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The Impact of Nitrogen Deposition on the Occurrence of Lichen Species in the UK: Evidence from National Records

Running head: The impact of nitrogen deposition on lichens

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Abstract

Large areas of the UK currently have nitrogen (N) deposition at rates which exceed the thresholds above which there is risk of damage to sensitive components of the ecosystem (critical loads for nutrient nitrogen and critical levels for ammonia), and are predicted to continue to do so. This excess nitrogen can be very damaging to semi-natural ecosystems. Lichens are potentially very sensitive to air quality because they are adapted for direct uptake of nutrients deposited from the atmosphere. They are therefore potentially one of the most sensitive components of the ecosystem. We used data from the British Lichen Society (BLS) database, which records the presence of all lichen species growing in Britain at 10 km resolution, to assess individual responses of terricolous lichen species in acid grasslands, calcareous grasslands, heathlands and bogs to N deposition. The probability of presence of a species at a given level of N deposition was analysed together with driver data for climate, change in sulphur deposition, land-use and N deposition using generalised additive models (GAMs). Many species showed clear negative responses to N deposition with reductions in the probability of presence as N deposition increased. In all of the habitats, there were a mix of terricolous species which responded negatively or showed no significant relationship with N deposition. Most of the species with negative responses to N deposition started to decline in prevalence at levels of deposition below 10 kg N ha^{-1} yr^{-1}. This implies that current critical loads may have been set too high to protect sensitive lichen species.

Introduction

Atmospheric nitrogen (N) deposition poses a serious threat to sensitive semi-natural habitats in the UK [1,2]. 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 [3]. Hallsworth *et al.* [4] estimated that 20% of the area of Special Areas of Conservation in the UK exceeded the 1 $\mu g\ m^{-3}$ critical level for ammonia concentration in air assigned to lichens and bryophytes. A wide range of impacts on semi-natural vegetation communities resulting from N deposition have been reported including changes in species richness and composition [e.g. 5,6,7], changes in soil chemistry [e.g. 8,9], changes in plant tissue chemistry [e.g. 10,11] and changes in susceptibility to pest, disease and extreme weather [e.g. 12,13,14].

Lichens are potentially very sensitive to air quality and they have been widely used for biomonitoring of air pollutants, especially sulphur dioxide [15]. Lichens are adapted for direct uptake of nutrients deposited from the atmosphere through their thallus surface making them vulnerable to changes in atmospheric chemistry [16]. Both changes in species composition and community structure have been observed in relation to N deposition [17,18]. In a regional survey, Mitchell *et al.* [19] 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. Changes in the chemistry of lichen tissues have also been associated with N deposition and may be implicated in changes in species' abundance [e.g. 20,21,22,23].

Some lichen species are more sensitive to N deposition than others and an index has been created with epiphytic lichen species classified according to their sensitivity to nitrogen and bark pH based on their response to ammonia concentration [24]. However, terricolous lichens have received much less research attention even though they form an important component of some habitats. Here we focus on the response of terricolous lichen species in acid grasslands, calcareous grasslands, heathlands and bogs to examine individual species responses to N deposition in a national data set.

Results

Distributions of deposition for each habitat for which data were analysed are given in Figure 1.

Acid grassland

The relationship with N deposition for each of the species analysed is given in table 1. Of seven acid grassland lichen species that were investigated for their response to N deposition, four showed a significant response to N deposition: *Catapyrenium lachneum*, *Cetraria aculeata*, *Peltigera didactyla* and *P. hymenina*. *Catapyrenium lachneum* only showed a very small humped shape change in its distribution across the deposition range maintaining a low probability of presence. The probability of presence of *Cetraria aculeata* was reduced with increasing N deposition reaching very low levels at 20 kg N ha^{-1} yr^{-1} whereas both *P. didactyla* and *P. hymenina* showed a clear decline in probability of presence as N deposition increased (Figure 2).

Calcareous grassland

Sixteen species were examined for calcareous grassland and three showed a significant response to N deposition, *Diploschistes muscorum*, *Toninia sedifolia* and *Cladonia foliacea*. *Cladonia foliacea* showed a reduced probability of occurrence above 20 kg N ha^{-1} yr^{-1} (Figure 3). *D. muscorum* showed a decrease followed by an increase and *Toninia sedifolia* showed an inconsistent response, increasing then decreasing and increasing again. The latter two responses do not look realistic and are influenced by large variability in occurrence at both low and high deposition.

