

# Atmospheric nitrogen pollution impacts on biodiversity: Phase 1 – Model development and testing

## Final report - APPENDICES

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## Appendix 1: Development of a statistical model to predict species richness in British plant communities.

Peter Rothery

### PART 1

#### **Application of Generalized Linear Mixed Models to predict number of species per plot**

In the initial analysis the response variable was the mean number of species per km square (averaged over the plots in each square). This was related to the explanatory variables soil  $pH$ , soil  $CN$ ,  $H$  (cover-weighted canopy height) and  $MC$  (%soil moisture content) using a loglinear or Poisson regression model. These variables were selected because they together reflect the primary abiotic factors controlling above-ground species richness.

Here we develop a model using the number of species in each plot as the response variable. In this case there are two levels of random variation to consider (a) between plots within km squares; (b) between km squares. One approach is to extend the Poisson regression by including a random effect for the km square, and to fit as a generalized linear mixed model (GLMM).

#### *GLMM structure*

Let  $Y_{ik}$  denote the number of species observed in the  $k$ th plot of the  $i$ th square. The structure of the GLMM is then as follows. The mean and variance of  $Y_{ik}$  for a given square are given by

$$E [Y_{ik}] = \mu_{ik} ; \text{var} [Y_{ik}] = c\mu_{ik}$$

where  $c$  is the dispersion parameter ( $c > 1$  indicating overdispersion, i.e. more variation than for a Poisson distribution).

Let  $pH_{ik}$ ,  $CN_{ik}$ ,  $H_{ik}$  and  $MC_{ik}$  denote the corresponding values of the explanatory variables. In the GLMM the effects the explanatory variables and the random effect for square are assumed to be linear on a logarithmic scale, i.e.

$$\ln \mu_{ik} = L(pH_{ik}, CN_{ik}, H_{ik}, MC_{ik}) + S_i$$

where  $L(\cdot)$  is a linear predictor (this means linear in the coefficients of the variables, so that it includes polynomials as well as linear functions of the variables). The random square effects ( $S_i$ ) are assumed to follow a Normal distribution with mean zero and variance  $V_S$ , independently between squares.

#### *Fitted model*

I used the same approach as previously starting with a model including linear, quadratic and line-interaction effects for all four variables. Quadratic and interaction terms were then removed from the model according to the statistical significance of

the effect. Note that the linear terms were always retained (irrespective of statistical significance) if any of the corresponding higher order interactions were included (this is the marginality principle).

Table 1 shows the results of fitting model and the reduced model with non-significant terms excluded (i.e. excluding  $pH^2$ ,  $CN^2$ ,  $Ph \times CN$ ,  $CN \times MC$ ).

It is interesting to see that the variables included in this model are not exactly the same as those in the previous analysis using mean number of species per plot in each km square.

### *Goodness-of-fit*

Figure 1a-b illustrates the fit of the model as a plot of (a) observed vs fitted values and (b) residuals vs fitted values. There is a suggestion that the model overestimates when the number of species is high.

Figure 2a-d shows residuals plotted against the explanatory variables. There is no evidence that an important effect of any of the variables has been omitted.

### *Trends at different scales*

The above analysis refers to overall trends between plots, allowing for random variation in the effect of km square. It is also of interest to estimate trends within plots to see if they are comparable to the overall trend. These trends can be estimated by fitting a model with fixed effects for plots, i.e. effectively taking out a plot mean and looking at the trends in the 'centred data'. Note that trends at the different scales need not be the same – an effect which is sometimes called the ecological fallacy.

Table 2 shows estimated coefficients for the two levels, confirming that they are very similar.

Note that in some cases the statistical significance of the within-square trends is reduced. This is probably reflecting the reduced range of variation within the km squares. The proportion of variation between squares for each of the variables is estimated as follows (Table 3):  $pH$  (73%);  $CN$  (67%);  $H$  (36%);  $MC$  (82%). Note the relatively large component of within square-variation for  $H$ .

### *Quadratic effects*

Statistically significant quadratic effects (negative) emerge for  $MC$  and  $H$ . These indicate a maximum in the fitted model. However, this maximum could fall within the observed range of the variable, or it might fall outside of the range in which case the quadratic effect is reflecting a curvilinear increase/decrease. To see which it is we examine the fitted model as follows.

For  $MC$ , the relevant terms in the model are

$$-0.00968MC - 0.00017MC^2 + 0.00594PhMC + 0.00165HMC$$

Setting the partial derivative with respect  $MC$  equal to zero gives

$$0.00034MC = -0.00968 + 0.00594Ph + 0.00165H$$

Using the average values of  $pH = 13.38$  and  $H = 3.33$  and solving gives the maximum at

$$MC = 221.5$$

A similar calculation for  $H$  gives the maximum at  $H = -0.80$ .

In both cases the maximum occurs outside of the range of the data (Figure 3). For  $MC$ , the fitted quadratic reflects the curvilinear monotonic increase in numbers. For  $H$ , the model reflects a decline with numbers highest at low  $H$ .

It would be also be useful to plot fitted values against  $MC$  and  $H$  for fixed values of the other variables to confirm the above analysis and to illustrate the form of the underlying curve.

#### *Check on variance proportional to mean*

As I check on the assumption that the variance of the count (within squares) is proportional to the mean I examined the standardised residuals from the model with fixed effects for km square (using fixed effects takes out the effect of random variation between squares). The residuals are standardised as  $(\text{count} - \text{mean}[\text{count}])/\sqrt{\text{mean}[\text{count}]}$ . If the variance is proportional to the mean a plot of the absolute standardised residual against the fitted value should show no trend. In fact, because the distribution of the absolute residuals is skewed it is better to plot the square root. Figure 4a shows that the data are consistent with the assumption.

The corresponding plot using residuals from the fitted model with a random effect for square shows an underlying increase (Figure 4b) which is consistent with the effect of the extra component for the km square which implies variance proportional to mean squared.

#### *Simulating data from the fitted model*

Counts can be simulated in two stages as follows.

First, we generate the mean count for the  $k$ th plot in the  $i$ th square as

$$\mu_{ik} = \text{Fit}_{ik} \exp(Z_{ik}\sqrt{V_S})$$

where  $Z_{ik}$  is drawn from a Normal distribution with mean zero and unit variance, and where  $V_S$  is estimated as 0.144.

Second, we generate a count with mean  $\mu_{ik}$  and variance  $c\mu_{ik}$ , where  $c$  is the estimated dispersion, i.e.  $c = 2.51$ . However, the presence of overdispersion means that a Poisson distribution ( $c = 1$ ) does not apply. One alternative is to use a negative

binomial distribution. If the mean count is  $M$  then the variance for the negative binomial distribution is given by  $\text{var}[\text{count}] = M + M^2/k$ , where  $k$  is a dispersion parameter. We require the variance of the count to be proportional to the mean, i.e.  $\text{var}[\text{count}] = cM$ . This can be achieved by setting  $M + M^2/k = cM$ , i.e.  $k = M/(c - 1)$ .

In other words, in the second step we generate a count from a negative binomial distribution with mean  $= \mu_{ik}$  and dispersion parameter  $k = \mu_{ik}/(c - 1)$ .

Figure 4a-b illustrates the procedure for a single set of simulated data. Figure 4c shows a plot of the actual data for comparison.

To assess whether the negative binomial provides a plausible distribution for the counts I examined the variation in the standardised residuals calculated as  $(\text{count} - \mu_{ik})/\sqrt{\mu_{ik}}$ . For comparison with the actual data I used the residuals from the model with fixed effects for km squares.

Figure 5 shows histograms of the standardised residuals. The agreement looks reasonable, although the negative binomial seems to be more skewed with a heavier upper tail.

**Table 1** Summary of fitted GLMMs relating number of species per plots to environmental variables.

Variable	Full model		Reduced model	
	Coefficient ( <i>se</i> )	<i>t</i> -value	Coefficient ( <i>se</i> )	<i>t</i> -value
<i>Constant</i>	2.349 (0.977)	2.40 *	2.316 (0.444)	5.21 ***
<i>pH</i>	-0.11560 (0.23734)	-0.48	-0.11840 (0.05887)	-2.01 *
<i>CN</i>	0.00867 (0.03605)	0.24	0.02743 (0.01168)	2.35 *
<i>H</i>	0.34560 (0.11918)	2.90 **	0.33890 (0.11629)	2.91 **
<i>MC</i>	-0.00504 (0.00971)	-0.52	-0.00968 (0.00808)	-1.20
<i>pH sq</i>	-0.00155 (0.01576)	-0.098	- (-)	-
<i>CN sq</i>	0.00035 (0.00036)	0.96	- (-)	-
<i>MC sq</i>	-0.00015 (0.000048)	-3.14 ***	-0.00017 (0.000041)	-4.00 ***
<i>H sq</i>	-0.03153 (0.00801)	-3.93 ***	-0.03067 (0.00798)	-3.84 ***
				-
<i>pH x CN</i>	0.00228 (0.00413)	0.55	- (-)	
<i>pH x H</i>	-0.03038 (0.01237)	-2.46 **	-0.02993 (0.01206)	-2.48 *
<i>pH x MC</i>	0.00543 (0.00111)	4.89 ***	0.00594 (0.00087)	6.84 ***
<i>CN x H</i>	-0.00984 (0.00332)	-2.97 **	-0.01025 (0.00324)	-3.16 **
<i>CN x MC</i>	-0.00017 (0.00022)	-0.75	- (-)	-
<i>H x MC</i>	0.00159 (0.00084)	1.89	0.00165 (0.00082)	2.00 *
<i>V<sub>S</sub> (se)</i>	0.144 (0.019)		0.144 (0.018)	
<i>c (se)</i>	2.51 (0.13)		2.51 (0.13)	
<i>r(Obs, Fit)</i>	0.575		0.573	

**Table 2** Estimated coefficients in reduced model showing (a) overall trend at population level and (b) trend within km squares

Variable	Between plots (overall)		Between plots within squares	
	Coefficient (se)	t-value	Coefficient (se)	t-value
<i>Constant</i>	2.316 (0.444)	5.21 ***	1.724 (0.61900)	2.78
<i>pH</i>	-0.11840 (0.05887)	-2.01 *	-0.10840 (0.06660)	-1.63
<i>CN</i>	0.02743 (0.01168)	2.35 *	0.02060 (0.01260)	1.63
<i>H</i>	0.33890 (0.11629)	2.91 **	0.35100 (0.12000)	2.94 **
<i>MC</i>	-0.00968 (0.00808)	-1.20	-0.01171 (0.00917)	-1.28
<i>pH sq</i>	- (-)	-	- (-)	
<i>CN sq</i>	- (-)	-	- (-)	
<i>MC sq</i>	-0.00017 (0.000041)	-4.00 ***	-0.00013 (0.000048)	-2.76 **
<i>H sq</i>	-0.03067 (0.00798)	-3.84 ***	-0.03546 (0.00844)	-4.20 **
<i>pH x CN</i>	- (-)	-	- (-)	
<i>pH x H</i>	-0.02993 (0.01206)	-2.48 *	-0.02250 (0.01220)	-1.84
<i>pH x MC</i>	0.00594 (0.00087)	6.84 ***	0.00522 (0.00100)	5.21 ***
<i>CN x H</i>	-0.01025 (0.00324)	-3.16 **	-0.00894 (0.00346)	-2.59 **
<i>CN x MC</i>	- (-)	-	- (-)	
<i>H x MC</i>	0.00165 (0.00082)	2.00 *	0.00149 (0.00092)	1.62

**Table 3** One-way ANOVA to estimate components of variation between and within squares for the explanatory variables

(a) *pH*

Analysis of Variance for *pH*, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
kmsq	239	1381.318	1381.318	5.780	12.31	0.000
Error	777	364.851	364.851	0.470		
Total	1016	1746.169				

Expected Mean Squares, using Adjusted SS

Source	Expected Mean Square for Each Term
1 kmsq	(2) + 4.2363(1)
2 Error	(2)

Variance Components, using Adjusted SS

Source	Estimated Value	(%)
kmsq	1.2535	73%
Error	0.4696	27%
Total	1.723	

(b) *CN*

Analysis of Variance for *CN*, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
kmsq	239	38516.45	38516.45	161.16	9.47	0.000
Error	777	13222.20	13222.20	17.02		
Total	1016	51738.64				

Expected Mean Squares, using Adjusted SS

Source	Expected Mean Square for Each Term
1 kmsq	(2) + 4.2363(1)
2 Error	(2)

Variance Components, using Adjusted SS

Source	Estimated Value	(%)
kmsq	34.03	67%
Error	17.02	33%
Total	51.05	

(c) *H*

Analysis of Variance for *H*, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
kmsq	239	1045.586	1045.586	4.375	3.38	0.000
Error	777	1006.422	1006.422	1.295		
Total	1016	2052.007				

Expected Mean Squares, using Adjusted SS

Source	Expected Mean Square for Each Term
1 kmsq	(2) + 4.2363(1)
2 Error	(2)

Variance Components, using Adjusted SS

Source	Estimated Value	(%)
kmsq	0.7270	36%
Error	1.2953	64%

Total 2.022

(d) MC

Analysis of Variance for MC, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
kmsq	239	552674.6	552674.6	2312.4	19.70	0.000
Error	777	91219.9	91219.9	117.4		
Total	1016	643894.5				

Expected Mean Squares, using Adjusted SS

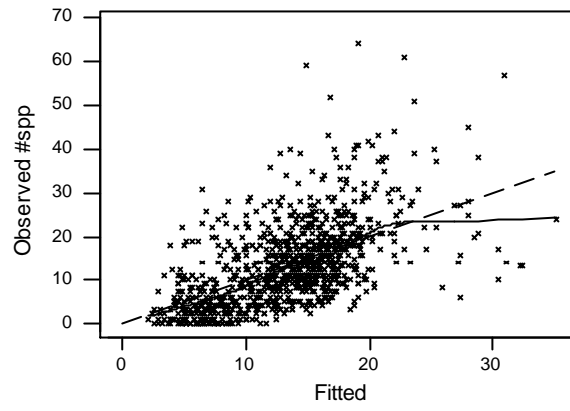
Source	Expected Mean Square for Each Term
1 kmsq	(2) + 4.2363(1)
2 Error	(2)

Variance Components, using Adjusted SS

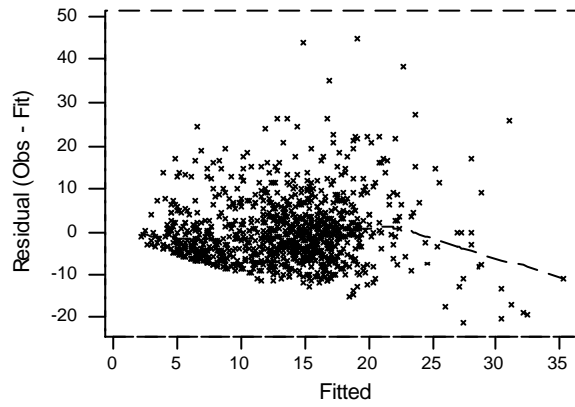
Source	Estimated Value	(%)
kmsq	518.2	82%
Error	117.4	18%

Total 635.6

**Figure 1a** Plot of observed vs fitted values. Lowess lines to help visualize underlying trend.

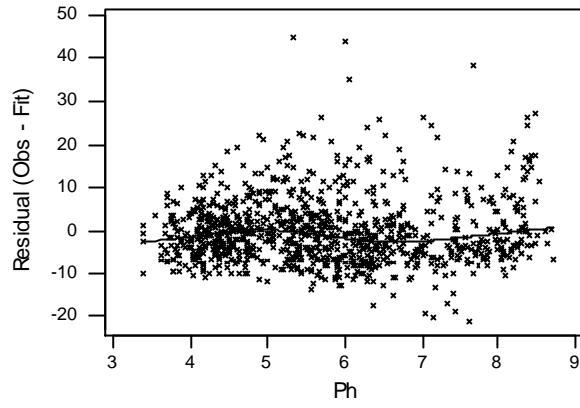


**Figure 1b** Plot of residuals vs fitted values

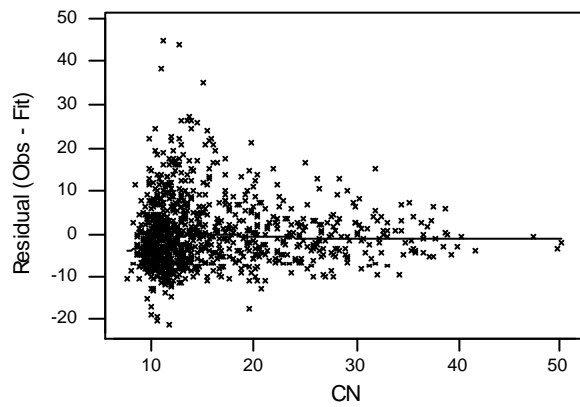


**Figure 2** Residuals plotted against explanatory variables. Lowess lines shown to help visualize underlying trend.

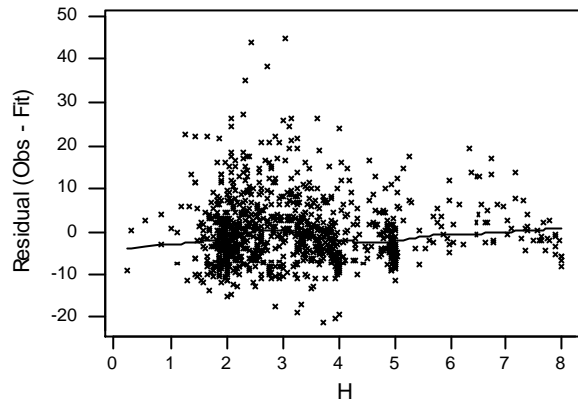
(a)



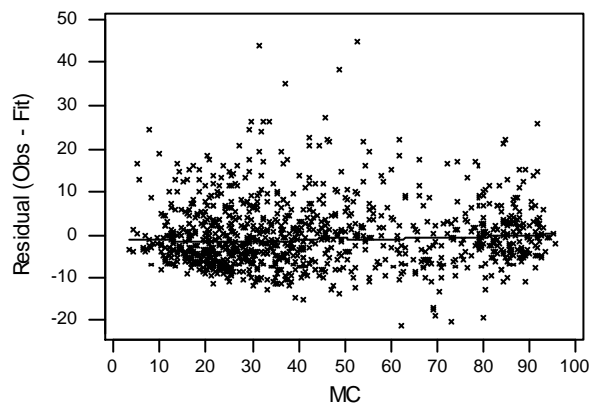
(b)



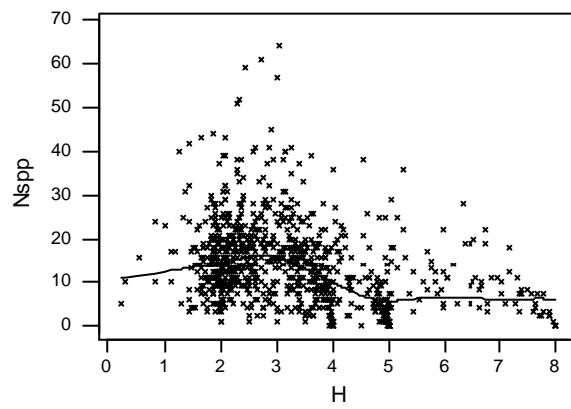
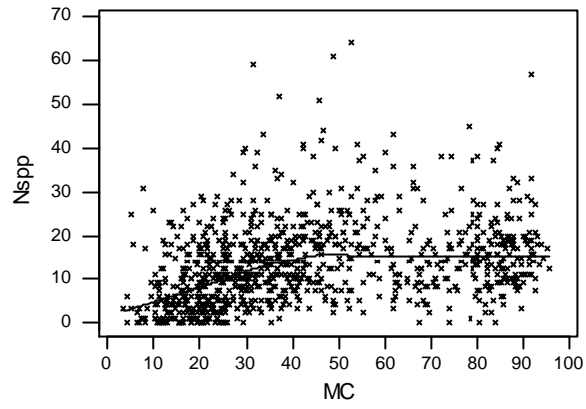
(c)



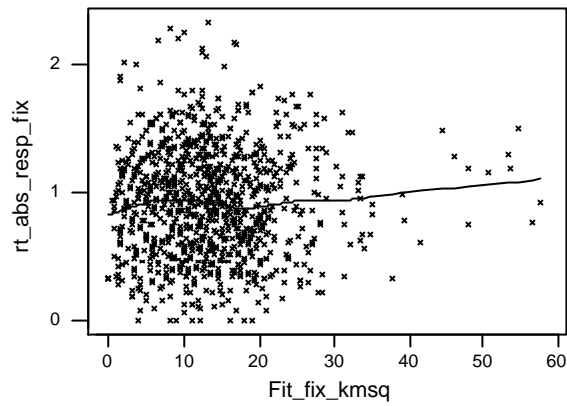
(d)



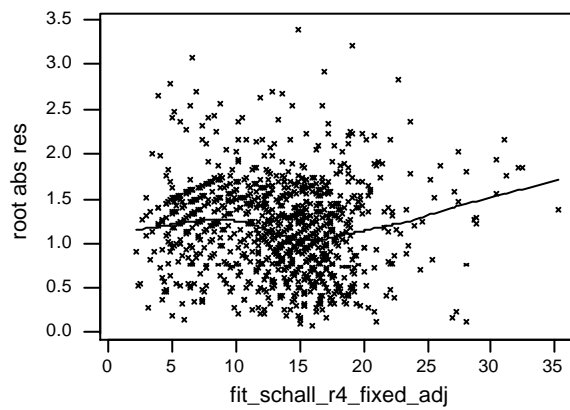
**Figure 3** Plots of number of species vs  $MC$  and  $H$  to examine form of quadratic effect in fitted model.



**Figure 4a** Plot of absolute standardised residual (square root transformed) against fitted values for model with fixed effects for km squares. Lowess line shown to help visualise underlying trend. Variance proportional to mean should give no trend.

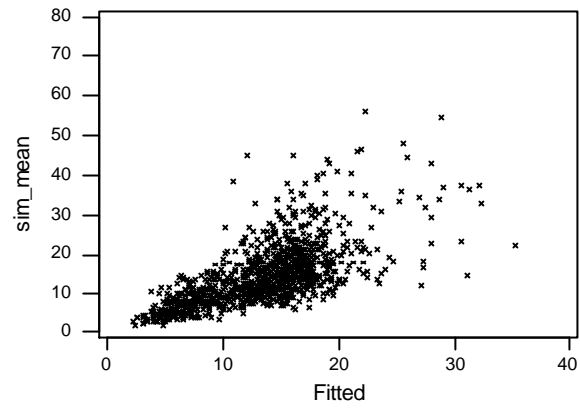


**Figure 4b** Corresponding plot to (a) using residual from fitted model with random effect for km square

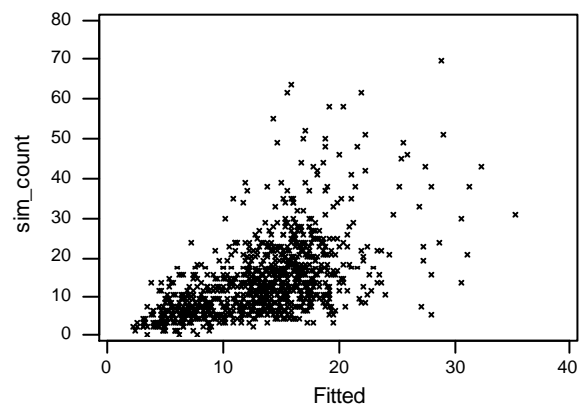


**Figure 5** Illustration of simulated data from fitted model. Figure 4c shows actual data for comparison

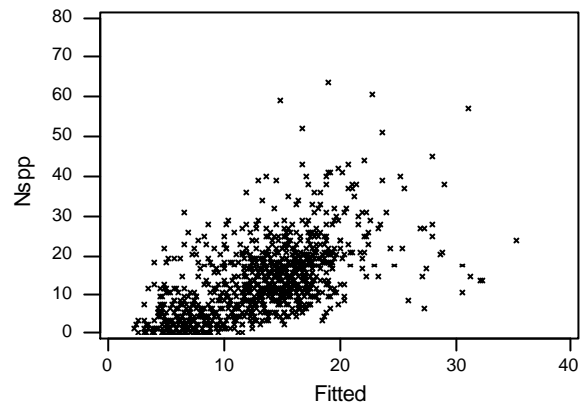
(a) Step 1 – simulating the mean count



(b) Step 2 – simulating the count

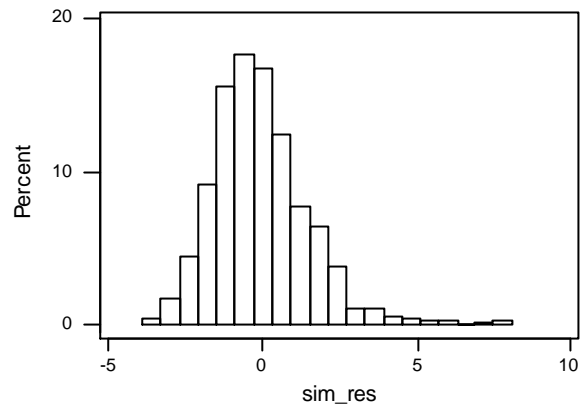


(c) Observed count vs fitted

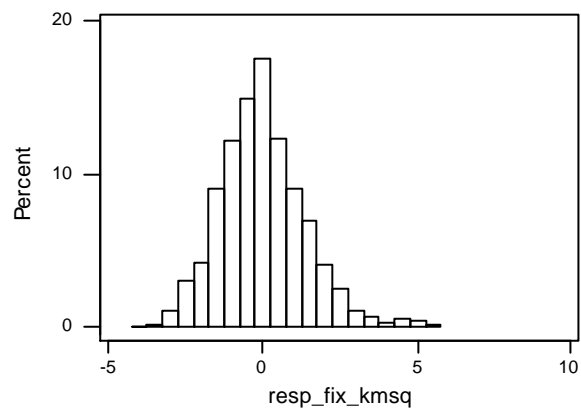


**Figure 6** Histograms of standardised residuals  $[\text{count} - \text{mean}(\text{count})]/\sqrt{\text{mean}(\text{count})}$  for simulated negative binomial data and observed counts.

