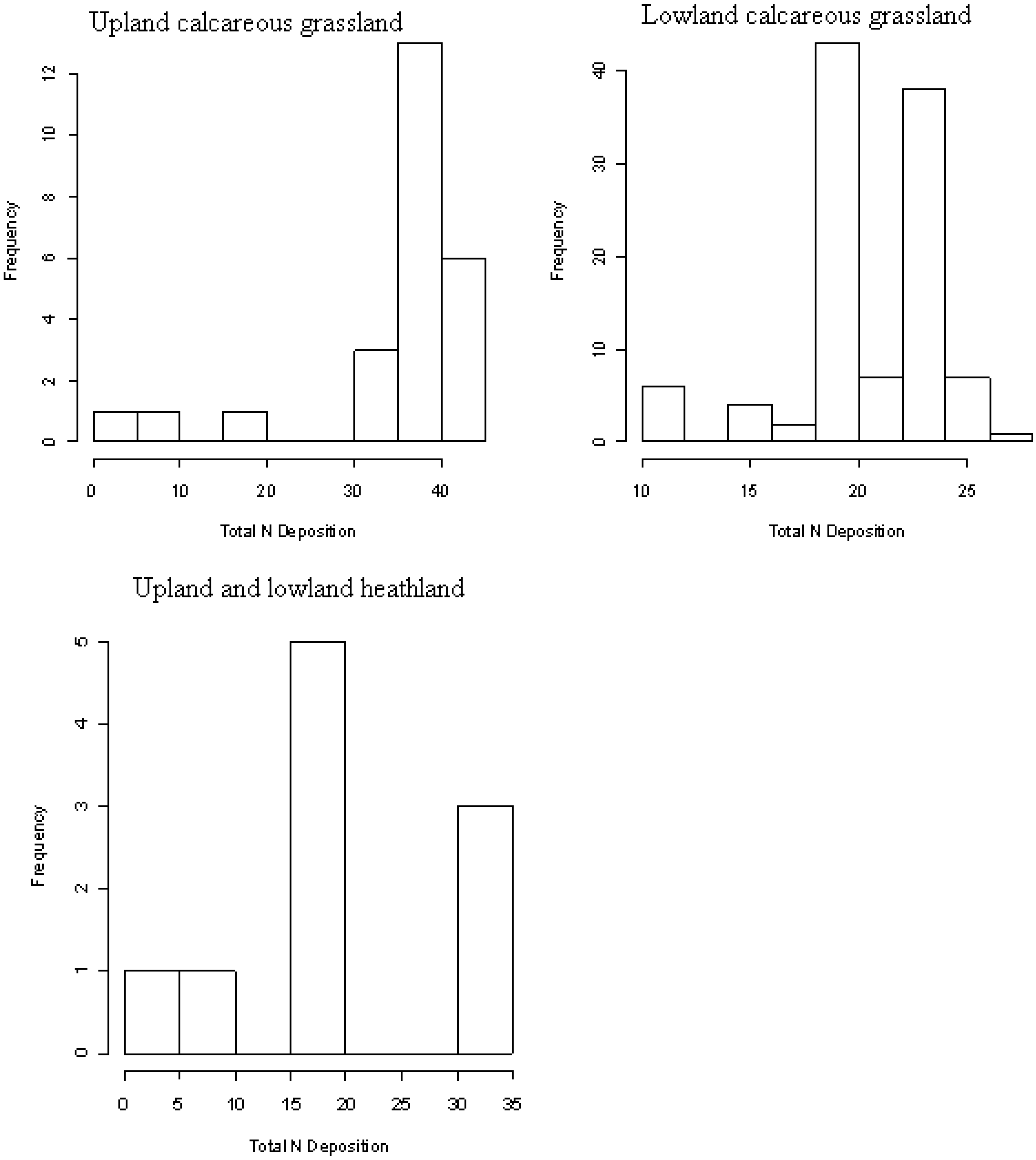


Figure 3.8.1. Range of total N deposition (kg N ha^{-1} yr^{-1}) covered by the Plantlife dataset. Calcareous grasslands have been split into upland and lowland but due to the very small dataset heathland have not.

The results presented are for change in presence between 2005 and 2008 (the period for which there was most data in the habitats of interest). As would be expected, during this relatively small time period few species showed changes in presence that could be related to N deposition. *Achillea millefolium* in calcareous grassland was the only species which showed a difference in change between these years that could be related to N deposition with a loss only apparent at high deposition. All species for which there were ten or more occurrences are shown in Figure 3.8.2.

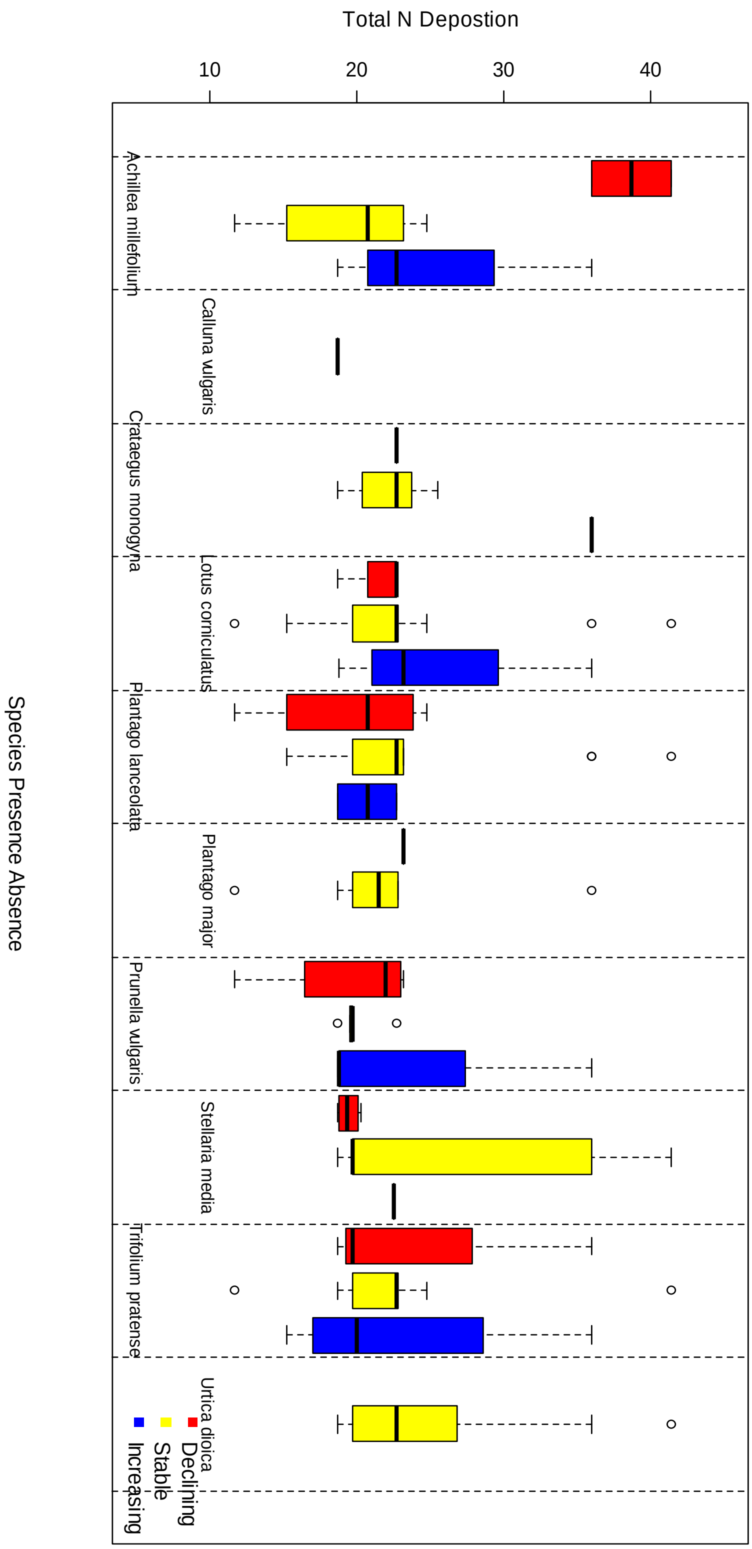


Figure 3.8.2. Change in presence between 2005 and 2008 for all species analysed. *Calluna vulgaris* is shown for heathland, all other species shown are in calcareous grassland. Data from Plantlife Common Plant Survey.

4 Discussion

This section of the report begins with a discussion on the models used to analyse the data (section 4.1.1). This is followed by an examination of specific issues or problems with each of the datasets that need to be considered when interpreting the data (section 4.1.2). The next section explores the responses of summary variables, beginning with a short general discussion (section 4.2), and then examining each habitat in turn (sections 4.3 to 4.6).

4.1 Interpretation of the analysis

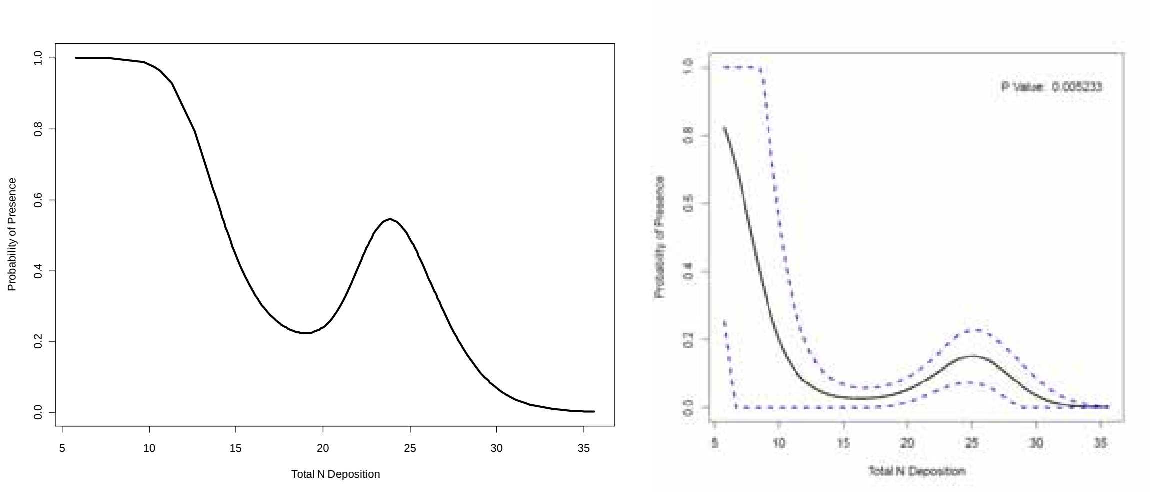
4.1.1 Data analysis

i Model Assessment

The unusual nature of some of the plots, which may not have an obvious ecological interpretation, reflects the fact that the natural world is a complex series of mechanistic and random processes that makes it hard to model. As such it is almost impossible to account for every single element that affects species occurrence. The approach taken here was to select a common list of driver variables thought to have the biggest influence on species distributions.

As can be seen in the results section and the appendices, there are a number of species that show relationships with N deposition that are not immediately ecologically interpretable. For example, some relationships show a clear hump at mid ranges of N deposition in addition to a general increasing or declining trend. To ensure that these relationships and inexplicable humps are not an artefact of the modelling technique, a number of species were re-analysed using a Markov Chain Monte Carlo (MCMC) approach. MCMC approaches, although time consuming to initialise and computationally demanding, require fewer assumptions in order to estimate the model parameters and are more flexible and detailed in the conceptual model that can be specified.

Results from these additional analyses showed the same relationships, including general trends and humps as in the original analysis. An example of *Bromopsis erecta* is shown in Figure 4.1.1, where we can see that, although there are slight differences between the two relationships, the “problematic” hump is present in both. As all analyses that were rerun showed the same relationships as in the original analysis, we can conclude that this was not an artefact of the modelling approach or the assumptions made within.



(A) **(B)**

Figure 4.1.1. Modelled relationship between presence of *Bromopsis erecta* in lowland calcareous grassland, using a) MCMC techniques and b) the original method outlined in section 2.

As we have discovered that some of the more unusual characteristics of the plots are not due to the statistical modelling approach adopted, we must stress circumstances, scenarios and caveats that could lead to such patterns. The first point to note is that when interpreting the model output we must be aware that although statistical models provide an excellent way of explaining, predicting and assessing data, we can only get out what we put in. That is to say that the model will return the best fit that the covariates we provide have to the data. The model will not tell us that any of these covariates are wrong, that they are serving as proxies for variables we have not accounted for or that they are highly correlated with a covariate not present in the model. So our ecological interpretation needs to take this into account as it is the user, rather than the model itself, that must draw the conclusions and make the ecological inference as opposed to the statistical inference.

ii Model covariates

As already mentioned, a number of covariates additional to N deposition were accounted for in the model as well as an extra purely spatial term. So any effect that these variables had on species occurrence was accounted for before looking into the effect that N deposition has. So if you believe sulphur deposition, for example, has the biggest influence on the outcome, then that has already been taken account of before we look at the relationship to N. Of course, N deposition may be correlated with other covariates in the model and this could have an effect on the relationships that we see in the plots. For example, some of the humps witnessed in the plots could be where mid-levels of N are highly correlated with favourable climates. So what the model sees is that there are a number of presences at the mid levels of N and models the relationship accordingly. In this case it would appear that mid levels of N lead to high species occurrence rather than our interpretation being connected with favourable climate, but it is extremely difficult to disentangle the effects of the two variables and determine which the true driver is.

If this was the case and the variables were correlated, we had a number of options: leave one of the correlated terms out; leave both terms out; or leave both terms in. In the approach we took, both terms were left in. This ensures that we accounted for all important terms in the model and did not subjectively leave out covariates. However, we had to be careful in our interpretation and, as with all statistical modelling, be careful to note that the resulting relationships are not necessarily cause and effect.

The inclusion of a purely spatial term accounted for differences over space that we cannot account for with the covariates we have available. Covariates with a strong spatial pattern, that we have not included, can be thought of as being accounted for by this term. Of course, missing covariates without a strong spatial pattern are missed altogether and if such a covariate was to be correlated in some way with N deposition, then this could also affect the relationships we see in the plots.

Finally, it is important to note that the data used in the analysis were not collected for the purpose of the modelling work undertaken. If we were to collect data specifically for this type of analysis, we should aim to sample evenly across the covariate space; we should aim to have as many observations at low N deposition values as we have observations at high N deposition levels. This would give a truer representation of the response at the extremes of the N distribution. Uneven sampling across the covariates could lead to the humps witnessed in some plots simply because there is more data in the mid region and hence possibly greater variability. For example, if we have only five observations with low N deposition, 50 at mid N deposition and five at high levels, then we may, by chance, see no presences at the low and high levels, but at the mid level see many presences and a few absences. This uneven sampling across the N deposition gradient and its effects can be seen when comparing some of the modelled relationships with the histograms of N deposition produced for each dataset.

iii Hectad and Tetrad Data

One of the problems with the grid cell data is that species presences apply to the tetrad or hectad species pool and not to specific habitat patches. The species pools were filtered to focus on those taxa likely to grow in the habitat of interest and grid squares were only included where they contained the habitat of interest. However, it cannot be assumed that all species were confined to just the focal habitat. The list is a filtered species pool rather than a sample from a stand of vegetation. This means that the results are not directly interpretable as expectations of change, nor of driver-state relationships on patches within any particular site. Within a tetrad or hectad, species populations on a specific SSSI may well not have changed in the way that the grid level mean Ellenberg N or species presence record had.