Bog

Six species were examined for bogs and two of these showed significant relationships with N deposition, *Cladonia arbuscula* subsp. *squarrosa* and *C. portentosa*. *C. arbuscula* subsp. *squarrosa* showed a humped response to N deposition, initially increasing in its probability of occurrence, peaking around 15 kg N ha^{-1} yr^{-1} and then declining. *C. 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 4). This increase is likely to be an artefact of few records at high deposition.

Heathland

In heathlands, 26 species were investigated and nine showed a significant relationship with N deposition (*Cetraria aculeata, Cladonia arbuscula* subsp. *squarrosa, C. cervicornis verticillata, C. glauca, C. portentosa, C. subulata, C. uncialis* subsp. *biuncialis, Dibaeis baeomyces* and *Peltigera hymenina*). All other species showing significant relationships showed negative relationships (Figure 5) with many of the species reaching a very low probability of presence by 20 kg N ha^{-1} yr^{-1}.

Discussion

Species responses to N deposition

The results of the analysis conducted in this project indicate that some lichen species are very sensitive to N deposition. In all of the habitats there were species which responded negatively to N deposition as well as those that showed no significant relationship with N deposition, but there were no species which showed a clear positive relationship with N deposition, which highlights the sensitivity of lichens to N deposition. Hauck [16] suggests that there are unlikely to be any terricolous lichens indicative of high N pollution because they will be suppressed by vascular plant cover.

In acid grasslands *Cetraria aculeata*, *Peltigera didactyla* and *P. hymenina* showed clear negative responses to N deposition. Both *C. aculeata* and *P. didactyla* showed a reduction in their probability of presence to approximately half by 15 kg N ha^{-1} yr^{-1}, with both species reaching very low probabilities of presence at high deposition. *P. hymenina* showed a less steep negative trend but nevertheless, probability of presence was consistently reduced with increasing N deposition. The sensitivity of *C. aculeata* to N deposition in acid grasslands is well known. In a survey of acid and calcareous dune grasslands, Remke et al. [25] found that *C. 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 *C. aculeata* is sensitive to acid deposition [26]. Acid deposition from NO_3 is a possible mechanism for its decline along the UK spatial gradient. *Peltigera* species form stable symbioses with nitrogen-fixing cyanobacteria which may influence their sensitivity to N deposition, but little has previously been reported regarding the sensitivity of this species to N deposition.

In calcareous grasslands, *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 the decline in probability of presence is apparent up to 30 kg N ha^{-1} yr^{-1} when *C. 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.

Two species showed significant relationships with N deposition in bogs, *Cladonia arbuscula* subsp. *squarrosa* and *C. portentosa*. *C. arbuscula* subsp. *squarrosa* shows a humped 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 rather than a response to N deposition. *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 tissue of *C. 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 [20,22,27].

In heathlands, 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. The probability of presence of *Cetraria aculeata*, *Cladonia cervicornis verticillata, C. subulata* and *C. uncialis* subsp. *biuncialis* at 15 kg N ha^{-1} yr^{-1} was reduced to approximately half that at 5 kg N ha^{-1} yr^{-1}. The majority of species that showed a negative relationship with N deposition did so starting from the lowest levels of deposition found in this study. This suggests that the critical load concept, which assumes that there is a level below which damage cannot be detected [28], is lower than the lowest deposition levels found in the UK. Indeed, only three species (*Cladonia glauca, Dibaeis baeomyces* and *Peltigera hymenina*) showed a threshold below which a negative relationship with N deposition was not observed. The probability of presence for all of these species had begun to fall by 15 kg N ha^{-1} yr^{-1}. Two of the species that have a negative relationship in heathlands 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.

Although there are species in the data set for which we may have expected to see negative trends 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. 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. There may also have been reductions in populations of individual species which this analysis has not assessed.

Data limitations

The BLS database is currently limited by patchy coverage of parts of England and Wales, although Scotland and northern England are well covered. The database also contains records from a range of different sources. This may have resulted in some geographical bias towards the more lichen-rich areas, but overall this is compensated by the inclusion in the analysis of the BLS Mapping Scheme dataset, which has more comprehensive coverage.

