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Tipping, E.; Henrys, P.A.; Maskell, L.C.; Smart, S.M**.** 2013. **Nitrogen deposition effects on plant species diversity; threshold loads from field data**

Nitrogen deposition effects on plant species diversity; threshold loads from field data

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Abstract

National-scale plant species richness data for Great Britain in 1998 were related to modelled contemporary N deposition (N_{dep}) using a broken stick median regression, to estimate thresholds above which N_{dep} definitely has had an effect. The thresholds (kgN ha^{-1} a^{-1}) are 7.9 for acid grassland 14.9 for bogs, 23.6 for calcareous grassland, 7.8 for deciduous woodland and 8.8 for heath. The woodland and heath thresholds are not significantly greater than the lowest N_{dep}, which implies that species loss may occur over the whole range of contemporary N_{dep}. This also applies to acid grassland if it is assumed that N_{dep} has substituted for previous N fixation. The thresholds for bog and calcareous grassland are both significantly above the lowest N_{dep}. The thresholds are lower than the mid-range empirical Critical Loads for acid grassland, deciduous woodland and heath, higher for bogs, and approximately equal for calcareous grassland.

Keywords: Countryside Survey, diversity, nitrogen deposition, plants, species richness

Capsule: Analysis of extensive field data provides estimates of nitrogen deposition rates above which plant species richness is reduced.

INTRODUCTION

The acidification and eutrophication of terrestrial ecosystems by atmospherically deposited nitrogen (N_{dep}), and resulting biodiversity loss, are of wide concern because of habitat degradation and the possibility that ecosystem impacts are hard to reverse (Bobbink et al., 2010; Strengbom et al. 2001). In Europe, international conventions designed to reduce or reverse unwanted effects of N, notably the Gothenburg Protocol, make use of Critical Loads, i.e. values of N_{dep} above which the effects of atmospherically-deposited N are deemed unacceptable (Bobbink et al., 2010, 2011). Critical Loads of nitrogen are set for different habitats; examples are 3-5 kgN ha^{-1} a^{-1} for tundra, 5-10 kgN ha^{-1} a^{-1} for raised and blanket bogs, and 10-20 kgN ha^{-1} a^{-1} for dry heaths (Bobbink et al., 2011). Their values are derived mainly from the results of experimental studies, usually small-scale field manipulations, in which known added N inputs have been related to observable short-term changes in plant species and growth, and biogeochemical effects. Expert judgement is also applied.

The indirect link to long-term biodiversity loss *per se* is seen as a drawback of this approach (van Hinsberg et al, 2008). However, although evidence from field surveys has been used as contextual information to set Critical Loads, its application has proved problematic because low signal-to-noise ratios weaken the ability of the data to identify quantitative thresholds (Bobbink et al., 2010). The importance of other factors in conditioning ecosystem responses to nitrogen deposition has also been emphasised. For example, historical acidification, starting soil pH, land-use intensity and climatic gradients also exert partial unique effects on enrichment indicators such as species richness (Maskell et al., 2010). The contributions of factors other than N deposition on differences in plant species diversity make it difficult to determine effects from conventional (multiple) regression analysis. Some of these factors might be known and quantifiable by survey data but others may not. For example, abiotic factors such as low levels of trace elements, or ecological filters such as species pool effects, are hard to quantify as explanatory variables.

Nonetheless, there is mounting field evidence from British and European ecosystems to show that plant diversity decreases with N_{dep} (Stevens et al. 2004; Duprè et al. 2010; Maskell et al. 2010; van den Berg et al. 2011), with N_{dep} assumed to be a proxy for ecosystem N enrichment. Weak but highly significant correlations have been found in cases where plant sampling has been randomised (Maskell et al., 2010), and stronger signals where surveys were optimised by well-replicated sampling along the deposition gradient and controlling for other sources of variation (Stevens et al., 2004).