(a) Simulated counts



(b) Observed counts



## PART 2

### **Predictions using fitted model**

The model will be used to predict the following.

1. The expected number of species in a plot with recorded values of the explanatory variables or predictors. This is partly for comparison with the expected number of species based on individual species logistic regressions relating presence/absence to the predictors.
2. The variation in number of species per plot in a sample of plots each with the same values for the predictors.

Before addressing these issues it is useful to recap on the fitted model.

#### *Fitted model*

Let  $Y_{ik}$  denote the number of species observed in the  $k$ th plot of the  $i$ th square. The structure of the GLMM is then as follows. The mean and variance of  $Y_{ik}$  for a given square are given by

$$E [Y_{ik}] = \mu_{ik} ; \text{var} [Y_{ik}] = c\mu_{ik}$$

where  $c$  is the dispersion parameter ( $c > 1$  indicating overdispersion, i.e. more variation than for a Poisson distribution).

Let  $pH_{ik}$ ,  $CN_{ik}$ ,  $H_{ik}$  and  $MC_{ik}$  denote the corresponding values of the explanatory variables. In the GLMM the effects the explanatory variables and the random effect for square are assumed to be linear on a logarithmic scale, i.e.

$$\ln \mu_{ik} = L(pH_{ik}, CN_{ik}, H_{ik}, MC_{ik}) + S_i$$

where  $L(\cdot)$  is a linear predictor (this means linear in the coefficients of the variables, so that it includes polynomials as well as linear functions of the variables). The random square effects ( $S_i$ ) are assumed to follow a Normal distribution with mean zero and variance  $V_S$ , independently between squares.

From the above equation the mean or expected number of species for the  $k$ th plot in the  $i$ th square is

$$\mu_{ik} = \exp\{L(pH_{ik}, CN_{ik}, H_{ik}, MC_{ik}) + S_i\}$$

#### *Expected number of species in a plotina randomly selected square*

We cannot use the above equation to predict the expected number of species in a plot with given values of  $pH$ ,  $CN$ ,  $H$  and  $MC$  because we do not know the value of the square effect. Instead we use a mean value averaged over the assumed distribution of random square effects, i.e. a Normal distribution with mean zero and variance  $V_S$ . This can be calculated theoretically as

$$\text{Expected \#species per plot} = \exp\{L(pH, CN, H, MC) + V_S/2\}$$

In other words, the value calculated by ignoring the random square effect is multiplied by a factor  $\exp(V_S/2)$ .

For the fitted model the estimated value of  $V_S$  is equal to 0.144, with factor  $\exp(0.072) = 1.075$ . So, the adjustment for random variation between squares is not particularly large, i.e. a 7.5% increase.

An illustration of why we need this adjustment to estimate the expected number of species follows by comparing the observed mean number of species per plot with that for the model based on values of  $\exp\{L(pH, CN, H, MC)\}$ .

Observed mean:                    13610/1017 = 13.38.  
 Mean of predicted values:    12581/1017 = 12.37

Ratio observed/predicted:                    1.082

In other words the predicted values need to be increased by a factor 1.082. This is slightly different to the value of 1.075 for the model because the latter is based on the assumption of a Normal distribution of random square effects.

#### *Predicting variation between individual plots*

In an earlier note I suggested that the model could be used to generate a distribution of counts for specified values of the predictors. The approach was to use a negative binomial distribution with the index of dispersion  $k$  chosen to achieve variance proportional to mean.

However, for the purposes of predicting the variation in counts of plots (within a square) each with the same values of the predictors we do not need to generate a distribution of random counts. We simply use the fact that the variance is proportional to the expected value, i.e.  $\text{var}[\text{count}] = cE[\text{count}]$ , where the dispersion parameter  $c$  is estimated as 2.51.

If we have a sample of sites each with a set of plots then we can examine the relationships of the observed variance to that predicted by the model to look for departures from the line of equality.

## **Appendices 2 and 3: Development of trait-based dispersal and grazing indices for UK higher plants.**

Ibby Moy, James Bullock

### ***Summary***

As plant traits affect the species composition and functioning of ecosystems (Diaz, Hodgson et al. 2004) it follows that weightings for relevant plant attributes need to be integrated for reliable predictions of changes to the species composition of plant communities when modelling altered conditions.

A summary list of the types of trait relevant to the construction of dispersal and grazing filters, shown below, was compiled by the end of April 2004.

### Grazing Traits

For the purposes of this study, these traits determine the inherent capacity of each species to colonise and persist under different grazing regimes:

Thorns/prickles e.g. gorse, thistles

Toughening – physical un-palatability e.g. *Nardus stricta*

Chemical palatability e.g. tannins in oak

Growth form (to avoid or withstand grazing) e.g. hemicryptophytes, trees

Regrowth ability

Strategy (CSR)

Life history

### Dispersal Traits

For the purposes of this study, these traits determine the inherent capacity of each species to disperse over different distances

Propagation method (seed, vegetative/clonal, viviparous = regenerative strategy)

Mechanism

- wind
- ballistic
- animal
- water
- no evident mechanism

Seed size

Number of seed

Height/spread of plant

Life history

Seed bank

## **Background for Clarification of definitions**

Each list of traits needs to be supported by information on the mechanisms that determine the role of these traits in governing the overall processes of grazing and dispersal. We also include some of the information supporting the identification of grazing and dispersal as critical components for the response of a species within the overall model.

Grazing, defined as the consumption of plant biomass by the activities of herbivores, has been established as a mechanism in the shaping of many plant communities of conservation value, particularly grasslands. It has also, been used increasingly in recent years as a management tool in conservation to maintain the species composition for many habitats of conservation value (WallisDeVries, Bakker et al. 1998) . However plant behavioural responses to grazing and the traits that govern their responses are not easy to characterize. Large herbivore grazing regimes can be at a range of intensities governed by stocking rates. Furthermore, the response of individual plant species may be altered by grazing periods, seasonal variation to the grazing regimes or factors such as the preferences of the herbivores. Individual plant species may have precise defences against certain herbivores. Small mammal herbivores or invertebrates may appear to have little impact on plant communities but undoubtedly have impacts at a local level. At the community level, grazing is inextricably linked with disturbance, the creation of gaps and hence dispersal.

Dispersal governs the ability of the balance of abundance to alter within a community as well as allowing new species to arrive.

The accumulated supporting information has been used to prioritise the traits and to develop a method for weighting designation where traits are qualitative.

Once the list of traits for the filters had been compiled, existing data sources were pursued and the relevant traits have been extracted and combined into database. The sources used, include the databases ECPE, ECOFLORA, PLANTATTR and SID. Unfortunately, after contacting a representative for LEDA, we established that it was not feasible to use data from LEDA (Life-history traits of the Northwest European Flora) at this stage as their project is still underway.

## **Practical limitations of data sources**

Within individual data-sources, fields for many of the applicable traits are incomplete. Furthermore the data for a trait completed for one species trait may be incomplete for the next species leading to a cumulative reduction in the number of species for which a filter can be derived. The lists of all traits for both filters were investigated during the early stages. Some of the information is duplicated, for example seed size is found from ECPE as well as SID and although there are many values that are not repeats some come from the same source. In addition there are some traits that would contribute to the precision of the filters that are not present in the databases examined so far. For example, some of the features determining the palatability of plants are well known for cultivars sown for fodder but are not well-documented for native species. Although some plant families (such as *Euphorbiaceae* – the spurge family,

plants with acrid latex) have features that deter grazing. Other families include both members that are poisonous and others that are highly palatable, such as the *Umbelliferae* with hemlock *Conium maculatum* at one extreme and wild carrot *Daucus carota*, the ancestor of the cultivated varieties, at the other extreme. There are also plants with physical features that are obvious grazing deterrents such as thorns but this information has not been found in database format and may well not have been collated.

There have been some compatibility issues for the different datasets resulting in problems matching data. These included inconsistencies with the format of the British Records Centre numbering which should be a useful tool for the extraction of corresponding data from different sources however, in practice, different formats have been used as well as different variants of the system. The formatting inconsistencies are easily rectified with time, however to facilitate the recognition of suitability of traits, the species names were employed for the data extraction at this stage. The species names exhibited discrepancies too but for the reduced species lists these have been amended.

There has been a surprising paucity of data for traits designated as components of dispersal and grazing filters within the existing databases. This emphasises the logistical problems collating information that probably exists somewhere as well as the cumbersome (and hence expensive) task to standardise, collate and input this data in an appropriate format. The lack of data on traits has been for both abundant and common species, as well as for some of the well-researched species that typify habitats of conservation value. It may also be that the data for a particular trait has not been determined by research or published, such as the seed production, say, as average number of seed per plant for example, for many common species of grass (bent-grasses *Agrostis* spp., fescues *Festuca* spp., meadow-grasses *Poa* spp.).

### **Grazing Filter Plant Traits –Overview**

The aim is to develop a 'rank' for each species from quantifiable plant traits that govern the response of the plant to grazing pressure. The presence or absence of grazing pressure on plant communities is a major determinant of the resultant vegetation type (Smith, Buckingham et al. 1996; Proulx and Mazumder 1998). This is a manifestation of the responses of individual plant species to grazing (Bullock and Marriott 2000; Dupré and Diekmann 2001; McIntyre and Lavorel 2001; de-Val and Crawley 2004). Given that the management of sites of conservation value is likely to be continued whether nitrogen deposition increases or decreases, when modelling the changes in biodiversity/species composition it may be essential to build in an assessment of plant responses to grazing pressure in order to realistically predict change.

The mechanisms conferring a plant with traits that are a manifestation of strategies for survival under grazing can be divided into two main groups: those reducing the likelihood or the intensity for a plant being grazed and those that increase plant growth when grazed. These mechanisms are the avoidance and tolerance strategies (Briske 1996). The traits listed fall into one or other of these categories with physical deterrents and palatability determining the plant's ability to avoid grazing and the growth form and re-growth ability characterising the plant's ability to tolerate grazing. The strategy (Grime 1974) as manifested by the competitive ability, the ruderality or

stress tolerance of a species combines aspects of avoidance and tolerance.

A further aspect of a plant's response to grazing is the susceptibility of seedlings to invertebrates, where selective pressure on the plant community is enhanced because plants are prevented from establishing. Aside from the inherent capacity of an individual species to respond under grazing regimes, it should be noted that an important aspect of grazing is the indirect link with dispersal in that grazing regimes have the capacity to open up the communities facilitating the colonisation by new species.

1. Avoidance – this includes adaptations to deter grazing, such thorns and prickles, factors affecting palatability including toughness, the presence/absence of chemical deterrents such as alkaloids and growth forms such as hemi-cryptophytes or trees/shrubs.
2. Life history traits enable plants to survive different cycles of grazing.
3. Re-growth ability (tolerance) – the ability of a plant to re-grow after grazing, many grasses do this well. Growth rate may also be considered as a component of tolerance.
4. Ruderality/Competitiveness - regeneration determined by the plant strategy affecting processes such as the ability to colonise gaps.

The components of innate avoidance including physical features and physiological compounds, are all different measures of palatability. There is little information in databases examined. Ecoflora contains fields for a range of physical defense features, however further investigations revealed that the simple features listed in these fields often give little indication of the plant's inbuilt palatability. For some species the glabrous, thickened cuticle may be a defense against saline conditions but may actually increase the palatability of the plant. Although the concentrations of nitrogen and phosphorus (or non-structural carbohydrates) in plant tissue might be a useful measure of palatability, there is little information on the relative nutritional value of native plant species. The effect of nutritional value on palatability is well-known in general terms but does not seem to have been quantified except for crops or fodder varieties. Where palatability has been examined for native plants the measures have been with invertebrates as grazers (Fenner, Hanley et al. 1999) . It might be possible to derive some kind of all-encompassing ranking for all these features putting species into functional groups. Indeed there is some work that shows patterns of response to grazing pressure are similar for species allocated to the same functional groups (however functional groups are not clearly defined in the literature, different authors use different groupings). So, in addition to the ranking of individual species for the grazing filter derived from database sources, further formulations to construct a palatability category devised from a variety of sources and incorporating assumptions based on field experience are under investigation.

Life history traits can furnish a plant with the potential to avoid grazing over time. Hence a summer grazing regime could encourage autumn germinating therophytes with the ability to complete their lifecycle before the grazing regime is implemented. The management history of a plant community determines the structure of the plant community in terms of the types of plants that comprise the vegetation (Jauffret and Lavorel 2003; Pausus and Lavorel 2003).

Growth form: can confer the mechanisms of avoidance and/or tolerance on the

individual by allowing the plant to withstand grazing e.g. hemicryptophytes or trees. There are several studies (Lavorel, McIntyre et al. 1999; Bullock, Franklin et al. 2001; McIntyre and Lavorel 2001) that have examined the plant response to grazing based on plant attribute and there is no doubt that plants with certain attributes are well-adapted to grazed conditions. This classification is a useful tool to differentiate apparent physical characteristics and a simple form of ranking has been suggested based on the level of resistance/ vulnerability to grazing that the typical form confers to the plant, see Table 8. However some caution needs exercising because the stage of development for the individual plant also alters the level of resistance/ vulnerability to grazing for that plant. For tree species (phanerophytes), seedlings are much more susceptible to grazing than mature trees. This anomaly may be compensated by the inclusion of other traits such as the length of time to maturity and the use of plant height to eliminate possible anomalies.

**Regrowth ability:** The method of regeneration and certain aspects of clonality allow some plants to tolerate grazing by colonization, recovery or persistence more than others. ECPE lists regenerative strategies and PLANTATTR has two fields for clonal traits with types ranging from not clonal to various forms of far-creeping clonality.

**Strategy (Competitor, Stress tolerator, or Ruderal)** a derived attribute (Grime, Hodgson et al. 1988) is listed within the ECPE database with numerical values given.

The information obtained indicates that it is possible to derive a well-informed index for grazing however the number of species where the information is comprehensive is likely to be limited.

**Validation of the traits:** In conjunction with the main task of filter development for both dispersal and grazing it is necessary to provide a method to validate the derived indices. For example, Ecoflora contains a “response to vertebrate grazing” field but this only has data for 100 species. This ‘field’ may be best used as a validation to assess **derived** grazing filter. Caution; note results from work on plant responses to grazing from Australia (Vesk and Westoby 2001) where it was shown that the response of a particular species to grazed conditions was often not consistent.

## **Development of Grazing Filter**

Initially, the components for a species response to grazing, identified from database sources, were collated.

An appraisal of the information available revealed that the physical features determining the overall palatability for species were only present within the database sources to a rather limited extent. For example Ecoflora contains fields on physical defenses but the features listed tend to relate to defence against invertebrate attack such as the presence of bristly hairs on leaves or stems. The scale renders this type of feature immaterial when gauging susceptibility of a plant to grazing by large herbivore. It was proposed that for each species from the resultant, reduced list of species should be designated a rank for the combination of physical traits, with grazing deterrents such as thorns and prickles giving a plant a higher chance for survival under intense grazing than a plant without this type of feature. In addition, plants known to be tough or with some form of chemical un-palatability rank higher than plants without these types of characteristics. These rankings were derived from

assessing any relevant features listed in the database sources (PLANTATTR and Ecoflora) supplemented by personal experience and with reference to other published sources (Grime, Hodgson et al. 1988; Stace 1997). For the avoidance traits we reversed our approach, leaving this group of traits until the rankings for all other traits had been constructed.

Life history traits for individual species were well-documented under the ECPE data-source as winter or summer annuals, biennials, monocarpic or polycarpic perennials with 502 species listed. This information needed ranking according to the effect on the ability of the plant to tolerate grazing. Whilst attempting to formulate the ranking for these traits however it became increasingly apparent that the processes that govern the life history response to grazing are subsumed within the recognised strategy for a species. The response of a plant to grazing by life history trait cannot be considered as a simple relationship linear relationship, therefore straightforward ranking is somewhat limited. To elucidate the relationship fully, some qualification for the features of grazing regime are required.

The growth form of a species is more clear-cut for assessment than the life history trait. Growth form also includes a major element of the life history characteristic. The growth form trait, usually described as life form in the data-sources, has records for 1884 species in PLANTATTR. These have been verified with other data-sources. Ecoflora held life form traits for 1699 species, ECPE included entries for just over 500 species and SID contains life forms for 422 species. Some of the entries were not identical but in most cases these were minor variations to classification e.g. hydrophyte read as equivalent to helophyte which describes a plant rooted in waterlogged soil. The number of species from these other sources that tallied with the longest list (PLANTATTR) was progressively reduced when matching the information however, as the information that matched on species name matched well for life form, the longest list has been used for ranking with a scale of 1-3 where the lowest value denotes a poor response to grazing whereas a high value indicates a species tends to show a good tolerance, see Table 8.

The level of grazing resistance that the growth form confers to a plant is further modified by the height of the plant with small, creeping or sprawling plants avoiding herbivores. Very tall plants (trees and large shrubs) already established in the vegetation avoid grazing pressure as they are beyond the reach of the herbivores. However within the plant canopy accessible to livestock, tall plants encounter proportionally greater biomass removal than shorter plants. All plants with the potential to grow very tall pass through the other height phases. A simplified inverse scale for plant height, shown in Table 9, helps to dispel the apparent anomaly for trees which are usually prevented from establishment in habitats where there are moderate to high grazing intensities.

In contrast to plant height where the order for the capacity of the plant to withstand grazing is inverted as compared to the potential for dispersal, the regrowth ability of a plant, as manifest in a combination of regenerative strategy and clonality remains similar for both dispersal and grazing. A species with a high regenerative capacity has an increased likelihood for the survival under grazed conditions. The same rankings for plant traits have been used in combination for both the Dispersal and the Grazing Filter to quantify the regenerative strategies (Source = ECPE), and for the 'Clonality'

trait (from PLANTATTR) for plants both where growth is usually clonal and for those where growth is not normally clonal, see Tables 1, 2 and 3.

The strategy of a plant, identified as a component of a species' capacity to resist grazing, is perhaps the most complex component considered for the filter. The strategy of a plant is based on a model of the effects of the balance between competition, stress and disturbance in vegetation. Hence the plant strategy derived from the triangular C-S-R model is an example of functional grouping where the strategy is derived from ordinations of quantifiable features.

When using an array of plant traits to define the characteristics of the strategy, it is difficult to determine which traits determine the response to grazing. Indeed it might be more robust if individual traits, where the governance of grazing response was apparent, were used, however the strategy as developed by Grime, Hodgson et al. (1988) encompasses and distils many of the relevant traits, primarily the life history traits, as mentioned earlier in this section.

A practical limitation for the use of strategy in the filter is that the equilibrium between the constraints on production (**S**tress), physical damage to vegetation (disturbance - **R**uderality) and the contest with neighbours for resources (**C**ompetition) vary from place to place as well as over diurnal, seasonal and successional timescales. The position of grazing as a component of the C-S-R model is a matter of interpretation and is highly dependent on the seasonal timing and intensity of grazing. At one extreme; high stocking rates lead to disturbance and gap creation so that ruderal species dominate the vegetation; whereas under minimal grazing competitors dominate. Positive responses by some plant species to grazing can be explained if selectivity is linked to regrowth ability so that competitors (often palatable with high nutrient content) can still grow faster than less competitive plants. Competitive plants are unlikely to retain their advantage if the nutrients become depleted. Stress-tolerators tend to be well-defended against herbivory. The picture may be further complicated by indirect effects, for example a species intolerant of grazing may also be intolerant of shading so does not persist under a low intensity grazing regime.

Where a plant community is already under conservation management a light to moderate grazing regime is a likely scenario. However many grassland habitats of high conservation value are often a product of a long history of intensive grazing management and stress-tolerant plants dominate the vegetation. Using the 501 species with a quantified strategy from the ECPE database a weighting has been designated summing the values for stress and ruderal, accounting for both the success of ruderal species under heavily grazed conditions and the ability of stress tolerators to persist under moderate grazing. The overall weighting for grazing tolerance can be boosted for competitors that do well under grazing by the contribution of other traits such as the capacity for regeneration. Ultimately ruderality and stress tolerance have been combined to calculate the contribution of a plant's strategy to the capacity to resist grazing.

The final stage for the production of values for a response to grazing amalgamated the different trait ranks once these values had been transformed. The accumulation of the traits was further transformed to produce a value between zero and one. The loss of

species because of the lack of trait data in the sources resulted in a list of just over 450 species with a grazing resistance value. A high value denotes a greater capacity to withstand grazing pressure than a low value. The timescale and dearth of available data has led to the omission of palatability (at this stage).

## **Dispersal Filter Plant Traits – Overview**

The principle behind this filter aimed to give a measure of the innate dispersal potential for individual species. The importance of dispersal is linked to the trade-off between competition and reproduction. A simplified system is where one species either allocates resources to one process or the other, so a poor competitor escapes to an available gap through the allocation of resources to dispersal. When assessing changes in the species composition for any habitat in response to altered resource availability, a key element is the potential of a species to invade the area. Indeed work (Tilman 1997) has shown that species richness in a native grassland is limited by dispersal and recruitment. Different species cannot colonise available gaps if they have no capacity to disperse (Coulson, Bullock et al. 2001). Hence dispersal ability is critical for predicting changes in species assemblages before the response of a particular species to altered resources and the biotic interactions between individual species within that habitat even come into play. Components of the dispersal filter included some features also determinant in a plant's response to grazing. Many of the features that were listed have, at least some data listed in the data-sources. The data has often required further adaptation, for example where the dispersal mechanism has been catalogued as 'animal' this has been differentiated into two groups; vertebrate and invertebrate. The two categories have potentially different dispersal distances with vertebrates carrying seed kilometres distant whereas invertebrates likely to take seed only a few metres.

Propagation method: Some appropriate information was under the regenerative strategies listed in ECPE. This information may be combined with the traits of regrowth ability already investigated for the grazing filter. The ability of many plants to disperse by clonality is constrained by the proximity of occurrence for that plant to the community likely to be colonized. A few aggressively clonal plants may colonise from some distance but, on the whole plants with clonal attributes need to occur near to or within a site for the feature to confer a dispersal advantage. That said, aggressively clonal plants may quickly dominate a site if they can out-compete other plants under altered conditions so that the clonality trait may facilitate the accelerated dispersal under particular conditions.

Dispersal mechanism: Some of the methodology has been alluded already. The type of mechanism can be ranked to differentiate plants as 'good' or 'poor' dispersers and these are afforded a numerical category. The availability of data is not insignificant with a dispersal agent records for 750 species in Ecoflora.

Seed size: Many species had several values recorded in more than one data source. Some of these values may be duplicates. Sources for the data were not always apparent so it is not always possible to know whether to treat the values as independent. Given that there is huge variability in the values listed for seed size, it may be best to select modal values rather than to calculate averages. Both methods are likely to be affected by duplicates so elimination of obvious duplicates is a priority.

Seed number: Ecoflora contained records for seed production per plant for 357 species. However, although annuals, often arable weeds, were well-represented, few values were recorded for grasses. There is wide variation for seed production and this trait is closely linked to alterations in the environment, with some species increasing seed production under one regime whereas another species may respond to the same conditions with a reduction in seed production. Different management regimes can also alter the capacity of a species to produce seed. In fact it is a wonder any values have been recorded at all and it is possible that some of these are highly debatable, ideally we require a value for a species grown in its optimal natural habitat on an average year, or values for all species grown in standard conditions.

Height and spread of plant: The records in ECPE are listed in categories. Ecoflora also contained information but spread is represented as a ratio of height to spread, confirming that spread tends to be coupled with height so the use of height alone is sufficient to characterise these traits.

Life history: This trait for individual species was well-documented (ECPE as winter or summer annuals, biennials, monocarpic or polycarpic perennials) but needs ranking according to the effect on the ability to disperse. Age at first flowering was recorded for 232 species in Ecoflora.

Seedbank: There was a range of information, mostly qualitative but this may have a strong effect on the ability of plants to disperse over time.

The construction of a formula to calculate values for the filters was not feasible with so many of the components derived by a ranking mechanism.

Building in a certainty ranking (as additional sets of values) has been proposed to indicate a level of confidence for the filter values. This should include a measure of how many traits have been used to build filter (data for some traits are not available for some species), and can also indicate the level of assurance for features such as palatability measures that are based on combinations of existing knowledge, not the main listed data sources. Initially we have focussed on deriving values for those species where data is available for the majority of the recognised components.

## **Development of Dispersal Filter**

The rank was constructed by assembling the listed available components into summary weightings.

The propagation method for a species was derived by the combination of the regenerative strategy from ECPE, see Table 1, and the regrowth ability from PLANTATTR, see Table 2 and Table 3. These components help predict the ability of the species to disperse by the production of seed or vegetative propagation. Further mechanisms and the physical characteristics build the probability for level of ability to disperse up (good dispersal – several kilometres) or down (poor dispersal – under a few metres).

For the dispersal mechanism, when converting the characteristic to a numerical value,

some reclassification was undertaken. The category for animal dispersal was further subdivided into two, with plants dispersed by vertebrates ranked as potentially good dispersers, whereas plants with seeds normally carried by invertebrates only a few metres as poor dispersers. Database information for this trait was available from more than one source (Ecoflora, ECPE and SID as well as the Countryside Survey summary) with the disperser not consistently the same for the same species in different sources, so the ranking for the trait has been built by a cumulative weighting.

Seed weight is well-documented, and actual values were available from various sources (Ecoflora, SID), however the data presented in the ECPE database had already been sorted classified into categories. The ECPE categories have been compared to values derived from actual values from the Ecoflora and SID sources and, whereas, for the purposes of this study we have reversed the order of the values, they are correlated, see Table 4. ECPE categories such that large seeds tend to be allocated to Category 5 and at the other extreme, small seeds fall in Category 1. However it seems that other attributes have contributed to these category allocations. Where there are several values for a species, occasionally the values are disparate. This may be the result of natural variability. Some caution has been exercised where information from different sources may have been drawn from the same origin. Further validation for a sub-set of seed data was performed by cross-reference to information on seed weight for seed from continental Europe (Šerá and Šerý 2004) and values for seed weight for the matching species were found to be highly comparable. The weighting has been based on the assumption that the smallest seeds are likely to be carried the furthest. This is over-simplistic but there is evidence of a general trend that heavier seeds fall where produced whereas light seed have a greater potential to be carried some distance particularly if wind dispersed (Willson 1993). Also small germinule size also facilitates dispersal through time by their assimilation into the soil and smaller seeds may also be less vulnerable to predation than large seeds explaining the persistence of small seeds in the seedbank.