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 as being species strongly associated with one or more of the habitats. However, it was necessary to take these as including dunes and calaminarian grasslands (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. 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. To identify trends over time and associate them with these different factors it would be necessary to use dated records and revisits to known sites. 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 for this purpose the records have been collated over a long period of time (1960 to 2009 inclusive), consequently species that have declined or been lost since 1960 will still be recorded as present. Visual examination maps of recent dated records compared with older records did not reveal any distinct distribution changes for the species of interest.

Although there are limitations with this data set, some species showed clear declines in their probability of presence with increasing N deposition 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.

Materials and methods

Data were taken from the British Lichen Society (BLS) database. This database records the presence of all lichen species growing within 10 km hectads. All of the UK is covered although data is more thoroughly collected in some areas than others. Records used in this study span the last 50 years.

Lichen species were selected for analysis where they were a) associated with, and largely limited to, the target habitats (according to expert opinion), b) terricolous, c) not too scarce or regionally distributed (excludes montane and coastal species), d) accurately represented in the BLS database, and e) as far as possible subject to geographically even recording effort.

Data for three types of ecological driver were included in the models as potential explanatory variables; land-use, atmospheric pollutant deposition and climate. 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 (http://www.ceh.ac.uk/sci_programmes/BioGeoChem/LandCoverMap2000.html). Long term annual average climate data (1980 to 2005) at the 5 x 5 km scale based on interpolated estimates provided by the Met Office (www.metoffice.gov.uk) were used. Minimum January temperature, maximum July temperature and annual rainfall were used in the analysis.

Estimates of total N deposition at the 5 x 5 km scale were provided by CEH Edinburgh using the CBED model for deposition to moorland [2,29] calculated as the mean of the estimates for 1996, '97 and '98. Change in sulphur (S) deposition was considered more important than current S deposition because reductions since the early 1970s have been dramatic in many parts of the UK. Change in S deposition since the early seventies was based on FRAME (Fine Resolution Ammonia Exchange) [30,31] model estimates calculated for 2005 and 1971. The explanatory variable was the difference between the two estimates for each 5 x 5 km.

GIS and database querying was used to spatially match botanical data with driver datasets. Where the resolution of the botanical records was larger than that of the driver variable data the driver data up-scaled by averaging over the botanical recording unit.

The probability of presence of each individual species in a hectad at a given level of N deposition was analysed together with driver data for climate, change in S deposition, land use and N deposition using generalised additive models (GAMs) [32]. Spatial dependence between the hectads was accounted for in the GAM by including an additional two dimensional smooth term, ie 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. To assess this approach, models were also set up in a Bayesian framework allowing for a localised, fine scale spatial dependence structure to be specified. In this model framework, the value in a hectad is modelled conditional on the values in all neighbouring hectads. Results from this analysis confirmed that the broader scale dependence method of the GAMs performed equally as well as the full Bayesian model. Due to the size of the dataset, and the attendant computational effort required, the GAMs were deemed the most appropriate modelling choice for the remainder of the data to be analysed.

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 fitted the model with all terms, individual terms were selected based on F tests, the AIC score [33] and the generalised cross validation score (GVC). Non significant terms were only removed if the AIC and GCV scores improved upon their removal. The covariate corresponding to N deposition was always included in the model whether it was significant or not, as it was this relationship ultimately we were interested in. The final models were checked by examining plots of residuals and quantile-quantile plots of the observed and predicted values.

To assess the impact of N deposition formally, the p value from the F test associated with the nitrogen covariate was returned along with a graphical plot of the estimated smooth term in the GAM for N deposition. 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 that N had in relation to the vegetation response variable, including predicted strength, direction and change points.

In the figures 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, not prediction intervals for individual observations. Plots show the relationships between the probability of presence of individual species and N deposition once the influence of other co-variables has been removed. Figures are plots of the marginal affect of N deposition, conditional on the median values for each of the co-variables.

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Table 1. P values and direction of spatial relationship with nitrogen deposition for species analysed. The direction of the relationship with N deposition is given in the column 'direction of change' for all species where the relationship was significant: positive and negative indicate a clear direction of change, U-shaped and humped indicate relationships with these shapes (although the shape of these relationship could not be specifically tested), small magnitude indicates that although the relationship was significant there was little change in the probability of presence across the deposition range, and inconsistent indicates a relationship that changes direction several times.