Here we report a new analysis of plant species richness data from nearly 2000 sites in the UK, in which we test for possible thresholds of N_{dep} above which plant species richness can be said to decline. We used data obtained during the Countryside Survey of Great Britain, carried out in 1998 (Smart et al., 2003), by the randomised sampling of a large number of spatially representative sites. These data are especially useful for our purposes since they are geographically comprehensive, derived from stratified, random sampling, and recorded at fine resolution. The data are therefore unbiased and also minimise the confounding between alpha and beta diversity (i.e. ‘within habitat’ versus ‘among habitat’ diversity) associated with species richness from large grid cells (Huston, 1999).

We analysed the plant species richness data for five broad habitats (acid grassland, bog, calcareous grassland, deciduous woodland and heath), in terms of N deposition estimated from national-scale measurement and spatial interpolation (Smith *et al*., 2000; NEGTAP, 2001). Rather than analyse the data by conventional regression, as done in previous work (Stevens et al., 2004, 2010; Maskell et al., 2010), we applied a “broken stick” model, the break in which corresponds to the threshold in N_{dep}. The results were assessed for statistical significance in order to estimate the deposition rate above which reductions in species diversity can confidently be said to occur, and to estimate species loss per additional unit of N_{dep} above the threshold. Comparisons of the thresholds with empirical Critical Loads were made.

METHODS

The Countryside Survey (CS) samples a large number of 1 km x 1 km squares randomly located within defined environmental strata across Great Britain to provide statistically representative coverage of the wider countryside and its habitat composition. Each square contains smaller subplots where detailed information on vegetation composition (both vascular plants and bryophytes) is recorded. Surveys have been carried out in 1978, 1984, 1990, 1998 and 2007. In this analysis, we used CS data collected in 1998 that had previously been assembled and analysed by Maskell et al. (2010). Further information is available from the Countryside Survey website (http://www.countrysidesurvey.org.uk/).

Vegetation plots were classified to the phyto-sociological units of the British National Vegetation Classification (NVC) (Rodwell, 1992). We used a new assignment of CS plots to the NVC based on the pseudo-quadrat approach (Critchley et al., 2002 and Supplementary Material). Plots were selected that were classified with a Jaccard similarity coefficient of >0.5 into one of five NVC habitat types; acid grassland (U1–9), calcareous grassland (CG2, 3, 4, 6, 8, 10, 11), heathland (H1–19 except H5, 6 and 17), bogs (M1-M4, M6, M15-M21, M25, H9, H12 (bog on deep peat)), and deciduous woodlands (included W4-W25 with no plots from W20 or W21). Plots were also assigned to the UK Biodiversity Action Plan Broad Habitat classification (Jackson, 2000) by referencing the habitat assignment of the mapped unit of land area within which each plot was located.

The data employed in this study are summarised in Table 1. Figure 1 shows the coverage of each of the habitats across Great Britain using data from Land Cover Map 2000 and also the distribution of the Countryside survey 1km sample squares. This highlights the comprehensive spatial coverage provided by Countryside Survey. The number of CS plots available for each of the five habitats were 873 (acid grassland), 92 (calcareous grassland), 457 (heathland), 203 (bog) and 361 (deciduous woodland). The numbers of sites are roughly proportional to the areal distribution of each habitat.

For N deposition we used estimates at the 5 x 5 km scale provided by CEH Edinburgh (Smith et al., 2000; NEGTAP, 2001;), calculated as the mean of the estimates for 1996-1998 from the CBED model for deposition to the appropriate habitat type. The ranges of N deposition covered by each of the habitats are given in Table 1 (see also Figure 2). The distribution of N_{dep} is approximately normally distributed for all habitats except bog, where there is a clear peak at low N_{dep}. The analysis is helped by the wide ranges of N_{dep} across GB.