The production of a plant as manifested by the number of seeds has a major effect on the ability to disperse. Ecoflora contains values (in size categories) for 357 species, these have been ranked numerically with plants producing large numbers of seeds given a higher rank as they have more opportunity to disperse, see Table 5. Of these only 167 species have values for seed weight.

Height categories have been derived from the maximum measured in centimetres for all plants with values in Ecoflora (1634 species), see Table 6. The minimum height recorded for 1257 species helped afford categorisation where there was some ambiguity. Cases where anomalous data entries in the data-set have been identified have been corrected.

502 species have life history characteristics described in the ECPE database. These have been numerically ranked and tallied with the less detailed perennation types listed in PLANTATTR, see Table 7. It is rather difficult to base a ranking on the summarised simple trait as, for example, some perennials establish over several years before flowering, whereas other perennials flower within a few weeks. A perennial that reaches sexual maturity quickly may have an advantage over an annual for dispersal. However a best generalised estimate has been based on annuals having more potential to disperse with a quicker lifecycle and this is supported by the

evidence that arable weeds and plants of early succession tend to be annuals. Individual perennial plants may have a high dispersal capacity; other traits, such as longevity may well boost their overall ranking for dispersal.

Seed persistence, as quantified by the presence of viable seed in the seedbank, is another factor determining the ability of a plant to invade an unoccupied gap and extends the potential of the plant to disperse over time so must be considered as another vital component for building a measure of the ability of a plant to disperse. Information on seed bank type was derived from the soil seed bank database for North West Europe (Thompson, Bakker et al. 1997). A major practical limitation on this data was multiple entries for individual species assigning individual species to more than one category in terms of their soil seed bank characteristics. To derive a value for ranking seed persistence we have used the longevity index (Thompson, Rickard et al. 2002) for the reduced list of species with seed weight ranking. The limitation of this index lies in the variability of the quantity of values for persistence; some well-researched species have numerous values whereas many have only a few.

Available data for these traits was collated in one database. Initially different traits were usually listed in different tables within the database for ease of recognition and because the species lists for each trait did not correspond. To be able to link the tables and combine the information to produce a summary list of species with a dispersal rating, some standardisation of species names was essential. Use of the BRC number as an identifier (Microsoft Access – primary key) was not practical since the format varied from one database to another or the numbers had not already been input with some of the data-sources. As one function of my role was to introduce an element of experience as a field botanist by recognition of the authenticity of the traits for species it was effective to allow quick recognition of species by using names.

The final stage in the production of an overall dispersal ranking was developing a method to amalgamate a set of somewhat disparate values for the different traits. The most straightforward method would be a simple accumulation; however the ranks have all been produced on different scales so conferring a weighting greater to one trait than another which does not reflect reality. A transformation to give all the traits fairly equal status within the calculation was undertaken as well as an assessment of any correlations between particular traits that could negate their inclusion as discrete factors with equal weight within an accumulated final weighting for dispersal. The use of the regenerative strategy and clonality as separate factors conferred a disproportionately weighted representation for these aspects of the plant life history in dispersal so they were amalgamated, then transformed. During an assessment of correlations between different methods for producing a final dispersal weighting, the omission of the Life History trait from correlations made little impact on the correlations. This was so even when the ranking of the Life History trait was transformed to give the same order of magnitude as the other components. Hence the use of the Life History trait in the overall calculation was found to have little contribution. The Life History trait had been difficult to rank with regard to influence on dispersal capacity with some evidence that plants that live longer or even taking longer to reach sexual maturity have higher dispersal potential over time. As the Life History trait was relatively neutral and was not a limiting trait in terms of availability in the data-sources it has remained in the overall calculation.

Where the component traits have been limiting in terms of records in the data-sources, as is the case with seed production, we have investigated the overall influence of the omission of this trait from the final calculation. Seed production is deemed a critical component in dispersal so rather a risky element to exclude. This has been tested and has made little difference overall to the majority of species in the reduced list (98% correlation for the two lists), so a rank has been derived for the list of species where seed production has been omitted. This second list, which includes all the species from the first list, has values for a dispersal rating for just under 300 species.

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## Appendix 4: Testing and development of a method to predict probability of occurrence of rare and subordinate plant species.

David Roy, Mark Hill

### Introduction

Previous work under the Defra Pollution Umbrella and in other components of this project have shown that response curves can be used to define the realised niche of plant species along of abiotic gradients. This approach works especially well for common plants that are well-recorded by national vegetation surveys, but cannot be applied to rarer plants, for which information on abiotic factors is lacking. Here we develop a method to predict the probability of occurrence of rare and scarce species, based on their association with assemblages of more common species.

### Data and methods

#### *Datasets*

Electronic datasets of species recorded in quadrats were available from several sources (Table 1). Datasets were selected to have wide geographical coverage. Only presences and absences were used and the total number of observations was almost 430000. Of the 1373 plant species covered by the dataset 913 have sufficient data to fit response surface models. For the remaining 460 species we have developed an alternative approach to predict their occurrence within quadrats, given that the complement of commoner species is known.

Dataset	Date recorded	Location	Source	Number of records
NVC	1965-1980	All Britain	I.M. Strachan (JNCC)	298129
CS2000	1999/1999	United Kingdom	S. Smart (CEH)	84326
Key Habitats	1990-2000	Britain	S. Smart (CEH)	2960
Woodland Survey	1971	All Britain	S. Smart (CEH)	37496

**Table 1.** Quadrat datasets used for development of subordinate/rare species model.

#### *Calculating a measure of association, the odds-ratio*

The aim of this method is to estimate the probability of finding a rare species in a given environment. To this end, the probability of finding each of the commoner species is calculated first. The probability finding a rare species is derived second, conditional on the common species that are present. The reason for this apparently circuitous method of reasoning is that we have relatively good data on the common plants that are associated with rare plants, but almost no direct measurements of the physical environment of most rare plants.

We use presence of species in quadrats to calculate the degree of association between pairs of species  $i$  and  $j$ . A 2 x 2 contingency table can be used to summarise the data:

		Species $i$		
		Present	Absent	Total
Species $j$	Present	$a$	$b$	$a + b$
	Absent	$c$	$d$	$c + d$

		$a + c$	$b + d$	$N$
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where the total number of quadrats  $N$  is partitioned into those in which both species are present ( $a$ ), those in which only one is present ( $b$  or  $c$ ), and those in which both species are absent ( $d$ ). Many different coefficients of similarity based on the quantities  $a$ ,  $b$ ,  $c$ , and  $d$  have been proposed (Digby and Kempton, 1987) but we adopt a measure based on the odds-ratio statistic.

An odds-ratio statistic can be derived from a 2 x 2 contingency table for a given rare species,  $i$ , and associated common species  $j$ . The odds ratio in favour of the association is

$$OR_{i,j} = (a \times d) / (c \times b)$$

the log odds ratio being

$$\log_e (OR_{i,j}) = \ln(a) + \ln(d) - \ln(c) - \ln(b) .$$

In the present example, when  $i$  is a rare species, for which one or other of  $a$  or  $b$  is likely to be zero, we use  $(1 + a)$  and  $(1 + c)$ , to avoid taking logarithms of zero. For any given rare species,  $i$ , we can define the suitability of a suite of  $n$  common species  $j$  as the mean odds ratio in favour of the rare species, given its associates

$$A_i = (1/n) \sum_{j=1}^{j=n} \log_e(OR_{i,j})$$

It is convenient to divide  $A_i$  into two components

$$A_i = B_i + C_i$$

where

$$B_i = (1/n) \sum_{j=1}^{j=n} ( \log_e(a) - \log_e(c) )$$

$$C_i = (1/n) \sum_{j=1}^{j=n} ( \log_e(d) - \log_e(b) )$$

In practice, because species  $i$  is a rare species the values of  $c$  and  $a$  are small, so that

$$d \sim c + d$$

$$b \sim a + b .$$

Thus, the term  $C_j$  hardly depends on which rare species  $i$  is being studied, but is a constant telling us about the common species but not the rare ones. Indeed, it is possible, as a thought experiment, to imagine that a large number of extra samples had been added from another part of the world, say the humid tropics. In that case,  $d$  would increase but the other values,  $a$ ,  $b$ , and  $c$ , would remain constant. The value of  $d$  and therefore of  $C_i$ , depending as it does on the essentially extraneous number of quadrats that were sampled in areas that are quite unsuitable for the rare species, is of little interest. Therefore, the test statistic selected was  $A_i$ .

*Probability of occurrence against test statistic*

The mean adjusted odds ratio in favour of rare species  $i$ ,  $B_i$ , was calculated for each quadrat in our dataset.  $B_i$  was used as the explanatory variable in a binary logistic regression to derive coefficients  $a_i, \beta_i$ , for estimating the probability  $P_i$  of occurrence of rare species,  $i$

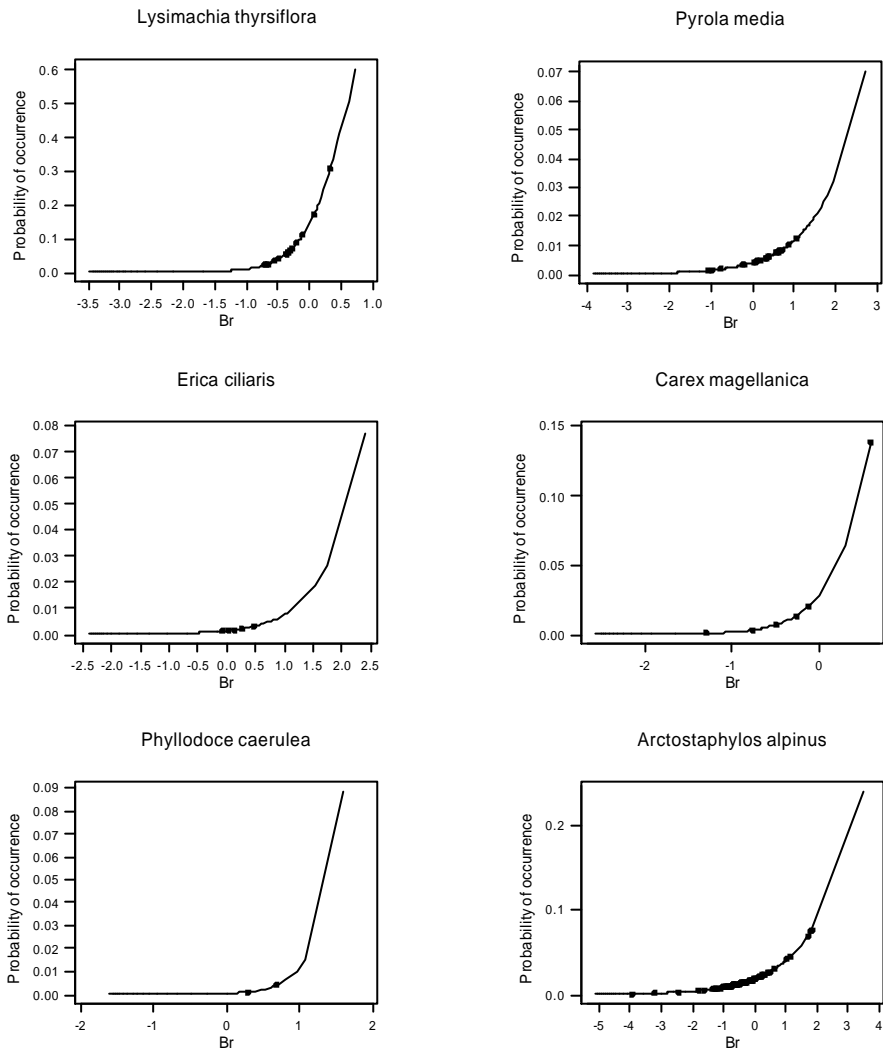
$$P_i = \frac{e^{a_i + b_i B_i}}{1 + e^{a_i + b_i B_i}} .$$

## Results

Regression equations for the probability of occurrence of rare species have been developed for ten rare species (Figure 1). In all cases the model was highly significant ( $p < 0.001$ ). For a further three species, regression models could not be fitted. For quadrats where the successfully modelled species occur in our dataset, the mean predicted probability of occurrence ranged from 0.2% (*Erica ciliaris*) to 7.7% (*Loiseleuria procumbens*), confirming that the likelihood of finding these species in quadrats is extremely small.

Species	N	Model Convergence	$a_i$	$\beta_i$	Mean probability where present
<i>Arctostaphylos alpinus</i>	85	Y	-3.99	0.81	0.016
<i>Carex chordorrhiza</i>	9	N	-	-	-
<i>Carex magellanica</i>	6	Y	-3.54	2.92	0.030
<i>Carex rariflora</i>	19	N	-3.99	1.75	0.019
<i>Erica ciliaris</i>	5	Y	-6.63	1.73	0.002
<i>Fritillaria meleagris</i>	9	Y	-6.49	3.11	0.026
<i>Gentiana pneumonanthe</i>	1	N	-	-	-
<i>Loiseleuria procumbens</i>	131	Y	-2.14	1.32	0.077
<i>Lysimachia thyrsoiflora</i>	16	Y	-1.79	2.98	0.074
<i>Phyllodoce caerulea</i>	2	Y	-7.94	3.48	0.002
<i>Pyrola media</i>	23	Y	-5.54	1.09	0.006
<i>Trifolium ochroleucon</i>	1	Y	-25.7	20.9	0.062
<i>Vaccinium microcarpum</i>	8	N	-	-	-

**Table 2.** Summary of models relating the presence of rare species to the test statistic  $B_i$ . N is the number of quadrats the species was recorded from in our dataset.  $a_i$  and  $\beta_i$  are the intercept and slope coefficients respectively.



**Figure 1.** Probability  $P_i$  of occurrence of rare species in relation to the test statistic  $B_i$ . Solid circles show quadrats where the rare species was recorded as present.

## Discussion and future developments

Predicting the presence of rare species in quadrats is problematic due to the lack of data on their distribution at fine scales and information on their ecological requirements. There is also a large element of chance in the precise position where rare species are found. The approach adopted here uses associated common species to predict the likelihood of finding rare species. The test statistic based on the mean log-odds ratio for occurrence of rare species shows promise. It now needs to be tested on a more extensive set of rare species.

**Acknowledgements**

For the supply of datasets in electronic form, we are grateful to Ian Strachan (Joint Nature Conservation Committee) and Simon Smart (CEH). We are grateful to Cassie Hoyland (CEH) for help with manipulation of NVC quadrata data. The project was funded by Defra as part of the project, Nitrogen Impacts on Biodiversity.

**Reference**

Digby, P.G.N. and Kempton, R.A. 1987. *Multivariate analysis of ecological communities*. Chapman and Hall, London.

## Appendix 5: Determination of environmental optima for higher and lower plants.

Andy Scott

Consider fitting a logistic regression describing the response of a species to a number of explanatory environmental variables. The fitted model (for just two variables can be described as:-

$$E(z) = \exp(\mathbf{h}) / (1 + \exp(\mathbf{h})) \quad \text{and} \quad \mathbf{h} = \mathbf{a} + \mathbf{b}x + \mathbf{g}x^2 + \mathbf{d}y + \mathbf{f}y^2 + \mathbf{j}xy$$

where  $z$  is the response variable of interest (in this case the probability of the species being observed),  $E$  is the expectation operator,  $x$  and  $y$  are explanatory variables,  $\mathbf{a}$ ,  $\mathbf{b}$ ,  $\mathbf{g}$ ,  $\mathbf{d}$ ,  $\mathbf{f}$  and  $\mathbf{j}$  are fitted parameters (or coefficients) and  $\mathbf{h}$  is referred to as the linear predictor. Additional explanatory variables are incorporated in the linear predictor in an obvious way with terms (and parameters) for the new explanatory variable, its square, and its interactions with existing variables. We will assume that no three or higher way interactions are included.

Let  $X$  represent the vector of explanatory variables, then the linear predictor can be reparameterised as

$$\mathbf{h} = \mathbf{a} + \mathbf{B}^T X - X^T \Sigma X$$

where  $\mathbf{B}$  is the vector of coefficients of the linear terms and  $\mathbf{S}$  is a symmetrical matrix whose diagonal values are *minus* the coefficients of the squared terms and whose off-diagonal elements are *minus half* the coefficients of the corresponding two-way interaction terms.

Subtract from the squared  $X$  term an arbitrary vector  $\mathbf{q}$  to give

$$\mathbf{h} = (\mathbf{a} + \mathbf{q}^T \Sigma \mathbf{q}) + (\mathbf{B}^T - 2\mathbf{q}^T \Sigma) X - (X - \mathbf{q})^T \Sigma (X - \mathbf{q})$$

If now  $\mathbf{q}$  is given a value that makes the linear term zero in this equation, whatever the value of  $X$ , then we are left (apart from an arbitrary constant) with a quadratic form whose maximum is known to be at the chosen value of  $\mathbf{q}$ . I.e. the value of  $X$  which maximises the linear predictor is

$$X = \mathbf{q} = 0.5 \Sigma^{-1} \mathbf{B}$$

as long as  $\mathbf{S}$  is invertible. Since the equation above relating the response variable to the linear predictor is a monotonic transformation of the linear predictor then this value of  $X$  is also the value which maximises the expected value of  $y$ , i.e. the required species optimum.

If  $\mathbf{S}$  is not invertible then a generalised inverse can be used. However it should be noted that this procedure may not give optimum values unless certain conditions are met even if  $\mathbf{S}$  can be inverted and the equation above is solvable. If, for example, any explanatory variable is included as just a linear term then the optimum is at either plus or minus infinity for that variable depending upon the sign of its coefficient.

Furthermore estimation of the optimum may not be accurate if it falls outside the range of the data.

### Restrictions on fitted values required to produce valid optima

1. All coefficients of quadratic terms must be negative. Positive quadratic coefficients indicate a minimum not a maximum, i.e. the species in question is more prevalent at the ends of the environmental range than in the centre.
2. A linear term without a corresponding quadratic term indicates that the species has no optimum but a probability of occurrence that increases steadily towards one end of the environmental gradient. This is most likely to be due to the optimum value being outside the observed range of the data leading to a non-significant quadratic term.
3. Including an interaction between a variable that has no quadratic term and another variable forces the other variable to have an optimum at plus or minus infinity. Hence quadratic terms must be included for all variables in an interaction term.
4. The coefficients of interaction terms must also be such as to make the matrix  $\Sigma$  satisfy the requirements of a covariance matrix. I.e. positive interaction coefficients must be less than twice the square root of the product of the two corresponding quadratic terms. If this is not the case then the variables concerned have no optima.

To illustrate these points we examine the simple case of just two environmental variables, x and y. The fitted linear predictor is  $h = a + bx + gx^2 + dy + fy^2 + jxy$ .  $\Sigma$  and B are therefore

$$\Sigma = \begin{bmatrix} -g & -0.5j \\ -0.5j & -f \end{bmatrix} \quad \text{and} \quad B = \begin{bmatrix} b \\ d \end{bmatrix}$$

and the inverse of  $\Sigma$  is

$$\Sigma^{-1} = (0.25j^2 - fg) \begin{bmatrix} f & -0.5j \\ -0.5j & g \end{bmatrix}$$

giving the solution to the optima equation

$$\begin{bmatrix} x \\ y \end{bmatrix} = 0.5(0.25j^2 - fg)^{-1} \begin{bmatrix} f & -0.5j \\ -0.5j & g \end{bmatrix} \begin{bmatrix} b \\ d \end{bmatrix} = \begin{bmatrix} 0.5(fb - 0.5jg)/(0.25j^2 - fg) \\ 0.5(gd - 0.5jb)/(0.25j^2 - fg) \end{bmatrix}$$

These equations give real values unless  $fg=0.25j^2$ , in which case  $\Sigma$  is singular, but the values produced may not represent an optimum, i.e. a point of maximum occurrence for the species concerned. If, for example  $b=d=j=1$ ,  $g=f=-1$  then the linear predictor is quadratic (Figure 1) and a unique optimum exists. If, however,  $g$  is set to zero so that y has no quadratic term then the solution represents what is called a saddlepoint (Figure 2) and not an optimum. In this case x has an optimum value for any given value of y but y has an infinite optimum for any value of x. Similarly if  $j$ , the interaction coefficient, is increased to 5 then again a saddlepoint results (Figure 3) even though both variables have a quadratic term. In this case both x and y have optimum values for any fixed value of the other variable but the overall optima is again at infinity.

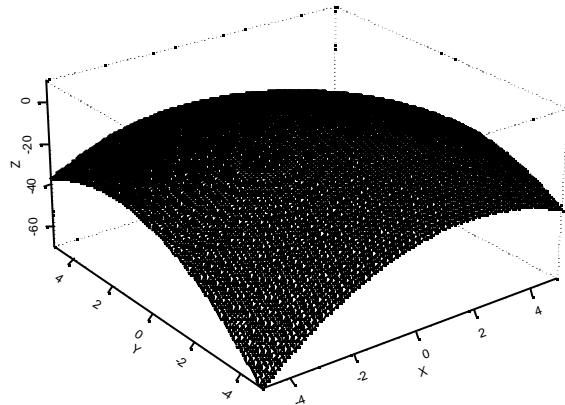


Figure 1. Both quadratic terms – unique optimum

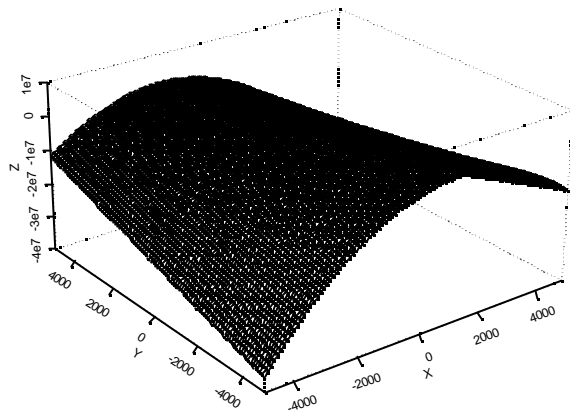


Figure 2. One quadratic term – saddlepoint

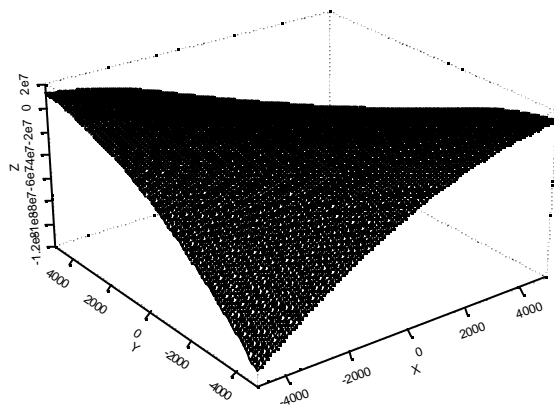


Figure 3. Interaction coefficient greater than quadratic coefficients – saddlepoint

## **Appendix 6: Coverage of Common Standards Monitoring indicator species by GBMOVE models.**

Simon Smart

### Introduction

We envisage that, given satisfactory model development and testing, outputs will be used to test the impact of various scenarios on changing suitability of conditions for individual species as well as changes in biomass of plant functional types (grasses, legumes, forbs, dwarf shrubs, pioneer trees and climax trees). The emphasis of the individual species models is on the suitability of conditions rather than predictions of actual occurrence. For species not present in a target patch, likelihood of actually reaching the target patch will be estimated by applying filters relating to the composition of the species pool in the surrounding area as well as the estimated dispersal potential of the species.

Individual species models have now been developed for as many lower and higher plants as possible. Therefore to determine attributes and targets that could be modelled in the N impacts project, CSM guidance was examined. We focussed only on those Priority Habitats that feature in the current project and hence those for which N deposition is thought to pose a past and current threat based on progress reporting for the Biodiversity Action Plan in 2002.

### Results

Out of 398 lower and higher plants mentioned by name or by group in the CSM guidance notes, regression models exist for 293. Those species for which models do not exist are listed in Table 1. They largely include the many separate species of *Cladonia* as well as rare sedges. It seems likely that lack of some of these species will not be relevant since they were included because the whole genus was mentioned in CSM guidance. Hence, the sedge list can be furthered filtered to weed out taxa not applicable to the Priority Habitats, while there is the possibility of modelling *Cladonia* as one entire group.

Table 1. + indicates a positive indicator. Models have been generated for *Alchemilla* species combined and *Dactylorhiza* species combined.