However, results from analysing the grid cell data do provide useful contextual information on wider changes across grid cells that contain the habitat of interest. It should provide a useful guide as to whether a designated site in a particular part of Britain is more or less vulnerable to N deposition based on the well characterised signal expressed at the larger scale. Filtering the species pool just for habitat preferentials also usefully focuses on species likely to be of concern on designated sites. This selection criterion means that more generalist species with high Ellenberg N values are under-represented and their changing patterns of occupancy cannot influence grid-square response variables. This is an important difference between the signals characterised in the grid cell data and those based on full species lists in the quadrat-scale data. Omitting these species is desirable since, at the hectad and tetrad scales, these species are by definition likely to have occurred in many other habitats and locations than just the focal habitat patches in the grid square. Also, generalist high Ellenberg N species would, in many cases, already be present at the grid square scale and so could not increase between surveys, thus dampening any signal of change.

iv Quadrat data

The quadrat datasets (CCW Grassland Survey, Natural England Grassland Database, and SNH NVC Survey) are not based on random or stratified random sampling so that they offer a somewhat biased representation of the variation in the vegetation types targeted (Smart and Scott, 2004). Some have cautioned against applying statistical tests to such data (Lájer, 2007) but this is a drastic step given the information that these large datasets potentially contain within them. The middle ground is to exercise caution in inferring analytical results to the wider population of vegetation types. This is particularly so if new randomly sampled monitoring data is placed within the ordination space defined by multivariate analysis.

While the biased sampling design used for the quadrat datasets poses statistical difficulties they were designed to represent as fully as possible the range of variation in vegetation types within each area of search. The datasets targeted patches of habitat where the species composition represents Priority Habitats, NVC units and Broad Habitats. This means that the constellations of quadrat data are ideally suited to defining an assessment space in which quadrats associated with the impact of higher N deposition could be compared with 'clean' quadrats from the same community type. An ordination of subsets of quadrat data could therefore provide the basis for a better quantitative visualisation of change over time in monitoring data on selected sites within the geographical range of the quadrat datasets. As with the options described for grid cell data, the approaches outlined are only useful if prior statistical analysis demonstrates a significant relationship between species composition and N deposition. We assume that these gradients have been found for the purposes of these illustrations.

4.1.2 Datasets

i Vascular Plant Database

The two surveys were both attempts to map the vascular plants of Britain and Ireland in 10-km grid squares. The first survey was pioneering; no such exercise had ever been attempted in the British Isles. By the time of the second survey such recording was a routine procedure for the botanical community (although not to all the individuals taking part, as inevitably some recorders for the New Atlas were inexperienced, at least at the start of the scheme). The two atlas volumes, the '1962 Atlas' (Perring and Walters, 1962) and the 'New Atlas' (Preston *et al* 2002) set out the history and methods of the surveys. Rich & Woodruff (1990) commented in more detail on some of the problems in interpreting data from the 1962 Atlas. Limitations of the data and possible problems of interpretation are discussed by Preston *et al* (2002) and summarised below.

a Time-spans

The 1930–69 survey covered a long period in which there was much floristic change, although the vast majority of records were made in the 1950s. However, the time period has to be extended back to 1930 as some areas (notably Dorset, Outer Hebrides) had been well-recorded in the 1930s and were not surveyed again.

b Recording intensity

The New Atlas was based on a more thorough survey than the 1962 Atlas (Preston *et al* 2002). More 10-km squares were recorded, and these were usually surveyed in more detail (particularly if the returns for the 1987–99 survey included the results of a county tetrad survey). Some coastal squares with only small areas of land were disregarded in the 1962 Atlas or the results were amalgamated with those in adjacent squares. For this reason, Telfer *et al* (2002) reported on the relative change of species rather than the absolute change, using results from only those squares which had been recorded to a certain minimum standard in the two surveys.

c Taxonomic problems

Taxa which were relatively new and unfamiliar in the 1950s were under-recorded in the 1962 Atlas; some of these were still under-recorded in the New Atlas but many were more familiar by 1987 and are much better recorded (e.g. *Dryopteris affinis*). As a rule of thumb, species described before 1850 are likely to have been well-understood by 1930 whereas most of the less inconspicuous segregates will have been described after 1850 and these are the species which may well be under-recorded in the first survey, or even in both.

d Alien species

Few alien species were recorded in the 1962 Atlas, in part because there were fewer species naturalised but also because the recording culture was different. The species, which were recorded, tended to be naturalised species well away from habitation, rather than planted in the wild or garden escapes growing only a few yards from gardens. However, a few species (e.g. *Aesculus hippocastanum*) were traditionally recorded even though they were rarely if ever naturalised. The main change in recording culture came about with the publication of the first edition of Stace's *New Flora* in 1991 (Stace, 1991), part-way though the second recording period.

ii BSBI Local Change

Broad-scale surveillance schemes, such as BSBI Local Change, cannot be repeated after an interval of 16 years with the same precision as a laboratory experiment or plot-based field trial. Such voluntary schemes are more challenging to standardise due to many factors. Those thought to have the greatest effect on the data gathered for BSBI Local Change are given below:

a Recording effort

Analyses of the raw data for BSBI Local Change showed a significant increase in recorded range in relation to the Monitoring Scheme for most species, typically by around 8%. As with the New Atlas dataset, this relates to better recording in the most recent survey over the first, presumably due to improvements in voluntary recording, taxonomy and field skills, as well as coordination of large-scale surveys.

b Geographic coverage

The sample design (A,J,W tetrads in 1 in 9 hectads on a systematic grid) gave a possible 811 tetrads for analyses across England, Scotland and Wales of which 755 were visited during both surveys. Of these 635 were deemed comparable for analyses after excluding difficult taxa, taxa displaying dramatic changes and tetrads where overall refined rates were lower than 57% (see Braithwaite *et al* 2006 for details). It is clear from the map given below (Figure 4.1.1) that these factors make data from some areas less 'comparable' although the extent to which these might affect spatial analyses is unknown. Having said that, a simplified analysis of three regional groupings of tetrads (based on January temperatures) showed no significant regional bias in refind rates (Braithwaite *et al* 2006).

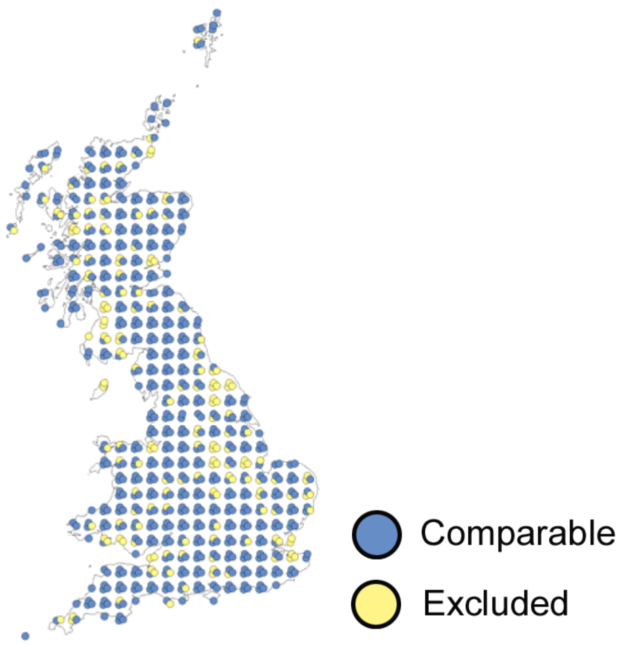


Figure 4.1.1. Map showing tetrads identified as comparable and not comparable in the BSBI Local Change survey.

c Approaches to field recording

One of the most pronounced differences between the two surveys was the treatment of alien species. The Monitoring Scheme instructions requested that plants obviously cultivated or planted should be excluded. In the second, BSBI Local Change survey, recorders were encouraged to record all species recorded in the 'wild' whether they were planted or not. This was made possible by the availability of Clive Stace's (1997) New Flora of the British Isles (second edition) which covers all taxa likely to be encountered in the wild. This different approach means that comparisons were not possible for species that are frequently found planted and more generally for alien species covered by Stace (1997) but not by earlier standard floras.

A second factor was the extent to which 'routes' surveyed during the Monitoring Scheme were available (as paper 1:25000 OS maps) and resurveyed exactly during BSBI Local Change. These were only available for some areas but no data were available to analyse if this had an effect on overall refind rates.

A third factor was the time taken to record a tetrad. Recorders were asked to spend no more than ten hours in a tetrad (broken into three visits) but, inevitably, more time was spent attempting to relocate species in BSBI Local Change. Unfortunately, no data were available to assess whether this had an effect on the overall results.

iii British Lichen Society Database

The suitability of the BLS database for this project is currently limited by patchy coverage of parts of England and Wales, although Scotland and northern England are well covered. The BLS is currently running a major project to collate all available records for England and Wales. To ensure that terricolous sites (those with significant populations of lichens growing directly on the soil) were well-represented in the database throughout the country for this project, BLS gave priority to loading some 16,000 records for grasslands, heathlands and metal mines. This may have resulted in some geographical bias towards the more lichen-rich areas, but overall this is compensated by the more comprehensive coverage of the mapping scheme data which was also included in the data analysis. There may also be some temporal bias, as many of these sites in the new records have not been surveyed recently.

Terricolous lichens are rarely entirely restricted to the target habitats and can also be found on associated rock outcrops, rotting wood, walls and other substrates. The species selected for analysis were chosen, based on expert opinion, as being species strongly associated with one or more of the habitats. However, it was necessary to include dunes and calaminarian grassland (metal mine spoil and other contaminated ground) within calcareous grassland. These subsidiary habitats often have characteristics of both acid and calcareous grassland, as pedogenesis leads to acidification, and are difficult to classify. If these habitats occur in the same hectad as the habitats that are the focus of this study, it is not possible to separate which habitat the lichen was recorded in.

Lichen populations are changing rapidly in some parts of the country. To identify trends over time and associate them with different factors it would be necessary to use dated records and revisits to known sites. Population changes are first apparent as a change in abundance as species increase or decline. Records of species presence without abundance conceal these changes until the species is lost, so there can be a significant delay before the effect shows in the data. There may be some temporal bias in the BLS databases as many of the terricolous sites have not been surveyed recently. Unfortunately, there were insufficient dated and repeat records for the species of interest to permit analysis of records on a temporal basis in this project. Therefore, care must be taken when interpreting the data because records were collated over a long period of time (1960 to 2009 inclusive), consequently species that have declined since 1960 will still be recorded as present.

This information is taken from an unpublished report from the BLS to JNCC (Simkin, unpublished).

iv British Bryological Society Database

The records of bryophytes in the BBS database held at BRC are those collected for the *Atlas of the Bryophytes of Britain and Ireland* (Hill *et al* 1991-94) plus those added to the database after publication. The source of the 0.75 million records on which the published *Atlas* was based is described therein; almost all were collected by volunteer recorders from 1950 onwards. For a brief discussion of the patterns of recording since then, which have resulted in an additional 1.25 million records, see Preston *et al* (2009). From the point of view of the current analysis, the accumulated records if aggregated from 1950 onwards represent a good national coverage (Figure 4.1.2). However, there may of course have been changes in the distribution of species since 1960 (although the habitats in which most change has been apparent are not included in the present study). Species which were not understood in 1950 will be recorded patchily and they will be known only from the areas which have been surveyed since their taxonomy was clarified; similarly species which are expanding in range may not be well recorded from areas which have not been well-surveyed in recent decades. Only a few areas have been surveyed and resurveyed since 1960 so it is not possible to analyse changes of distribution over time using the same methods as those employed for vascular plants.

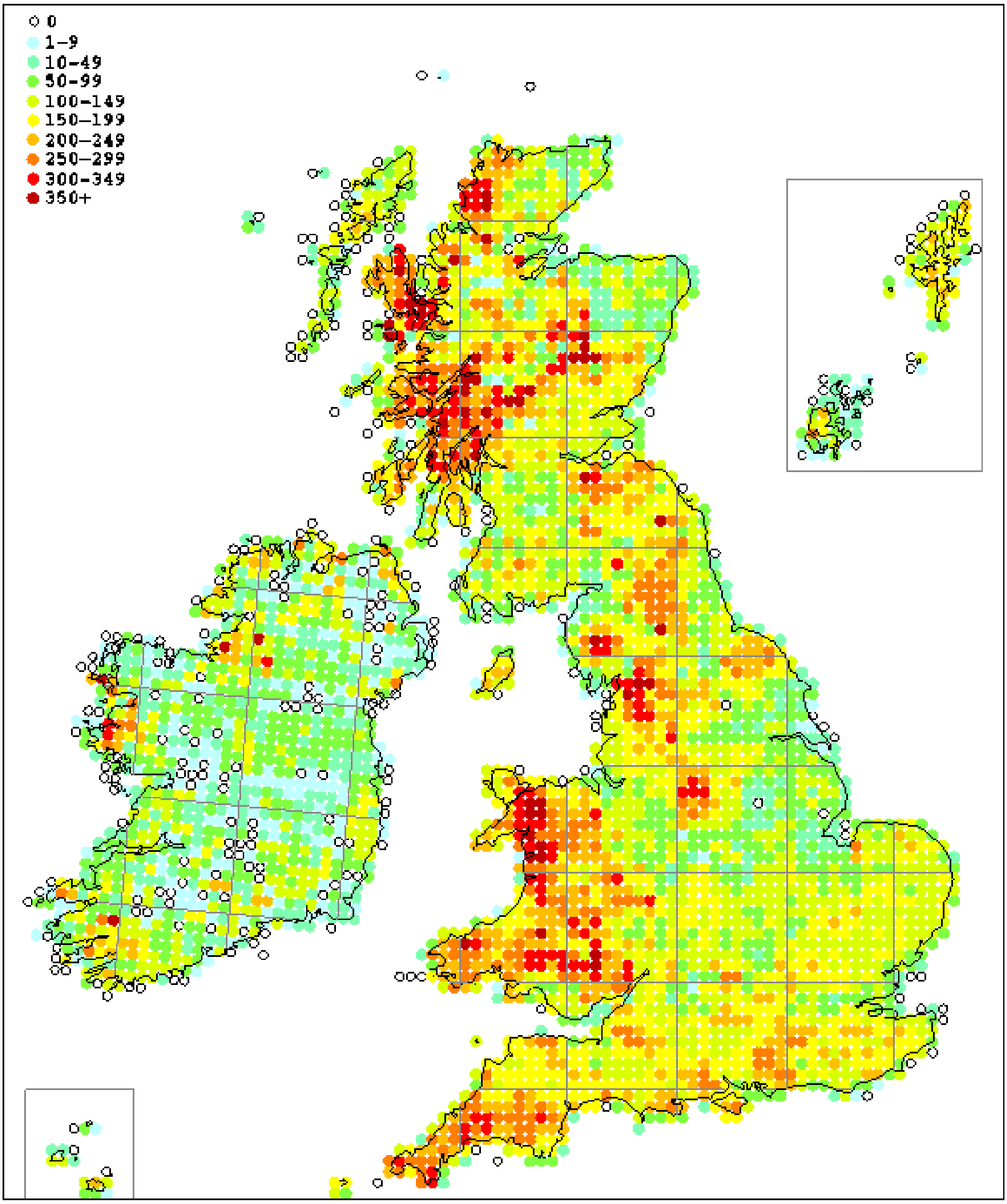


Figure 4.1.2. Bryophyte species richness in accumulated records if aggregated from 1950 onwards. BBS data.

a Quadrat datasets

CCW Grassland Survey, Natural England Grassland Database and SNH NVC Survey.

b Unequal sampling along the N deposition gradient

It was apparent that the numbers of plots varied greatly along the deposition gradient. Because sampling was not designed to achieve equal coverage, variation in sampling effort translated into uneven representation of the N deposition gradient such that modal deposition was naturally represented by more plots than less common values of N deposition within each sampled region.

c Biased sampling

NVC methodology requires that sampled vegetation is homogenous and representative of the stand. Thus, sampling is consistent with a phytosociological approach (Rodwell, 1991 *et seq*). However, if N deposition results in a species composition with a poorer fit to an NVC unit it is likely that such assemblages will not be targeted as representative samples by surveyors. Indeed the more impacted the vegetation type then the greater the chances that surveyors will avoid the assemblage. This is also a weakness of spatial analyses where datasets are classified by floristic criteria used to define each vegetation type. For example if all plots selected for analysis are initially chosen on the basis that they are representative of the range of calcareous grassland NVC units then any plots whose floristic match to calcareous grassland has been weakened by eutrophication or acidification are less likely to be included thus reducing the chance of detecting these impacts. Smart & Scott (2004) showed that samples constrained by the need to represent phytosociological units such as the NVC, result in constrained distributions of Ellenberg indicator values. This reduces the power of detecting vegetation-environment relationships. These issues probably explain why few or only weak relationships were found in these data even though others have found stronger relationships based on analysis of stratified random samples (Maskell *et al* 2010; Stevens *et al* 2004). The impact of bias in quadrat data sampled to be representative of plant communities, rather than sampled at random, are well known (e.g. Palmer, 1993). Lájer (2007) viewed the biased nature of phytosociological datasets as so severe that they should never be subject to statistical analysis. Others have taken a more liberal approach since the results of analyzing such datasets can still be interpreted if the impacts of sampling bias are recognized and to some extent expected to show themselves in the patterns detected. However, it is apparent that the issue of bias needs careful consideration. The key message seems to be that the absence of a clear signal in such data is not good evidence of the absence of large-scale impacts. There was a large amount of variability in the results of driver variables for the quadrat data. With further analysis, variability could be reduced by taking average values at a site level rather than a quadrat level; however, it may be that these data are unsuitable for this type of analysis.