We used non-parametric quantile regression to estimate the relationship, including a threshold, between N_{dep} and species richness. Using this method, one would estimate the parameters of a standard multivariate linear model by minimising the following function:

$$\arg\min_{\beta}\left\{\sum_{i=1}^{n}\rho_{\tau}(y_i-\beta X_i)\right\}$$

where $\rho_\tau(z) = z(\tau - I(z<0))$ with $I(\cdot)$ representing the indicator function and τ the quantile estimate. The main analysis was performed with τ set to 0.5, i.e. a median regression. The median is less sensitive to extreme values than the mean and provides a robust estimate of the underlying relationship. We also carried out comparative analyses with τ set to 0.25 and 0.75.

As we are seeking to estimate a threshold from the field data, rather than fitting a standard linear slope, we fit a model that includes a breakpoint, which defines the point at which a constant relationship changes into a declining linear trend. We therefore seek to minimise the quantile error (defined in above) between the observed data and a function expressed by three variables that control the constant value up to the breakpoint (n_{max}), the breakpoint location ($N_{dep,T}$) and the slope of decline after the breakpoint, known as species loss rate (r_{sl}). As this function is a three parameter equation, it is minimised using a numerical based technique, in this case we used the Nelder-Mead algorithm (Nelder and Mead, 1965).

Because we estimate the regression coefficients non-parametrically by minimising the quantile error, with no distributional assumptions placed on the data or the parameters, we are unable to directly obtain estimates of upper and lower limits for the estimated threshold values. Therefore, in order to estimate a confidence interval on the estimated threshold load, we use a bootstrap based procedure (Efron and Tibshirani, 1993). This involves randomly sampling *n* observations from the data with replacement, where *n* is the total sample number. The quantile regression function as described above is then fitted to this new pseudo data set to obtain estimates for each of the three parameters. Estimated parameters are stored and then the whole process is repeated 999 times, producing (including the original data) 1000 sets of breakpoints. Confidence intervals for the breakpoint parameter are then obtained simply by taking the 2.5th and 97.5th percentile from these estimates.

RESULTS AND DISCUSSION

Median regression analysis was carried out on each of the five habitats separately, firstly including all species and secondly only vascular species. There were only minor differences in the derived thresholds with or without the bryophytes, and we report only the results for the combined data (Table 1). Figure 2 shows the fitted relationships using the mean parameters. Confidence intervals around the threshold value are also plotted with the upper and lower 95% interval values. For acid grassland, bog and calcareous grassland, the lower 95% limit of the threshold is greater than the lowest N_{dep}, indicating that a significant threshold value is identified. But this does not apply to deciduous woodland and heath, for which the lower 95% confidence limits are less than the lowest N_{dep}; therefore for these two habitats it appears that species richness is reduced at all current values of N_{dep}.

The other information that comes from the fitting is the decrease in species number per additional N_{dep}, r_{sl}. This varies among the habitats, ranging in absolute terms from 0.19 species per kg N ha^{-1} yr^{-1} in deciduous woodland to 0.85 species per kg N ha^{-1} yr^{-1} in calcareous grassland. When expressed as a relative percentage to the maximum species number (n_{max}), the range is from 1.3 – 3.0 % per kg N ha^{-1} yr^{-1} again from deciduous woodland to bog.

The high scatter in the data (Figure 2) reflects the numerous factors that influence species richness (Grace 1999; Dodd et al 1994). As well as variables that may be affected by N_{dep}, principally soil fertility and acidity, other factors include seed bank availability, species-area and species pool effects, grazing and other disturbances, climate, land-use legacies and the acidifying effect of (non-marine) sulphur deposition (which is likely to have different effects than N_{dep} because the two are not strongly correlated; $r^2 = 0.33$).