Species	P value	Direction of change
Acid grassland		
Baeomyces rufus	0.503	
Catapyrenium lachneum	**0.007**	Small magnitude
Cetraria aculeata	**0.000**	Negative
Cladonia cariosa	0.066	
Leptogium palmatum	0.154	
Peltigera didactyla	**0.030**	Negative
Peltigera hymenina	**0.020**	Negative
Calcareous grassland		
Catapyreneum squamulosum	0.884	
Cladonia foliacea	**0.002**	Negative
Cladonia furcata subsp. *subrangiformis*	0.131	
Cladonia pocillum	0.500	
Cladonia rangiformis	0.730	
Diploschistes muscorum	**0.033**	U-shaped
Fulgensia fulgens	0.931	
Heterodermia leucomela	0.758	
Lecidea lichenicola	0.692	
Megaspora verrucosa	0.065	
Peltigera leucophlebia	0.338	
Peltigera neckeri	0.278	
Peltigera rufescens	0.713	
Placidiopsis custnani	0.489	
Psora decipiens	0.073	
Toninia sedifolia	**0.005**	Inconsistent
Bog		
Cladonia arbuscula subsp. *squarrosa*	**0.003**	Humped
Cladonia ciliata	0.877	
Cladonia portentosa	**0.000**	Negative

Cladonia uncialis biuncialis	0.290	
Icmadophila ericitorum	0.523	
Lichenomphalia umbellifera	0.058	
Heathland		
Baeomyces placophyllus	0.565	
Baeomyces rufus	0.141	
Catapyrenium lachneum	**0.027**	Small magnitude
Cetraria aculeata	**0.000**	Negative
Cetraria islandica islandica	0.493	
Cetraria muricata	0.074	
Cladonia arbuscula subsp. *squarrosa*	**0.007**	Negative
Cladonia cariosa	0.227	
Cladonia cervicornis subsp. *cervicornis*	0.083	
Cladonia cervicornis subsp. *verticillata*	**0.022**	Negative
Cladonia ciliata	0.160	
Cladonia crispata subsp. *cetrariiformis*	0.102	
Cladonia floerkeana	0.153	
Cladonia glauca	**0.002**	Negative
Cladonia portentosa	**0.003**	Negative
Cladonia strepsilis	0.105	
Cladonia subulata	**0.002**	Negative
Cladonia uncialis subsp.*biuncialis*	**0.002**	Negative
Dibaeis baeomyces	**0.008**	Negative
Diploschistes muscorum	0.105	
Icmadophila ericitorum	0.280	
Lichenomphalia hudsoniana	0.122	
Lichenomphalia umbellifera	0.137	
Peltigera hymenina	**0.000**	Negative
Placynthiella uliginosa	0.096	
Pycnothelia papillaria	0.086	

Figure legends

Figure 1. Range of nitrogen deposition for habitats investigated. Frequency histograms of N deposition (kg N ha^{-1} yr^{-1}) for each of the habitats for acid grassland, calcareous grassland, bog and heathland.

Figure 2. Spatial change in probability of presence of lichen species in acid grassland. Modelled spatial change in probability of presence of *Cetraria aculeata, Catapyrenium lachneum, Peltigera didactyla* and *P. hymenina* in acid grassland hectads with increasing total inorganic N deposition (kg N ha^{-1} yr^{-1}).

Figure 3. Spatial change in probability of presence of lichen species in calcarous grassland. Modelled spatial change in probability of presence of *Cladonia foliacea* in calcareous grassland hectads with increasing total inorganic N deposition (kg N ha^{-1} yr^{-1}).

Figure 4. Spatial change in probability of presence of lichen species in bog. Modelled spatial change in probability of presence of *Cladonia arbuscula* subsp. *squarrosa* and *C. portentosa* in bog hectads with increasing total inorganic N deposition (kg N ha^{-1} yr^{-1}).

Figure 5. Spatial change in probability of presence of lichen species in heathland. Modelled spatial change in probability of presence of *Cetraria aculeata, Cladonia arbuscula* subsp. *squarrosa, Cladonia cervicornis* subsp. *verticillata, Cladonia glauca, Cladonia portentosa, Cladonia subulata, Cladonia uncialis* subsp. *biuncialis, Dibaeis baeomyces, Peltigera hymenina,* and *Placynthiella uliginosa* in heathland hectads with increasing total inorganic N deposition (kg N ha^{-1} yr^{-1}).