On balance the NVC quadrat datasets analysed in this report did not present signals consistent with Countryside Survey regarding changes in species richness, mean Ellenberg N and mean SLA. However, the results for mean Ellenberg N change based on the hectad and tetrad species pools, were highly consistent between habitats and datasets, with ten significant positive correlations between N deposition and mean Ellenberg N, and two negative correlations. This suggests that, despite high sample numbers and adequate coverage of N deposition gradients, properties of the NVC quadrat datasets may be reducing the detectability of expected correlative relationships.

As a consequence of the problems with the quadrat data we place less emphasis on it in the following discussion.

4.2 General discussion of habitat responses

4.2.1 Summary variables

i Ellenberg N

For all of the habitats there was a general trend for increasing Ellenberg N in the spatial analysis scores indicating an increase in fertility with increasing N deposition. Generally, the quadrat data results (CCW Grassland Survey, Natural England Grassland Database, and SNH NVC Survey) were not as clear as the large scale data with much variability and few significant results but this may be because the data is not suitable for showing that relationships exist (see section 4.1.2).

In general there were stronger results from spatial analysis than the temporal analysis. This could indicate that the change had already occurred prior to the data in the temporal analysis being recorded, although it could also be, that without cover-weighting, Ellenberg N is less suited to detecting change on a temporal basis. Difficulties in detecting temporal trends were also found in Countryside Survey; Smart *et al* (2004) found a significant positive relationship between temporal change in mean Ellenberg N and total N deposition between 1990 and 1998 but only when a cover-weighting was applied.

Across all habitats the bryophyte changes in Ellenberg N are all very small and scores remain low.

ii Ellenberg R

Ellenberg R showed very few significant changes with N deposition within the datasets analysed. This is surprising, as several studies have found clear evidence of soil acidification (e.g. Skiba *et al* 1989; Stevens *et al* 2009a) in the UK associated with acid deposition. The lack of relationship found in this analysis is presumably due to the removal of S deposition (and consequently all co-variation with N deposition) as a driver in the statistical modelling method. While N deposition is of increasing importance for acidification, historic levels of S deposition remain an important factor determining soil acidification.

iii Specific leaf area and canopy height

Specific leaf area has been suggested as an indicator of plant strategies (e.g. Wilson *et al* 1999) with higher SLA indicating increased competitive ability. Competitive species also tend to be taller, forming a higher canopy. With the potential for increased N availability at high N deposition we might expect competitive species to increase. We would expect these measures to perform in a similar way to Ellenberg N scores; however, neither measure seemed to be as sensitive a measure as Ellenberg N scores, sometimes returning non-significant results when Ellenberg N score returned significant ones. There was one case where SLA returned a significant positive result but Ellenberg N score did not; this was for upland acid grassland in the Vascular Plant Database.

iv Species diversity and richness

Analysis of species diversity and richness could only be conducted on quadrat data although these datasets are subject to the problems outlined in section 4.1.2. This means that we are less likely to detect trends using data collected from an NVC rather than survey data collected using random sampling. Although some significant results were detected very few of these showed clear trends, many being subject to large amounts of scatter and/or the influence of outlying points. From previous work we may have expected to see a negative relationship between species richness and diversity and N deposition (Dupré *et al* 2010; Maskell *et al* 2010; Stevens *et al* 2004) and, although this was the case in some habitats and datasets (species diversity and richness in lowland acid grassland, species diversity in upland acid grassland - Countryside Council for Wales Grassland Survey, species diversity and richness in lowland bog and species diversity in lowland heathland - Scottish Natural Heritage NVC Survey), for many the results were less clear. Several habitats showed hump-backed relationships with N deposition but in all cases the scatter was too great to suggest that these are ecologically relevant relationships. Using a site average for species richness and diversity would have reduced the scatter in the relationship but although this may have increased the number of relationships, in many cases looking at the data suggests that relationships would still not have shown clear increases or decreases in richness and diversity.

Because species richness does not account for evenness of species distribution, species diversity is more likely to detect changes in the NVC data. Although assessing cover can be time consuming, this must be done for the assessment of NVC community so in this case it would certainly be preferable to use species diversity rather than richness to assess impacts.

Tables for the results of the summary variables are presented below (Tables 4.1 and 4.2).

Table 4.1. Results of analysis of summary variables (Ellenberg N score, Ellenberg R score, plant height and SLA) for different habitats in: Vascular Plant Database (VPD) from spatial and temporal analysis, BSBI Local Change Survey (BSBI) from spatial and temporal analysis, British Bryological Society Database (BBS), Natural England Grassland Database (NE), Countryside Council for Wales Grassland Survey (CCW) and Scottish Natural Heritage NVC Survey (SNH). + indicates a positive relationship with N deposition, - indicates a negative relationship, ns no significant relationship, Hb a hump-backed distribution (a significant quadratic relationship, possibly due to greater variation at intermediate values) and a blank cell that there was insufficient data for analysis or that the analysis was not performed.

	VPD spatial	VPD temporal	BSBI spatial	BSBI temporal	BBS	NE	CCW	SNH
Lowland acid grassland								
Ellenberg N	+	+	+	-	+	ns	ns	Hb
Ellenberg R	ns	ns	ns	ns	ns	ns	ns	Hb
Plant height	+		ns			ns	Hb	ns
SLA	+		ns			ns	ns	Hb
Upland acid grassland								
Ellenberg N	ns	ns	ns		+		Hb	-
Ellenberg R	ns	ns	ns	ns	ns		Hb	-
Plant height	ns		ns				ns	ns
SLA	+		ns				ns	-
Lowland calcareous grassland								
Ellenberg N	Hb	ns	+	ns	ns	-	ns	
Ellenberg R	ns	ns	ns	+	ns	-	Hb	
Plant height	ns		ns			ns	Hb	
SLA	ns		+			-	+	
Upland calcareous grassland								
Ellenberg N	+	ns	ns	+	ns			+
Ellenberg R	ns	ns	ns	+	ns			ns
Plant height	+		ns					ns
SLA	+		ns					+
Lowland bog								
Ellenberg N								+
Ellenberg R	ns	ns						ns
Plant height	ns	ns						ns
SLA	ns		ns					ns
Upland bog								
Ellenberg N	+	ns	ns		+			Hb
Ellenberg R	ns	ns	ns	-	+			Hb
Plant height			ns					-
SLA	ns		ns					Hb
Lowland heathland								
Ellenberg N	+	ns	+	-	ns			-
Ellenberg R	ns	+	-	ns	ns			ns
Plant height	+		-					ns
SLA	ns		ns					-
Upland heathland								
Ellenberg N	+	Hb	ns		+			ns
Ellenberg R	ns	ns	ns	+	ns			-
Plant height	ns		ns					-
SLA	ns		ns					Hb

Table 4.2. Results of analysis of summary variables (species richness and diversity (Shannon-Wiener diversity index)) for different habitats in: Natural England Grassland Database (NE), Countryside Council for Wales Grassland Survey (CCW) and Scottish Natural Heritage NVC Surveys (SNH). + indicates a positive relationship with N deposition, - indicates a negative relationship, ns no significant relationship, Hb a hump-backed distribution and a blank cell that there were insufficient data for analysis or that the analysis was not performed.

	NE	CCW	SNH
Lowland acid grassland			
Species richness	Hb	-	+
Species diversity		-	+
Upland acid grassland			
Species richness		ns	Ns
Species diversity		-	Ns
Lowland calcareous grassland			
Species richness	Hb	ns	
Species diversity		ns	
Upland calcareous grassland			
Species richness			Ns
Species diversity			Ns
Lowland bog			
Species richness			-
Species diversity			-
Upland bog			
Species richness			Ns
Species diversity			Hb
Lowland heathland			
Species richness			Ns
Species diversity			-
Lowland heathland			
Species richness			Hb
Species diversity			Hb

4.2.2 Individual species responses

i Vascular plants

a Spatial and temporal analyses of the effects of N deposition

Spatial and temporal analysis of individual species responses to N deposition are presented for each habitat below. It is very difficult to identify common features for the species which show positive or negative responses to N deposition. It seems that many of the species responding negatively to N deposition have low Ellenberg N values as we may expect. However, a low Ellenberg N value does not mean that a species will be negatively associated with N deposition.

b Quadrat data

Comparison between the CCAs for the different quadrat datasets (CCW Grassland Survey, Natural England Grassland Database, and SNH NVC Survey) is not straightforward because the range of deposition differs between the datasets; the Scottish Natural Heritage data has a much more limited range of deposition than the other two datasets with maximum deposition of 25 kg N ha^{-1} yr^{-1}. Species also occurred in some of the datasets but not in others and it must be considered that if a species is rare within a dataset its result may not be reliable. Therefore, in order to compare the outcomes of the ordinations for the different datasets, the species identified as most strongly associated with high or low deposition that occurred in more than 10% of quadrats for each dataset will be compared, considering their axis scores in the other datasets.

As a consequence of the problems with the data identified in section 4.1.2, although comparisons can be made between the quadrat data and the tetrad and hectad data, we must place more emphasis on the larger scale data in drawing conclusions.

ii Bryophytes

The individual species data for bryophytes are difficult to interpret with some species increasing and other decreasing but we cannot identify any general trends in the data. Bryophytes are small and most live in a world which is restricted to a few cubic centimetres at the air/substrate interface. Their habitats are therefore often best characterised by features of the microhabitat rather than of the broad habitat (they might grow, for example, on shaded calcareous stones or masonry or on disturbed acidic soils wherever these are found). Many therefore occur in many Broad Habitats. Statements below on the habitat requirements of species are based on Hill *et al* (1991-94) unless otherwise stated. Few of the species have been investigated previously in terms of their response to N deposition. The species selected for analysis were those for which the relevant Broad Habitat is one of their usual habitats; the species analysed therefore include many which often grow just as frequently (or more frequently) in several other Broad Habitats. An alternative approach is to select for specialists but this reduces the list to a much smaller number of species, many of which are rare. Another potential problem is whether the wetness of the climate is adequately described for bryophytes by the total annual precipitation term which is included in the model, rather than a measure such as the number of ‘wet days’ which Ratcliffe (1968) argued was a better predictor of the distribution of oceanic bryophytes. Finally, any interpretation is handicapped by the paucity of experimental studies of the response of bryophyte species to varied levels of N.

iii Lichens

Lichens are potentially very sensitive to air quality and they have been widely used for biomonitoring of air pollutants, especially sulphur dioxide (Hawksworth and Rose, 1970). Lichens are adapted for direct uptake of nutrients deposited from the atmosphere through their thallus surface making them vulnerable to changes in atmospheric chemistry. Both changes in species composition and community structure (Davies *et al* 2007; Welch *et al* 2006) and changes in the chemistry of lichen tissues have been associated with N deposition (Britton and Fisher, 2008; Hogan *et al* 2010a; Hyvarinen and Crittenden, 1998). Some lichen species are more sensitive to N deposition than others and an index has been created with lichen species found on trees classified according to their sensitivity to N and bark pH based on their response to ammonia concentration (Wolseley *et al* 2008). Epiphytic lichen species show a range of sensitivities to N deposition and, as such, have been suggested as indicators of N deposition in Atlantic oak woodlands (Mitchell *et al* 2005). Due to the habitats selected for this study the focus of this project was on terricolous lichens which have received much less research attention than epiphytic lichens.

The results of the analysis conducted in this project also indicate that some species are more sensitive than others. In all of the habitats there was a mix of species which responded negatively to N deposition as well as those that showed no significant relationship with N deposition. There were no species which showed a positive relationship with N deposition which highlights the sensitivity of terricolous lichens to N deposition.

4.3 Acid grassland

4.3.1 Summary variables

i Ellenberg N

In lowland acid grassland Ellenberg N showed an increase in the spatial analysis of all of the large-scale datasets. This gives a very clear signal that mean Ellenberg N is higher at high deposition, indicating increased fertility. However, the magnitude of these changes was generally quite small. Spatial analysis of both the Vascular Plant Database and BSBI Local Change Survey data showed an increase of approximately one unit on the Ellenberg N scale between deposition of 5 and 35 kg N ha^{-1} yr^{-1}. Both showed approximately linear increases across the deposition range. Bryophytes showed a much smaller response and a slightly different shape curve with a change of 0.2 units between 5 and 20 kg N ha^{-1} yr^{-1} and then no further change.

Temporal analysis of the Vascular Plant Database also showed an increase in Ellenberg N score over time in areas of high N deposition but not in areas of low deposition. The results of the Vascular Plant Database analysis show that between the two survey periods (1930 to 1969 and 1987 to 1999) Ellenberg N scores changed very little or were even slightly reduced at lowest levels of deposition but between 10 and 35 kg N ha^{-1} yr^{-1} they showed small increases (<1 unit). Above 35 kg N ha^{-1} yr^{-1} increases were much larger. The BSBI Local Change Survey data showed small reductions in Ellenberg N score over time which may represent different changes during the more recent time period of the survey (1987-88 and 2003-04). Here, Ellenberg N score shows very little change up to 25 kg N ha^{-1} yr^{-1} and then shows a reduction between the two surveys at higher levels. This could indicate recovery but given that total deposition of N has not changed significantly since 1990 (RoTAP, In Preparation) the result should be interpreted with caution.

For upland acid grassland only bryophytes showed a significant change in Ellenberg N score with results very similar to lowland acid grassland. It is somewhat surprising that lowland acid grassland appears to show more change than upland acid grassland. Due to their tendency to have soils with a lower nutrient status, we might expect upland grassland to be more sensitive. However, for upland acid grassland the lack of a convincing Ellenberg N score response to N deposition is not entirely surprising, as this has also been found in Countryside Survey and a research scale spatial survey (Maskell *et al* 2010; Stevens *et al* 2010b). Analysis of the most recent survey datasets from 1998 and 2007 have found a positive spatial correlation but this analysis combined acid, calcareous and neutral grassland from upland and lowland Britain (ROTAP, In Preparation).

ii Ellenberg R

The lack of response of Ellenberg R to N deposition may be due to the restricted number of vascular plant species used in the tetrad and hectad surveys analysed. In acid grassland, Stevens *et al* (2010b) and Maskell *et al* (2010) found a clear signal from Ellenberg R scores and an index of soil acidity preference. It may be that changes in preference for acidity are best detected with the full range of species so that changes in species that are less typical of the acid habitat or do not have a strong preference for an acid habitat can be seen. A negative relationship was detected in the Natural England Grassland Database indicating acidification with N deposition.

iii Specific leaf area and canopy height

We would expect both SLA and canopy height to perform in a similar way to Ellenberg N scores; however, neither measure seemed to be as sensitive a measure as Ellenberg N scores, sometimes returning non-significant results when Ellenberg N score returned significant ones. However, in upland acid grassland in the Vascular Plant Database SLA returned a significant positive result but Ellenberg N score did not.