The use of median (0.5 quantile) regression implies that combinations of these other factors both increase and decrease diversity, on average equally. But bias in one or other direction may exist, which would mean that other quantiles might be more suitable for data fitting (cf. Cade and Noon, 2003). Fitting the data to the 0.75 quantile produced thresholds and confidence ranges similar to the median regression values (Table 2). The same is true for the 0.25 quantile for acid and calcareous grasslands and heath, but for bog and deciduous woodland the thresholds are higher. Of course the absolute slopes of the diversity-N_{dep} relationship differ, but the relative slopes do not.

Although N_{dep} is an obvious choice for the independent variable, being the driving variable of interest and subject to emission control, it presents some problems with respect to interpretation. Firstly, the effects on diversity are mediated through biogeochemical processing of additional N inputs due to deposition. In the case of acidification, this is by the generation of excess nitrate, when the soil cannot immobilise nitrogen (Emmett, 2007), so that soil pH is decreased which reduces diversity (Grime, 2001). Eutrophication depends upon the rate of cycling of N, and control of net primary productivity, potentially producing both increases in diversity at low levels of input and decreases at high levels (Grime, 2001). While both of these effects will depend upon N_{dep} they will be separate.

Secondly, although N_{dep} may be a guide to N enrichment, the relationship must be time dependent, due to the accumulation of N in the ecosystem. Therefore, a plot like those in Figure 2 for earlier years would be expected to show a higher threshold and perhaps a lower slope, while a future plot might have a lower threshold and steeper slope. The use of cumulative N_{dep} as employed by Dupre et al. (2009) resolves this to some extent, although not completely if the evolution of the soil N status is nonlinear with respect to N_{dep}. The thresholds of Figure 2 are therefore time-dependent, determined more by historical N build-up than contemporary N_{dep}. A more precise statement of their meaning is that, for N_{dep} values below the current threshold, there is no evidence for diversity loss due to N enrichment brought about by cumulative N_{dep}.

A third confounding issue is the relationship between N_{dep} and inputs from N fixation, which will have been the main supply prior to the recent decades and centuries of elevated N_{dep}. According to DeLuca et al. (2008) N fixation is down-regulated by N deposition, so that at N_{dep} below or equal to the "pristine" N fixation rate, the total N input is approximately unchanged. A representative "pristine" N fixation rate of 3 kg ha^{-1} a^{-1} has been estimated for NW Europe (Tipping et al., 2012). Therefore "excess N_{dep}" thresholds might be derived by subtracting this value from the thresholds of Table 1, i.e. only this excess N_{dep} will have enriched the soils. This suggests that for acid grassland, deciduous woodland and heath, effects are seen at all N_{dep} values above the N fixation rate, whereas for bog and calcareous grassland there is evidence only at higher thresholds.

Empirical Critical Loads are derived from short term treatments, usually focused on measurable single processes or effects (Bobbink et al., 2010, 2011). Such experiments in themselves will not have added as much N to the systems as long-term accumulation over decades or centuries, although the systems under study will often have experienced loads higher than our thresholds, i.e. the applied loads will operate to increase the rate of enrichment. By the same arguments as above, empirical loads must be time-dependent, but with a different time constant; thus Hornung et al (1995) suggested that empirical Critical Loads might be applicable on a time scale of only 20-30 years. Therefore one perhaps should not expect agreement in absolute values, although Table 1 and Figure 3 show that the thresholds and empirical Critical Loads are of similar magnitude. However, it might be expected that the order of habitats should be the same in the two systems, and this is the case for deciduous woodland, heath and calcareous grassland, with acid grassland quite close. The one habitat that does not fit well into the pattern is bog, for which the threshold deposition is considerably higher than the empirical Critical Load, and is significantly greater than the lowest N_{dep}. Differences between the thresholds and Critical Loads must arise because the latter are set on the basis of changes in species composition, physiology and bigeochemical variables, as well as in diversity, the exact combination varying amongst habitats. It may therefore be significant that the two habitats for which the threshold and Critical Load agree best (acid and calcareous grasslands) are the only two of the five habitats for which changes in plant species richness were used to set the Critical Load, whereas for bogs changesin plant species composition was the principal criterion (Bobbink et al., 2011).