CSM_spp_with_no GBMOVE models	
Notes	BRC names
CG1 +	Acinos arvensis
MG3 +	Alchemilla acutiloba
“	Alchemilla alpina
“	Alchemilla conjuncta
“	Alchemilla filicaulis
“	Alchemilla glabra
“	Alchemilla glaucescens
“	Alchemilla glomerulans
“	Alchemilla gracilis
“	Alchemilla minima
“	Alchemilla mollis
“	Alchemilla monticola
“	Alchemilla subcrenata
“	Alchemilla tythantha
“	Alchemilla wichurae
“	Alchemilla xanthochlora
CG7 +	Aphanes arvensis
Hay meadow -	Berberis vulgaris
Upland dry heath -	Campylopus polytrichoides
“	Campylopus schimperi
“	Campylopus schwarzii
“	Campylopus shawii
“	Campylopus subulatus
“	Carex atrofusca
	Carex buxbaumii
	Carex chordorrhiza
	Carex depauperata
CG8,9 +?	Carex digitata
	Carex divisa
	Carex filiformis
	Carex lachenalii
	Carex magellanica
	Carex microglochin
CG8,9 +?	Carex ornithopoda
	Carex punctata
	Carex rariflora

<b>CSM_spp_with_no GBMOVE models</b>	
<b>Notes</b>	<b>BRC names</b>
	Carex recta
	Carex trinervis
Lowland calc grass -	Cetranthus ruber
CG7 +	Cetraria chlorophylla
“	Cetraria commixta
“	Cetraria cucullata
“	Cetraria hepaticum
“	Cetraria pinastri
“	Cetraria sepincola
“	Cladonia acuminata
“	Cladonia alcicornis
“	Cladonia alpestris
“	Cladonia amaurocraea
“	Cladonia caespiticia
“	Cladonia cariosa
“	Cladonia carneola
“	Cladonia cenotea
“	Cladonia cf.coccifera
“	Cladonia cf.polydactyla
“	Cladonia cf.subcervicornis
“	Cladonia ciliata
“	Cladonia conista
“	Cladonia convoluta
“	Cladonia cyathomorpha
“	Cladonia degenerans
“	Cladonia destriata
“	Cladonia ecmocyna
“	Cladonia gonecha
“	Cladonia incrassata
“	Cladonia luteoalba
“	Cladonia macrophylla
“	Cladonia mitis
“	Cladonia nylanderii
“	Cladonia ochrochlora
“	Cladonia parasitica
“	Cladonia pityrea
“	Cladonia portentosa
“	Cladonia ramulosa
“	Cladonia subrangiformis

CSM_spp_with_no GBMOVE models	
Notes	BRC names
“	<i>Cladonia subsquamosa</i>
“	<i>Cladonia turgida</i>
Lowland calc grass -	<i>Cotoneaster</i> spp.
These were amalgamated but worth revisiting for some species to run individual models.	<i>Dactylorhiza fuchsii</i>
	<i>Dactylorhiza incarnata</i>
	<i>Dactylorhiza maculata</i>
	<i>Dactylorhiza majalis</i>
	<i>Dactylorhiza majalis praetermissa</i>
<i>Dactylorhiza purpurella</i>	
CG7 +	<i>Dianthus deltoides</i>
Lowland heath +	<i>Erica ciliaris</i>
CG9 +	<i>Galium sternerii</i>
Lowland heath -	<i>Gaultheria shallon</i>
Lowland heath/upland dry heath +	<i>Gentianella anglica</i>
CG8 +	<i>Gentianella ciliata</i>
“	<i>Gentianella germanica</i>
“	<i>Gentianella uliginosa</i>
CG9 +	<i>Helianthemum appeninum</i>
MG4 +	<i>Oenanthe silaifolia</i>
Blanket bog + (Needs checking)	<i>Rubus chamaemorus</i>
Upland wet heath/Blanket bog +	<i>Sphagnum balticum</i>
“	<i>Sphagnum platyphyllum</i>
“	<i>Sphagnum riparium</i>
“	<i>Sphagnum strictum</i>
CG1 +	<i>Trinia glauca</i>

## **Appendix 7: Literature review of experimental evidence for the influence of multiple drivers on plant community dynamics.**

### **OBJECTIVE**

Three recent reviews amply cover the subject of atmospheric N deposition impacts on temperate ecosystems across Europe (NEGTAP 2001; Achermann & Bobbink 2003; Cunha et al 2002). This brief review avoids covering the same ground but instead uses these sources to identify gaps in the existing experimental evidence base relating to interactions between different potential factors that promote or inhibit vegetation change on UK Priority Habitats. By interactions we mean the dependence of a response to one factor on levels of one or more other factors.

This issue is important for two reasons. Firstly, phase 1 of the N impacts project aims to produce a model framework for predicting A/SSSI condition on terrestrial Priority Habitats. Clearly, sites of conservation importance are impacted simultaneously by driving forces other than heightened atmospheric N deposition. If predictions are to be accurate, developing model components need to reproduce the impacts of these other drivers and a review of the evidence will therefore inform the model development and testing process. Secondly, the operation of multiple factors is of growing ecological significance in its own right. Multiple factors can act simultaneously or in sequence to produce ecosystem effects not predictable by studying the action of each driver independently. Examples include the increased susceptibility of *Calluna* to Heather Beetle attack given N enrichment and favourable climate and the dependence of a response to N enrichment on addition of P.

The issue of multiple drivers also appears to have increasing ecological significance in an age when ecosystem perturbations are a complex consequence of many driving forces operating at different scales. There is increasing evidence that the consequence of these interactions can lead to so-called alternative stable states (Suding et al.2004). These states are often species-poor variants of previous ecosystems that have been pushed to the point where they are resistant to further perturbation but, importantly, are also resistant to restoration efforts even if management conditions are right. These alternative stable states are particularly associated with the operation of multiple drivers of change (Scheffer and Carpenter 2003).

The consequences of multiple factors operating together maybe hard to predict if they combine to cause non-linear, step changes. Sudden shifts can be triggered by unpredictable catastrophic events such as major flooding or pathogen outbreak. By definition, short-term experiments will have difficulty in describing the dynamics of such events and their underlying processes. However, experiments remain an obvious way of studying how responses to varying levels of one factor, such as grazing intensity, are affected by simultaneously varying one or more other factors such as N deposition, propagule availability and climate. This review addresses these issues by firstly identifying the major threats to UK Priority Habitats and then focussing on the complexes of factors likely to impact Priority Habitats in which N deposition is thought to be a current risk factor. The review ends by assessing the extent to which published experiments have studied interactions between these risk factors.

## APPROACH

A current ranking of risk factors associated with UK terrestrial Priority Habitats can be found in the 2002 Biodiversity Action Plan Progress report<sup>1</sup>. Marine Priority Habitats were excluded (Table 1). Seven Priority Habitats were thought to be threatened by atmospheric N deposition and the intention is to develop models for six of these (Lowland Wood-pasture and Parkland excluded). The review of experimental evidence therefore focussed on these six only.

A literature review was carried out for each Priority Habitat to identify experiments where each threat factor had been manipulated alongside N deposition treatments. (Table 2 and Appendix 1). Knowledge gaps were identified for each habitat. Threat factors that destroy habitat such as quarrying, peat extraction, urban development and ploughing were not included. Information sources were principally based on UK studies with additional information incorporated from the European literature as summarised in Achermann & Bobbink (2003). While the review relied largely on published evidence, we also refer to the latest results from the long-term experiments sponsored by the NERC/DEFRA Terrestrial Pollution Umbrella project reported in Emmett & McShane (2004).

## RESULTS

### Lowland heath

The effects of N deposition on lowland heath have been well studied, not least because of sustained research efforts on a small number of long-term experimental sites, three of which (Thursley Common, Wardlow Hay Cop and Budworth Common) will be used to test Phase 1 models. Results indicate that N addition invariably leads to increased shoot growth, canopy height and density, flowering and litter production. Temperature and drought treatments were also crossed with N addition in the mesocosm experiments of Ashenden and Jones (2000). They showed that N addition on its own increased *Calluna* susceptibility to frost and drought. Caporn et al (2004) have also seen an increase in the susceptibility of *Calluna* to drought, frost and heather beetle attack following N addition treatments that began at Budworth Common in 1996. These additional stresses can promote canopy gap formation, facilitating the invasion of nitrophilous species including grasses (Power et al 1998a,b; Uren et al 1997; Cawley 2001). However climate x eutrophication effects as well as the desirability of managed disturbance in ameliorating eutrophication effects, remain somewhat uncertain given the inconsistency of responses between sites. For example, Power & Green (2004) found that P availability was increased following experimental burning but this was presumably a transient effect. At the same time the legacy of previous N addition was lower in plots subjected to the higher intensity burn, at least in terms of enhanced soil microbial activity and *Calluna* growth.

Several studies also indicate that difficulties generalizing the extent to which managed disturbance can ameliorate increased N deposition can reflect differences in drought or frost sensitivity (Gordon et al 1999 – Bracken versus *Calluna*) or possibly in the relative palatability and shade-tolerance of competing pairs of species (Alonso et al. 2001; Alonso and Hartley 1998 – *Deschampsia flexuosa* and *Nardus stricta*

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<sup>1</sup> On line at [www.ukbap.org.uk/asp/2002\\_main.asp](http://www.ukbap.org.uk/asp/2002_main.asp)

versus *Calluna*). In this respect it is significant that in Dutch heathlands sheep grazing is used to check the vigour of *D.flexuosa* and maintain *Calluna* dominance (W.Wamelink pers comm.) while in Britain *Calluna* is avidly consumed by sheep when co-existing with *Nardus* presumably because it is relatively more palatable. If the asymmetry of these competitive relations can be understood by reference to a common attribute such as relative palatability then prospects for developing a generalised cross-species modelling approach will be improved.

The evidence for an N related increase in *Calluna* frost sensitivity is also equivocal. Increases in sensitivity have mostly followed from unusually high N loading while the more realistic application of 7.7 and 15.4 kg N ha yr showed no significant effect even after seven years (Power et al 1998). The relationship between frost sensitivity and N deposition at ambient levels therefore remains very uncertain.

The increase in drought sensitivity following increased N appears to be more clearly supported but disentangling the relative importance of different mechanisms e.g. reduced mycorrhizal infection, reduced root:shoot ratio, increased attack by heather beetle, requires further experiment. However the outcomes of induced *Calluna* drought stress have recently been demonstrated following the experimental application of a Summer drought to lowland heath at Budworth. Increased *Calluna* stress was followed by a heather beetle outbreak, which was more severe in the droughted plots, and a correlated increase in *Deschampsia flexuosa* exploiting gaps in the stand (Lee and Caporn 2001).

Two recent modelling studies provide new indications of the impact of management and N deposition interactions on lowland heathland in the UK. In contrast to the Netherlands, where a 50-year cycle of sod-cutting serves to dramatically set back heathland succession and nutrient accumulation, less intensive UK management regimes such as mowing on a 15 year rotation offer less amelioration of the effects of heightened N deposition (Allchin et al 2001 cited in Achermann & Bobbink 2003). Intensive management of UK lowland heaths is predicted to lead to recovery from N enhanced grass-dominance with 20-30 years but low intensity grazing or burning may lead to recovery times of the order of 50 years. Uncertainty in these predictions was also related to outbreaks of Heather beetle highlighting the potential impacts of climate change that are likely to be seen at these timescales (Terry et al 2004).

Studies that have changed N and P availability also concluded that these factors can substantially alter the response of lowland heathland plant species to increased N deposition (eg. Roem et al 2002).

Knowledge gaps: There is limited recent experimental or observational evidence for the effects of burning on heathland (eg. Allchin et al. 1996) and most of the literature dates back to the late eighties (eg. Hobbs and Gimmingham 1987). However, some of the UK long-term experiments have crossed N addition with burning treatments. These showed that the effect of high intensity burning or mowing tended to dampen the effects of N addition on *Calluna* growth. At low intensity management and high N, litter decomposition and *Calluna* growth were enhanced suggesting more rapid nutrient cycling (Barker 2001; Power et al 2001). While Caporn et al (2004) concluded that “..a raised level of management activities using light cutting and burning can partly compensate for current [nitrogen] inputs”, they highlighted the greater leaching of inorganic N following more intensive, deeper burns. Hence, management recommendations need to balance the contrasting needs for nutrient retention and removal. In light of current evidence from UK long-term experiments,

Caporn et al (2004) concluded that “..the value of burning in general as a tool to remove the accumulated nitrogen stores in heathlands is uncertain.”

Given the timescales involved it is not surprising that experimental evidence is currently lacking for the effects of enhanced N deposition on succession in neglected heaths. Understanding of these interactions has however, been successfully explored using observational data (Marrs et al. 1986 – succession only), chronosequence studies (Mitchell et al., 1999 - succession and soil fertility only) and modelling (Britton et al 2001; Heil and Bobbink, 1993).

### **Upland heath**

A number of studies have examined the interactions between enhanced N deposition and grazing. Hartley (1997) crossed grazed and ungrazed treatments with N additions and found that *Nardus stricta* was only favoured in the grazed treatments. Where sheep and deer were excluded, *Calluna* dominated at the expense of the shade-intolerant *Nardus*. They concluded that reduction of grazing pressure would prevent transition to *Nardus* grassland in upland moorlands despite elevated N and therefore that canopy disturbance might be needed to trigger the displacement of *Calluna* by grasses (Alonso and Hartley 1998). *Deschampsia flexuosa* has also been shown to respond in a similar fashion when grazed and receiving elevated N (Emmett et al 2001). A recent synthesis of the relationship between N deposition and grazing has also emphasised the interplay between the increasing nutritional quality of enriched *Calluna*, increased grazing pressure and subsequent increases in grass cover at the expense of Ericoids (van der Wal et al. 2003).

The sensitivity of characteristic moss and lichens appears species-specific, with different optima at different N loading (Achermann & Bobbink 2003; Jones et al 2002). Effects are also strongly modified by P supply (Caporn et al 2004). Addition of both N and P at Ruabon upland heath led to a dense bryophyte layer while N on its own, reduced the abundance of moss (especially *Rhytidiadelphus loreus* and *Pleurozium schreberi*) and lichen species (Emmett et al 2001). Burning at high N addition also stimulates bryophyte growth in the years immediately following treatment but species tend to be shade-intolerant and nitrophilous (Ashmore 2004).

Knowledge gaps: In terms of risk factors identified for Upland Heath (Table 2), no experimental evidence exists that has crossed N addition with burning treatments with or without grazing – the Ruabon study has crossed N and P loading and burning but not grazing. In reality all three factors can operate together since intense and large-scale burns have been used in parts of upland Britain to encourage greater grass growth to support greater sheep numbers (Yeo and Blackstock, 2003). The positive effects of grazing, N addition as a result of local fertiliser application, and reseeded on the establishment of nutrient demanding species in nearby grazed heathland have been highlighted, though not fully explored for UK upland heathland (Welch and Scott, 1995).

### **Calcareous Grassland**

Atmospheric N deposition only appears in the current threat list for Upland Calcareous Grassland but at present only a Lowland Calcareous Grassland site has been identified for phase 1 modelling. Available UK evidence for understanding the interaction of N deposition and other factors appears to rest entirely on the long-term experiments carried out at Wardlow Hay Cop in Derbyshire with some additional

information available from relatively short (2 growing seasons) field and greenhouse experiments carried out on Cotswold limestone grasslands (Hewins 2000). These experiments provide information on interactions between N deposition, grazing management and P addition and therefore cover all the highest threat factors other than global warming. Both studies confirm major and persistent effects of P limitation in these systems (also Leake & Lee 2004). For example in her field survey and spatial comparison of between-site factors, Hewins (2000) found that high mean Ellenberg N values were more highly correlated with high soil P rather than high N. However, high N deposition ( $20\text{kg N ha}^{-1}\text{ yr}^{-1}$ ) was still capable of stimulating the tillering of the two most important potential dominants in these grasslands – *Bromus erectus* and *Brachypodium pinnatum*. Cattle grazing could however successfully control both grasses but they were still likely to increase in cover even if canopy height and hence competition for light was checked by defoliation (Hewins 2000). Similar evidence of the compensatory impact of grazing has recently come from the mesocosm study of Jones (2004) where clipping was intended to simulate grazing. Here though, the inherent resistance of calcareous versus acid grassland assemblages, in the absence of grazing, was evidenced by the lack of change in both mean Ellenberg N and species richness in response to 6 years of high N loading ( $55\text{kg N ha}^{-1}\text{ yr}^{-1}$ ). Despite this, the medium to long term impact of lack of management on calcareous grasslands inevitably results in succession and the loss of characteristic species but the role of high N deposition in accelerating and changing the floristic course of succession is likely to be reduced as long as P availability remains low. The critical importance of P limitation, however seems to rest on the reduced timescale for effects to be seen in above-ground vegetation rather than complete suppression of a response. Both the Wardlow Haycop study and evidence from European modelling work (Vergeer & Heil 1998 cited in Achermann & Bobbink 2003) have shown that increases in monocot:forb ratio occur within 10-15 years above the  $15\text{-}25\text{kg ha}^{-1}\text{ yr}^{-1}$  critical load despite low P supply.

Interestingly, the resistance to floristic change conferred by P limitation may exacerbate the problem of N leaching if N uptake by plants and immobilisation in the soil are reduced (Jones 2004). However, the extent of N leaching in calcareous grasslands in response to N addition still appears hard to generalise. At Wardlow, 70% of the N added to the limestone grassland was immobilised in the soil (Leake & Lee 2004) yet appreciable leaching was seen in mesocosms taken from the same site and subjected to N addition treatments by Jones (2004). Significant soil immobilisation of added N was also seen in the Wytham chalk grassland experiment where, in contrast to other studies, no additional response was seen to added P (Unkovich et al 1998). Nevertheless, the greater likelihood of N leaching in P limited calcareous grassland has been recently used to justify discarding a higher critical load (Achermann & Bobbink 2003) where P availability is low.

A unique 6-year study where fertilizer application, disturbance, climate change and seed additions were simultaneously applied to a *Brachypodium pinnatum* grassland illustrated the scope for existing plant communities to acquire new subordinates and dominants given climate change and propagule availability (Buckland et al. 2001). The identity of newly establishing colonists differed predictably, depending upon levels of disturbance and fertility.

Knowledge gaps: Interactions between threat factors have been well studied relative to other Priority Habitats however, available experiments are concentrated on three sites only, raising the question of their representativeness given the range of floristic

variation across the UK. Studies on calcareous grasslands are more numerous on the European mainland and provide additional information on interaction effects (Appendix 1).

### **Blanket Bog**

N addition experiments on blanket bog vegetation are reasonably plentiful across Europe although only one UK example was found (Press et al 1986). No UK studies were identified that involved crossing N application with other key treatment effects.

Summaries of the potential for other factors to influence the response of blanket bog vegetation to N addition have highlighted the effects of climate (particularly precipitation) and P availability. Hence, high precipitation or ground water levels and low P, slow ecosystem responses to increased N loading. In the extreme case, drying bog surfaces can lead to oxidation and rapid mineralization of previously unavailable N and P. The vulnerability of the moss layer to enhanced N has also been well established. Bryophytes intercept nutrients directly from rainfall and in doing so may divert nutrient supply from vascular plants, however their susceptibility differs between species leading to changes in species competition as a result of competition between bryophyte species as well as local extinction as a result of direct toxicity, as for example in parts of the Pennines.

Response to heightened N deposition in UK blanket bog may depend upon the availability of propagules of species inherently capable of greater relative growth rate than stress-tolerators *in situ*. Climatic constraints on establishment and growth would also be expected to impact the behaviour of immigrants yet no experiment has attempted a factorial crossing of climate change, seed availability and N addition. Tomassen et al (2000; 2002 cited in Achermann & Bobbink 2003) introduced plants of *Betula pubescens* and *Molinia caerulea* into ombrotrophic bog turves in the Netherlands and found a growth response after 3 years at 40 kg ha<sup>-1</sup> yr<sup>-1</sup>. Correlation between increased atmospheric NH<sub>x</sub> deposition and shifts in species composition in favour of trees and more nutrient-demanding grasses was also seen in a national survey of Danish ombrotrophic bogs (Aaby 1994).

Knowledge gaps: Effects of climate change on blanket bog communities have been covered in other parts of the temperate world (Weltzin et al. 2003; Weltzin et al. 2000). However, UK studies that modelled, measured or manipulated climate and management appear to have focussed on hydrological effects or other ecosystem functions rather than changes in plant species composition (eg. Bragg, 2002; Garnett et al. 2000). An exception is the Hard Hills burning experiment that has applied replicated 10 or 20 year burning treatments to grazed and ungrazed plots since 1954 at Moorhouse NNR. While the experiment provides an unrivalled time-series, N addition treatments have not been part of the experiment.

### **Lowland raised bog**

Interaction studies involving N deposition treatments in UK raised bogs appear to be very limited. While European studies have been carried out on the importance of threat factors such as neglect, eutrophication and dewatering in lowland fen and mire systems (Diemer et al. 2001; Fossati and Pautou, 1986; Pfadenhauer and Klotzli 1996; Jauhiainen et al. 2002) little evidence exists recording interactions

between other threat factors. No study was found that crossed N addition with burning. The scarcity of the habitat is probably the obvious reason. The only UK interaction study located was that of Hogg et al (1995) who applied N addition and cutting treatments to *Sphagnum* rich valley mire. They showed that biomass removal of the dominant grass *Molinia caerulea* could alleviate the suppressive effect of enhanced grass growth on *Sphagnum*. Hence, the asymmetry of competition for light between dominants and subordinate species is likely to be amplified by nutrient enrichment. They also noted that *Molinia* appeared to be well adapted to low P concentrations although no P treatment was applied.

Dutch evidence has shown that the characteristic dominant of wet heaths, *Erica tetralix*, is less able to tolerate above-ground competition with *Molinia caerulea* than with *Calluna*, because of its shorter canopy height. This has been linked to the widespread shift to *Molinia*-dominated wet heath in the Netherlands (Aerts & Berendse 1988). Lack of heathland management combined with evidence of the link between N deposition, litter and humus accumulation and enhanced N mineralization has resulted in the adoption of sod-cutting as an effective way of setting back succession and removing accumulated nutrients.

Knowledge gaps: Evidence is lacking on the time-scale and dynamics of vegetation change following tree growth and clear-felling of secondary woodland on neglected raised mire remnants and interactions with drainage and N deposition.

### **Lowland meadows**

Numerous studies have examined the effects of different combinations of agricultural treatments on plant communities referable to the Upland and Lowland Meadows Priority Habitats. These have involved crossed and replicated grazing, cutting, manure and mineral fertilizer applications often in an attempt to explicitly tease apart the relative contribution of each type of impact in shaping the plant communities present (eg. Smith and Rushton 1994). Some studies have also been running long enough to study the initial effect of declines in species richness following NPK application and the subsequent course of recovery (eg. Mountford et al., 1996; Tallowin et al. 1998; Bekker et al 1998; Acreman et al. 2002).

Knowledge gaps: While these and many other UK studies provide considerable insight into the impact of agricultural improvement, none were identified that addressed agricultural impacts in the context of global warming as well as varying ambient N deposition. No studies were identified that explicitly attempted to mimic N loading from atmospheric sources with an emphasis instead on FYM or mineral fertiliser. The primary importance of direct agricultural inputs is presumably reflected by the fact that N deposition was ranked as the fifth most important threat factor to the Lowland Meadows Priority Habitat in the 2002 BAP Progress Report.

Although neglect was identified as a key threat to lowland meadows, little UK-based research appears to have been carried out on the impact of abandonment and subsequent restoration with most published work of European origin (Mitlacher et al. 2002; Huhta et al. 2001). The Rothamsted Park Grass experiment appears to be unique in having examined management impacts in addition to changes in atmospheric pollutant inputs and seasonal weather variation within semi-improved and unimproved grassland communities (Jenkinson et al, 1994).

## **CONCLUSIONS**

Research findings that address the requirements of conservation policy will often lag behind the current policy agenda especially if the answers can only be provided by long-term studies and if threats to habitats quickly change in their perceived importance to conservation managers and policy makers. This is one reason why the current evidence base can be expected to have gaps. Moreover, the importance of studying multiple interactions between factors operating at different scales has only recently become more widely publicised and is still a matter for debate (Carpenter 2002). It is also fair to say that the size of the challenge of community restoration and maintenance differs between Priority Habitats so that the lack of experimental evidence for some combinations of threat factors reflects the fact that practical solutions are known to work and do not need experimental confirmation. An example might be restoration of drying and neglected raised mires where intact peat bodies still exist (Rowell, 1989).

More challenging is the quantification of ecosystem dynamics where local factors, such as habitat abandonment, interact with larger-scale factors such as propagule availability and atmospheric N deposition. Realistic experiments maybe needed at complementary scales. These are likely to be rare simply because of their cost and the requirement for cross-institutional funding and collaboration over long-periods with no guarantee that the policy agenda will stay still. In the absence of such experiments, modelling approaches have become an increasingly popular way of exploring vegetation dynamics at large and long timescales (Britton et al 2001). The disadvantage is that their validation maybe restricted to much smaller scales consistent with the availability of independent observations. This is not to downplay the crucial importance of existing experimental studies since the detailed understanding gained about the impact of one or two factors can be used to generate hypotheses and model predictions. Deviations from expectation can then focus attention on the possible influence of other constraints. It is in this spirit that the range of existing studies are intended to be applied in Phase 1 of the N impacts project.

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(see **Bibliography to Appendix 1 for additional references**)

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Figure 1. Risk factors and their importance across UK terrestrial Priority Habitats. Summarised from the 2002 UK BAP Progress Report.

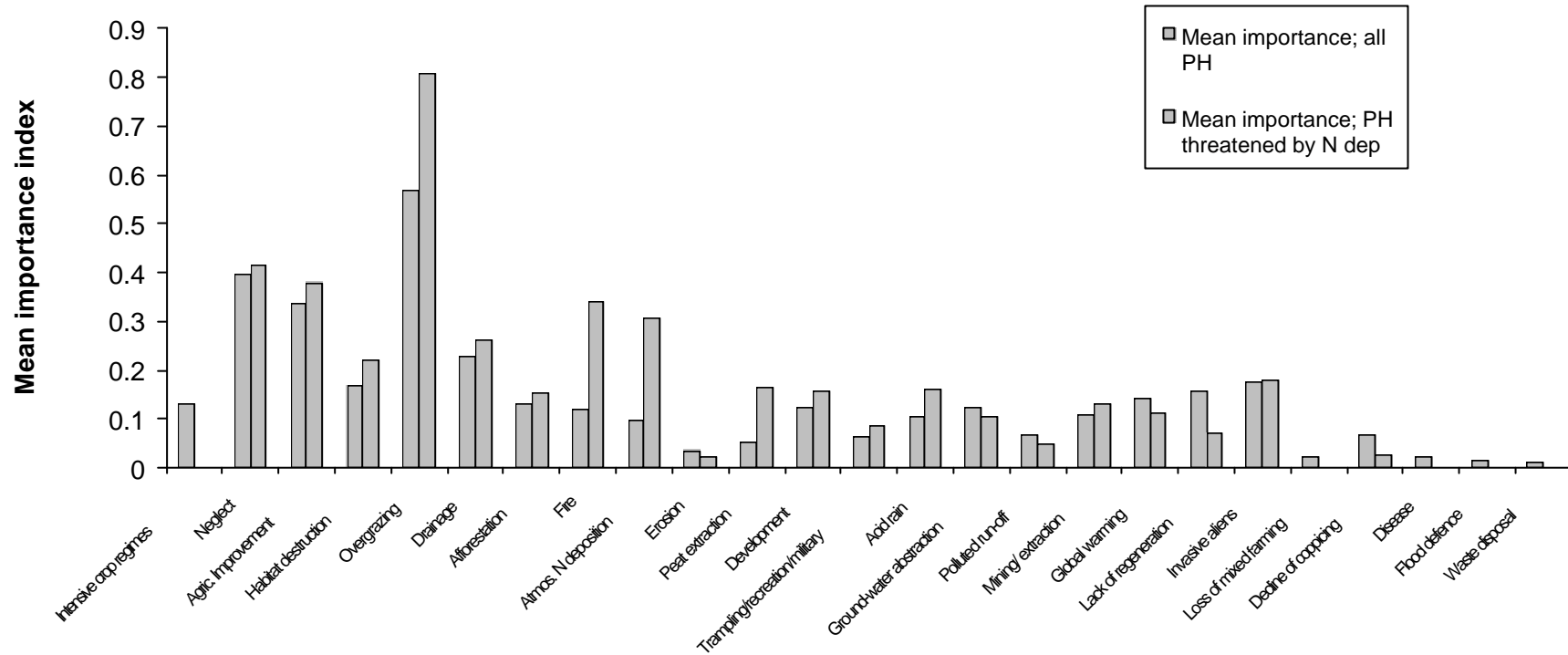


Table 1. Current risk factors for UK Priority Habitats.