Analyses of mean SLA in Countryside Survey plots in semi-natural grassland have detected correlations consistent with an eutrophication effect. These were spatial rather than temporal signals and only detected across the most recent two surveys in 1998 and 2007 (ROTAP, In Preparation).

iv Species diversity and richness

From previous work in acid grasslands we may have expected to see a negative relationship between species richness and diversity and N deposition (Dupré *et al* 2010; Maskell *et al* 2010; Stevens *et al* 2004) and although this was the case in some of the acid grassland datasets in this study (species diversity and richness in lowland acid grassland, species diversity in upland acid grassland - Countryside Council for Wales Grassland Survey), for others, the results were less clear.

Positive relationships reported for species richness and diversity in lowland acid grassland in the Scottish Natural Heritage NVC Survey were accompanied by much residual scatter and cannot be considered of ecological significance. In contrast, negative species richness and N deposition relationships for acid grassland have been very apparent in Countryside Survey and other analytical surveys (Maskell *et al* 2010; Stevens *et al* 2004; 2006). Analysis of all semi-natural grassland plots in Countryside Survey also showed a temporal relationship between 1978 through to 1998, with species richness declining more over time at higher N deposition (ROTAP, In Preparation).

4.3.2 Individual species responses

i Vascular plants

a Spatial analyses of the effects of N deposition

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 above c.20 kg N ha^{-1} yr^{-1}. With the exception of *Viola canina* all are small, low-growing or prostrate species of dry acid grassland in the south and east of England (i.e. *Cerastium arvense*, *C. semidecandrum*, *Trifolium arvense*, *Vicia lathyroides*). All have low Ellenberg N values. There are a number of species with low Ellenberg N values which do not show negative responses as might have been expected, but the reasons for this are likely to differ between species and could be related to levels of other soil nutrients.

Unfortunately, the BSBI Local Change Survey dataset did not contain sufficient data for lowland acid grassland species to test the effects of N deposition and to enable us to confirm whether there were consistent trends. 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 Survey dataset.

b Temporal analyses of the effects of N deposition

For lowland acid grassland, five of the eight species with significant trends in the Vascular Plant Database displayed negative responses suggesting an overall negative impact with increasing N deposition in this habitat. The small magnitude negative responses of two of these species were consistent with the spatial analyses (*Cerastium semidecandrum*, *Trifolium arvense*). Two other species displayed a similar small magnitude response (*Trifolium ornithopodioides*, *T*. *subterraneum*). All these species are very small low-growing or prostate plants (<10 cm tall) of open vegetation on nutrient-poor soils that might be expected to decline under increased competition in taller swards (e.g. *Myosotis ramosissima*, *Ornithopus perpusillus*, *Trifolium micranthum*). All of these species have low Ellenberg N values. Only *Senecio sylvaticus* displayed a different response increasing to an optimum at around c.20 kg N ha^{-1} yr^{-1} and then falling. The reason for this hump-backed relationship is not understood but might reflect an expansion in range in more westerly populations, where much suitable habitat still exists, but a contraction in areas of high N deposition where its habitat has declined.

Unfortunately, the BSBI Local Change Survey dataset did not contain sufficient data for lowland acid grassland species to test the effects of N deposition and to enable us to confirm whether there were consistent trends.

In comparison there were only sufficient data to analyse two upland acid grassland species, both in the Vascular Plants Database (*Nardus stricta*, *Viola lutea*), but neither displayed significant responses.

c Quadrat data

All NVC communities of type ‘U’ were included in this analysis which includes some tall herb grasslands. This means some species identified are not typical of all acid grassland community types. Of the species identified as positively associated with N deposition in lowland acid grassland, three species showed a consistent effect across the datasets. The first of these was *Calluna vulgaris*. In heathland in the Netherlands *Calluna vulgaris* has been shown to decline dramatically with high N deposition in combination with attacks from the heather beetle, drought and frost (e.g. Brunsting and Heil, 1985; Heil and Diemont, 1983; Power *et al* 1998). However, although stress tolerant and able to withstand low nutrient conditions and very acid soils, *Calluna vulgaris* is a relatively competitive species (Grime *et al* 2007) and some experiments have shown beneficial effects of N deposition on *Calluna vulgaris* including increased growth (Britton and Fisher, 2008). The majority of work has been focussed on *Calluna vulgaris* in heathland but Dupré *et al* (2010) found no change in the relative frequency of *Calluna vulgaris* in quadrats from acid grassland in Great Britain pre- and post-1975. It is possible that this positive association results from an increase in heathland heavily damaged by N deposition and undergoing conversion to grassland being classified as grassland rather than heathland; the result must be interpreted with caution and further investigation is needed to confirm this. *Cirsium palustre* also showed a positive response in all datasets; this is a species whose life history strategy is intermediate between competitor and ruderal (Grime *et al* 2007) so is the type of species we may expect to increase with N deposition.

The final species to show a positive response in lowland acid grassland was *Deschampsia flexuosa*. This species showed a positive response in the Natural England and Countryside Council for Wales' datasets although there was no response in the Scottish Natural Heritage data. However, given the lower range of deposition covered by the lowland acid grassland in Scotland, this may be because there are insufficient sites of high deposition for this to be apparent or that deposition is not high enough to have an effect on this species. *Deschampsia flexuosa* is a species that has been observed to increase in response to N deposition in heathlands, replacing *Calluna vulgaris* as the dominant species, so is a species we may expect to increase (Britton *et al* 2003; Brunsting and Heil, 1985). As with *Calluna vulgaris*, described above, it is difficult to determine in this dataset whether the grasslands evaluated here are all grasslands or if some of the grasslands recorded at high deposition are in fact degraded heathland.

Veronica chamaedrys showed a negative response in all three datasets although this response was not as strong in the Scottish Natural Heritage data. *Veronica chamaedrys* is typical of intermediate fertility situations so it is somewhat surprising that it is identified as responding negatively to N deposition, but as a species of typically small stature it may be out-competed by taller plants. It is a species typical of weakly acid or neutral soils so may be impacted by acidification (Hill *et al* 1999). The same is true of *Poa pratensis*. This species showed a negative response in the Natural England and Countryside Council for Wales' datasets but showed a slightly positive response in the lower deposition Scottish Natural Heritage data. Several of the species identified as associated with low deposition were only found in one dataset. Although this does not mean that the effect is not real, it does mean we have less confidence in it than if it were apparent in several independent datasets.

Both of the upland acid grassland datasets were biased towards low deposition, with no sites with deposition greater than 25 kg N ha^{-1} yr^{-1}. This makes it difficult to interpret in terms of national deposition patterns. Many of the species identified as being associated with high or low deposition were only found on one or other dataset and the large number of tree and scrub species identified in the SNH data suggested that NVC classification might have been problematic in upland and lowland acid grassland. One species from the Countryside Council for Wales' survey, *Ajuga reptans,* did show a common association with low deposition. Although not a species of particularly low nutrient status, this species is commonly associated with weakly acid to neutral soils (Hill *et al* 1999) so may be impacted by acidification.

ii Bryophytes

Very few bryophytes are grassland specialists, although many occur in open grassland communities as well as in other habitats. For upland acid grassland there is a significant decrease in the probability of the presence of *Frullania tamarisci*, *Racomitrium lanuginosum* and *Scapania gracilis* with increasing N deposition. Although *F. tamarisci* is a plant of many habitats (it also grows on rocks and as an epiphyte), it is very sensitive to competition in grassland and there is evidence that it has decreased in calcareous grassland in S. England as a result of lack of grazing and agricultural improvement (Porley and Rose, 2001). Its exclusion from grassland with high levels of N deposition is therefore plausible. *R. lanuginosum* is a species that is particularly sensitive to N deposition and experiments and regional surveys have both shown strong reductions in this species in relation to N deposition (Baddeley *et al* 1994; Pearce and van der Wal, 2002). *Scapania gracilis* is an ecologically wide-ranging species (often found in abundance on rocks, tree bases and decaying wood) but it is one which is much more restricted to the north and west. The result of the analysis is intriguing and deserves further investigation, as it is a species which one would expect to be limited by climatic factors.

The species which show a positive correlation with N deposition in upland acid grassland are a heterogeneous group. *Racomitrium ericoides* is a relatively recent segregate of the *R. canescens* aggregate and is not well-recorded. *Gymnocolea inflata* is a low-growing liverwort of bare, very acidic soils, often in seasonally droughted habitats; it is very tolerant of both SO_2 and heavy-metal pollution. *Sanionia uncinata* is not as frequent as one might expect from its wide habitat range; in both Wales and Scotland it is notably commoner in the east than the west. *Archidium alternifolium* is a calcifuge of open, often trampled soil, especially in coastal areas. Like the result for *Scapania gracilis*, these results invite further and more detailed study.

There were insufficient data to analyse lowland habitats for bryophytes.

iii Lichens

In acid grassland *Cetraria aculeata* and *Peltigera didactyla* both showed clear negative responses to N deposition. For both of these species their probability of presence was reduced to approximately half by 15 kg N ha^{-1} yr^{-1} with both species reaching very low probabilities of presence at high deposition. The sensitivity of *Cetraria aculeata* to N deposition in acid grassland is well known. In a survey of acid and calcareous dune grassland, Remke *et al* (2009) found that *Cetraria aculeata* was absent from high N deposition sites although they suggest no mechanism for this loss. Experimental studies concerned with SO_2 deposition have shown that *Cetraria aculeata* is sensitive to acid deposition (Hauck, 2008). Acid deposition from NO_3 is a possible mechanism for its decline along the GB spatial gradient. *Peltigera didactyla* forms stable symbioses with N-fixing cyanobacteria but little has previously been reported regarding its sensitivity to N deposition.

Although there are other species in the dataset for which we may have expected to see declines in relation to N deposition these may not be apparent for several reasons. The collation of data over such a long time period means that the analysis conducted is somewhat insensitive. Although current S deposition was removed from the models before N deposition so changes are isolated to N deposition, the distribution of current S deposition does not necessarily reflect historic levels. If lichen populations were lost from hectads since 1960 this would not have been detected from the data. This means that species which did not show significant results in this analysis cannot be described as insensitive to N deposition as their distribution may have changed in the last 50 years. Further analysis using only dated records could be used to confirm these responses. There may also have been reductions in populations of individual species which this analysis has not assessed.

Although there are limitations with this dataset some species show clear declines in their probability of presence highlighting their sensitivity to N deposition. There is a need for further investigation into the response of lichens to N deposition; although they are widely thought to be sensitive, lichens, and particularly terricolous lichens, have received relatively little research attention.

4.4 Calcareous grassland

4.4.1 Summary variables

i Ellenberg N

In lowland calcareous grassland the Vascular Plant Database spatial analysis showed a hump-backed response of Ellenberg N score against N deposition. The BSBI Local Change data showed a linear increase, but this is actually in close agreement, as both show an increase in Ellenberg N of around 1 unit between 5 and 35 kg N ha^{-1} yr^{-1}. The decline in Ellenberg N score at the highest levels of deposition in the Vascular Plant Database may be an artefact resulting from the small number of sites with deposition above 40 kg N ha^{-1} yr^{-1}. Temporal analysis of both datasets shows no significant change.

For upland calcareous grassland the Vascular Plant Database shows an increase in Ellenberg N score of approximately one unit between 5 and 35 kg N ha^{-1} yr^{-1}. The BSBI Local Change data also showed an increase in Ellenberg N, although the relationship was not significant, possibly due to the smaller number of tetrads in this dataset. Temporal analysis of the BSBI Local Change upland calcareous grassland data showed a positive relationship between change in Ellenberg N and N deposition. This relationship was not seen in the Vascular Plant Database analysis, which may indicate that changes have occurred relatively recently. Bryophytes did not show any significant results in calcareous grassland which is not surprising given the limited bryophyte flora in this habitat.

There was a positive spatial correlation between N deposition and Ellenberg N in the SNH upland calcareous grassland NVC Survey data. In lowland calcareous grassland, mean Ellenberg N showed a negative spatial correlation in the NE Grassland Database but limitations with quadrat data (see section 4.1.2) mean that this result is not reliable.

ii Ellenberg R

Some changes in Ellenberg R score were detected in the temporal analysis in the Vascular Plant Database and BSBI Local Change data. Both upland and lowland calcareous grassland showed a positive relationship between N deposition and change in Ellenberg R scores, indicating less acidification at high deposition although both showed negative change over time across the deposition gradient, i.e. acidification of the habitat. In lowland grassland the magnitude of the change was very small, but for upland calcareous grassland the magnitude of change was much higher; in areas of the lowest N deposition (5 kg N ha^{-1} yr^{-1}) a reduction in Ellenberg R of approximately two units occurred between survey periods. It is possible that in areas of high deposition changes in Ellenberg R score occurred before the survey took place.

iii Specific leaf area and canopy height

A positive relationship of canopy height with N deposition was identified for upland calcareous grassland in the Vascular Plant Database indicating an increase in competitive species. However, this relationship was not seen in the BSBI Local Change analysis, or for lowland calcareous grassland. A hump-backed relationship was found in the Countryside Council for Wales' data but this relationship was not convincing.

Specific leaf area showed results that are more significant. In the spatial analyses, the Vascular Plant Database analysis showed a positive relationship between SLA and N deposition in upland calcareous grassland, and the BSBI Local Change analysis showed a positive relationship in lowland calcareous grassland.

The NVC quadrat data, although subject to the limitations discussed in section 4.1.2, also showed some relationships; the Countryside Council for Wales Grassland Survey showed a positive relationship for lowland grassland, and the Scottish Natural Heritage NVC Survey showed a positive relationship for upland grassland. Only the Natural England data showed a negative relationship (for lowland calcareous grassland) but there was a lot of scatter in this relationship.

iv Species diversity and richness

Species diversity and richness did not show significant relationships with N deposition, possibly due to the difficulties of using quadrat data (discussed in section 4.1.2). This is in contrast to the results found by Maskell *et al* (2010) for Countryside Survey but may be as a result of relationships with N deposition being secondary to other drivers as found by Bennie *et al* (2006). The latter two datasets used randomly selected quadrats so were more likely to detect impacts of N deposition than NVC quadrats.

4.4.2 Individual species responses

i Vascular plants

a Spatial analyses of the effects of N deposition

Overall, the results for lowland calcareous grassland were broadly similar for the Vascular Plant Database and the BSBI Local Change Survey with around half the species which displayed significant responses showing negative trends in occupancy in relation to increasing N deposition. However, only one species (*Ononis repens*) showed this significant negative response in both datasets. Clear examples of negative responses in only one dataset included *Bromopsis erecta* in the BSBI Local Change Survey and *Allium vineale*, *Anacamptis pyramidalis*, *Carlina vulgaris* and *Spiranthes spiralis* in the Vascular Plant Database. In general lowland calcareous grassland species had shallower slopes than for acid grassland suggesting a greater probability of occurrence for some species at intermediate N deposition rates (e.g. between 20-40 kg N ha^{-1} yr^{-1}).

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 (e.g. *Anacamptis pyramidalis*, *Bromopsis erectus*, *Campanula glomerata*, *Carlina vulgaris*, *Spiranthes spiralis*) and were species with low Ellenberg N values whereas species displaying more complex (hump-backed) or positive trends in the Vascular Plant Database are more typical of taller mesotrophic swards, often subject to some shade (e.g. *Carex spicata*, *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. For example, *Spiranthes spiralis* has suffered a dramatic decline in recent decades mainly due to habitat loss and under-grazing, but also in species-rich grassland where subtle changes in vegetation structure and composition may be causing localised extinction.