Figures

Figure 1.

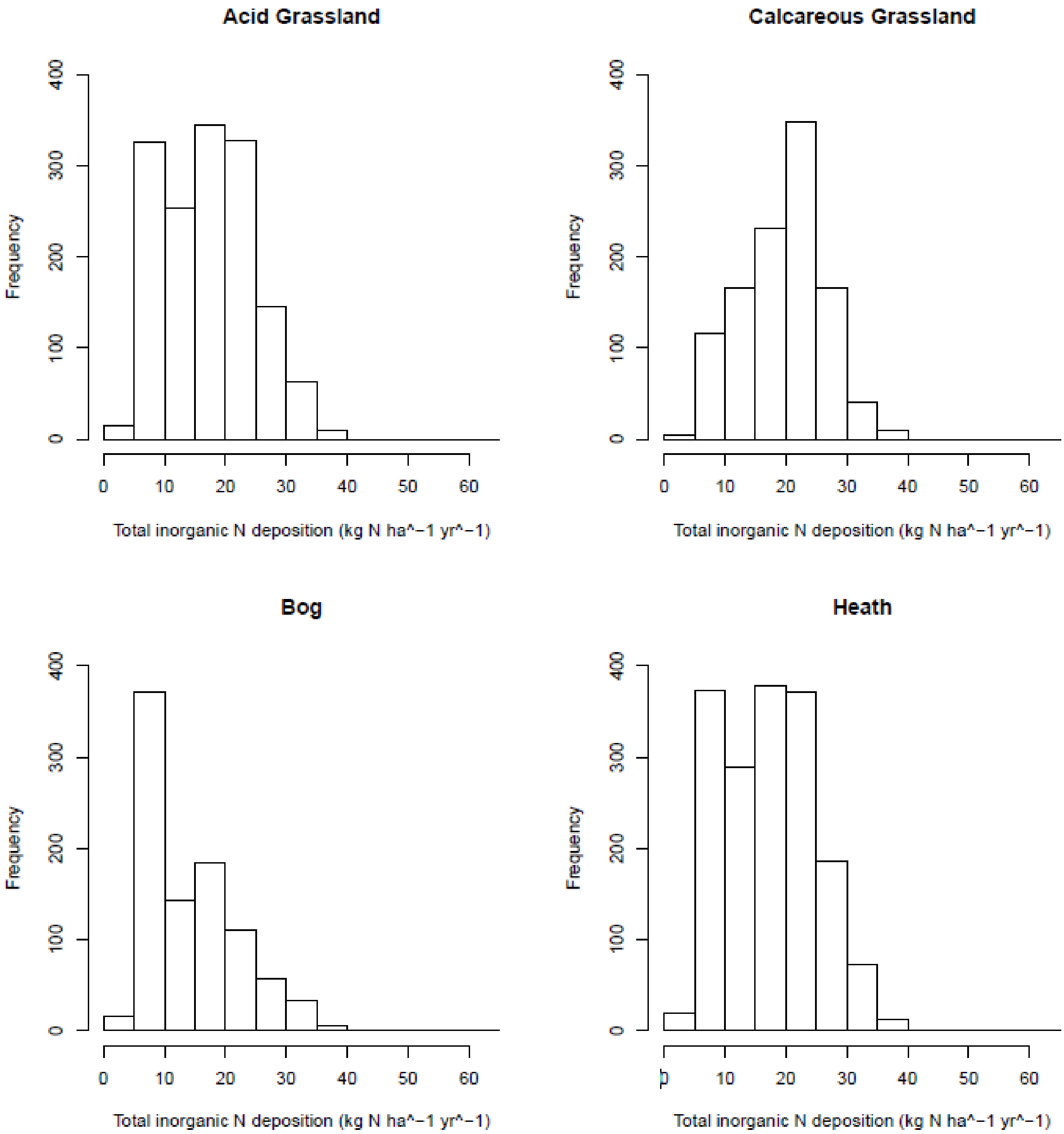


Figure 2.