Interpretation of the large-scale spatial results presented here would likely be enhanced by the use of dynamic biogeochemical modelling (see De Vries et al., 2010) to translate the primary driving variable

N_{dep} to more direct predictors of species diversity, for example the N cycling flux through the soil, net primary production and soil pH. By taking into account differences in climatic and soil properties, as well as habitat type and deposition, this could distinguish the acidifying and eutrophying effects of N, and, through space-for-time substitution, provide insights into the temporal evolution of effects on biodiversity. Such modelling could further draw together the different kinds of information about ecosystem N enrichment to provide a more comprehensive and robust assessment of the relationship between N deposition and species richness decline.

CONCLUSIONS

- Threshold N_{dep} values above which plant species diversity is reduced have been derived from field observations for five terrestrial British habitats.
- In two cases, deciduous woodland and heath, the thresholds (7.8 and 8.8 kgN ha^{-1} a^{-1} respectively) are not significantly greater than the lowest N_{dep}, which implies that species loss has occured over the whole range of contemporary N_{dep}. This also applies to acid grassland (threshold 7.8 kgN ha^{-1} a^{-1}) if it is assumed that N_{dep} has substituted for previous N fixation. For bog and calcareous grassland, the thresholds of 14 kgN ha^{-1} a^{-1} and 24 kgN ha^{-1} a^{-1} respectively are both significantly above the lowest N_{dep}.
- Median species numbers at N_{dep} below the thresholds are; acid grassland 18, bog 18, calcareous grassland 28, deciduous woodland 14, and heath 13.
- The average relative loss of species with increasing N_{dep} is 2% per (kgN ha^{-1} a^{-1}). The values range from 1.3% for deciduous woodland to 3.0% for calcareous grassland. Absolute losses range from 0.19 species per (kgN ha^{-1} a^{-1}) for deciduous woodland to 0.85 species per (kgN ha^{-1} a^{-1}) for calcareous grassland.
- The derived thresholds are broadly similar in magnitude to empirical Critical Loads, assigned from collated manipulation studies. The thresholds are lower than the mid-range Critical Loads for acid grassland, deciduous woodland and heath, higher for bogs, and approximately equal for calcareous grassland.

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Table 1. Summary of data and fitting results. Key: n_{max} maximum species number; $N_{dep,T}$ threshold N deposition; r_{sl} no. of species lost per unit N_{dep}; $\%r_{sl}$ % species lost per unit N_{dep}. The 95% confidence limits of $N_{dep,T}$ are given.

	unit	acid grassland	bog	calcareous grassland	deciduous woodland	heath
EUNIS code	-	E1.7	D1	E1.26	G1	F4.2, F4.11
no. of sites	-	883	203	92	361	457
range of N_{dep}	kg ha^{-1} a^{-1}	4.9-40	5.3-40	4.9-36.5	6.9-56.7	4.9-40
range of critical load*	kg ha^{-1} a^{-1}	10-15	5-10	15-25	10-20	10-20
n_{max}	-	18.0	18.0	28.0	14.0	13.0
$N_{dep,T}$	kg ha^{-1} a^{-1}	7.8	14.3	23.6	7.8	8.8
		6.3-8.1	*13.2-15.9*	*15.5-29.3*	*6.8-15.0*	*4.7-10.1*
r_{sl}	(kg ha^{-1} $a^{-1})^{-1}$	0.28	0.31	0.85	0.19	0.30
$\%r_{sl}$	(kg ha^{-1} $a^{-1})^{-1}$	1.6	1.7	3.0	1.3	2.3

* values employed for national mapping of Critical Loads in the UK (Hall et al., 2011)

Table 2. Threshold values and 95% confidence limits for different quantiles.