Priority Habitats:	Major threats; 1=most important												
	Intensive crop regimes	Neglect	Agric. Improvement	Habitat destruction	Overgrazing	Drainage	Afforestation	Fire	Atmos. N deposition	Erosion	Peat extraction	Development	Trampling/recreation/military
Ancient and/or species-rich hedgerows	1	2	3	4									
Blanket bog			8		1	2	3	4	5	6	7	9	10
Cereal field margins	1												
Fens		2	1				3						
Limestone pavements		2			1								3
Lowland beech and yew woodland					6		4					5	
Lowland calcareous grassland	8	1	4	5	3		8					6	8
Lowland dry acid grassland		1	1	2	6		6					4	
Lowland heathland		1	5	7	1			1	3			2	4
Lowland meadows		2	1	6	2				5				
Lowland raised bog		5	3		7	1	4	7	4		1	4	
Lowland wood-pasture and parkland		1	4	1	1				3				
Machair	4	3	6		3					2			
Native pine woodlands				1									
Purple moor grass and rush pastures		2	1		2	1	4	4				4	
Upland calcareous grassland		5	4		1				3				
Upland hay meadows	2	7	1	5	3	6							
Upland heathland			2	4	1	3	2	1	2			4	4
Upland mixed ashwoods					1		4						
Upland oakwood					1		3					4	
Wet woodland		3			1	1						3	
Coastal sand dunes		1			1		9			8		6	3

Table 2. Published interaction studies where responses due to variation in N deposition and other risk factors were quantified using experiments. Risk factors applying to each Priority Habitat are listed under their ranked importance (1=highest threat from the factor) as set out in the 2002 BAP Progress Report. Only Priority Habitats in which N deposition featured as an identified risk are included. The last column identifies the type of interaction studied. All interactions involve N deposition treatments and either a risk factor listed in the left hand columns (identified by its rank) or with other factors. For example N\*3\*P in the lowland heathland row indicates an experiment in which phosphorus levels (P) were crossed with grazing (ie. threat rank=3) and N deposition treatment. The number of such published studies based on UK sites is shown in brackets.

Threat rank (excluding habitat destruction factors)	1	2	3	4	N deposition rank	Interactions investigated on at least 1 UK site
Blanket bog	<b>overgrazing</b>	drainage	<b>afforestation</b>	<b>fire</b>	5	N*2 (1) N*P (1)
Lowland calcareous grassland	neglect	overgrazing	improvement <sup>#</sup>	<b>global warming</b>	3 <sup>@</sup>	N*3*1*2 (1) N*3 (3) N*3 (1)
Lowland heathland	<b>neglect</b>	<b>invasive aliens</b>	overgrazing	fire	3	N*4*mowing (1) N*climate (3) N*4 (1) N*3*P (1)
Lowland meadows	<b>improvement<sup>#</sup></b>	<b>neglect</b>	<b>drainage</b>	<b>global warming</b>	5	N*grazing*mowing (>10)
Lowland raised bog	<b>drainage</b>	<b>improvement<sup>#</sup></b>	<b>neglect</b>	<b>fire</b>	4	N*mowing (1)
Upland heathland	overgrazing	<b>fire</b>	<b>improvement<sup>#</sup></b>	<b>drainage</b>	2	N*mowing (1) N*1 (2)

# includes factors in addition to N application ie. P addition, reseeding, early cutting.

@ Applies to Upland Calcareous Grassland only but Lowland Calcareous Grassland site identified for Phase 1 modelling.

## **Appendix 8: Literature review of evidence and techniques for disentangling signals due to N deposition and other drivers of ecological change.**

### **OBJECTIVE**

This brief review seeks to identify and summarise the application of the most popular currently used methods for attributing spatial or temporal variation in the abundance of species to causal factors. A detailed description of each method is beyond the scope of the review since these are well covered in other sources. Our aim is rather to examine the extent to which key issues such as scale of study and the importance of detecting multiple drivers of ecological change have affected the choice of quantitative techniques. In particular, we aim to highlight the challenges posed by the demand for estimating causes of change using data collected at the large-scale and the extent to which these challenges are being met by currently available quantitative tools.

The review is in three parts. Part 1 reviews the type of techniques available and their preferred use at different scales. Part 2 summarises the results of four recent reviews that involved comparisons of the performance of the most popular methods for modelling spatial and temporal change in plant species abundance in terms of multiple drivers. Part 3 consists of a spreadsheet outlining the objectives and quantitative techniques employed in recently published studies involving the impact of N addition.

### **Approaches to partitioning spatial and temporal change**

Explaining the distribution and abundance of organisms is the basic project that occupies the science of ecology, hence quantitative methods have developed over its lifetime. The most influential and popular techniques can be classified as analyses of variance. These are inseparable from the idea of hypothesis testing by designed experiments where the quantification of independent and interacting effects of planned treatments are compared against controls (Underwood 1997). However recognition that human activity is having chronic, negative effects on ecosystems has led to the accumulation of long-term and large-scale datasets recording ecosystem response to stressors that, by definition, were not applied as part of an experimental design (Stow et al. 1998). Estimating the causes of change in these datasets requires quantitative methods that firstly identify signals of change (signal detection) and secondly, attribute parts of these signals to different potential drivers (signal attribution). The distinction between these two tasks is important (Figure 1). For example, climate change studies clearly separate the problem of detecting long-term global warming from the attribution of some proportion of this trend to factors other than natural cycles (IPCC, 2000). Large-scale eutrophication effects are another example of the challenge of signal attribution: Across British terrestrial ecosystems a eutrophication signal has been clearly detected in the sense that nutrient-demanding species have been favoured while stress-tolerators have declined since at least the 1950s (Thompson 1994; Preston et al 2002; Smart et al, 2003). Yet, the challenge of attributing this signal to different nutrient sources is a different question and requires joint analyses of biological response data with spatially and temporally coincident records of driving

variables such as grazing, agricultural conversion, climate and N deposition (Smart et al 2003; cf. Stevens et al 2004). These kinds of analyses incorporate response data from sampling domains where treatments, ie. environmental drivers, have not been applied following an experimental design. This is the crucial point of departure from the classical application of ANOVA to planned experiments. Although it is still important to approach the problem with the rigour of hypothesis generation and the precision of ANOVA-like techniques, the community level nature of the response data and the lack of experimental design pose particular problems of interpretation and analysis.

### **The problem of uncontrolled sampling domains**

Large-scale sampling domains, such as national territories, are naturally heterogenous and this variation inevitably and predictably influences the responsiveness of ecosystems to drivers such as pollutant deposition or agricultural management. Thus change is likely to be a function of both the inherent stability of a perturbed ecosystem and the source of the perturbation. The question is what proportion of observed change across an ecosystem mosaic is uniquely attributable to which of several factors? This requires apportioning percentage variance between sets of variables and is usually carried out by treating one set as covariables and then examining the variation explained by the remainder (Cushman and McGarrigal 2002). Covariables refers to factors whose variation is removed in order to focus in on the unique explanatory power of another variable before analysing the species versus environment relationships. The process involves centring the response data by working out the mean response within each different level of the covariable eg. soil type or crop cover, and then taking this mean away from each of the individual data points within that level. Hence, the response data are converted into residuals after having fitted the covariable. These residuals no longer express the influence of the covariable and can be related to other explanatory variables to determine their unique explanatory power (Pysek and Leps 1991).

This step is central to the idea of signal attribution since the approach partitions observed variation into independent components that reflect only the factor of interest. This technique will only work however, if the environmental variables (covariables and other driving variables) are sufficiently uncorrelated across the sampling domain. This does not guarantee that biological responses will be uncorrelated but does guarantee that such an outcome can be discovered. In experimental situations this is achieved by a carefully planned experimental design in which gradients of one factor are crossed with or nested within levels of another factor (Underwood 1997). In the more critical situation where signal attribution is attempted across undesigned, large-scale sampling domains, it maybe an accident of nature whether gradients of potential drivers are sufficiently crossed and replicated to enable such variation partitioning to take place. A good example is the natural lack of crossing between early grass cutting and high fertiliser application rates. In real agricultural systems, the two practices invariably go together so that a planned experiment offers the only way of estimating the unique importance of each effect. The influence of this critical aspect on the power of large-scale signal attribution studies has not been well addressed in the literature but is a particular feature of terrestrial systems impacted by multiple drivers.

Ways of expressing the natural extent of crossing and intercorrelation between uncontrolled factors in large-scale studies are sorely needed to help avoid conclusions

that a particular driver has had little effect, when in fact lack of a signal was related to undersampling of different levels of the driver. An outstanding and unique example of successful variation partitioning of temporal change at the large scale has been the analysis of the joint effects of acidification and eutrophication across Scandinavian woodlands (Diekmann and Falkengren-Grerup, 2002). Notable large-scale studies that have partitioned spatial variation rather than change in time include Yeo and Blackstock (2003) and Duckworth et al (2000).

Additional sources of uncertainty will predictably reduce the goodness-of-fit between prediction and observation. An important issue is that ecological responses recovered from large-scale surveys are often faced with weak but realistically-scaled signals of environmental drivers. However, the response data may reflect cumulative effects of long-term change that are themselves not well quantified by available explanatory variables. For example, high residual error when fitting national-scale vegetation change in Countryside Survey plots to modelled N deposition, is almost certainly due to historical land-use effects as well as the cumulative effect of pollutant deposition through the 20<sup>th</sup> century. In the former case, no explanatory data exists at the plot level. In the latter case, N deposition is estimated at the 5x5 km square scale. These estimates may be poor surrogates for cumulative deposition affecting each plot while their scale also means that the limit of possible signal attribution is set at the 1km square, hence between-plot variation within each 1km square could not be explained (Smart et al in press). In the absence of explanatory data scaled exactly to the level of the measured response, residual error will inevitably be high. This affects the interpretation of such studies in two ways: firstly, low  $r^2$  values should be expected and second, results are unlikely to be useful as predictive models. Both aspects are conveyed by applying 95% prediction intervals to regression lines. These show the uncertainty in the model when asked to predict new individual cases. Unlike 95% confidence intervals that delimiting where the line of best fit should pass, prediction intervals tend to be wider because they directly incorporate the error in the observed dataset.

### **The problem of scale**

In Britain, a range of research initiatives can be identified that have been used to explain different aspects of ecosystem change in terms of multiple drivers (Figure 2). These studies can be arranged along an axis relating to their scale of data collection. Their scale of observation limits their expected accuracy in predicting species versus environment relations in any specific place throughout Britain. Hence, detailed experiments on a single site may give an accurate quantification of ecosystem dynamics at this site but predictions may be inaccurate at other sites with different climate, management and soil type. Large-scale studies such as BSBI/BRC recording and Countryside Survey also display their own trade-offs. BSBI/BRC plant species data on presence in every 10km square in GB have amply demonstrated ecologically significant changes in species distribution during the last half of the 20<sup>th</sup> century, however in seeking to model species presence in 10km squares, factors will be ignored that affect abundance within the square. For example, a 10km square could have a richness of 100 species but these could be distributed in very different ways; 10 species in 10 different habitats or 100 species everywhere. The factors correlated with the same overall richness could differ markedly between the two situations. Examining finer-scale phenomena such as abundance in 1km squares or cover in small plots also has a cost because it is impossible to record all species in all smaller

sampling units across the same large sampling domain. Hence, sampling of a random subset of areas can be carried out but rare species and plant communities will inevitably be missed, thus limiting the applicability of such data to the most vulnerable species in Britain. This is the trade-off exemplified by the BRC Atlas recording scheme versus the CS recording program. Both schemes also do little to simultaneously record evidence of potential drivers of change.

Costs and benefits attach to all the studies shown. Each was set up and optimised for specific objectives focussed on measuring change in particular attributes in particular ecosystems. The objectives of each scheme also inevitably reflect what was achievable with available resources. Hence the diagonal line in Figure 2, represents a line of cost-constraint in the sense that there is never sufficient resources available at one time to fund studies that achieve high accuracy, by recording many attributes frequently, but also high generality because detailed recording goes on over a large geographical area. Movement away from this idealised cost-constraint line could therefore be achieved by either increasing resources or by increasing the sophistication of data recording and modelling on intensive monitoring sites such as the ECN network.

Despite their various shortcomings the value of existing studies in helping explain rather than just describe, real large-scale ecosystem change is likely to increase the longer they operate and the more datasets are combined in cross-scale research (Parr et al 2002). The possibility of cross-scale analyses where the results of experiments or modelling at small scales are used to test hypotheses at larger scales is implicitly acknowledged by the many studies that take as their starting point results of hypothesis tests first conducted at smaller scales. But, perhaps as a result of the tendency for modelling, experiments and large-scale observation to be seen as competing enterprises, there has been a lack of development of mathematical tools to aid quantitative cross-scale research and in particular, the challenge of signal attribution at large-scales where, by definition, potential drivers have not been crossed, replicated and randomised. Recent work has started to address these challenges in several key areas. For example the influence of differences in scale on the outcomes and inferential power of experiments was examined by Englund and Cooper (2003) who provided a wide range of examples where patterns studied at large scales were inconsistent with expectations based on experiments at small scales. They also set out quantitative approaches to estimating scale effects. The problems of variation partitioning and hence signal attribution at the large scale have also seen recent new treatments: Gadbury and Schreuder (2003) provide a statistical framework based on maximum likelihood while Shipley (2000) has popularised the powerful technique of path analysis that explicitly handles intercorrelations between sequences of factors organised into hypothesised chains of causation.

Lastly, small-scale intensive studies will be better able to control surveyor errors. These include taxonomic misidentification and variation in estimating cover/abundance. A good example is the poor recording of bryophyte data in the Countryside Surveys (Haworth, unpublished PhD thesis in prep). Each roughly decadal survey has to meet the challenge of recruiting large numbers of botanists whose competence is at least consistent with previous surveys. The increasing scarcity of good botanists means that bryophyte expertise is particularly rare. As a result bryophytes plus a range of other critical or difficult taxa have been selectively omitted from most analyses of change. The particular sensitivity of bryophytes to pollutant deposition has led to focussed efforts to establish a reliable subset of the more

common species upon which signal attribution analyses could be carried out (Haworth, unpublished PhD thesis, Ashmore 2004).

Figure 1. Redrawn from Stow et al (1998). Constraints to signal attribution studies along a continuum from small scale studies (eg. experiments at single sites) to large-scale studies (eg. analysis of surveillance or monitoring data across large, uncontrolled regions).

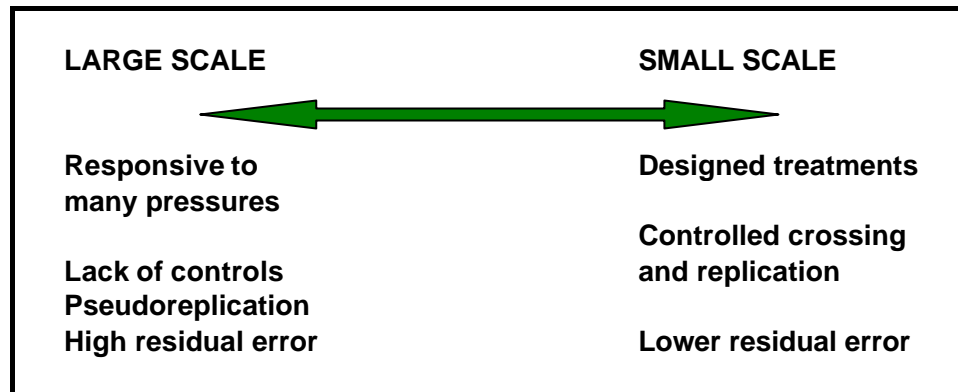
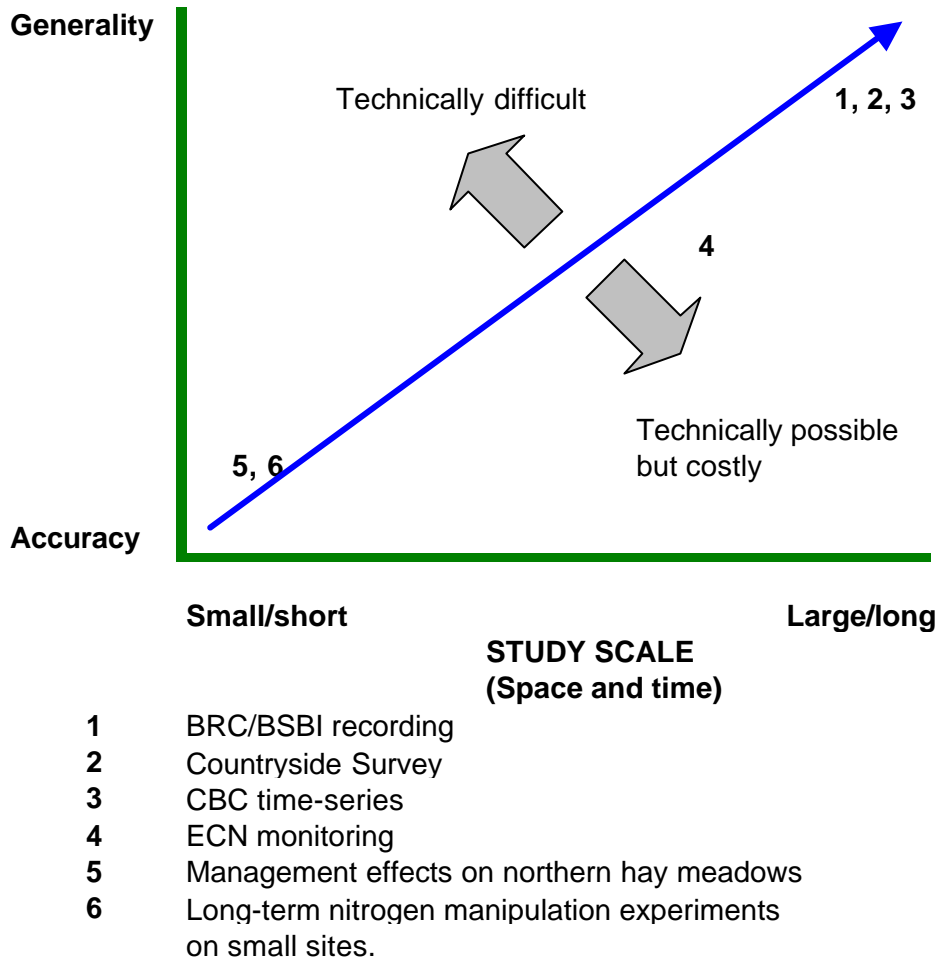


Figure 2. The positions of some British initiatives that contribute to signal attribution at different scales in relation to a cost-constrained trade-off between study scale and the local accuracy versus geographical generality of the results. See text for explanation. 1 Preston et al (2002), 2 Firbank et al (2003), 3 Crick et al. (1997), 4 [www.ecn.ac.uk](http://www.ecn.ac.uk), 5 Smith et al (1996), 6 Cunha et al (2002).



## Summaries of conclusions from recent reviews of species modelling approaches

### Miller and Franklin (2002)

Three complimentary techniques were used to predict the presence of 4 vegetation alliances. These were General Linear Models, classification trees and General Additive Models (GAM). Environmental explanatory variables used to model the distribution of the alliances included temperature, precipitation, elevation, derived terrain variables including slope and aspect, topographic moisture index, solar radiation and landscape position- and categorical landform/surface composition variables. Vegetation models exhibited spatial dependence (ie. the nearer things are the more similar they tend to be) so the geostatistical interpolation technique known as kriging was employed to derive neighbourhood values of presence also used as predictors in the model.

Decision tree models express complex relationships among predictor variables. Decision trees are particularly effective at recovering non-linear, non-additive and hierarchical relationships between species and environment. Rather than estimating a mean value for a range of environmental variables associated with the vegetation types, decision trees identify specific thresholds of environmental conditions above or below which species or vegetation type can be found. Decision tree models can be used with continuous response variables such as species abundance or with categorical response variables such as species type.

General Linear Models include the whole family of ANOVA-like methods where variation in a response is modelled as a systematic component related to the error-free, hypothesised effect of an explanatory variable plus a random component related to the error or unexplained variation in the measured response. This family of models have the advantage that parameters (means and variances) are estimated, thus generating equations that can be readily tested on new cases. However, the resulting model may not actually be the best description of the response data. The random component can usually be specified as a so-called link function between the response and predictor variables. Specifically, the link function takes a form appropriate to the type of response being modelled, for example a logit link for presence/absence data consistent with a binomial error distribution, or a log link for count data (eg. species richness) consistent with a Poisson error distribution.

Alternatives to models based on a prior choice of statistical distribution are GAMs. Here the relationship between the response and predictor variables is driven by the data itself via a number of smoothing functions that reflect the density of the response at a sequence of points along the gradient of the explanatory variable. These models often generate a better fit to the data but may therefore be less applicable to new datasets. In fact, since these models do not result in statistical parameter estimates in the same way that a parametric regression model yields an intercept and a number of regression coefficients, they cannot be transparently applied to predict new observations. Their major benefit is as data exploration tools that are a better summary of the response shapes in the data and can therefore aid the selection of parametric model forms.

### Pysek and Leps (1991)

This review highlighted the difference between the problem of modelling a single response variable, such as species richness, biomass or a mean Ellenberg score versus the problem of modelling the response of an entire species assemblage. The statistical analysis of the effect of a fertiliser on a single variable, say crop yield, is routinely done by ANOVA. However, the evaluation of the effect at the community level is a more difficult task because the response consists of matrices of species abundance by sample plots. Hence, the response is an aggregation of all the individual, inter-correlated responses of each species. The problem is typically addressed by multivariate analysis techniques such as Canonical Correspondence Analysis (CCA). CCA enables an evaluation of the influence of the environment on the composition of the community using a distribution free Monte-carlo test of significance. This approach basically assesses the ability of independent variables to explain the observed data by comparing the observed relationships with those generated by many random allocations of responses to the environment. In this study environmental variables consisted of fertiliser dose, cover of the crop and type of fertiliser (nominal variable for N, P or K). To separate the influence of cover from the direct influence of fertilisers CCA was computed as follows:

1. With dose of fertiliser and composition of fertiliser as environmental variables and cover as a covariable.
2. Cover as environmental variable and dose and composition of fertiliser as covariables.

CCA is a subtle combination of linear regression and weighted reciprocal averaging. In essence, the major species compositional gradients in a species by sample matrix are determined by weighted averaging but at each successive iteration the weighted averages are substituted with the predicted values that arise from a multiple regression of the weighted averages on available explanatory variables.

### Guisan (2002)

GLM's are mathematical extensions of linear models that do not force data into unnatural scales and allow for non-linearity and non-constant variance structures. They are based on an assumed relationship between the mean of the response variable and the linear combination of the explanatory variables. Data may be assumed to be from a family of probability distributions including the normal, binomial, poisson, negative binomial or gamma distribution. GAM's are semi parametric extensions of GLM's the only underlying assumption is that the functions are additive and the components are smooth. The strength of GAMs is their ability to deal with highly non-linear and non-monotonic relationships between the response and the set of explanatory variables. GAMs are data rather than model driven and are better thought of as explanatory models that provide insights into ecological processes and patterns rather than predictive models based on a statistical relationship between response and a series of predictor variables. GAMs are a useful addition to the family of regression techniques used to model the spatial distribution of species or communities in terms of environmental variables.

Implicit in the application of regression tools is pseudo-equilibrium between the organisms and their environment. The more sampled patterns are influenced by

disequilibrium the less reliable will be their application to new cases. For example, if species are undergoing rapid range expansion then static, spatial models may not predict more recent spatial patterns. This highlights the fact that spatial patterns may not validly translate into temporal predictions.

### **Linear regression**

Assumptions;

1. errors assumed to be identically and independently distributed
2. errors assumed to follow a normal Gaussian distribution
3. regression function linear in the predictors

A common way of dealing with assumptions 1 and 2 is to transform the response variable, several approaches for transforming data are available.

### Austin (2002)

Improvements in statistical modelling can be achieved based on ecological concepts. Examples include incorporating interspecific competition from dominant species, more proximal predictors based on water balance models and spatial autocorrelation procedures to accommodate non-equilibrium vegetation.

Predicting species distribution has been achieved using regression analysis techniques including GLM (essentially ANOVA but this describes the general family of approaches to linear modelling including mixed-models and logistic regression). In addition non-parametric Generalized Additive Models can be used together parametric statistical models.