A key finding in terms of changes to the composition of British calcareous grassland was the negative response of *Bromopsis erecta* in the BSBI Local Change Survey to increasing N deposition (although this was not supported by the Vascular Plant Database results where the response was not significant). This species is an important component of National Vegetation Classification types CG2-3, 5 and 8 and therefore declines could impact on the overall quality of these grasslands in areas of high N deposition. In many of these grasslands in southern England there is increasing concern over the spread of *Brachypodium pinnatum* (NVC CG4) at the expense of these types, possibly in response to eutrophication. However, the responses of *B. pinnatum* in both datasets in this study do not support this hypothesis.

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 but showed no significant relationship with N deposition (both Vascular Plant Database). The latter trend is difficult to explain as *A. xanthochlora* 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 Survey, with an optimum in occupancy between 10-20 kg N ha^{-1} 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.

In general, species with higher Ellenberg N values tended not to show responses to N deposition as might be expected, but there were also a number of species with low values which did not show negative changes. The reasons for this are not clear.

b Temporal analyses of the effects of N deposition

Several negative trends, mostly of small magnitude, were detected in the Vascular Plant Database. These include a number of low-growing, low Ellenberg N value species that would be predicted to decline in more productive swards (e.g. *Anacamptis pyramidalis*, *Orchis morio*, *Rosa rubiginosa*). Unlike acid grassland, however, these results suggest that in lowland Britain at least, calcareous grasslands have been largely resistant to the effects of increased N deposition, possibly due to their well buffered soils and management. Alternatively, it might be argued that the bulk of the losses for these species took place for other reasons before the first recording period covered by these analyses and consequently only a very weak effect can be determined.

For upland calcareous grassland, only four species in the Vascular Plant Database showed significant trends, three of which were of small magnitude and one was inconclusive. It is therefore difficult to reach any general conclusions but, as mentioned above for the spatial analysis, this may reflect the localised distribution of many of these species to a narrow altitudinal and geographical range in the uplands.

The BSBI Local Change Survey did not contain sufficient data for lowland or upland calcareous grassland species to test the temporal effects of N deposition.

c Quadrat data

In lowland calcareous grassland all of the species associated with high N deposition in the Countryside Council for Wales Grassland Survey were centrally located in the ordination diagram for the Natural England data. However, several different species identified as associated with high or low N deposition in the Natural England data gave a similar response in the Countryside Council for Wales' data. *Poa pratensis* was negatively associated with deposition in both datasets, the opposite response to that observed in acid grassland above. As this species is not typical of fertile situations (Hill *et al* 1999) it could again be a response to acidification, in this case responding to the increased acidity on the calcareous soils. *Anthoxanthum odoratum* was associated with low deposition, although less strongly in the Countryside Council for Wales Grassland Survey. *Anthoxanthum odoratum* is typically a species of less fertile situations but is commonly associated with lower pH soils so again may be responding to acidification.

Only the Scottish Natural Heritage data had sufficient upland calcareous grassland sites for analysis, and this dataset has a limited range of deposition with no sites above 22 kg N ha^{-1} yr^{-1}. None of the three species associated with high deposition (*Chrysosplenium oppositifolium, Epilobium anagallidifolium* and *Rubus idaeus*) are particularly typical of acidified or nutrient rich soils (Hill *et al* 1999) so would not be expected to respond in this way. Some of the results for species associated with low deposition were also unexpected, with the exception of *Triglochin palustre* and *Arcostaphylos uva-ursi* which are typical of infertile situations (Hill *et al* 1999). However, the results of the quadrat analyses should be viewed with caution due to the limitations of the data discussed in section 4.1. None of the species for SNH upland calcareous grassland identified as associated with either low or high N deposition were included in the hectad/tetrad analysis, providing little scope for comparison.

In the Plantlife Common Plant Survey only one species showed a change that could be associated with N deposition. *Achillea millefolium* in calcareous grassland was reduced in cover at high deposition. This species was not covered by the hectad and tetrad analysis, and had inconsistent associations in the Countryside Council for Wales and Scottish Natural Heritage dataset analyses. Calcareous grasslands are not sampled with sufficient intensity in Countryside Survey to allow meaningful analysis.

ii Bryophytes

There are only two significant results for upland calcareous grassland, and both are for species which are much commoner in lowland habitats, *Didymodon vinealis* (basic rocks and walls) and *Leiocolea turbinata* (damp, disturbed or shaded chalk or limestone rocks and soils). Both showed positive relationships with N deposition.

iii Lichens

In calcareous grassland *Cladonia foliacea* was the only species which showed a clear response to N deposition. High variability in the data at low deposition means that the gradient of the negative relationship cannot be reliably interpreted but this inhibition in probability of presence is apparent up to 30 kg N ha^{-1} yr^{-1} when *Cladonia foliacea* reaches a probability of presence of 0.2, one third of its probability of presence at 5 kg N ha^{-1} yr^{-1}. This species has received little, if any, research attention in relation to N deposition. *Diploschistes muscorum* showed a significant relationship to N deposition but its U-shaped relationship is difficult to interpret and explain ecologically and may be influenced by a driver not included in this analysis.

4.5 Bog

4.5.1 Summary variables

i Ellenberg N

Spatial analysis of the Vascular Plant Database showed a significant increase in Ellenberg N score with N deposition for upland bog, but this change was of a very small magnitude. The BSBI Local Change Survey spatial analysis for upland bog gave a non-significant relationship. Vascular plants make up a relatively small component of this habitat leaving less potential for changes in the community compared to others investigated in this project, which may be one reason that the response was only small and difficult to detect. Interestingly, analysis of the bryophyte data also showed an increase in Ellenberg N score with N deposition. There were insufficient data to conduct any of these analyses for lowland bog.

Similarly, few signals have been detected from Countryside Survey. Smart *et al* (2004) found a significant positive temporal correlation between 1990 and 1998 but only when change in cover-weighted mean Ellenberg N scores were analysed across all heath and bog plots combined.

ii Ellenberg R

There were no significant relationships between Ellenberg R and N deposition in lowland bog in either spatial or temporal analyses. This is surprising as peat soils are vulnerable to acidification (Skiba *et al* 1989). The lack of relationship found in this analysis is presumably associated with the removal of S deposition as a driver in the statistical modelling method which also removes covariation between N and S deposition. While N deposition is of increasing importance for acidification, historic levels of S deposition remain an important factor determining soil acidification.

In upland bog there was a negative relationship in the BSBI Local Change temporal analysis i.e. becomes more acidic over time in areas of high N deposition. A positive relationship was found in the bryophyte spatial analysis indicating more acidification at lower N deposition although the magnitude of the change was very small.

iii Specific leaf area and canopy height

Specific leaf area and canopy height showed few significant relationships, none at all in lowland bog. There was a negative relationship with N deposition of upland bog in the Scottish Natural Heritage NVC Survey for SLA and a hump-backed one for canopy height but neither relationship were convincing as there was a lot of scatter in the relationship.

In Countryside Survey positive spatial correlations have been detected between SLA and N deposition (ROTAP, in preparation). These patterns are consistent with an eutrophication effect and can be seen even in the 1978 data. Again, Countryside Survey analyses are based on combining heath and bog plots into one group. No temporal relationships between mean SLA and N deposition have been found with the Countryside Survey data.

iv Species diversity and richness

The Scottish Natural Heritage dataset was the only dataset with sufficient data for bogs to be able to analyse species diversity and richness. Lowland bog showed a reduction in species diversity and richness with increasing N deposition suggesting sensitivity to N inputs. In upland bog there was no significant relationship between N deposition and species richness but there was a negative relationship with diversity. This indicates that the changes observed are mainly caused by a change in the evenness of species (i.e. the relative area that they cover) rather than richness. At higher deposition than is seen in the Scottish Natural Heritage dataset we may see changes in species richness as species with low cover become infrequent in quadrats.

In Countryside Survey, a clear negative spatial relationship between species richness in heathlands and bog and total N deposition has been found within all survey years from 1978 through to 2007 (ROTAP, in preparation).

4.5.2 Individual species responses

i Vascular plants

a Spatial analyses of the effects of N deposition

There were very few species in upland and lowland bog with sufficient data for analysis and none of these showed significant relationships with N deposition. This is surprising as bogs contain many species which are typical of very infertile environments. We would suggest that a more targeted survey of bogs is needed to determine N deposition impact.

b Temporal analyses of the effects of N deposition

For bog, the only flowering plant displaying a significant temporal trend in relation to N deposition was *Carex limosa* (upland bog, Vascular Plant Database). Consequently, it was not possible to assess general temporal trends for this habitat.

c Quadrat data

For bogs, data were only available from the Scottish Natural Heritage NVC survey. The inclusion of non-bog communities (i.e. M communities that are not bogs) in this analysis is likely to have had an impact on the ordination results which makes them difficult to interpret. The species identified as associated with high deposition in lowland bog were *Lychnis flos-cuculi* and *Hypericum pulchrum*. Neither species are typical of nutrient rich environments (Hill *et al* 1999) nor are they particularly competitive (Grime *et al* 2007) so further investigation is needed into why these species are associated with high deposition. Species associated with low deposition were *Stellaria holostea, Carex bigelowii, Myosotis* sp. and *Carex limosa*. Both *Carex bigelowii* and *Carex limosa* are typical of very infertile environments (Hill *et al* 1999) so may be expected to be out-competed by other species as nutrients are added through N deposition. *Carex limosa* was also identified as responding negatively to N deposition in the temporal analysis of the Vascular Plant Database although it showed no significant response in the spatial analysis. The difference between the response reported here and the spatial analysis of the Vascular Plant Database is most likely to be due to the presence absence nature of the data in the Vascular Plant Database. *Stellaria holostea* is more surprising as this is a species of intermediate fertility (Hill *et al* 1999) but it is also not a typical bog species and so may illustrate a problem with the assignment of NVC classes in the data. Because the ordination uses all quadrats in the dataset to identify the relative positions of species, if quadrats are incorrectly attributed to habitats the whole ordination becomes less reliable.

The species associated with high deposition in upland bog were *Ilex aquifolium, Quercus robur, Scutellaria galericulata* and *Lycopus europaeus*. *Ilex aquifolium* and *Quercus robur* are both tree species that would not be expected in bogs. *Scutellaria galericulata* and *Lycopus europaeus* are species of intermediate fertility (Hill *et al* 1999) which in a nutrient poor habitat like a bog would tend to be in the richer situations. Of the species associated with low deposition, none are common in bog communities.

This dataset highlights one of the problems with the data. The grouping of species not identified to a species level presents many problems as it is impossible to identify which species are changing, and in this case, whether there is a shift from one *Myosotis* species to another across the gradient.

ii Bryophytes

All the upland bog species with negative correlations with N deposition are liverworts, but otherwise they have little in common and have received little research attention in relation to N deposition. The species with a positive association with N deposition comprise two mosses and four liverworts. One of the mosses, *Warnstorfia fluitans*, is characteristic of degraded bog and is tolerant of very acidic conditions; it is less common in the extreme western areas of Wales and Scotland than it is further east.

iii Lichens

Two species showed significant relationships with N deposition in bogs, *Cladonia arbuscula squarrosa* and *Cladonia portentosa*. *Cladonia arbuscula squarrosa* shows a hump-backed relationship with N deposition but the shape of this curve is largely driven by the large variability in the data between 10 and 25 kg N ha^{-1} yr^{-1}. This may reflect the limited and patchy nature of the distribution of this species or a response to a driver not included in this study rather than a response to N deposition. *Cladonia portentosa* showed a steep negative relationship between probability of presence and N deposition between 15 and 25 kg N ha^{-1} yr^{-1} with data becoming too variable to interpret above 30 kg N ha^{-1} yr^{-1}. In heathlands the chemistry of *Cladonia portentosa* has been demonstrated to be very sensitive to N deposition with increases in N and P concentrations of the thallus and the activity of the enzyme phosphomonoesterase affected by N deposition (Hogan *et al* 2010a; Hogan *et al* 2010b; Hyvarinen and Crittenden, 1998).

4.6 Heathland

4.6.1 Summary variables

i Ellenberg N

Lowland heathland spatial analysis of both the Vascular Plant Database and BSBI Local Change Survey showed an increase in Ellenberg N score with N deposition. The Vascular Plant Database showed a change of approximately one unit between 5 and 35 kg N ha^{-1} yr^{-1}. BSBI Local Change Survey data showed a greater increase of 1.5 units between 5 and 20 kg N ha^{-1} yr^{-1}.

Temporal analysis of the BSBI Local Change Survey data showed a significant relationship between N deposition and change in Ellenberg N. At high deposition Ellenberg N values have fallen in recent years, although scores remain higher than in areas of low deposition.

Upland heathland also showed a spatial increase in Ellenberg N score with N deposition but this was only apparent in the larger Vascular Plant Database analysis and not in the BSBI Local Change Survey where there was no change apparent.

Temporal analysis for upland heathland was only significant in the Vascular Plant Database, but the change was of a very small magnitude.

Bryophytes showed a larger increase in Ellenberg N score with N deposition in upland heathland than in other habitats, but it was still only 0.5 units. Across all habitats the bryophyte changes are all very small and scores remain low indicating infertile habitats.

In Countryside Survey, plots in heathland have been analysed together with plots in bog. Overall, few signals have been detected in Countryside Survey. Smart *et al* (2004) found a significant positive temporal correlation between 1990 and 1998 but only when change in cover-weighted mean Ellenberg N scores were analysed across all heath and bog plots combined.

ii Ellenberg R

Lowland heathland is the only community to have shown a relationship in the large-scale spatial data for vascular plants, showing a reduction in Ellenberg R score above 15 kg N ha^{-1} yr^{-1} in the BSBI Local Change Survey data. Temporal analysis showed an increase in Ellenberg R score in the Vascular Plant Database, showing an increase at highest deposition levels. This could suggest some recovery from acidification in high deposition areas.

Upland heathland showed a positive relationship between N deposition and Ellenberg R score, although again the changes are of a very small magnitude, in this case less than 0.1 units.

iii Specific leaf area and canopy height

Canopy height showed somewhat contradictory results in lowland heathland, with a significant positive relationship in the Vascular Plant Database but a negative one in the BSBI Local Change Survey data. This requires further investigation. Upland heathland only showed a positive relationship between N deposition and canopy height in the quadrat data but again this was not clear.

In lowland heathland in the BSBI Local Change Survey spatial analysis, Ellenberg N score showed a positive relationship with N deposition, but plant height showed a negative relationship which we would not expect to see. However, in this instance, the shape of the plant canopy height versus N deposition relationship may be an artefact of high variability in heights at low deposition.

In Countryside Survey, no temporal relationships between mean SLA and N deposition have been found in the heathlands and bogs. However, positive spatial correlations have been detected (ROTAP, in preparation), and these patterns are clearly consistent with an eutrophication effect, seen even in the 1978 data.

iv Species richness and diversity

In lowland heathland hump-backed relationships were found in the Scottish Natural Heritage data for both diversity and species richness, but in neither analysis were the relationships convincing. In upland heathland, there was no significant relationship between N deposition and species richness, but there was a negative relationship with diversity. This indicates that the changes observed are mainly caused by a change in the evenness of species (i.e. the relative area that they cover) rather than richness. At higher deposition than is seen in the Scottish Natural Heritage dataset we may see changes in species richness as species with low cover become infrequent in quadrats.

In Countryside Survey, a clear negative spatial relationship between species richness in heathlands and bogs and total N deposition has been found within all survey years from 1978 through to 2007 (ROTAP, in preparation).

4.6.2 Individual species responses

i Vascular plants

a Spatial analyses of the effects of N deposition

In the Vascular Plant Database, only two species displayed significant trends, *Viola canina* decreasing 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.