quantile	acid grassland	bog	calcareous grassland	deciduous woodland	heath
0.25	7.8	20.0	23.7	19.3	7.8
	6.7-8.8	*5.7-22.8*	*11.1-25.8*	*14.9-20.2*	*4.7-24.8*
0.50	7.8	14.3	23.6	7.8	8.8
	6.3-8.1	*13.2-15.9*	*15.5-29.3*	*6.8-15.0*	*4.7-10.1*
0.75	8.0	14.1	25.8	8.0	7.8
	4.7-9.1	*11.1-16.9*	*18.9-26.6*	*6.7-29.9*	*6.0-10.4*

Figure captions

Figure 1. Map of sites

Figure 2. Variation of species richness with N_{dep} and broken-stick model fits. The vertical dashed lines are the 95% limits.

Figure 3. Plots of contemporary (1998) thresholds against empirical Critical Loads. Key: AG acid grassland, B bog, CG calcareous grassland, DW deciduous woodland, H heath. The points for AG and DW lie very close and so appear as a single point. The ranges for the threshold values are 95% confidence limits. The Critical Load ranges are from Table 1, and the centre-range values are plotted as points.

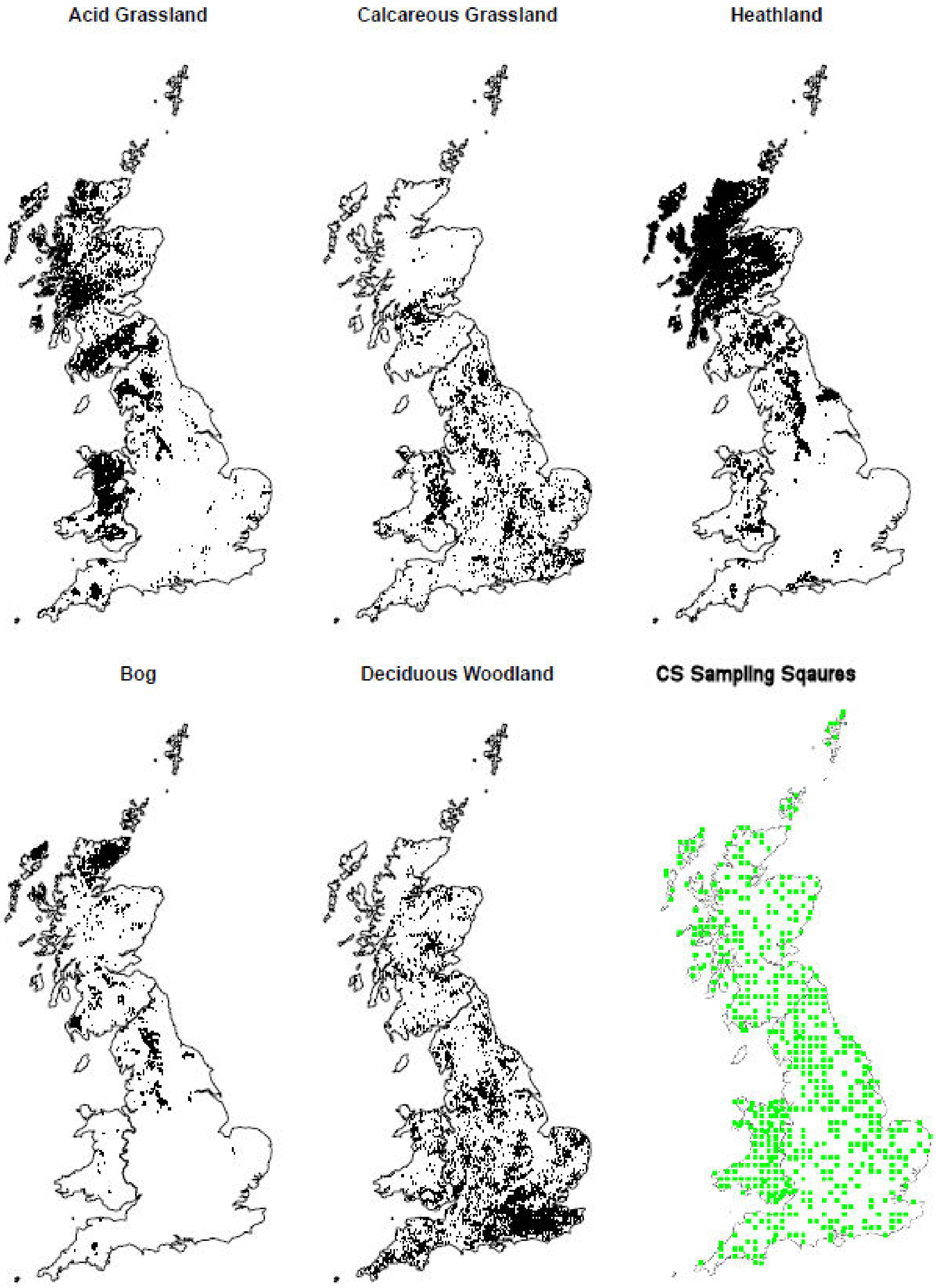

Acid Grassland
Calcareous Grassland
Heathland
Bog
Deciduous Woodland
CS Sampling Sqaures

Figure 1.