Statistical models are based on correlation and have as their purpose prediction. It is not possible to determine causation from correlation but a description of functional relationships can be achieved. The reality should be pursued by experiment, theoretical analysis or repeating the study at a different location, Three components in a framework for statistical modelling comprise an ecological model based on ecological knowledge and theory, a data model that includes decisions made regarding how the data are collected and a statistical model, which prescribes a model of the distribution of the error in the data and hence explicitly predicts the form that uncertainty will take. The more that ecological knowledge can be incorporated the more robust the prediction. Where it is accepted that it is important to maximise knowledge of the functional relationships between plants and environment current ecological concepts need to be considered, e.g. consensus is emerging that the continuum concept is a more appropriate model of vegetation organisation than the community or association that predicates communities as discontinuous blocks of vegetation that are correlated with similarly discontinuous underlying abiotic gradients. Another fundamental assumption is that species distribution and abundance models provide a description of the realised niche not the fundamental niche. Hence, species distributions reflect the tolerance of species to competition, the intensity of which varies along abiotic gradients in ways specific to each species.

Assumptions about the shape of the response of a species to an environmental variable are central to any predictive modelling effort. Niche theory assumes that

1. Both the fundamental and realised niches of a species are bell shaped curves
2. Competition restricts niche breadth
3. Maximum abundance occurs at the optimum for niche breadth
4. Species maxima are equally spaced along the gradient
5. Species maxima are of equal amplitude
6. Collective properties of species show no patterns of response along the gradient

### **Straight line relationships**

CCA assumes that species responses are unimodal to the underlying environmental gradients as specified by the ordination axes. Current practice is to estimate the underlying gradient as a linear combination of environmental variables ie. a regression equation of additive terms; intercept plus regression coefficients 1 to  $n$ . A review of papers using CCA gave 11 that did not mention the linear basis of the correlation, 20 out of 22 do not consider the possibility of curvilinear relationships or that distal indirect variables may have very different relationships with the ordination gradient than direct or resource. Leps et al (2000) explicitly use interactions between their variables in constrained regression but they use PCA rather than CCA because the axes were short hence a linear rather than unimodal relationship was assumed

### **Assumptions of CCA**

1. Species tolerances (niche breadths) are equal
2. Species maxima are equal
3. Species optima are homogeneously distributed along a gradient that is long compared with niche breadth

The influence of changes in species richness along gradients is not addressed in CCA. Guisan et al decided that the spatial distribution of individual species is better modelled by GLM than CCA. CCA may have advantages for rare species with few positive observations but is not well adapted to deal with unimodal species response. The relative neglect of interaction terms in recent vegetation modelling is also a current limitation to progressing beyond a one dimensional theory of vegetation composition. GAM may produce a complex function where an equivalent parametric would do whilst CART must produce discontinuities when a continuous function may be more realistic. Best practice may be to analyse data with CART and GAM using the results to construct a GLM. It will need to incorporate spatial autocorrelation. The role of ecotypic variation within a species influencing species response curves remains to be examined.

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## Appendix 9: Case studies – Model application to future scenarios of change on test sites based on Common Standards Monitoring guidelines

### Methods

In this section, predictions of change in habitat suitability for CSM indicator species are given for a series of management and deposition scenarios on each test site. Most scenarios assume constant management and apply a FRAME/GANE projection of future N and S deposition to 2050. Additional examples are given where management or climate (annual average temperature) is varied to examine expected impacts on biomass of functional types, using SMART/SUMO, and habitat suitability for CSM indicators, using MAGIC/GBMOVE.

Changes in habitat suitability were graphed as indicator species groups defined by CSM guidance for each Priority Habitat. Suitability values were defined as the probability from GBMOVE divided by the maximum probability solved at the optimum environmental conditions for each plant species modelled where an optimum could be calculated (see Box 6 and Appendix 5).

CSM indicator species NOT present in each monitored patch are tabulated along with information that helps highlight their potential for dispersing into a target patch given suitable habitat conditions as predicted by MAGIC+GBMOVE. Tabulated data comprise indices of abundance in the site pool and two site buffer zones. For species with trait-based dispersal indices, this index is combined with the index of species pool abundance to give an overall ranking of species pool members in terms of their local abundance and ease of dispersal assuming that appropriate vectors are in place. Issues concerning the reliability of the indices and a description of their construction are given in Box 7.

The number of CSM indicator species for the Priority Habitats tested that have GBMOVE models are enumerated in Appendix 6.

Table 13. List of case study model applications. Note that SMART/SUMO simulations of biomass growth are only applied at Moorhouse and Rothamsted since SUMO was validated using observed biomass data at these sites. On other sites, change in CSM indicators were modelled using MAGIC linked to GBMOVE.

Site	Scenario
R1. Rothamsted Park Grass – <b>lowland meadow</b>	FRAME/GANE prediction of N and S to 2050. Continued annual hay crop with no fertilizer addition.
R2. “	As above but hay cropping ceased in 2005.
C1. Climoor – <b>upland heath</b>	FRAME/GANE prediction of N and S to 2050. Management stable.
M1. Moorhouse – <b>blanket bog</b>	FRAME/GANE prediction of N and S between 1973 and 2001. Match of observed versus predicted change in CSM indicator species in the Hard Hills control plots; 0.1 sheep per hectare and no burn since 1954.

M2. “	FRAME/GANE prediction of N and S to 2050. Grazing pressure increased to 5 sheep per hectare in 2005 and no burning.
M3. “	FRAME/GANE prediction of N and S to 2100. Annual temperature increase based on UKCIP high emissions scenario with no grazing.
M4. “	FRAME/GANE prediction of N and S to 2100. Annual temperature increase based on UKCIP high emissions scenario with 0.1 sheep per hectare.
M5. “	FRAME/GANE prediction of N and S to 2100. Annual temperature increase based on UKCIP high emissions scenario with 0.1 sheep per hectare and 20 year rotational burn.
P1. Porton Down – <b>lowland calcareous grassland</b>	FRAME/GANE prediction of N and S to 2050. Site management unchanged.
Ca 1. Cairngorm – <b>upland heath</b>	FRAME/GANE prediction of N and S to 2050. Zero deer and sheep grazing pressure.
B1. Budworth Common – <b>lowland heath</b>	FRAME/GANE prediction of N and S to 2050. Site management unchanged.
NI 1. Dead Island Bog – <b>raised bog</b>	FRAME/GANE prediction of N and S to 2050. Site management unchanged.
NI 2. Dromore Motte – <b>lowland meadow</b>	FRAME/GANE prediction of N and S to 2050. Site management unchanged.

## R1. Rothamsted Park Grass: FRAME/GANE prediction of N and S to 2050. Continued annual hay crop with no fertilizer addition.

### Species richness

Despite high variation about the model line, species richness is not expected to change over the scenario (Fig R1.1).

### CSM indicator species

Species projections suggest that positive indicators will find conditions more favourable as N deposition continues to decline and inputs are increasingly outweighed by continued N offtake (Fig R1.2). Uncertainty here relates to the fact that the amount of N removed will itself decrease as biomass production declines. Effects of N removal are therefore likely to stabilise because less N will be available for removal. This could be modelled using SMART/SUMO.

For some positive indicator species including *Centaurea nigra* and *Lathyrus pratensis*, increasing C/N actually suggests declining suitability in the last decade of the projection, implying a move away from the species optima at intermediate productivity into an increasingly infertile, low yielding system (Fig R1.2).

Most negative indicators including Agricultural weeds and Agriculturally Favoured Species also decline with only *Senecio jacobaea* predicted to find soil conditions more suitable even though presently absent from the Park Grass control plots.

Fig R1.1 Predicted species richness change. 95% prediction intervals are also shown.

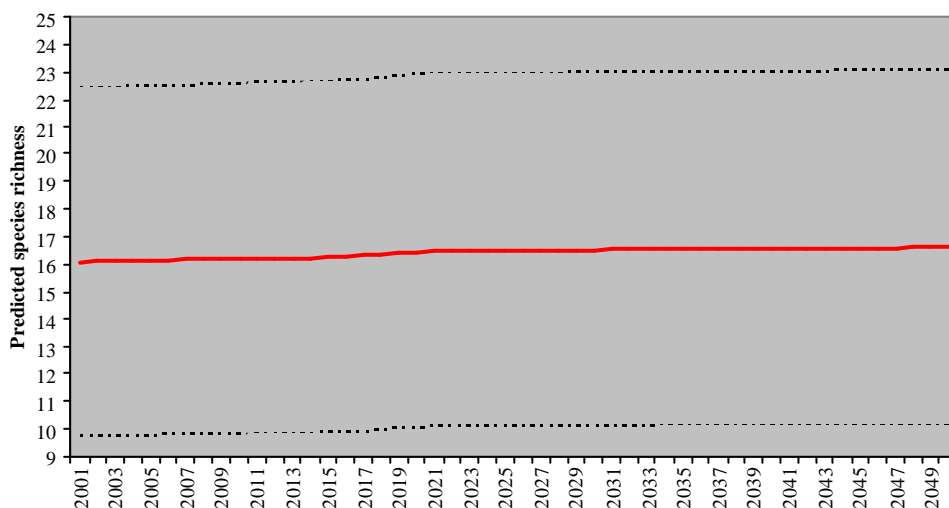
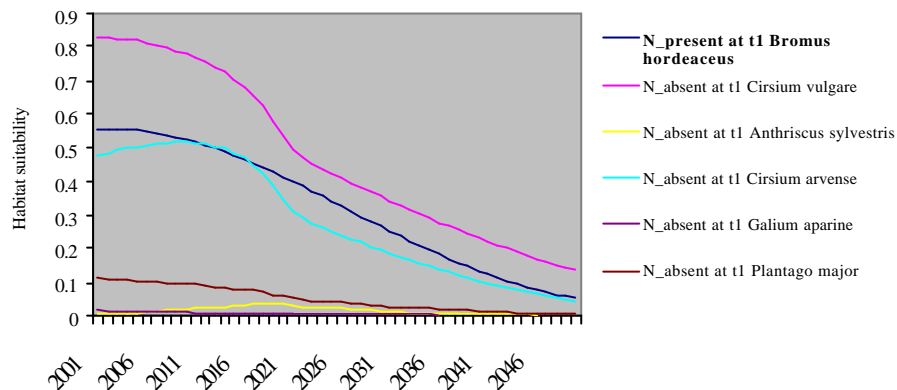
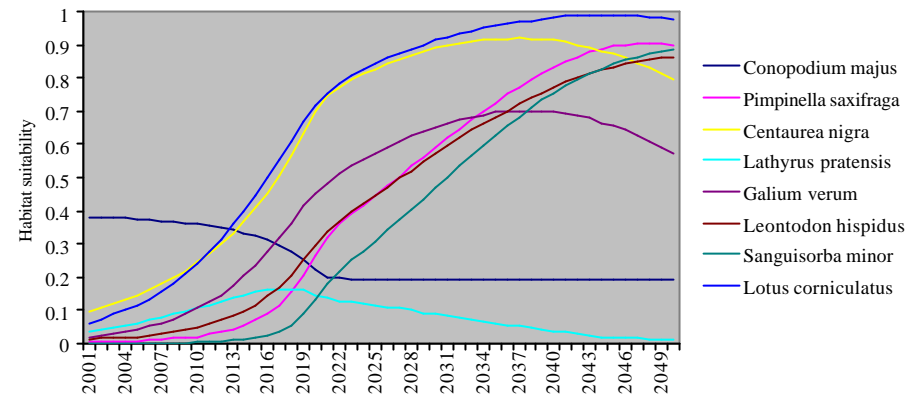


Fig R1.2. CSM indicator prediction for Rothamsted Park Grass control plots (MG5). Assuming FRAME/GANE N and S deposition with continued hay offtake and no fertilizer inputs. Modelled by MAGIC+GBMOVE. Species in bold were recorded in Park Grass plots. Non-bold are present in the local species pool.

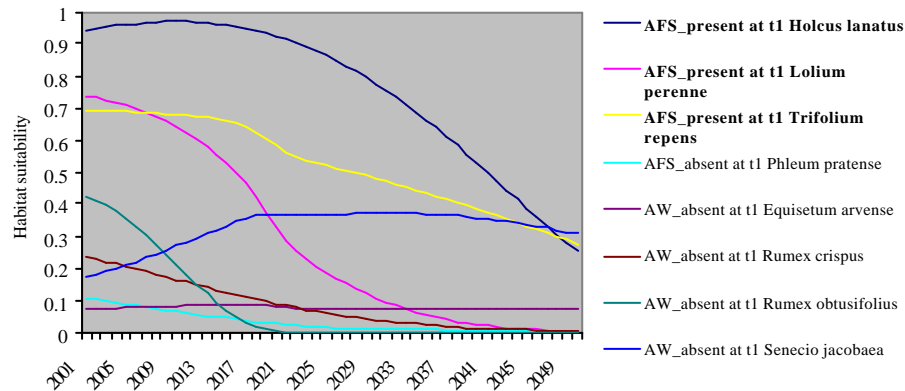
a) Negative indicators



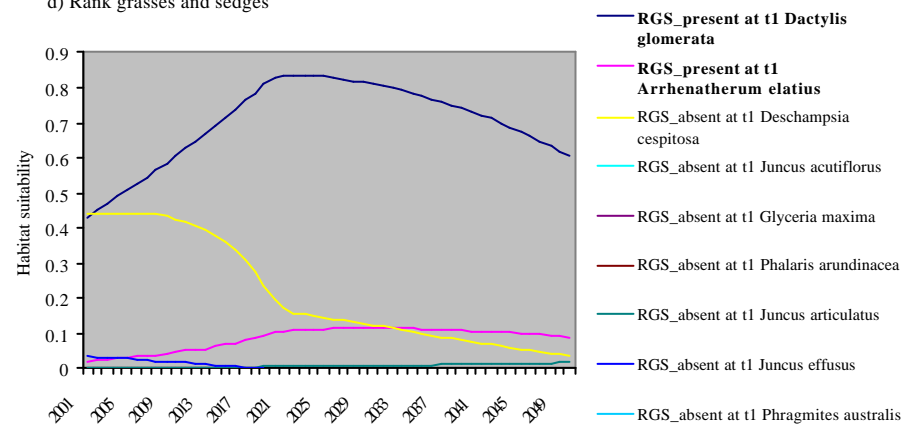
c) Positive indicators - present t1



b) Agriculturally Favoured Species



d) Rank grasses and sedges



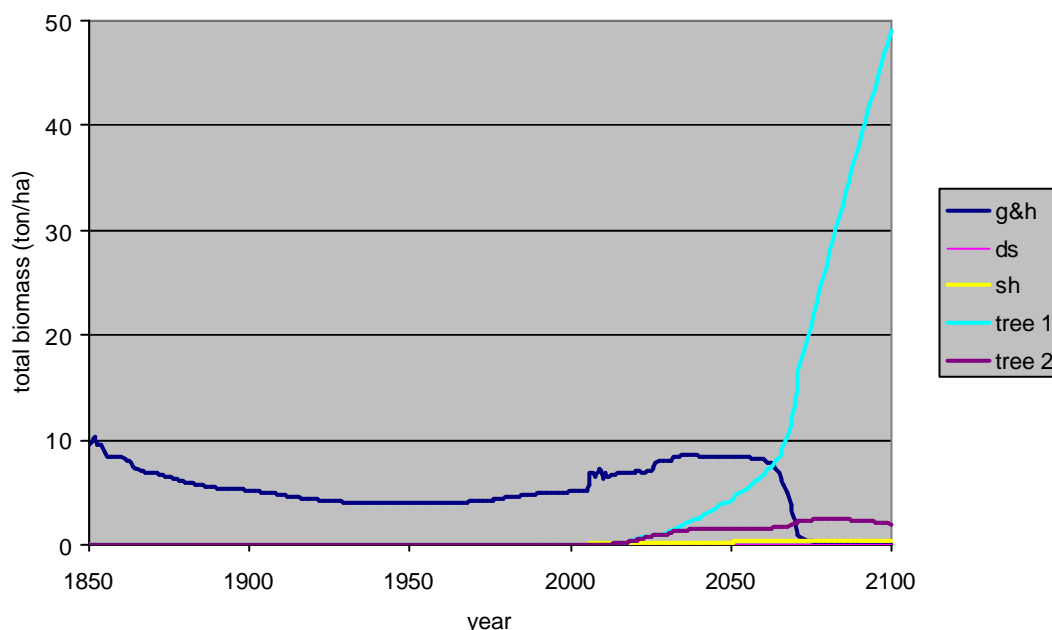
## R2. Rothamsted Park Grass: FRAME/GANE prediction of N and S to 2050. All management stopped in 2005. Grazing at 1 deer and 5 rabbits per hectare.

### Changes in biomass of plant functional types

SMART/SUMO predicted a gradual and then accelerating increase in tree biomass with an abrupt down turn in the herbaceous component as the tree canopy increased markedly from 2070 onwards (Fig R2.1). The rate of predicted succession appears reasonably consistent with that seen on the nearby Broadbalk wilderness where Sycamore, Ash and Oak appeared and then dominated from between 10 to 40 years after management stopped (Harmer et al 2001). In this simulation, succession is based on the regeneration dynamics of Oak and Beech, for which SUMO uses specific growth parameters. At Rothamsted, Ash would have been a better canopy dominant to model. Inclusion of Field Maple and Sycamore would require new parameters tailored to these particular species.

An additional simulation was also carried out with no wild grazers present. Under these conditions succession took much longer because vigorous herbaceous biomass was expected to inhibit tree regeneration. Even after 100 years herbaceous biomass still exceeded the sparse tree canopy.

Fig R2.1 Hay offtake ie. all management, stopped in 2005 plus 1 deer per hectare and 5 rabbits. Tree 1 = Oak, Tree 2 = Beech.



### Changes in plant species composition using GBMOVE and MAGIC

Ideally, future developments should see SMART/SUMO or MAGIC/SUMO integrated with GBMOVE so that predicted changes in habitat suitability for different species proceed at an appropriate rate given local climatic and edaphic constraints on the pace of succession. However, it is still possible to do a test of the ability of

GBMOVE+MAGIC to assemble a woodland community on the Rothamsted Park Grass that resembles as far as possible, the kind of broadleaved woodland known to develop on similar soils in the area. For example, Harmer et al (2001) showed that abandonment of arable land on soil types similar to the Park Grass plot led to the establishment of broadleaved woodland within 25-30 years. On the Broadbalk wilderness this led to a community closest to W8d, the *Hedera helix* sub-community of the *Fraxinus excelsior-Acer campestre-Mercurialis perennis* woodland. On the nearby Geesecroft wilderness a more acidic community developed reflecting the lack of bicarbonate buffering capacity in the soil. The Geesecroft site was also successfully modelled using SAFE by Sverdrup et al (1995) who attributed the long-term drop in pH (from 7.1 in 1881 to 4.5 in 1965) to a century of changing N and S deposition. In the Broadbalk wilderness greater buffering reflected liming in the early 1800s hence pH remained stable.

Using the pace of successional change observed in the Broadbalk wilderness, we simulated change in canopy height in the Rothamsted Park Grass control plots using a positive exponential model to yield in 2050 a mean cover-weighted canopy height typical of mature Oak and Ash dominated woodland in lowland Britain (mean value extracted from the 'Bunce' NCC/CEH woodland survey database – see Smart et al 2001). Soil C/N and pH change were driven by MAGIC assuming no N offtake and hence no hay removal from 2005 onwards. The goal was therefore to arrive at a species composition most closely resembling that of the Broadbalk woodland by empirically changing canopy height given the known rate of succession and by modelling change in soil conditions, albeit without considering litterfall and changes in N uptake rate with change in dominance of functional types as in SUMO. Species selection was also constrained to draw only on the local 10km square species pool based on BRC data.

Trajectories of predicted change are shown in Fig R2.2. NVC matching of the predicted frequency table in 2050, gave an impressive top similarity coefficient of 62.3% with W8d indicating a very good match between the observed, present-day Broadbalk community and the predicted outcome of 50 years succession on the Park Grass control. Although MAGIC+GBMOVE produced a good predicted match to current woodland on the site, MAGIC does not simulate the effects of biomass accumulation and death on nutrient cycling constrained by the differential growth rate of the functional types, the nutrient content of their tissues and the impact of local climate. A capability for doing this is again important if scenarios of climate change and their interaction with management and changing pollutant deposition are to be tested. This is the domain of SUMO. In this simulation the successional trajectory was mimicked empirically by simply incrementing canopy height so that a height typical of lowland neutral broadleaved woodland was reached in 2050. Thus the case-study is really a test of the GBMOVE regression models in accurately capturing the niche dimensions of sufficient plant species to build the target community based only on soil C/N and pH from the MAGIC simulation plus empirical change in canopy height. SUMO can predict canopy height so that linkage is possible with GBMOVE.

Species richness was expected to decline as succession proceeded to 2050 (Fig R2.3).

Figure R2.3. Predicted change in species richness as Park Grass controls tumble down to scrub and woodland. 95% prediction intervals are also shown.

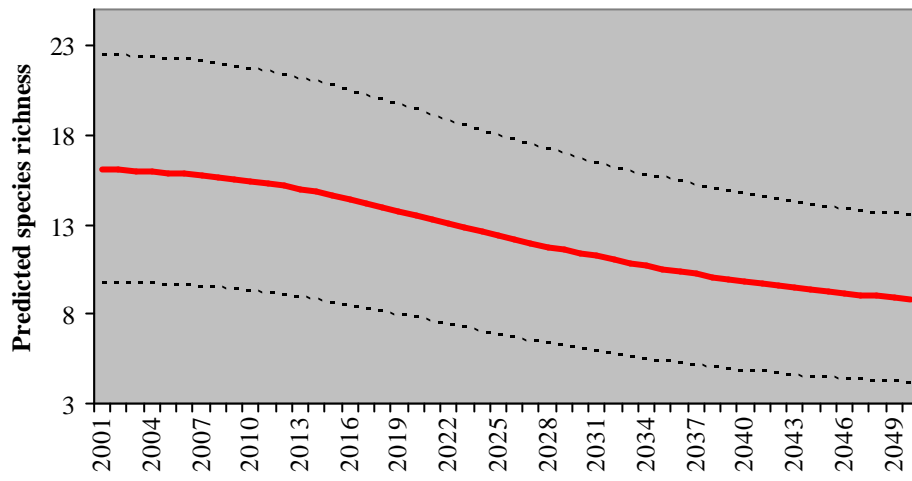
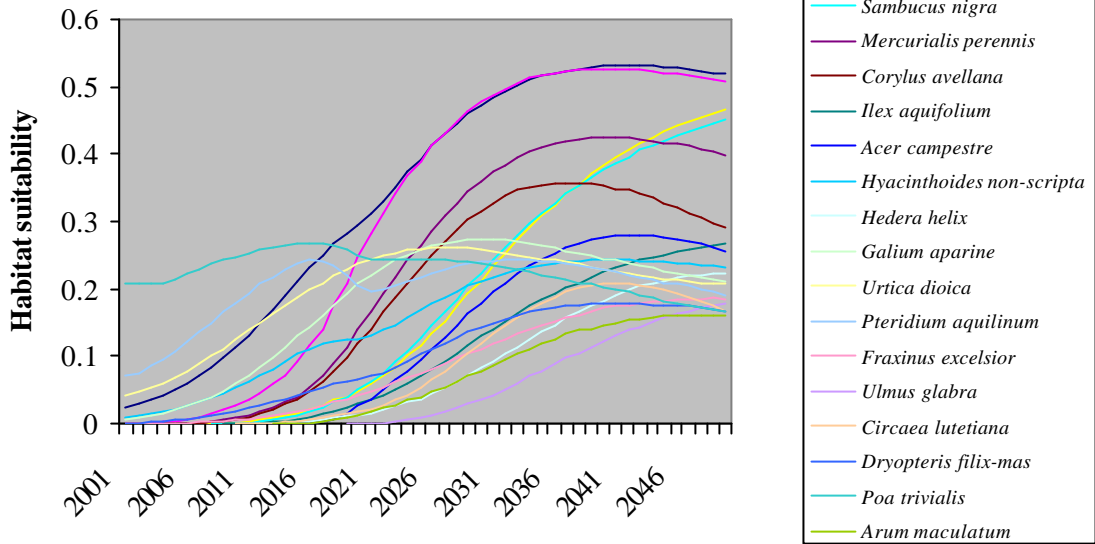
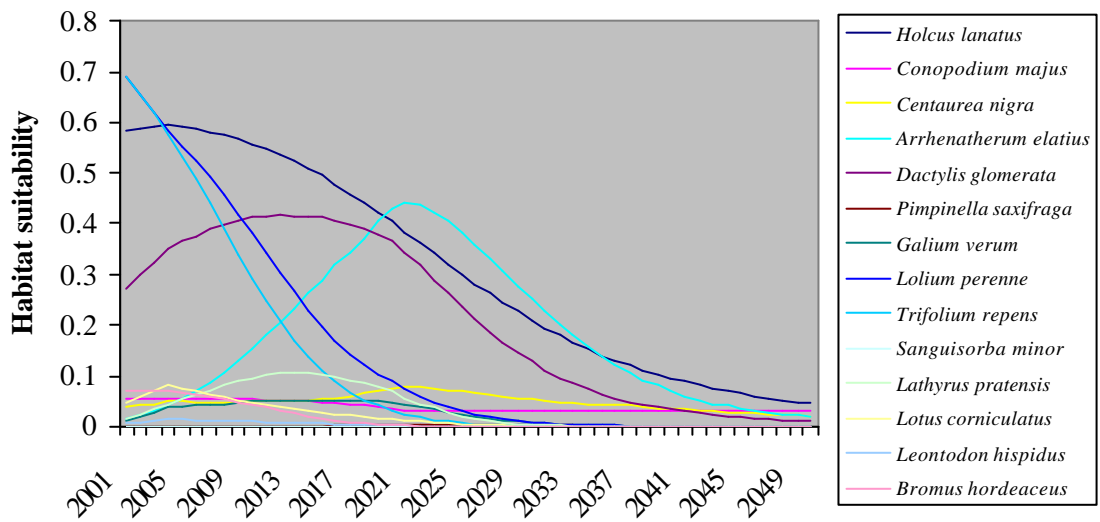


Fig R2.2. Trajectories of change in plant species predicted to dominate in the last decades of the time period (a) and species present in the Park Grass control plots at time 1 (b).