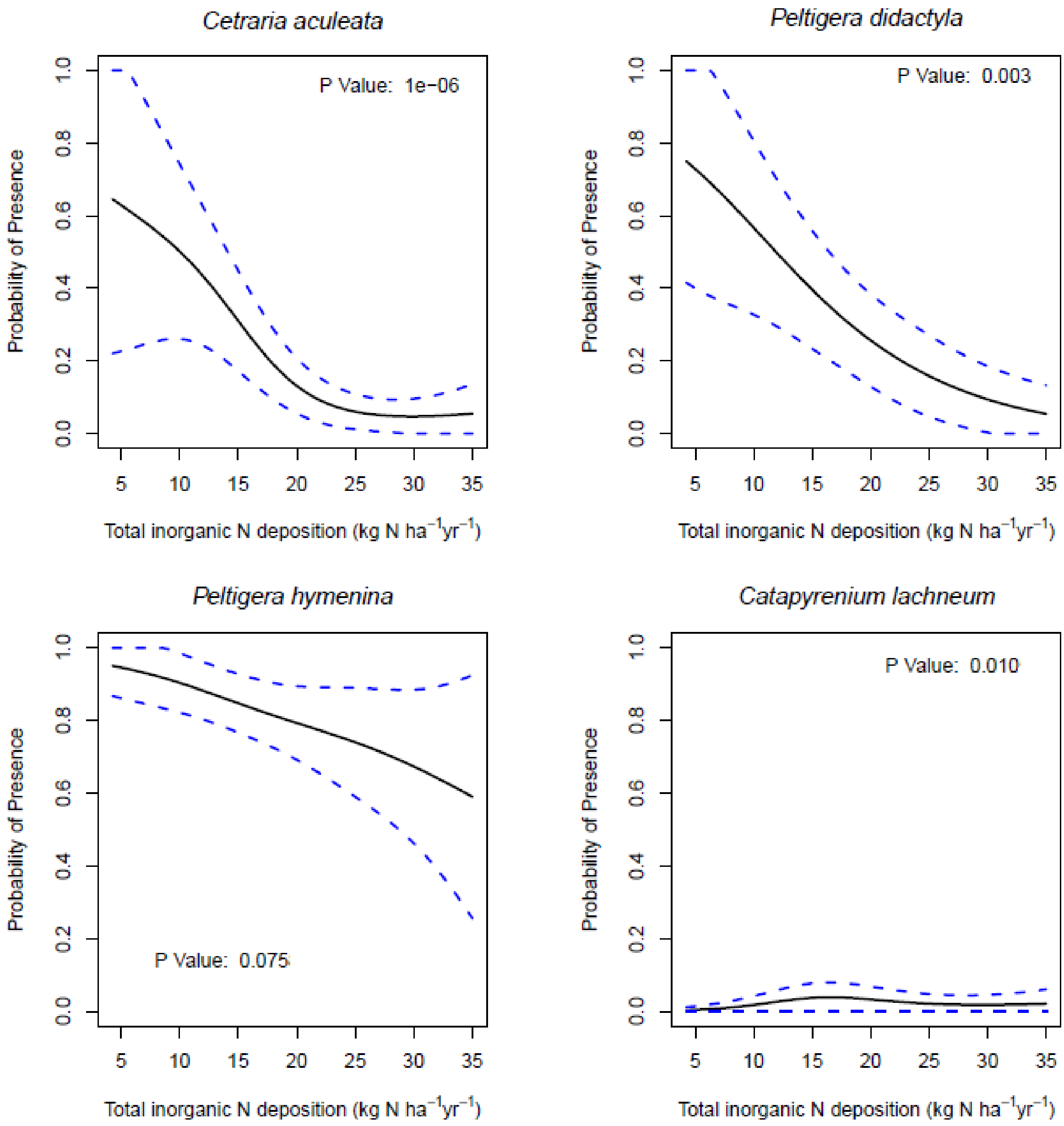

Cetraria aculeata
P Value: 1e−06
Peltigera didactyla
P Value: 0.003
Peltigera hymenina
P Value: 0.075
Catapyrenium lachneum
P Value: 0.010
Probability of Presence
0.0
0.2
0.4
0.6
0.8
1.0
5
10
15
20
25
30
35
Total inorganic N deposition (kg N ha^{-1}yr^{-1})

Figure 3.