The BSBI Local Change Survey did not contain sufficient data for lowland heathland species to test 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 being limited to areas with N deposition rates of less than 20 and 30 kg N ha^{-1} yr^{-1} respectively, although within this range they are very uncommon or absent from large areas of more southerly distributed upland heathlands where N deposition rates have been historically highest (e.g. South Pennines). Two species associated with more humid heathlands (or at least more humid conditions within 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. 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.

As with other habitats, there are a number of species with low Ellenberg N values, which may have been expected to respond negatively to N deposition but do not show a significant relationship with N deposition here. Further investigation would be needed to identify the reasons for this.

b Temporal analyses of the effects of N deposition

No general conclusions can be drawn for temporal trends in species of lowland heathlands as only two were significant, both from the BSBI Local Change Survey. *Scleranthus annuus* displayed the only clear negative relationship with increasing N deposition whereas for *Viola lactea* there was a small tendency for it to have increased in areas of higher N deposition. The result for *V. lactea* is very surprising as this is a typical plant of maritime heathlands. There is a possibility that for species which have increased at low deposition this is a consequence of more recording in recent times.

Although significant results were found for upland heathland species in both the Vascular Plant Database and BSBI Local Change Survey the results were inconclusive with many results showing changes of a very small magnitude. Both *Lycopodium annotinum* and *Trientalis europaeus* showed clear negative temporal trends with increased N deposition presumably reflecting historical losses of lowland populations where N deposition rates have been highest. A similar, albeit weak, negative relationship was also found for *Trientalis europaeus* in the Vascular Plant Database and for *Rubus chamaemorus,* whereas *Cryptogramma crispa* and *Lycopodium clavatum* appear to have persisted better at higher N deposition rates. These species are all typical of infertile environments but there were also other species typical of such environments which have not shown significant responses.

c Quadrat data

For heathland, data were only available from the Scottish Natural Heritage NVC Survey so comparisons between datasets cannot be made. The data selected only included dry heathland. The assignment of NVC habitat also appears to be problematic in the lowland heathland habitats where several of the species associated with high deposition are more typically of wetter habitats. This relatively small dataset also has a very restricted distribution of N deposition with a maximum of 19 kg N ha^{-1} yr^{-1}. *Salix aurita* and *Sorbus aucuparia* were both species associated with high deposition which may indicate an increased incidence of scrub invasion at higher deposition. The other two species were *Tricophorum cespitosum* and *Carex nigra*. *Carex nigra* is not a common species in heathland but is typical of one heathland community, H7 *Calluna vulgaris-Scilla verna* heath (Rodwell, 1991). It is typical of neither fertile nor strongly acidic situations (Hill *et al* 1999) hence it is surprising that it was associated with high N deposition. Species associated with low deposition were *Holcus mollis, Jasione montana* and *Rumex acetosa*. None are species of particularly fertile environments and all are tolerant of acid conditions (Hill *et al* 1999), although neither *Holcus mollis* nor *Rumex acetosa* are species one would expect to decline with increasing N deposition.

The upland heathland ordinations also contained a number of species which would not be considered typical of heathland, but normally of wetter habitats including *Myrica gale*, *Saussurea alpina, Ajuga reptans, Juncus bulbosus* and to a slightly lesser extent *Anagallis tenella*. Of the remaining species associated with either high or low deposition, *Euphrasia* were not identified to a species level. This is particularly problematic since *Euphrasia nemorosa*, which at some sites would have been included in *Euphrasia* spp., was identified as associated with high deposition. *Sagina procumbens* was associated with high deposition; as a somewhat ruderal species typically associated with intermediate fertility this is perhaps not surprising. *Helianthemum nummularium* was associated with low deposition. This species is commonly associated with infertile situations (Hill *et al* 1999) but is also a species typical of reasonably base rich or weakly acid soils.

ii Bryophytes

The long list of upland heathland species for which data are presented in Appendix 4 include many which also occur in many other Broad Habitats. These include some of the very few species which have a negative association with N deposition (e.g. *Fossombronia wondraczekii, Microlejeunea ulicina*). Very many more species have positive associations and again these include some species which are more closely associated with other habitats (e.g. *Calypogeia arguta, Dicranella schreberiana*, *Fissidens bryoides*). For the other species, it is again difficult to generalise about the types of species with positive and negative associations. It is striking that there were six positive and no negative responses in the 13 *Sphagnum* species included in the analysis.

iii Lichens

In heathland, there were a large number of species showing negative responses to N deposition. Some of these species occurred at relatively low probability of presence in the data but, for the more common species, several are dramatically reduced in their probability of presence by increasing N deposition. *Cetraria aculeata, Cetraria muricata, Cladonia cervicornis verticillata, Cladonia subulata* and *Cladonia uncialis biuncialis* are all reduced to approximately half of their probability of presence or less by 15 kg N ha^{-1} yr^{-1}. The majority of the species that are inhibited in their probability of presence do so from the lowest levels of deposition found in this country, implying that the critical load is actually below the lowest levels of deposition found in this country, or that there is not threshold below which damage cannot be detected. Indeed, only three species showed a level below which they did not decline (*Cladonia glauca, Dibaeis baeomyces* and *Peltigera hymenina*). All of these species had begun to fall by 15 kg N ha^{-1} yr^{-1}. Two of the species that declined in heathland have been discussed above for other habitats (*Cetraria aculeata* and *Cladonia portentosa*) but for the remainder of the species there was no published literature on their response to N deposition.

5 Evidence summary and conclusion

There is clear evidence, both from experiments and field surveys in Great Britain (outlined in section 1.1) and from this study, that N deposition has an impact on vegetation. The chemistry of plant tissues can be affected with increases in foliar N content (e.g. Carroll *et al* 2003; Kirkham, 2001; Pilkington *et al* 2005a), changes in enzyme activity (e.g. Arroniz-Crespo *et al* 2008; Edmondson, 2007), and changes in metabolic fingerprint (Gidman *et al* 2005) in species exposed to excess N. The physiological changes in plants can be reflected in their growth, ability to withstand stress and disease and their palatability to pests and grazing animals, potentially leading to ecosystem impacts. Changes in species composition, richness and diversity have also been directly observed in a wide range of habitats (e.g. Edmondson, 2007; Mountford *et al* 1994; Stevens *et al* 2004; Wilson *et al* 1995). In the majority of cases, N deposition leads to a reduction in species richness and diversity either through an increase in primary productivity leading to an increase in competitive species at the expense of less competitive species or a reduction in species less tolerant of acidified soils. Changes in the abundance of individual species along the deposition gradient and over time have been demonstrated in this study. Many of these changes have been observed over a range of spatial and temporal scales in both large-scale gradient studies and controlled experiments. These impacts for each of the habitats we have investigated are summarised in Table 5.1.

Further to evidence from research scale surveys and experiments (section 1.1) and Countryside Survey, the spatial analysis in this study has demonstrated clear species level impacts in all four of the habitats investigated demonstrating both increases and decreases in individual higher and lower plant species (section 3.1 and 3.2 and Appendices 1 to 4) and community composition (section 3.5). In some of the habitats and datasets we have also shown changes in fertility through the use of Ellenberg N scores and the competitive ability of plants through SLA and canopy height (see section 4.2 for a summary). We have also shown reductions in species richness and diversity in some habitats (see section 4.2 for a summary).

The temporal analysis also revealed changes in the distribution of some vascular plant species that could be related to N deposition (sections 3.1 and 3.2 and Appendices 1 and 2). The changes we have detected are mainly in species that are not so common in the UK because these are the species whose changes can be detected at the coarse tetrad and hectad scales. These findings could be considered in tandem with those of Dupré *et al* (2010) that showed increases and decreases in common species in Great Britain between 1939 and 2009.

There are clearly a large number of changes that are occurring in semi-natural ecosystems in response to N deposition but assessing the ecological and policy relevance of these changes is very difficult. To do this we need to consider how much, and what type of change we can tolerate before it becomes a concern. This is a very difficult question and one which we will begin the process of addressing in the second report for this project. However, it seems clear that detectable reductions in species richness, impacts on the distribution of individual species at the coarse resolution assessed in this project and the shift towards more eutrophic communities as measured by change in mean Ellenberg N scores are all changes in the fundamental characteristics of plant communities and even small changes indicate deterioration.

Table 5.1. Summary of changes observed that have been related to N deposition in acid grassland, calcareous grassland, bog and heathland in the UK.

Habitat	Impact of N deposition/addition	Example references	Comment
Acid grassland	Reduction in species richness	This report Dupré *et al* 2010 Maskell *et al* 2010 Stevens *et al* 2004	Not always apparent in this report
	Reduction in species diversity	This report Stevens *et al* 2004	Not always apparent in this report
	Change in species composition	This report Carroll *et al* 2000 Dupré *et al* 2010 Emmett, 2007 Morecroft *et al* 1994 Stevens *et al* 2006	
	Reduced forb richness	ROTAP, in preparation Stevens *et al* 2004 Stevens *et al* In press Maskell *et al* 2010	
	Reduced forb cover	O'Sullivan, 2008 Stevens *et al* 2006	
	Reduced bryophyte cover	Arroniz-Crespo *et al* 2008 Carroll *et al* 2000 Emmett, 2007	
	Increased grass cover	O'Sullivan, 2008 Stevens *et al* 2006	
	Increase in grass:forb ratio	Stevens *et al* 2009 Maskell *et al* 2010	
	Changes in the occurrence of individual higher plant species	This report Stevens *et al* 2006 Stevens *et al* 2009	
	Changes in the occurrence of individual bryophyte species	This report Carroll *et al* 2000 Stevens *et al* 2006	
	Changes in the occurrence of individual lichen species	This report	
	Increase in Ellenberg N score	This report Dupré *et al* 2010	Not apparent in all surveys
	Reduction in Ellenberg R score	Maskell *et al* 2010 Stevens *et al* 2010	Not apparent in this report
	Increase in species acidity index	Maskell *et al* 2010 Stevens *et al* 2010	
	Increase in mean specific leaf area	This report	Not apparent in all datasets
	Increase in mean canopy height	This report Maskell *et al* 2010	Not apparent in all datasets
	Increased bryophyte N content	Arroniz-Crespo *et al* 2008	Not found in species investigated in Stevens *et al* 2006

Habitat	**Impact of N deposition/addition**	**Example references**	**Comment**
	Increased higher plant N content	Carroll *et al* 2003 Kirkham, 2001 Morecroft *et al* 1994	Not found in all species in Emmett, 2007 and Stevens *et al* 2006
	Reduced flowering	O'Sullivan, 2008	
	Changed enzyme activity	Arroniz-Crespo *et al* 2008 Phoenix *et al* 2003	
	Change in metabolic fingerprint	Gidman *et al* 2006	
Calcareous grassland	Increasing then decreasing species richness	ROTAP, in preparation	Not apparent in Maskell *et al* 2010, not always apparent in this report
	Changed species composition	This report Morecroft *et al* 1994 ROTAP, in preparation	
	Increased grass cover	ROTAP, in preparation	
	Reduced forb cover	ROTAP, in preparation	
	Reduced bryophyte cover	ROTAP, in preparation	
	Changes in the occurrence of individual higher plant species	This report	
	Changes in the occurrence of individual bryophyte species	This report	
	Changes in the occurrence of individual lichen species	This report	
	Increased Ellenberg N score	This report Bennie *et al* 2006 ROTAP, in preparation	Not all datasets in this report
	Increase in mean specific leaf area	This report Maskell *et al* 2010	Not apparent in all datasets
	Increase in mean canopy height	This report Maskell *et al* 2010	Not apparent in all datasets
	Reduced flowering	O'Sullivan, 2008	
	Increased higher plant N content	Carroll *et al* 2003 Morecroft *et al* 1994	
Bog	Reduced species richness	This report	
	Reduced species diversity	This report	
	Changes in species composition	This report	
	Reduced bryophyte cover	ROTAP, in preparation	Some increases reported, wet and dry deposition
	Reduced lichen cover	ROTAP, in preparation	Wet and dry deposition
	Changes in *Calluna* cover and growth	Sheppard *et al* 2008	Increase for wet deposition, decrease for dry deposition

Habitat	Impact of N deposition/addition	Example references	Comment
	Increase in graminoid cover	ROTAP, in preparation	
	Changes in the occurrence of individual higher plant species	This report	
	Changes in the occurrence of individual bryophyte species	This report	
	Changes in the occurrence of individual lichen species	This report	
	Increased Ellenberg N score	This report	Not apparent in all datasets
	Increased sensitivity to frost	Sheppard *et al* 2008	
	Increased sensitivity to drought	Sheppard *et al* 2008	
	Increased pathogen outbreaks	Sheppard *et al* 2008	
	Increased bryophyte N content	ROTAP, in preparation	wet and dry deposition
	Increased higher plant N content	Sheppard *et al* 2008	wet and dry deposition, not consistent year to year
Heathland	Reduced species richness	This report Edmondson, 2007 Maskell *et al* 2010 ROTAP, in preparation	No change also reported in ROTAP, in preparation
	Reduced forb richness	Edmondson, 2007 ROTAP, in preparation Maskell *et al* 2010	No change also reported in ROTAP, in preparation
	Reduced forb cover		Increase and no change also reported in ROTAP, in preparation
	Reduced bryophyte cover	Pilkington *et al* 2007 ROTAP, in preparation	
	Reduced bryophyte richness	Edmondson, 2007	
	Increased ericoid cover	ROTAP, in preparation	Also reduced in ROTAP, in preparation
	Increased ericoid richness	ROTAP, in preparation	Also reduced in ROTAP, in preparation
	Increased graminoid cover	ROTAP, in preparation	
	Reduced graminoid richness	ROTAP, in preparation	
	Reduced lichen cover	Britton and Fisher, 2008 Pilkington *et al* 2007 Power *et al* 2006 ROTAP, in preparation	

Habitat	Impact of N deposition/addition	Example references	Comment
	Reduced lichen richness	ROTAP, in preparation	
	Increased Calluna growth	Britton and Fisher, 2008 Pilkington, 2003 Power *et al* 2006 Wilson, 2003	
	Increased bryophyte N content	Pilkington, 2003 Power *et al* 1995	
	Increased higher plant N content	Britton and Fisher, 2008 Pilkington *et al* 2005 Power *et al* 1995 Wilson, 2003	Not always apparent in all years
	Increased flowering of Calluna	Britton and Fisher, 2008 Power *et al* 1995 ROTAP, in preparation	
	Increased sensitivity to frost	Caporn *et al* 2000 Sheppard and Leith, 2002	
	Increased sensitivity to drought	Britton *et al* 2003	
	Changes in the occurrence of individual higher plant species	This report Edmondson, 2007	
	Changes in the occurrence of individual bryophyte species	This report Edmondson, 2007	
	Changes in the occurrence of individual lichen species	This report	
	Increased Ellenberg N score	This report	Not apparent in all datasets
	Reduced Ellenberg R score	This report Maskell *et al* 2010	Not apparent in all datasets
	Increase in mean canopy height	This report Maskell *et al* 2010	Not apparent in all datasets
	Changes in enzyme activity	Edmondson, 2007 Hogan *et al* 2010a Hogan *et al* 2010b	
	Change in metabolic fingerprint	Gidman *et al* 2005	

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8 Appendices

Appendices 1 to 4 show results for all species analysed, results from the Vascular Plant Database are given in Appendix 1 with results from the spatial analysis for each habitat (upland and lowland) followed by temporal analysis. Appendices 2 to 4 are set out in the same way presenting results for BSBI Local Change Survey (Appendix 2), British Lichen Society Database (Appendix 3) and British Bryological Society Database. Blank cells indicate insufficient data for analysis, ns indicates not significant, small magnitude indicates a small magnitude of change that is too small to show a clear direction. For all other significant results the direction or shape of the relationship is indicated (positive, negative, U-shaped, hump-backed or inconsistent (i.e. other shape)).