**a) Predicted increasers**



**b) Species present - t1**



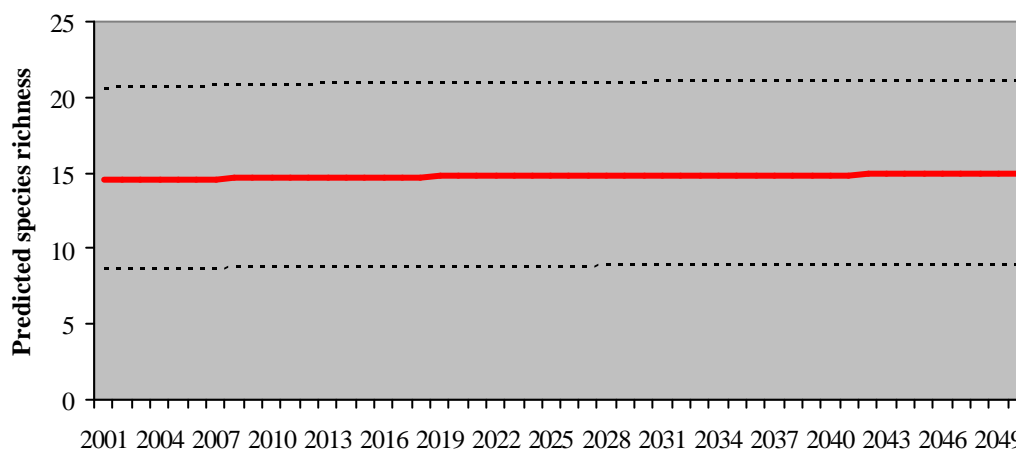
## C1. Climoor -Upland heath: FRAME/GANE prediction of N and S to 2050. Management stable.

### Predicted change in CSM indicator species

Overall current and future change is expected to be very slight in response to expected change in N and S deposition. Positive indicators that were present at time 1 were well predicted with largely high habitat suitability values (Fig C1.1). Hence, *Calluna* is expected to remain dominant over the interval while other positive indicators remain stable as do members of the Trees & Shrubs group.

Negative indicators are expected to increase very slightly over time but their habitat suitability predictions remain very low so that they would be highly atypical and would presumably find establishment and persistence difficult. It is particularly significant that *Agrostis stolonifera* was predicted to have the highest habitat suitability since this species actually increased the most among mesophytes in heath/bog vegetation sampled by Countryside Survey between 1978 and 1998 (Smart et al 2005). Species richness was also not expected to change in response to predicted pollutant deposition and its effect on soil C/N and pH (Fig C1.2).

Fig C1.2. Species richness prediction.



### CSM indicators in the wider species pool

All indicator species in the 10km<sup>2</sup> were estimated to be present in the site pool (Table C1.1). Species estimated to be most abundant in the site pool but with no dispersal information were mainly positive indicators such as *Erica cinerea* and *Carex binervis* or Trees & Shrubs such as *Picea sitchensis* and *Betula* spp. The only negative indicator estimated to be at low abundance in the site pool was *Pteridium aquilinum*.

Of those species with dispersal estimates, the positive indicator *Erica tetralix* and the negative indicator *Agrostis capillaris*, ranked highest in the pool list (Table C1.1). Most negative indicators were estimated to be scarce in the local site pool.

Fig C1.2. CSM indicator predictions for **Climoor** upland heath. Species present in quadrats at time 1 are shown in bold in the legend.

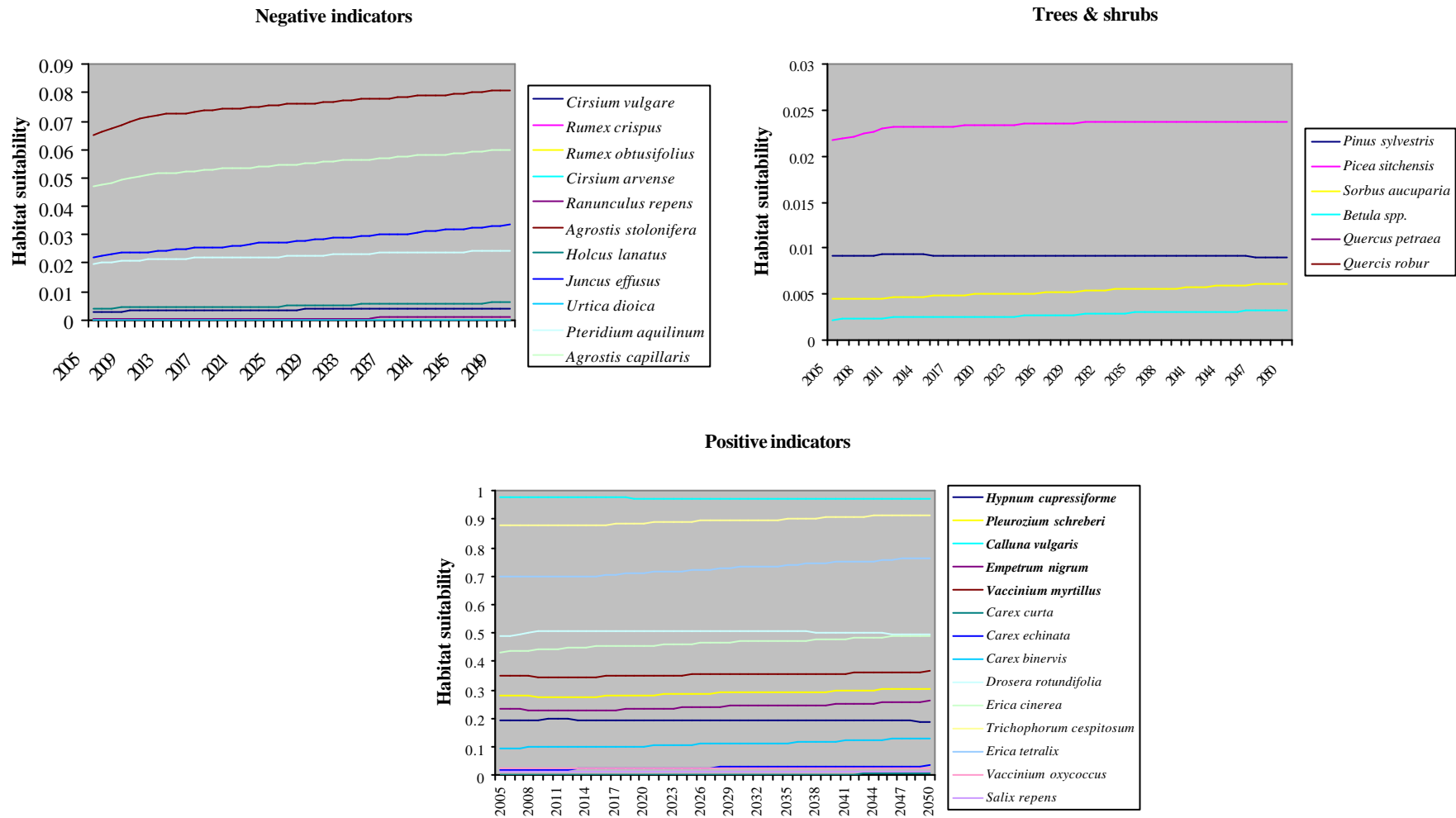


Table C1.1. Empirical immigration ranking for CSM indicators not present in the monitored patch but present in the local species pool at **Climoor**. See text above and Box 7 for explanation. CSM categories = Positive (P), Negative (N), Trees & Shrubs (TS). Site, b1 and b2 are indices estimating species abundance in the site pool or buffer zones. S\*DISP etc give the abundance index multiplied by the dispersal index where this was estimated. Null indicates that no dispersal index was attributed.

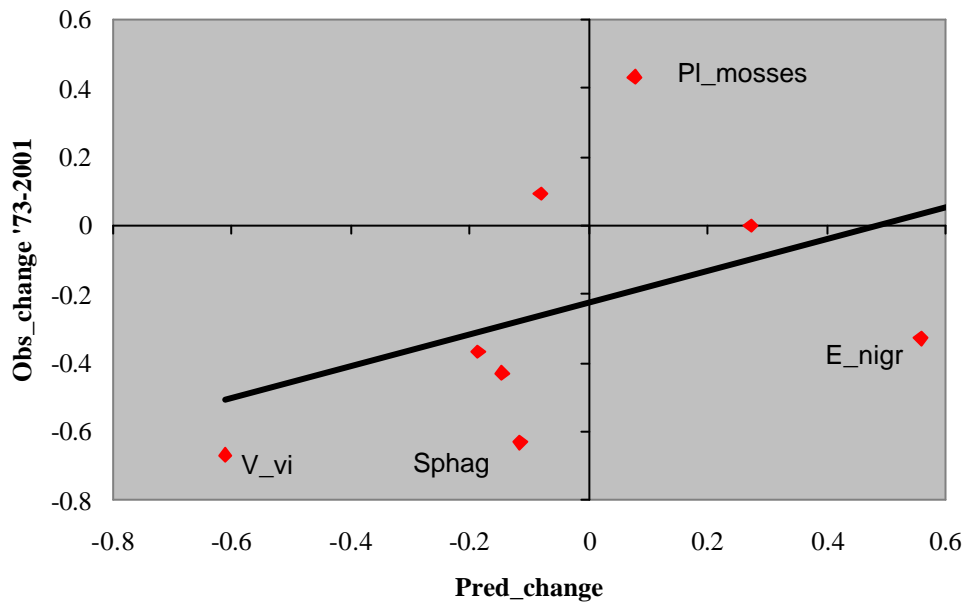
<b>BRC_names</b>	<b>CSM category</b>	<b>site</b>	<b>b1</b>	<b>b2</b>	<b>S*DISP</b>
<i>Erica cinerea</i>	P	0.94	0.54	0.39	null
<i>Carex binervis</i>	P	0.73	0.53	0.47	null
<i>Trichophorum cespitosum</i>	P	0.72	0.16	0.21	null
<i>Picea sitchensis</i>	TS	0.70	0.70	0.70	null
<i>Betula spp.</i>	TS	0.70	0.70	0.70	null
<i>Drosera rotundifolia</i>	P	0.47	0.09	0.07	null
<i>Salix repens</i>	P	0.47	0.09	0.07	null
<i>Carex echinata</i>	P	0.25	0.25	0.24	null
<i>Pteridium aquilinum</i>	N	0.24	0.24	0.20	null
<i>Vaccinium oxycoccus</i>	P	0.24	0.23	0.19	null
<i>Carex curta</i>	P	0.01	0.02	0.05	null
<i>Pinus sylvestris</i>	TS	0.00	0.70	0.40	null
<i>Quercus petraea</i>	TS	0.00	0.00	0.01	null
<i>Quercus robur</i>	TS	0.00	0.00	0.01	null
<i>Erica tetralix</i>	P	0.71	0.49	0.36	0.36
<i>Agrostis capillaris</i>	N	0.26	0.11	0.25	0.14
<i>Sorbus aucuparia</i>	TS	0.24	0.57	0.34	0.09
<i>Juncus effusus</i>	N	0.04	0.25	0.34	0.03
<i>Cirsium arvense</i>	N	0.03	0.02	0.12	0.02
<i>Holcus lanatus</i>	N	0.04	0.03	0.17	0.02
<i>Agrostis stolonifera</i>	N	0.03	0.02	0.12	0.02
<i>Rumex crispus</i>	N	0.03	0.02	0.12	0.02
<i>Ranunculus repens</i>	N	0.03	0.02	0.12	0.02
<i>Cirsium vulgare</i>	N	0.02	0.04	0.18	0.01
<i>Urtica dioica</i>	N	0.01	0.00	0.03	0.01
<i>Rumex obtusifolius</i>	N	0.01	0.00	0.03	0.00

**M1. Moorhouse – blanket bog:** FRAME/GANE prediction of N and S deposition between 1973 and 2001. Observed versus predicted change in CSM indicator species in the Hard Hills control plots; 0.1 sheep per hectare and no burn since 1954.

Predicted versus observed change in CSM indicators

Despite high residual variation, an overall positive correlation was observed between the direction of change in CSM indicators in the Hard Hills plots versus observed directions of change in frequency. The implication is that observed changes have been at least partly consistent with predicted impacts of N and S deposition.

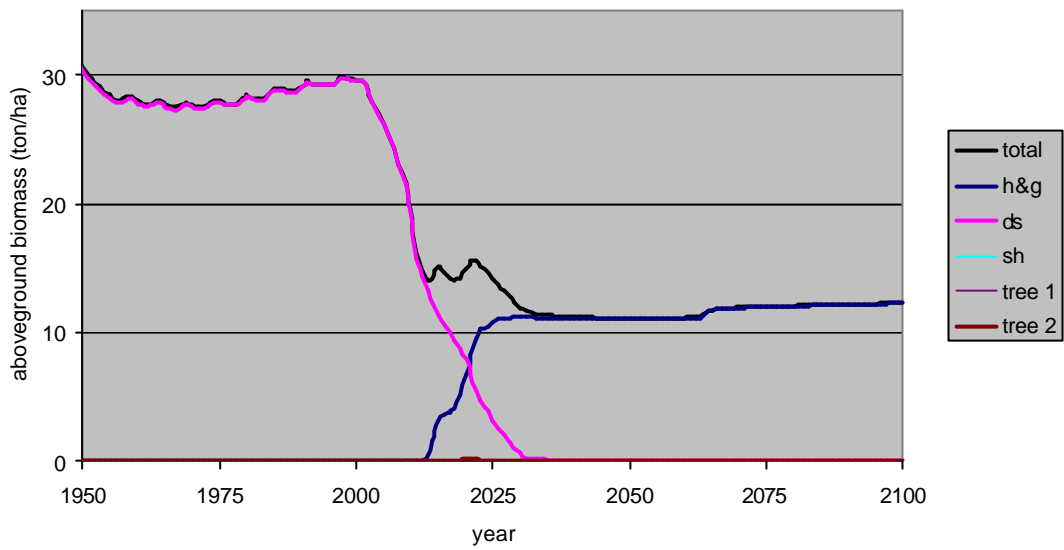
Fig M1.1. Observed versus predicted change in CSM indicator species for blanket bog. E\_nigr = *Empetrum nigrum*, PI\_mosses = average change for pleurocarpous mosses, Sphag = average change for *Sphagnum* species, V\_vi = *Vaccinium vitis-idaea*.



**M2. Moorhouse – blanket bog:** FRAME/GANE prediction of N and S to 2050. Grazing pressure increased to 5 sheep per hectare in 2005 and no burning.

SMART/SUMO was used to simulate expected changes in biomass of functional types given a dramatic increase in sheep grazing pressure starting in 2005. Dwarf Shrub Heath is expected to disappear completely after 30 years at this grazing intensity and the system stabilises at a lower productivity herb and grass dominated vegetation type.

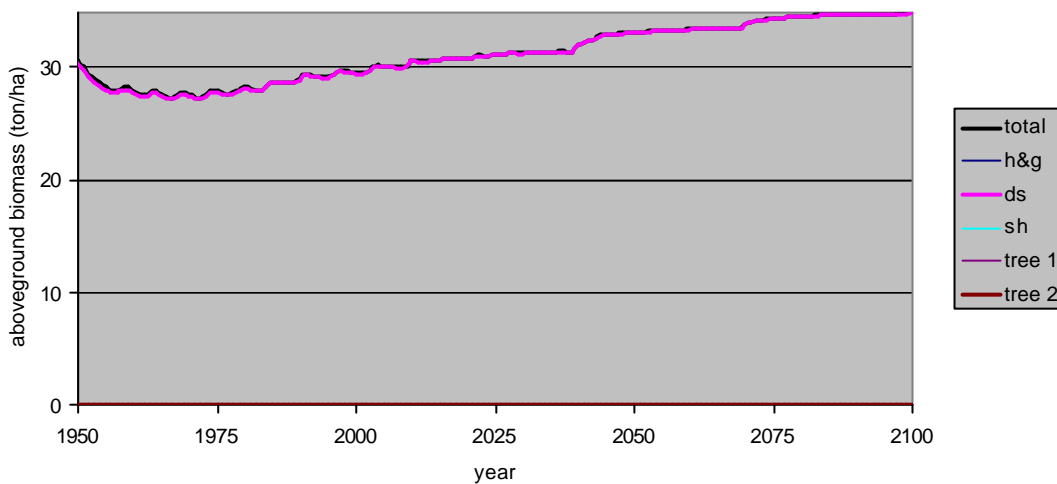
Fig M2.1 Prediction of change in biomass production by functional type at Moorhouse. Scenario based on FRAME N and S deposition and a shift from 0.1 to 5 sheep per ha in 2001.



**M3. Moorhouse – blanket bog:** FRAME/GANE prediction of N and S to 2100. Annual temperature increase based on UKCIP high emissions scenario with no grazing.

Biomass production is predicted to increase with each step change in temperature. However, no changes are predicted in functional type composition. Since the Hard Hills plots at Moorhouse are thought to be at the climatic tree line, it would be desirable to further modify SUMO to take account of changes in the likelihood of tree establishment as climate shifts. In this simulation, low pH and ground wetness are the only explicit constraints on tree growth in the model.

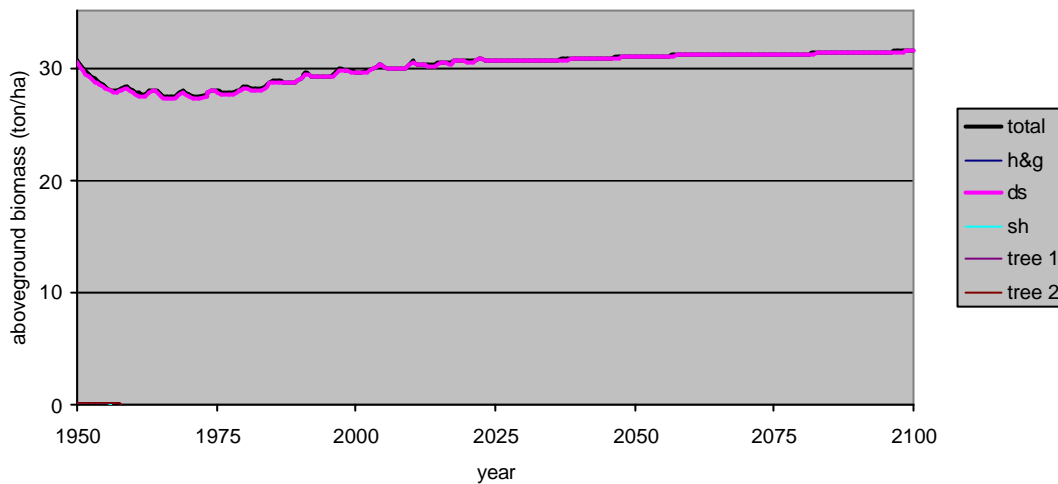
Fig M3.1. Prediction of change in biomass production by functional type at Moorhouse. Scenario based on FRAME N and S deposition and a shift in mean annual average temperature based on UKCIP high emissions with grazing and burning stopped.



**M4. Moorhouse – blanket bog:** FRAME/GANE prediction of N and S to 2100. Annual temperature increase based on UKCIP high emissions scenario with 0.1 sheep per hectare.

The only difference between this simulation and M3 was that grazing is kept here at the existing level on site of 0.1 sheep per ha. Not surprisingly, the effect is to reduce the standing crop and dampen the temperature stimulated increase in biomass growth. Grazing is still too low to generate a shift in the balance from dwarf shrub heath to herb/grass (Fig M4.1).

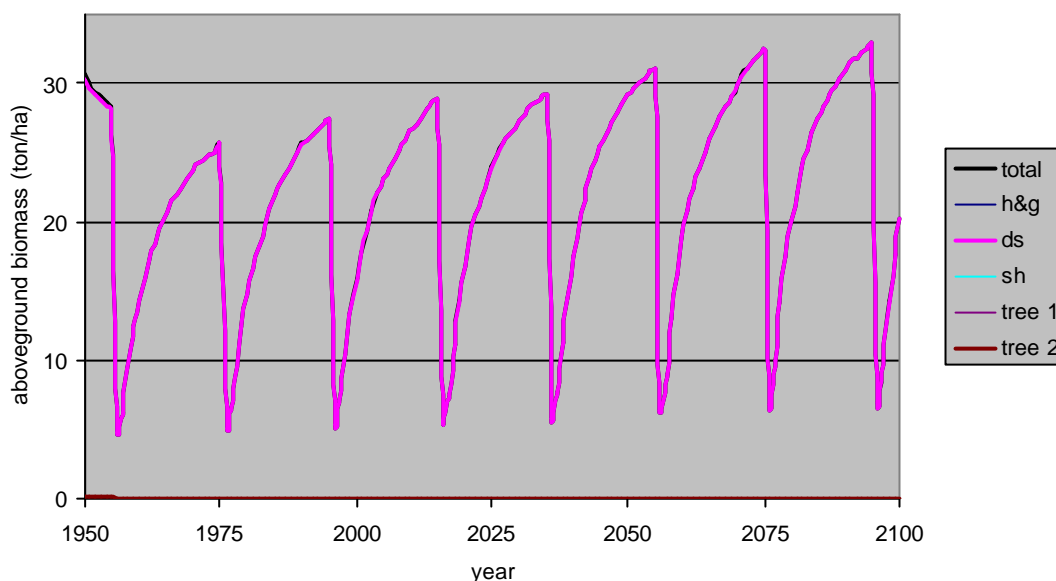
Fig M4.1. SMART/SUMO simulation of change in biomass production. Scenario based on FRAME/GANE N and S deposition and a shift in mean annual average temperature based on UKCIP high emissions with grazing maintained at 0.1 sheep per ha.



**M5. Moorhouse – blanket bog:** FRAME/GANE prediction of N and S to 2100. Annual temperature increase based on UKCIP high emissions scenario with 0.1 sheep per hectare and 20 year rotational burn.

When a 20 year burning rotation is added to the scenario in M4, biomass fluctuates predictably but with a steady increase due to temperature change. Again no change in the balance of functional types is predicted and the blanket bog remains dominated by dwarf shrubs.

Fig M5.1 As above for temperature but with 20 year burn rotation.



**P1. Porton Down – lowland calcareous grassland:** FRAME/GANE prediction of N and S to 2050. Constant management (wild rabbit grazing).

Change in CSM indicator species

Positive indicators are probably underestimated in their habitat suitability reflecting the fact that MAGIC did not calibrate well to the observed pH value in 2000. Soil CN was well matched to observed data and is predicted to decrease further giving rise to increasing fertility which clearly does not outweigh the predicted moderate increase in pH, in terms of driving change in species habitat suitability (Fig P1.1). In any event, typical calcicoles are predicted to decline markedly in the next 8 to 15 years.

Among negative indicator species, low habitat suitability is predicted for all species present apart from *Cirsium vulgare* and *Plantago major* which are expected to find conditions increasingly favourable with time. *Sonchus arvensis* is predicted to find conditions more suitable at first but then decreases toward the end of the interval.

Among Agriculturally Favoured Species, *Lolium perenne* and *Trifolium repens* are expected to find conditions somewhat more amenable as time passes but *Lolium* is

predicted to decrease again after about 2025, presumably in response to the predicted increase in pH.

Rank grasses are predicted to decline throughout the interval including the three present at time 1, *Bromus erectus*, *Helictotrichon pubescens* and *Arrhenatherum elatius*. Overall changes in habitat suitability are expected to favour negative indicators over positive indicators as conditions become more fertile and deviate increasingly from the pre-existing CG2 grassland. The prediction may give grounds for increased vigilance and more frequent soil analysis.

#### Status of CSM indicators in the local species pool

Of those species with no dispersal index (column = site in Table P1.1), local abundance estimates suggest that negative indicators should be scarce in the site pool with positive indicators likely to be much more abundant. However, when the bottom half of table P1.1 is examined, the implication is that several negative indicator species could disperse readily from the site pool. These include *Holcus lanatus*, *Brachypodium pinnatum* and *Phleum pratense*. Species such as *Plantago major*, *Lolium perenne* and *Trifolium repens* are estimated to be less common but are nevertheless present. Since soil conditions are expected to become increasingly favourable for these three species, vigilance would be advised.

Fig P1.1. CSM indicator predictions for **Porton Down** lowland calcareous grassland. Species present in quadrats at time 1 are shown in bold in the legend or shown on separate graphs.