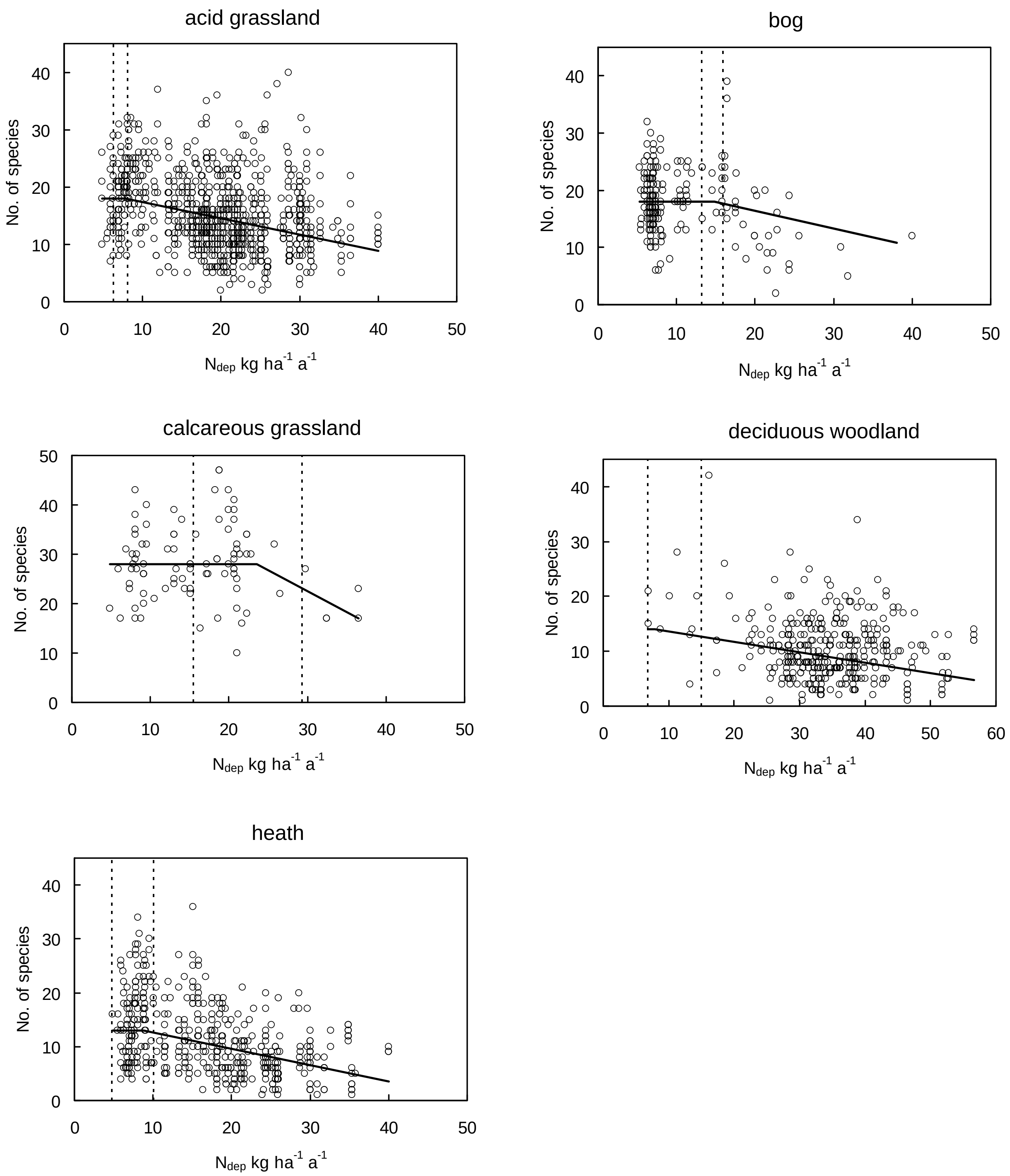
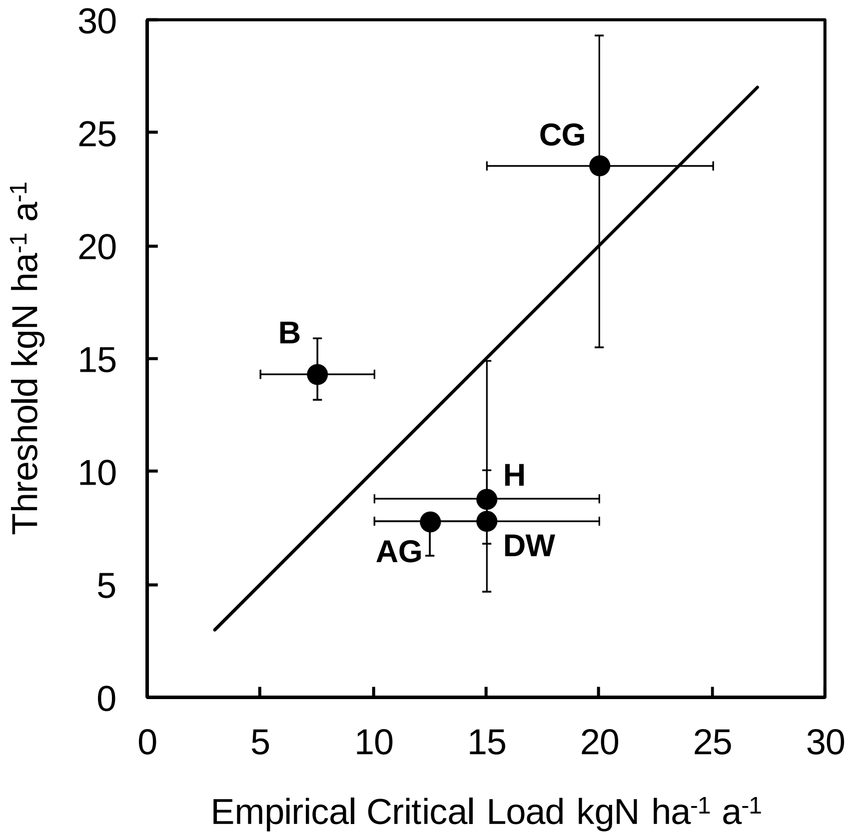

acid grassland
bog
calcareous grassland
deciduous woodland
heath
No. of species
N_{dep} kg ha^{-1} a^{-1}

Figure 2.



419

420 Figure 3.