Appendix 1

Spatial Analysis	Vascular Plant Database
Species	**Direction of change**
Acid grassland	
Lowland	
Anthriscus caucalis	ns
Aphanes australis	ns
Arabis glabra	
Artemisia campestris	
Cerastium arvense	Negative
Cerastium semidecandrum	Negative
Chamaemelum nobile	
Festuca longifolia	
Gentiana pneumonanthe	
Gladiolus illyricus	
Herniaria glabra	
Hypochaeris glabra	
Lobelia urens	
Lotus angustissimus	
Lotus subbiflorus	
Medicago minima	
Medicago polymorpha	
Moenchia erecta	
Muscari neglectum	
Myosotis ramosissima	ns
Ophioglossum azoricum	
Ophioglossum lusitanicum	
Ornithopus perpusillus	ns
Phleum phleoides	
Poa angustifolia	
Potentilla argentea	
Pulicaria vulgaris	
Scleranthus annuus	ns
Senecio sylvaticus	ns
Silene conica	
Silene otites	
Thymus serpyllum	
Trifolium arvense	Negative
Trifolium glomeratum	
Trifolium micranthum	
Trifolium ornithopodioides	
Trifolium scabrum	
Trifolium striatum	
Trifolium subterraneum	
Trifolium suffocatum	
Veronica verna	
Vicia lathyroides	Negative

Viola canina	Negative
Vulpia ciliata	
Upland	
Agrostis vinealis	
Alchemilla glomerulans	
Nardus stricta	
Viola lutea	ns
Calcareous grassland	
Lowland	
Ajuga chamaepitys	
Allium oleraceum	
Allium vineale	Negative
Anacamptis pyramidalis	Negative
Asperula cynanchica	
Blackstonia perfoliata	ns
Brachypodium pinnatum	ns
Bromopsis erecta	ns
Campanula glomerata	
Carex filiformis	
Carex humilis	
Carex spicata	Hump-backed
Carlina vulgaris	Negative
Catapodium rigidum	ns
Centaurium erythraea	U-shaped
Centaurea scabiosa	ns
Cerastium pumilum	
Cirsium acaule	ns
Cirsium eriophorum	ns
Cirsium tuberosum	
Clinopodium vulgare	ns
Convallaria majalis	
Crepis capillaris	
Cynoglossum officinale	Negative
Daucus carota	ns
Dianthus deltoides	
Echium vulgare	Negative
Epipactis helleborine	Hump-backed
Euphrasia pseudokerneri	
Filago vulgaris	ns
Galium pumilum	
Gastridium ventricosum	
Genista anglica	
Gentianella ciliata	
Gentianella germanica	
Geranium columbinum	Negative
Geranium sanguineum	ns
Helianthemum apenninum	
Herminium monorchis	

Himantoglossum hircinum	
Hypericum hirsutum	ns
Hypericum maculatum	
Iberis amara	
Inula conyzae	ns
Knautia arvensis	Hump-backed
Koeleria vallesiana	
Lathyrus aphaca	
Lathyrus nissolia	Positive
Linum bienne	Small magnitude
Linum perenne	
Lotus glaber	
Marrubium vulgare	
Minuartia hybrida	
Ononis repens	Negative
Ononis spinosa	ns
Onobrychis viciifolia	
Ophrys apifera	ns
Ophrys fuciflora	
Ophrys insectifera	
Ophrys sphegodes	
Orchis militaris	
Orchis morio	ns
Orchis simia	
Orchis ustulata	
Origanum vulgare	ns
Orobanche elatior	
Orobanche reticulata	
Pastinaca sativa	Small magnitude
Phyteuma orbiculare	
Picris hieracioides	ns
Pilosella peleteriana	
Poa angustifolia	ns
Polygala calcarea	
Pulsatilla vulgaris	
Rosa agrestis	
Rosa micrantha	Negative
Rosa rubiginosa	ns
Salvia pratensis	
Salvia verbenaca	
Sanguisorba minor	ns
Seseli libanotis	
Sherardia arvensis	ns
Spiranthes spiralis	Negative
Stachys officinalis	Positive
Tephroseris integrifolia	
Thesium humifusum	
Thymus pulegioides	

Trinia glauca	
Verbascum lychnitis	
Veronica spicata	
Viola odorata	ns
Upland	
Alchemilla alpina	
Alchemilla glaucescens	
Alchemilla micans	
Alchemilla minima	
Alchemilla wichurae	
Alchemilla xanthochlora	ns
Astragalus alpinus	
Bartsia alpina	
Carex capillaris	
Crepis mollis	
Crepis praemorsa	
Cypripedium calceolus	
Dryas octopetala	
Galium boreale	ns
Gentiana verna	
Luzula spicata	
Melica nutans	Negative
Myosotis alpestris	
Oxytropis campestris	
Oxytropis halleri	
Persicaria vivipara	ns
Polystichum lonchitis	
Potentilla crantzii	
Rubus saxatilis	ns
Sagina saginoides	
Saussurea alpina	
Saxifraga aizoides	
Saxifraga hypnoides	ns
Saxifraga oppositifolia	
Selaginella selaginoides	ns
Sesleria caerulea	
Silene acaulis	
Thalictrum alpinum	ns
Tofieldia pusilla	
Viola lutea	ns
Bog	
Lowland	
Deschampsia setacea	
Drosera intermedia	ns
Drosera longifolia	
Erica ciliaris	
Lycopodiella inundata	
Rhynchospora fusca	

Scheuchzeria palustris	
Upland	
Carex limosa	ns
Listera cordata	ns
Rubus chamaemorus	ns
Trichophorum cespitosum	
Vaccinium microcarpum	
Vaccinium uliginosum	ns
Heathland	
Lowland	
Centaurium scilloides	
Cicendia filiformis	
Cuscuta epithymum	
Erica ciliaris	
Erica vagans	
Juncus capitatus	
Lysimachia nummularia	
Orobanche rapum-genistae	
Physospermum cornubiense	
Pinguicula lusitanica	
Platanthera bifolia	Positive
Radiola linoides	ns
Scilla autumnalis	
Scilla verna	
Scleranthus annuus	ns
Tuberaria guttata	
Ulex minor	
Viola canina	Negative
Viola lactea	
Upland	
Arctostaphylos uva-ursi	Negative
Betula nana	
Cornus suecica	ns
Cryptogramma crispa	ns
Diphasiastrum complanatum	
Empetrum nigrum	ns
Listera cordata	
Lycopodium annotinum	
Lycopodium clavatum	ns
Phyllodoce caerulea	
Rubus chamaemorus	ns
Trichophorum cespitosum	ns
Trientalis europaea	Hump-backed
Vaccinium myrtillus	
Vaccinium vitis-idaea	ns

Acid grassland	
Lowland	
Anthriscus caucalis	
Aphanes australis	ns
Arabis glabra	ns
Artemisia campestris	
Cerastium arvense	ns
Cerastium semidecandrum	Negative
Chamaemelum nobile	ns
Festuca longifolia	ns
Gentiana pneumonanthe	ns
Gladiolus illyricus	ns
Herniaria glabra	
Hypochaeris glabra	ns
Lobelia urens	
Lotus angustissimus	
Lotus subbiflorus	
Medicago minima	
Medicago polymorpha	
Moenchia erecta	
Muscari neglectum	
Myosotis ramosissima	Negative
Ophioglossum azoricum	
Ophioglossum lusitanicum	
Ornithopus perpusillus	Negative
Phleum phleoides	
Poa angustifolia	
Potentilla argentea	ns
Pulicaria vulgaris	
Scleranthus annuus	ns
Scleranthus perennis	
Senecio sylvaticus	Hump-backed
Silene conica	
Thymus serpyllum	
Trifolium arvense	Negative
Trifolium glomeratum	
Trifolium micranthum	Negative
Trifolium ornithopodioides	Small magnitude
Trifolium scabrum	ns
Trifolium striatum	ns
Trifolium subterraneum	Small magnitude
Trifolium suffocatum	
Veronica verna	
Vicia lathyroides	ns
Viola canina	
Upland	
Alchemilla glomerulans	

Nardus stricta	ns
Viola lutea	ns
Calcareous grassland	
Lowland	
Ajuga chamaepitys	
Allium oleraceum	ns
Allium vineale	ns
Anacamptis pyramidalis	Small magnitude
Asperula cynanchica	
Blackstonia perfoliata	ns
Brachypodium pinnatum	ns
Bromopsis erecta	ns
Campanula glomerata	ns
Carex filiformis	
Carex humilis	
Carex spicata	Negative
Carlina vulgaris	ns
Catapodium rigidum	ns
Centaurium erythraea	
Centaurea scabiosa	Small magnitude
Cerastium pumilum	
Cirsium acaule	ns
Cirsium eriophorum	ns
Cirsium tuberosum	
Clinopodium vulgare	ns
Convallaria majalis	Small magnitude
Crepis capillaris	ns
Cynoglossum officinale	ns
Daucus carota	
Dianthus deltoides	
Echium vulgare	ns
Epipactis helleborine	ns
Euphrasia pseudokerneri	
Filago vulgaris	ns
Galium pumilum	
Gastridium ventricosum	
Genista anglica	
Gentianella germanica	
Geranium columbinum	ns
Geranium sanguineum	ns
Herminium monorchis	
Himantoglossum hircinum	
Hypericum hirsutum	ns
Hypericum maculatum	
Iberis amara	
Inula conyzae	ns
Knautia arvensis	ns
Lathyrus aphaca	

Lathyrus nissolia	ns
Linum bienne	ns
Linum perenne	
Lotus glaber	ns
Marrubium vulgare	
Minuartia hybrida	ns
Ononis repens	ns
Ononis spinosa	ns
Onobrychis viciifolia	ns
Ophrys apifera	ns
Ophrys insectifera	ns
Ophrys sphegodes	
Orchis militaris	
Orchis morio	Small magnitude
Orchis ustulata	ns
Origanum vulgare	ns
Orobanche elatior	ns
Orobanche reticulata	
Pastinaca sativa	ns
Phyteuma orbiculare	
Picris hieracioides	ns
Poa angustifolia	ns
Polygala calcarea	ns
Pulsatilla vulgaris	
Rosa agrestis	
Rosa micrantha	ns
Rosa rubiginosa	Small magnitude
Salvia pratensis	
Salvia verbenaca	ns
Sanguisorba minor	ns
Sherardia arvensis	ns
Spiranthes spiralis	ns
Stachys officinalis	ns
Tephroseris integrifolia	
Thesium humifusum	
Thymus pulegioides	ns
Verbascum lychnitis	
Viola odorata	ns
Upland	
Alchemilla alpina	Small magnitude
Alchemilla glaucescens	
Alchemilla minima	
Alchemilla wichurae	
Alchemilla xanthochlora	ns
Bartsia alpina	
Carex capillaris	
Crepis mollis	
Cypripedium calceolus	

Dryas octopetala	ns
Galium boreale	ns
Gentiana verna	
Luzula spicata	ns
Melica nutans	Inconsistent
Myosotis alpestris	
Oxytropis campestris	
Oxytropis halleri	
Persicaria vivipara	Small magnitude
Polystichum lonchitis	ns
Potentilla crantzii	ns
Rubus saxatilis	ns
Sagina saginoides	
Saussurea alpina	Small magnitude
Saxifraga aizoides	ns
Saxifraga hypnoides	ns
Saxifraga oppositifolia	ns
Selaginella selaginoides	ns
Sesleria caerulea	ns
Silene acaulis	ns
Thalictrum alpinum	ns
Tofieldia pusilla	
Viola lutea	ns
Bog	
Lowland	
Deschampsia setacea	ns
Drosera intermedia	ns
Drosera longifolia	ns
Lycopodiella inundata	ns
Rhynchospora fusca	
Upland	
Carex limosa	Negative
Listera cordata	ns
Rubus chamaemorus	ns
Trichophorum cespitosum	ns
Vaccinium microcarpum	ns
Vaccinium uliginosum	ns
Heathland	
Lowland	
Centaurium scilloides	
Cicendia filiformis	
Cuscuta epithymum	ns
Erica ciliaris	
Erica vagans	
Juncus capitatus	
Lycopodiella inundata	ns
Orobanche rapum-genistae	
Physospermum cornubiense	

Pinguicula lusitanica	ns
Platanthera bifolia	ns
Radiola linoides	ns
Scilla autumnalis	
Scilla verna	ns
Scleranthus annuus	ns
Tuberaria guttata	
Ulex minor	ns
Viola canina	ns
Upland	
Arctostaphylos uva-ursi	ns
Betula nana	ns
Cornus suecica	ns
Cryptogramma crispa	Small magnitude
Empetrum nigrum	
Listera cordata	ns
Lycopodium annotinum	ns
Lycopodium clavatum	Small magnitude
Phyllodoce caerulea	
Rubus chamaemorus	Small magnitude
Trichophorum cespitosum	ns
Trientalis europaea	Small magnitude
Vaccinium myrtillus	ns
Vaccinium vitis-idaea	ns

Appendix 2

Spatial Analysis	BSBI Local Change Survey
Species	**Direction of change**
Acid grassland	
Lowland	
Anthriscus caucalis	
Aphanes australis	
Arabis glabra	
Carex muricata	
Cerastium arvense	
Cerastium semidecandrum	
Chamaemelum nobile	
Herniaria glabra	
Hypochaeris glabra	
Lobelia urens	
Lotus angustissimus	
Lotus subbiflorus	
Medicago polymorpha	
Moenchia erecta	
Muscari neglectum	
Myosotis ramosissima	
Ophioglossum azoricum	
Ornithogalum angustifolium	
Ornithopus perpusillus	
Poa angustifolia	
Poa pratensis	
Potentilla argentea	
Senecio sylvaticus	ns
Trifolium arvense	
Trifolium glomeratum	
Trifolium micranthum	
Trifolium ornithopodioides	
Trifolium scabrum	
Trifolium striatum	
Trifolium subterraneum	
Trifolium suffocatum	
Vicia lathyroides	
Viola canina	
Upland	
Agrostis vinealis	Hump-backed
Alchemilla glomerulans	
Nardus stricta	
Viola lutea	

Calcareous grassland	
Lowland	
Aceras anthropophorum	
Allium oleraceum	
Allium vineale	
Anacamptis pyramidalis	
Asperula cynanchica	
Blackstonia perfoliata	
Brachypodium pinnatum	ns
Bromopsis erecta	Negative
Campanula glomerata	Negative
Carex divulsa	
Carex humilis	
Carex muricata	
Carex spicata	Negative
Carlina vulgaris	
Catapodium rigidum	ns
Centaurea scabiosa	Negative
Centaurium erythraea	ns
Cirsium acaule	
Cirsium eriophorum	
Clinopodium vulgare	
Convallaria majalis	
Crepis capillaris	ns
Cynoglossum officinale	
Daucus carota	Negative
Dianthus deltoides	
Echium vulgare	
Epipactis helleborine	
Euphorbia cyparissias	
Filago vulgaris	
Genista anglica	
Gentianella germanica	
Geranium columbinum	
Geranium sanguineum	
Herminium monorchis	
Hypericum hirsutum	
Iberis amara	
Inula conyzae	
Knautia arvensis	ns
Lathyrus aphaca	
Lathyrus nissolia	
Linaria repens	
Linum bienne	
Lotus glaber	
Marrubium vulgare	
Minuartia hybrida	
Nepeta cataria	

Onobrychis viciifolia	
Ononis repens	Negative
Ononis spinosa	
Ophrys apifera	
Ophrys insectifera	
Orchis morio	
Origanum vulgare	ns
Ornithogalum angustifolium	
Orobanche elatior	
Pastinaca sativa	ns
Phyteuma orbiculare	
Picris hieracioides	
Poa angustifolia	
Polygala calcarea	
Rosa micrantha	
Rosa rubiginosa	
Salvia pratensis	
Salvia verbenaca	ns
Sanguisorba minor	Inconsistent
Sherardia arvensis	
Spiranthes spiralis	
Stachys officinalis	ns
Tephroseris integrifolia	
Thesium humifusum	
Thymus pulegioides	
Verbascum lychnitis	
Veronica spicata	
Viola odorata	Inconsistent
Upland	
Alchemilla alpina	ns
Alchemilla glaucescens	
Alchemilla xanthochlora	
Bartsia alpina	
Carex capillaris	
Dryas octopetala	
Galium boreale	ns
Luzula spicata	
Melica nutans	
Persicaria vivipara	Hump-backed
Polystichum lonchitis	
Potentilla crantzii	
Rubus saxatilis	Hump-backed
Saussurea alpina	
Saxifraga aizoides	ns
Saxifraga hypnoides	
Saxifraga oppositifolia	ns
Selaginella selaginoides	ns
Sesleria caerulea	