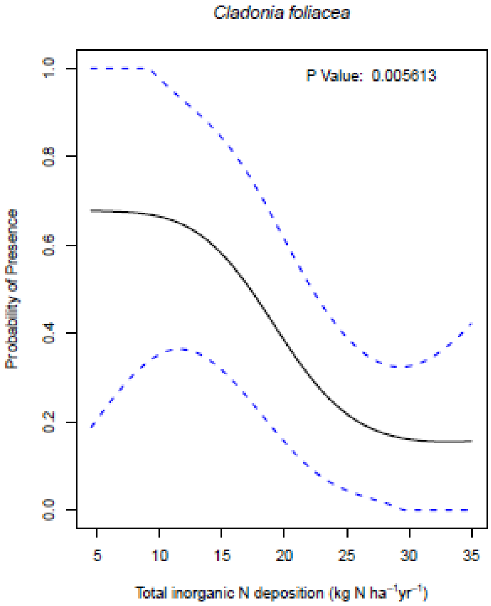

Cladonia foliacea
P Value: 0.005613
Probability of Presence
0.0
0.2
0.4
0.6
0.8
1.0
5
10
15
20
25
30
35
Total inorganic N deposition (kg N ha^{-1}yr^{-1})

Figure 4.

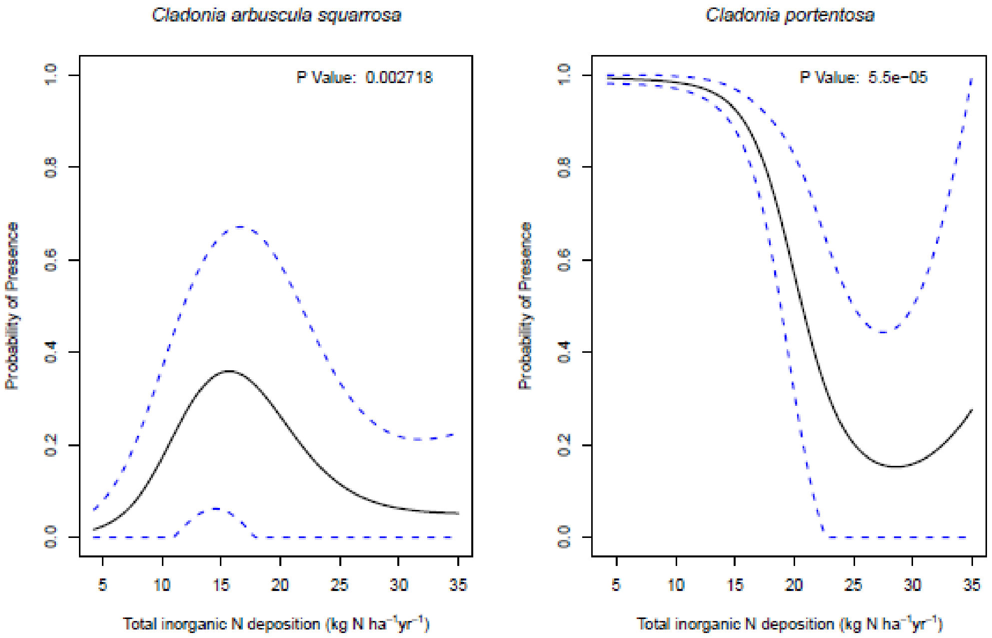
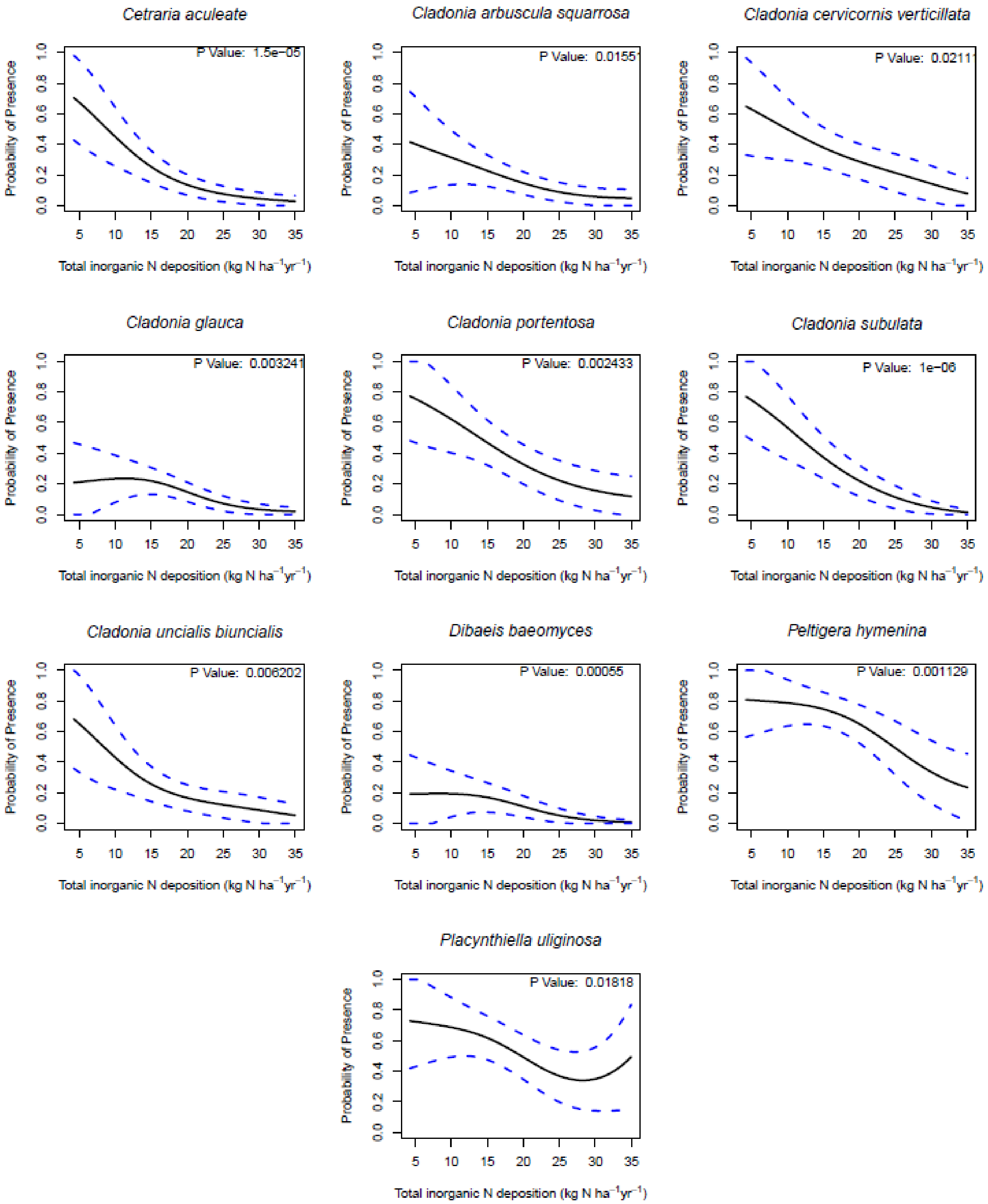

Cladonia arbuscula squarrosa
P Value: 0.002718
Probability of Presence
0.0
0.2
0.4
0.6
0.8
1.0
5
10
15
20
25
30
35
Total inorganic N deposition (kg N ha^{-1}yr^{-1})
Cladonia portentosa
P Value: 5.5e−05
Probability of Presence
0.0
0.2
0.4
0.6
0.8
1.0
5
10
15
20
25
30
35
Total inorganic N deposition (kg N ha^{-1}yr^{-1})

Figure 5.


Cetraria aculeate
P Value: 1.5e−05
Cladonia arbuscula squarrosa
P Value: 0.0155
Cladonia cervicornis verticillata
P Value: 0.0211
Cladonia glauca
P Value: 0.003241
Cladonia portentosa
P Value: 0.002433
Cladonia subulata
P Value: 1e−06
Cladonia uncialis biuncialis
P Value: 0.006202
Dibaeis baeomyces
P Value: 0.00055
Peltigera hymenina
P Value: 0.001129
Placynthiella uliginosa
P Value: 0.01818
Probability of Presence
0.0 0.2 0.4 0.6 0.8 1.0
5 10 15 20 25 30 35
Total inorganic N deposition (kg N ha⁻¹yr⁻¹)