Silene acaulis	
Thalictrum alpinum	Hump-backed
Tofieldia pusilla	
Viola lutea	
Heathland	
Lowland	
Acaena novae-zelandiae	
Cicendia filiformis	
Cuscuta epithymum	
Erica ciliaris	
Erica vagans	
Gaultheria shallon	
Lycopodiella inundata	
Pinguicula lusitanica	
Platanthera bifolia	
Radiola linoides	
Scilla autumnalis	
Scilla verna	
Scleranthus annuus	
Ulex minor	
Viola canina	
Viola lactea	
Upland	
Agrostis vinealis	Inconsistent
Arctostaphylos uva-ursi	ns
Betula nana	
Cornus suecica	
Cryptogramma crispa	
Empetrum nigrum	
Listera cordata	Hump-backed
Lycopodium annotinum	
Lycopodium clavatum	ns
Rubus chamaemorus	ns
Trichophorum cespitosum	ns
Trientalis europaea	
Vaccinium myrtillus	
Vaccinium vitis-idaea	Negative
Temporal analysis	
Acid grassland	
Lowland	
Anthriscus caucalis	
Aphanes australis	
Carex muricata	
Cerastium arvense	
Cerastium semidecandrum	
Chamaemelum nobile	
Lotus angustissimus	
Lotus subbiflorus	

Myosotis ramosissima
Ornithogalum angustifolium
Ornithopus perpusillus
Poa angustifolia
Poa pratensis
Senecio sylvaticus
Trifolium micranthum
Trifolium scabrum
Trifolium striatum
Viola canina
Upland
Agrostis vinealis
Nardus stricta
Viola lutea
Calcareous grassland
Lowland
Allium vineale
Blackstonia perfoliata
Brachypodium pinnatum
Bromopsis erecta
Campanula glomerata
Carex divulsa
Carex muricata
Carex spicata
Carlina vulgaris
Catapodium rigidum
Centaurea scabiosa
Centaurium erythraea
Cirsium acaule
Cirsium eriophorum
Clinopodium vulgare
Convallaria majalis
Crepis capillaris
Cynoglossum officinale
Daucus carota
Dianthus deltoides
Echium vulgare
Epipactis helleborine
Filago vulgaris
Geranium columbinum
Geranium sanguineum
Herminium monorchis
Hypericum hirsutum
Inula conyzae
Knautia arvensis
Lathyrus aphaca
Lathyrus nissolia

Linaria repens	
Linum bienne	
Lotus glaber	
Marrubium vulgare	
Minuartia hybrida	
Nepeta cataria	
Onobrychis viciifolia	
Ononis repens	
Ononis spinosa	
Ophrys apifera	
Ophrys insectifera	
Orchis morio	
Origanum vulgare	
Ornithogalum angustifolium	
Orobanche elatior	
Pastinaca sativa	
Picris hieracioides	
Poa angustifolia	
Polygala calcarea	
Rosa micrantha	
Rosa rubiginosa	
Salvia verbenaca	
Sanguisorba minor	
Sherardia arvensis	
Spiranthes spiralis	
Stachys officinalis	
Thesium humifusum	
Thymus pulegioides	
Verbascum lychnitis	
Viola odorata	
Heathland	
Lowland	
Cicendia filiformis	
Cuscuta epithymum	
Gaultheria shallon	
Lycopodiella inundata	
Pinguicula lusitanica	
Platanthera bifolia	
Radiola linoides	
Scilla autumnalis	
Scilla verna	
Scleranthus annuus	Negative
Ulex minor	
Viola canina	
Viola lactea	Small magnitude
Upland	
Agrostis vinealis	

Arctostaphylos uva-ursi	
Cornus suecica	
Cryptogramma crispa	
Empetrum nigrum	
Listera cordata	
Lycopodium annotinum	Negative
Lycopodium clavatum	
Rubus chamaemorus	
Trichophorum cespitosum	
Trientalis europaea	Negative
Vaccinium myrtillus	
Vaccinium vitis-idaea	

Appendix 3

Spatial Analysis	BLS Database
Species	**Direction of change**
Acid grassland	
Baeomyces rufus	ns
Catapyreneum lachneum	Small magnitude
Cetraria aculeata	Negative
Cladonia cariosa	ns
Leptogium palmatum	ns
Peltigera didactyla	Negative
Peltigera hymenina	ns
Calcareous grassland	
Catapyreneum squamulosum	ns
Cladonia foliacea	Negative
Cladonia furcata subrangiformis	ns
Cladonia pocillum	ns
Cladonia rangiformis	ns
Diploschistes muscorum	U-shaped
Fulgensia fulgens	ns
Heterodermia leucomela	ns
Lecidea lichenicola	ns
Megaspora verrucosa	ns
Peltigera leucophlebia	ns
Peltigera neckeri	ns
Peltigera rufescens	ns
Placidiopsis custnani	ns
Psora decipiens	ns
Toninia sedifolia	ns
Bog	
Cladonia arbuscula squarrosa	Hump-backed
Cladonia ciliata	ns
Cladonia portentosa	Negative
Cladonia uncialis biuncialis	ns
Icmadophila ericitorum	ns
Lichenomphalia umbellifera	ns
Heathland	
Baeomyces placophyllus	ns
Baeomyces rufus	ns
Catapyreneu lachneum	ns
Cetraria aculeata	Negative
Cetraria islandica islandica	ns
Cetraria muricata	Negative
Cladonia arbuscula squarrosa	U-shaped
Cladonia cariosa	ns
Cladonia cervicornis cervicornis	Negative
Cladonia cervicornis verticillata	Negative
Cladonia ciliata	ns

Cladonia crispata cetrariiformis	ns
Cladonia floerkeana	U-shaped
Cladonia glauca	Negative
Cladonia portentosa	Negative
Cladonia strepsilis	Negative
Cladonia subulata	Negative
Cladonia uncialis biuncialis	Negative
Dibaeis baeomyces	Negative
Diploschistes muscorum	Inconsistent
Icmadophila ericitorum	ns
Lichenomphalia hudsoniana	Negative
Lichenomphalia umbellifera	Negative
Peltigera hymenina	Negative
Placynthiella uliginosa	ns
Pycnothelia papillaria	ns

Appendix 4

Species	BBS Database Direction of change
Acid grassland	
Upland	
Archidium alternifolium	Positive
Barbilophozia floerkei	ns
Bazzania tricrenata	ns
Blasia pusilla	ns
Campylopus flexuosus	ns
Campylopus introflexus	ns
Campylopus pyriformis	ns
Cephalozia bicuspidata	ns
Cephaloziella divaricata	ns
Dicranum fuscescens	U-shaped
Dicranella heteromalla	ns
Dicranum majus	ns
Ditrichum heteromallum	ns
Frullania tamarisci	Negative
Gymnomitrion concinnatum	ns
Gymnocolea inflata	Positive
Gymnomitrion obtusum	ns
Herbertus aduncus	ns
Hylocomium splendens	Small magnitude
Hypnum jutlandicum	ns
Lejeunea patens	ns
Leptodontium flexifolium	Positive
Lophocolea bidentata	ns
Lophozia sudetica	ns
Lophozia ventricosa	Positive
Marsupella emarginata	U-shaped
Mylia taylorii	ns
Nardia scalaris	ns
Pleurozia purpurea	ns
Pogonatum nanum	ns
Pogonatum urnigerum	ns
Pohlia annotina	ns
Pohlia drummondii	ns
Pohlia nutans	ns
Polytrichum juniperinum	ns
Polytrichum piliferum	ns
Pseudotaxiphyllum elegans	ns
Ptilidium ciliare	ns
Racomitrium ericoides	Positive

Racomitrium lanuginosum	Negative
Rhytidiadelphus loreus	ns
Sanionia uncinata	Positive
Scapania gracilis	Negative
Scapania scandica	ns
Tetraplodon mnioides	ns
Tritomaria quinquedentata	ns
Calcareous grassland	
Upland	
Brachythecium glareosum	ns
Bryum radiculosum	ns
Campyliadelphus chrysophyllus	ns
Didymodon vinealis	Positive
Encalypta streptocarpa	ns
Encalypta vulgaris	ns
Homalothecium lutescens	ns
Leiocolea turbinata	Positive
Neckera crispa	ns
Trichostomum crispulum	ns
Bog	
Upland	
Anastrophyllum minutum	Negative
Aneura pinguis	ns
Aulacomnium palustre	ns
Calypogeia fissa	ns
Calypogeia muelleriana	ns
Calypogeia neesiana	Positive
Calypogeia sphagnicola	Negative
Campylopus atrovirens	ns
Campylopus brevipilus	ns
Campylopus flexuosus	ns
Campylopus introflexus	ns
Campylopus pyriformis	ns
Cephalozia bicuspidata	ns
Cephalozia connivens	ns
Cephaloziella divaricata	ns
Cephaloziella hampeana	ns
Cephalozia leucantha	ns
Cephalozia lunulifolia	ns
Ceratodon purpureus	ns
Cladopodiella fluitans	Small magnitude
Dicranum bonjeanii	Positive
Dicranella cerviculata	ns

Dicranella heteromalla	ns
Diplophyllum albicans	ns
Gymnocolea inflata	Positive
Hylocomium splendens	ns
Hypnum jutlandicum	ns
Kindbergia praelonga	ns
Kurzia pauciflora	ns
Kurzia trichoclados	ns
Lepidozia pearsonii	Negative
Leucobryum glaucum	ns
Lophocolea bidentata	ns
Lophozia incisa	Positive
Lophozia ventricosa	ns
Mylia anomala	ns
Mylia taylorii	ns
Nowellia curvifolia	ns
Odontoschisma denudatum	Negative
Odontoschisma sphagni	ns
Pellia epiphylla	ns
Pellia neesiana	ns
Plagiochila asplenioides	ns
Pleurozia purpurea	Positive
Pohlia nutans	ns
Polytrichum strictum	ns
Ptilidium ciliare	ns
Racomitrium lanuginosum	U-shaped
Rhytidiadelphus loreus	ns
Riccardia latifrons	ns
Scapania gracilis	ns
Scapania irrigua	ns
Scapania nemorea	ns
Scapania scandica	ns
Scapania umbrosa	Negative
Scapania undulata	U-shaped
Sphagnum austinii	Inconsistent
Sphagnum capillifolium	ns
Sphagnum cuspidatum	ns
Sphagnum denticulatum	ns
Sphagnum fallax	ns
Sphagnum fuscum	ns
Sphagnum girgensohnii	ns
Sphagnum magellanicum	ns
Sphagnum molle	ns
Sphagnum palustre	ns

Sphagnum papillosum	ns
Sphagnum strictum	ns
Sphagnum tenellum	ns
Splachnum ampullaceum	ns
Splachnum sphaericum	ns
Warnstorfia fluitans	Positive
Heathland	
Upland	
Anastrophyllum minutum	Negative
Anastrepta orcadensis	ns
Aneura pinguis	ns
Archidium alternifolium	ns
Aulacomnium palustre	Positive
Barbilophozia atlantica	U-shaped
Barbilophozia attenuata	U-shaped
Barbilophozia floerkei	ns
Barbilophozia hatcheri	Positive
Bazzania tricrenata	ns
Bazzania trilobata	ns
Blepharostoma trichophyllum	ns
Breutelia chrysocoma	ns
Bryum alpinum	U-shaped
Bryum subapiculatum	ns
Calypogeia arguta	Positive
Calypogeia fissa	ns
Calypogeia muelleriana	ns
Campylopus atrovirens	ns
Campylopus brevipilus	ns
Campylopus flexuosus	ns
Campylopus fragilis	ns
Campylopus introflexus	ns
Campylopus pyriformis	ns
Cephalozia bicuspidata	ns
Cephalozia connivens	Positive
Cephaloziella divaricata	ns
Cephaloziella hampeana	ns
Cephalozia lunulifolia	ns
Ceratodon purpureus	ns
Cladopodiella fluitans	ns
Colura calyptrifolia	ns
Dicranum bonjeanii	ns
Dicranodontium denudatum	ns
Dicranella heteromalla	ns
Dicranum majus	ns

Dicranella schreberiana	Positive
Diplophyllum albicans	ns
Ditrichum heteromallum	ns
Douinia ovata	U-shaped
Drepanocladus aduncus	ns
Entosthodon attenuatus	Small magnitude
Entosthodon obtusus	ns
Fissidens bryoides s.l.	Positive
Fossombronia wondraczekii	Negative
Frullania dilatata	ns
Frullania fragilifolia	ns
Frullania tamarisci	ns
Frullania teneriffae	ns
Funaria hygrometrica	ns
Gymnocolea inflata	Positive
Herbertus aduncus	ns
Hylocomium splendens	Positive
Hypnum jutlandicum	ns
Isothecium myosuroides	ns
Kurzia pauciflora	ns
Kurzia trichoclados	ns
Lepidozia cupressina	ns
Lepidozia pearsonii	Negative
Lepidozia reptans	ns
Leptodontium flexifolium	U-shaped
Leucobryum glaucum	Negative
Lophozia bicrenata	ns
Lophocolea bidentata	ns
Lophozia excisa	ns
Lophocolea heterophylla	ns
Lophozia incisa	ns
Lophozia ventricosa	ns
Marsupella funckii	ns
Microlejeunea ulicina	Negative
Mylia anomala	Positive
Mylia taylorii	ns
Nardia scalaris	ns
Nowellia curvifolia	ns
Odontoschisma denudatum	ns
Odontoschisma sphagni	Positive
Orthodontium lineare	ns
Pellia epiphylla	ns
Plagiothecium succulentum	ns
Pleuridium acuminatum	ns

Pleurozia purpurea	ns
Pleurozium schreberi	ns
Pogonatum nanum	ns
Pohlia drummondii	ns
Pohlia nutans	ns
Polytrichum commune	Positive
Polytrichum juniperinum	ns
Polytrichum piliferum	ns
Polytrichum strictum	ns
Pseudotaxiphyllum elegans	ns
Pseudoscleropodium purum	ns
Ptilidium ciliare	ns
Ptilium crista-castrensis	ns
Racomitrium ericoides	Positive
Racomitrium lanuginosum	ns
Rhytidiadelphus loreus	ns
Riccardia palmata	U-shaped
Saccogyna viticulosa	ns
Scapania compacta	ns
Scapania gracilis	ns
Scapania irrigua	Positive
Scapania nemorea	ns
Scapania scandica	ns
Scapania umbrosa	ns
Scapania undulata	ns
Sphagnum capillifolium	U-shaped
Sphagnum compactum	ns
Sphagnum denticulatum	Positive
Sphagnum fallax	Positive
Sphagnum fimbriatum	ns
Sphagnum girgensohnii	ns
Sphagnum molle	ns
Sphagnum quinquefarium	ns
Sphagnum russowii	Positive
Sphagnum squarrosum	Positive
Sphagnum strictum	ns
Sphagnum subnitens	Positive
Sphagnum tenellum	Positive
Sphagnum teres	ns
Sphagnum warnstorfii	ns
Splachnum ampullaceum	ns
Splachnum sphaericum	ns
Tetraplodon mnioides	ns
Tetraphis pellucida	ns

Tritomaria exsecta	ns
Tritomaria quinquedentata	ns
Warnstorfia fluitans	Positive