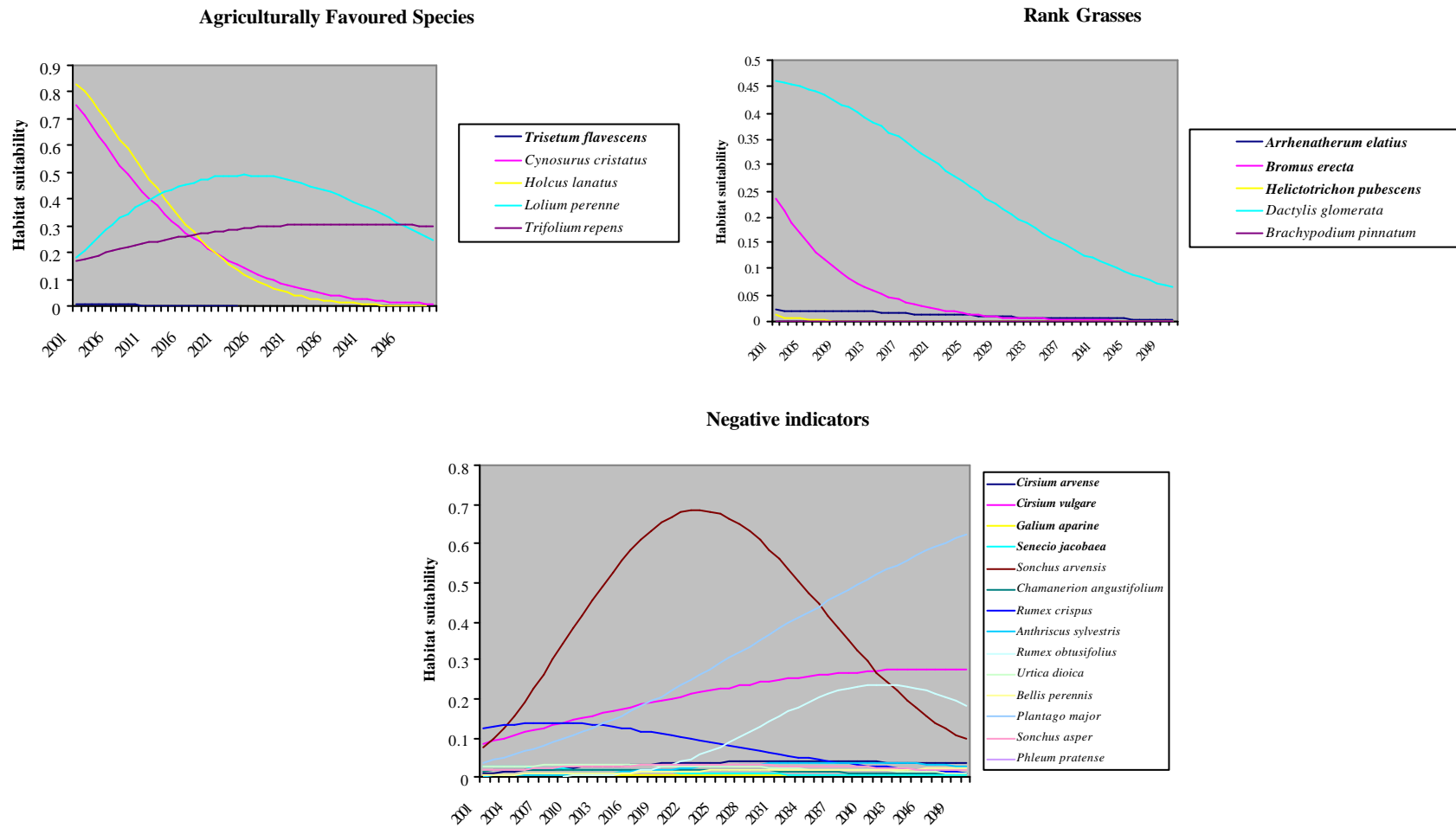
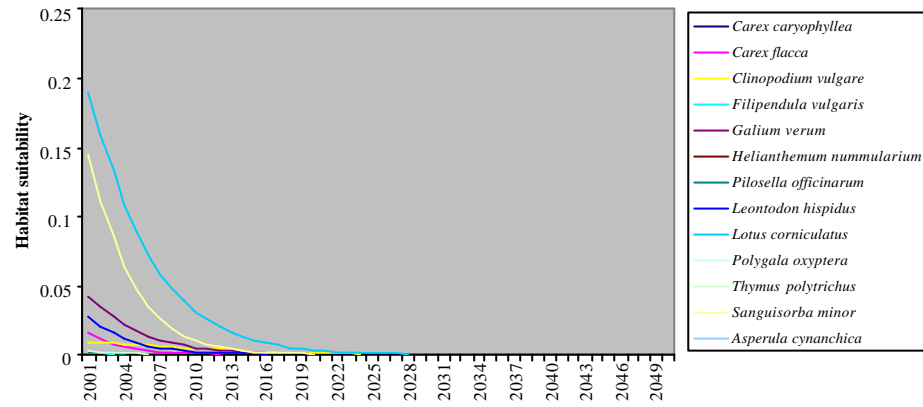


Fig P1 1 Contd

Positive indicators - present at t1



Positive indicators - absent at t1

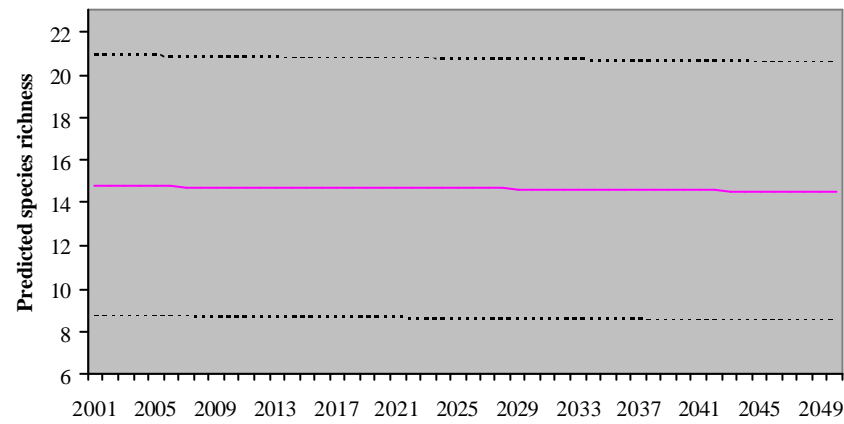
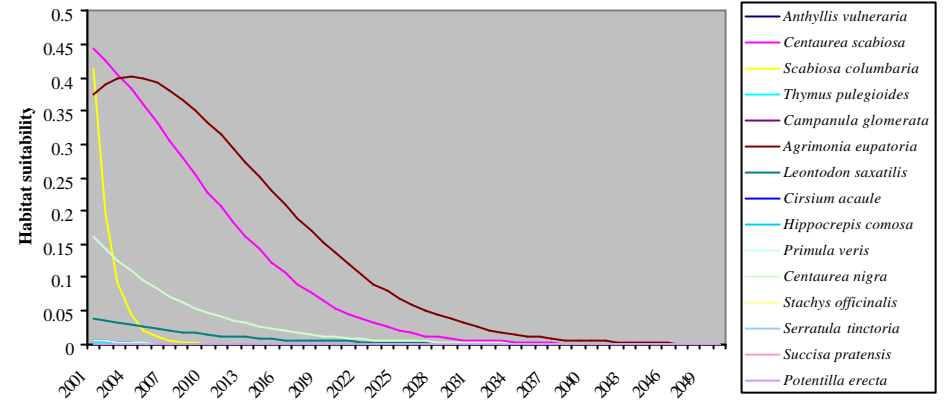


Table P1.1. Empirical immigration ranking for CSM indicators not present in the monitored patch but present in the local species pool at **Porton Down**. See text above and Box 7 for explanation. CSM categories = Positive (P), Negative (N), Introduced & Exotic (I), Agriculturally Favoured Species (AFS), Rank Grasses (RG). Site, b1 and b2 are indices estimating species abundance in the site pool or buffer zones. S\*DISP etc give the abundance index multiplied by the dispersal index where this was estimated. Null indicates that no dispersal index was attributed. Positive indicators by NVC community types relevant to the monitored patch, are also shown.

CSM category	CG2	CG3,4,5	BRC_names	site	b1	b2	S*DISP
P		1	<i>Thymus pulegioides</i>	0.60	0.05	0.04	null
P	1		<i>Campanula glomerata</i>	0.60	0.05	0.04	null
P	1		<i>Cirsium acaule</i>	0.60	0.05	0.04	null
P	1	1	<i>Hippocrepis comosa</i>	0.60	0.05	0.04	null
P	1	1	<i>Leontodon saxatilis</i>	0.45	0.04	0.03	null
P	1		<i>Serratula tinctoria</i>	0.45	0.04	0.03	null
P		1	<i>Agrimonia eupatoria</i>	0.34	0.10	0.12	null
N			<i>Chamanerion angustifolium</i>	0.07	0.06	0.09	null
I			<i>Parietaria judaica</i>	0.06	0.10	0.06	null
I			<i>Sedum album</i>	0.06	0.10	0.06	null
P	1	1	<i>Scabiosa columbaria</i>	0.62	0.07	0.05	0.31
AFS			<i>Holcus lanatus</i>	0.60	0.14	0.17	0.28
RG			<i>Brachypodium pinnatum</i>	0.60	0.05	0.04	0.26
N			<i>Phleum pratense</i>	0.38	0.17	0.19	0.23
P	1	1	<i>Primula veris</i>	0.60	0.05	0.04	0.21
AFS			<i>Cynosurus cristatus</i>	0.34	0.10	0.11	0.18
P		1	<i>Centaurea scabiosa</i>	0.62	0.07	0.05	0.18
P	1	1	<i>Centaurea nigra</i>	0.45	0.04	0.03	0.18
RG			<i>Dactylis glomerata</i>	0.34	0.11	0.13	0.18
P	1	1	<i>Succisa pratensis</i>	0.33	0.06	0.03	0.17
P	1	1	<i>Anthyllis vulneraria</i>	0.60	0.05	0.04	0.16
P	1		<i>Stachys officinalis</i>	0.45	0.04	0.03	0.15
N			<i>Bellis perennis</i>	0.34	0.10	0.11	0.14
AFS			<i>Trifolium repens</i>	0.19	0.08	0.10	0.12
N			<i>Anthriscus sylvestris</i>	0.34	0.10	0.11	0.12
N			<i>Rumex obtusifolius</i>	0.15	0.49	0.52	0.09
N			<i>Sonchus asper</i>	0.07	0.51	0.46	0.05
AFS			<i>Lolium perenne</i>	0.08	0.14	0.17	0.04
N			<i>Sonchus arvensis</i>	0.05	0.38	0.35	0.03
N			<i>Urtica dioica</i>	0.03	0.04	0.06	0.02
N			<i>Plantago major</i>	0.04	0.07	0.09	0.02
N			<i>Rumex crispus</i>	0.04	0.07	0.09	0.02
P	1		<i>Potentilla erecta</i>	0.02	0.02	0.01	0.01

## **Ca 1. Cairngorm – upland heath: FRAME/GANE prediction of N and S to 2050. Zero deer and sheep grazing pressure.**

The lower valley slopes below the Cairngorm ECN site have seen gradual succession in the past 15 or more years with *Pinus sylvestris* increasing (Thurlow et al 1999). Sheep grazing was effectively reduced to zero from the early 70s onward and currently the only grazing is by occasional reindeer from the Cairngorm herd (R.Brooker pers.comm.).

MAGIC+GBMOVE was therefore used to predict changes in habitat suitability for CSM indicators of upland heath. Canopy height was incrementally increased over the 50 years of the prediction interval in a similar empirical fashion to the approach taken to force woodland growth at Rothamsted Park Grass (Case study R2 above).

### Change in CSM indicator species

Since many of the negative indicators were predicted to have higher habitat suitability than positive indicators actually present at the site, it seems likely that some species have not been reliably predicted unless soil conditions are to some degree out of equilibrium with above-ground vegetation. Since Cairngorm is a historically low deposition site this seems unlikely.

Most of the predicted changes were clearly driven by the incremental increase in canopy height implemented to force niche changes along a successional gradient. Hence *Calluna vulgaris* was predicted to decline while more shaded conditions are predicted to favour *Sphagnum palustre* and *S.cuspidatum* (Fig Ca 1.1).

Habitat conditions were expected to be moderately suitable for *Agrostis stolonifera* at the start of the interval but canopy growth was expected to make conditions increasingly less suitable. On the other hand, predicted change in habitat conditions was expected to favour the two negative indicator species *Pteridium aquilinum* and *Ranunculus repens* (Fig Ca 1.1).

### Status of CSM indicators in the local species pool

Most of the indicator species estimated to be most abundant in the site species pool were positive indicators for upland heath (Table Ca 1.1) apart from *Picea sitchensis* and *Betula* spp. *Pinus sylvestris* has a relatively low local abundance index which is at odds with its known local proliferation close to the ECN sampling site. Of those negative indicator species with dispersal indices all except *Agrostis capillaris* and *Sorbus aucuparia* are estimated to be extremely scarce in the site pool (indices <0.00 in table Ca 1.1).

Fig Ca 1.1. CSM indicator predictions for Cairngorm ECN site – upland heath. Species present in quadrats at time 1 are shown in bold in the legend.

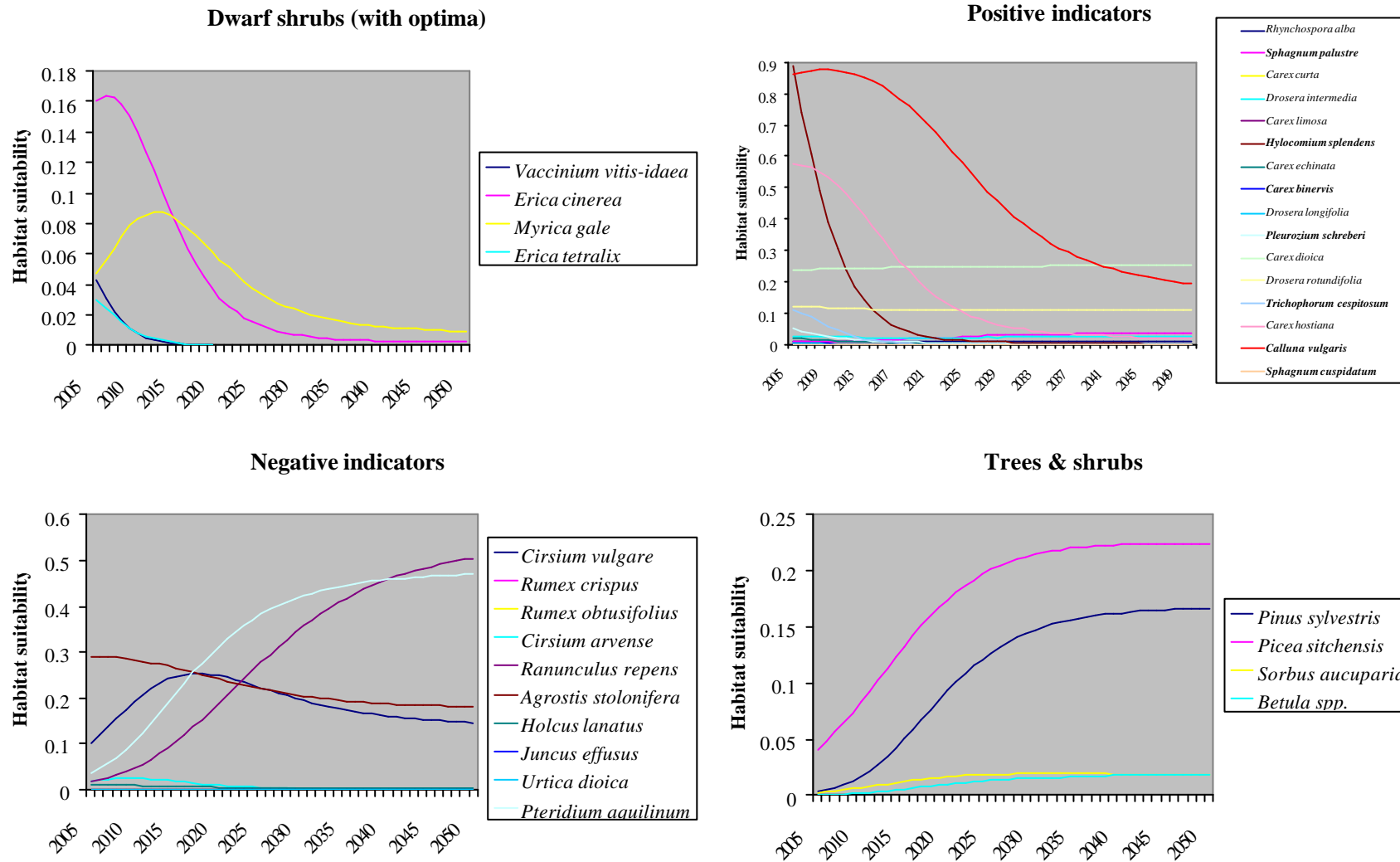


Table Ca 1.1. Empirical immigration ranking for CSM indicators not present in the monitored patch but present in the local species pool at **Cairngorm**. See text above and Box 7 for explanation. CSM categories = Positive (P), Negative (N), Dwarf Shrubs (DSH), Trees & Shrubs (TS). Site, b1 and b2 are indices estimating species abundance in the site pool or buffer zones. S\*DISP etc give the abundance index multiplied by the dispersal index where this was estimated. Null indicates that no dispersal index was attributed.

CSM category	BRC_names	site	b1	b2	S*DISP
DSH	<i>Arctostaphylos alpinus</i>	0.81	0.62	0.54	null
P	<i>Carex hostiana</i>	0.80	0.40	0.40	null
TS	<i>Betula nana</i>	0.68	0.57	0.57	null
TS	<i>Picea sitchensis</i>	0.50	0.40	0.40	null
TS	<i>Betula spp.</i>	0.20	0.60	0.70	null
P	<i>Myrica gale</i>	0.12	0.19	0.25	null
P	<i>Drosera intermedia</i>	0.10	0.15	0.22	null
P	<i>Drosera rotundifolia</i>	0.10	0.15	0.22	null
DSH	<i>Salix repens</i>	0.10	0.14	0.21	null
P	<i>Carex echinata</i>	0.07	0.13	0.16	null
DSH	<i>Vaccinium oxycoccus</i>	0.07	0.13	0.16	null
N	<i>Pteridium aquilinum</i>	0.07	0.13	0.17	null
TS	<i>Pinus sylvestris</i>	0.06	0.17	0.16	null
P	<i>Drosera longifolia</i>	0.05	0.08	0.11	null
P	<i>Rhynchospora alba</i>	0.01	0.01	0.01	null
P	<i>Carex limosa</i>	0.01	0.01	0.01	null
P	<i>Carex curta</i>	0.00	0.01	0.01	null
TS	<i>Quercus petraea</i>	0.00	0.02	0.02	null
TS	<i>Quercis robur</i>	0.00	0.02	0.02	null
P	<i>Carex dioica</i>	0.00	0.00	0.00	null
N	<i>Agrostis capillaris</i>	0.24	0.22	0.21	0.12
TS	<i>Sorbus aucuparia</i>	0.10	0.22	0.24	0.04
N	<i>Juncus effusus</i>	0.03	0.07	0.07	0.02
N	<i>Holcus lanatus</i>	0.01	0.02	0.02	0.00
N	<i>Cirsium arvense</i>	0.00	0.01	0.01	0.00
N	<i>Cirsium vulgare</i>	0.00	0.02	0.02	0.00
N	<i>Rumex crispus</i>	0.00	0.01	0.01	0.00
N	<i>Agrostis stolonifera</i>	0.00	0.01	0.01	0.00
N	<i>Ranunculus repens</i>	0.00	0.01	0.01	0.00
N	<i>Urtica dioica</i>	0.00	0.01	0.01	0.00
N	<i>Rumex obtusifolius</i>	0.00	0.01	0.02	0.00
N	<i>Phragmites australis</i>	0.00	0.00	0.01	0.00

## **B1. Budworth Common – lowland heath: FRAME/GANE prediction of N and S to 2050. Constant management.**

### Change in CSM indicator species

Overall no substantial changes in the suitability of the habitat were indicated over the 45 year period (Fig B1.1). All of the four species present in plots or immediately adjacent (in bold) had the highest predicted suitability values while *Calluna*, the community dominant, is predicted to remain dominant throughout the interval. Although conditions are expected to become more favourable for the negative indicators *Pteridium aquilinum* and *Chamaenerion angustifolium*, habitat suitability is still much lower than values for the community dominants.

At present conditions are predicted to remain unsuitable for all negative tree & shrub indicators.

### Status of CSM indicators in the local species pool

Given its lowland situation, it is not surprising that a large number of negative indicators plus trees and shrubs are estimated to be abundant in the site species pool (Table B1.1). These include *Betula* spp., *Quercus* spp., *Rhododendron*, *Chamaenerion angustifolium*, *Pinus sylvestris* and *Rubus fruticosus* agg. High dispersal and local abundance indices suggest a higher probability of reaching the recorded patch, but at present establishment is predicted to be less likely because habitat suitability for all these indicators except *Chamaenerion*, is low and expected to remain so.

Fig B1.1. CSM indicator predictions for **Budworth Common** – lowland heath. Species present in quadrats at time 1 are shown in bold in the legend.

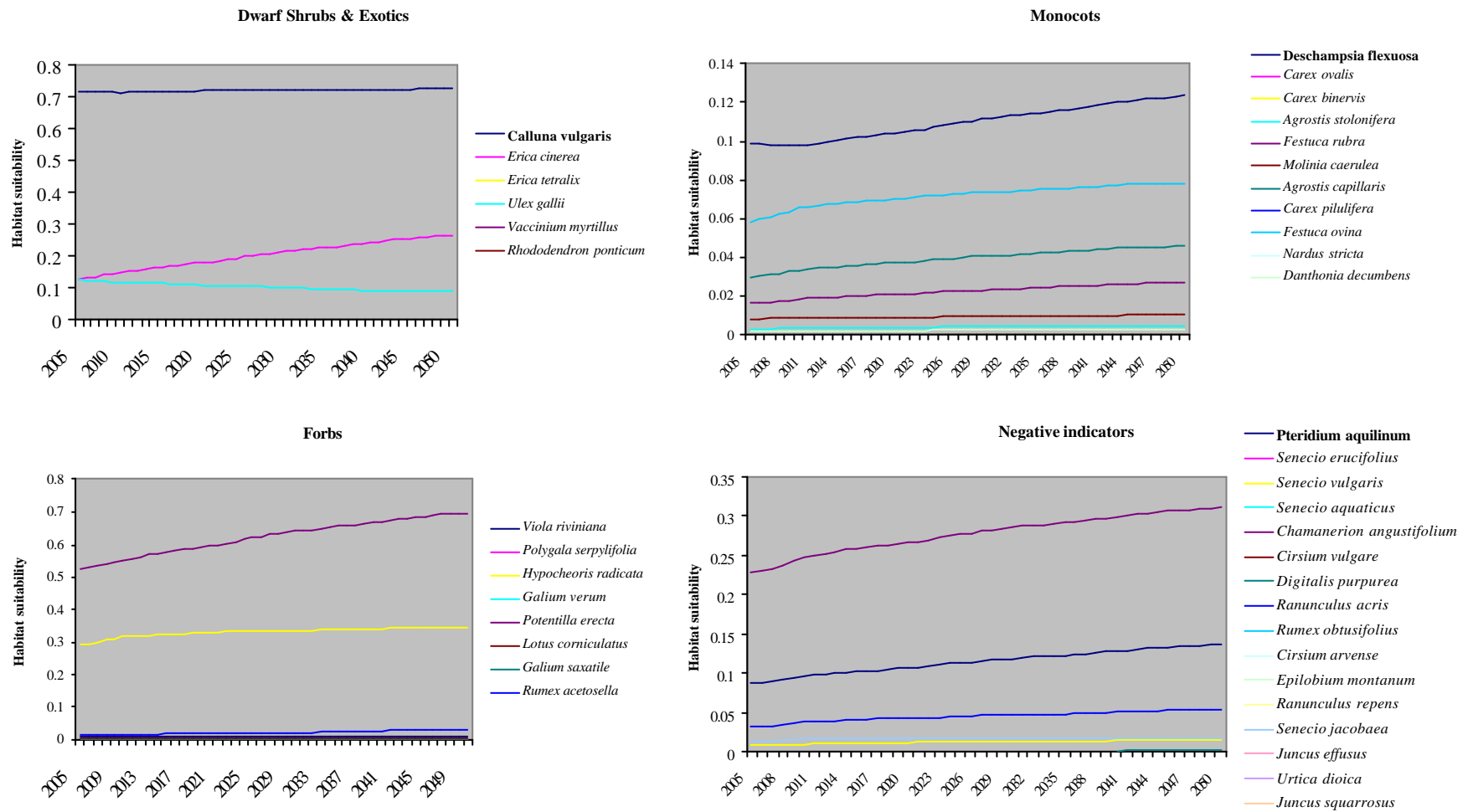


Fig B1.1 Contd.

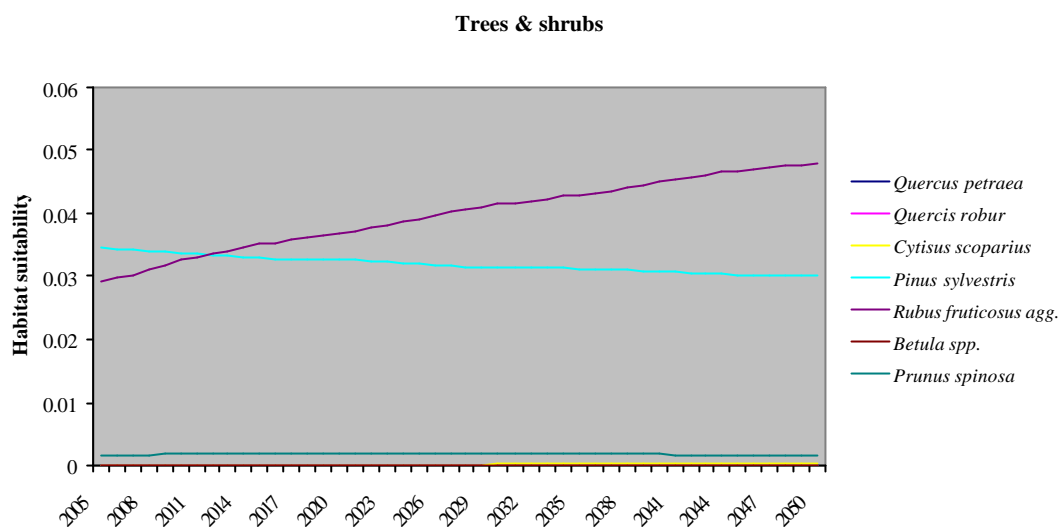


Table B1.1 Empirical immigration ranking for CSM indicators not present in the monitored patch but present in the local species pool at **Budworth Common**. See text above and Box 7 for explanation. CSM categories = Negative (N), Dwarf Shrubs (DSH), Trees & Shrubs (TS), forbs (f), monocots (g). Site, b1 and b2 are indices estimating species abundance in the site pool or buffer zones. S\*DISP etc give the abundance index multiplied by the dispersal index where this was estimated. Null indicates that no dispersal index was attributed.

CSM category	BRC_names	site	b1	b2	S*DISP
TS	<i>Betula spp.</i>	0.90	0.40	0.40	null
TS	<i>Quercus petraea</i>	0.84	0.10	0.06	null
TS	<i>Quercus robur</i>	0.84	0.10	0.06	null
EX	<i>Rhododendron ponticum</i>	0.80	0.02	0.03	null
N	<i>Chamaenerion angustifolium</i>	0.45	0.17	0.13	null
f	<i>Viola riviniana</i>	0.43	0.09	0.06	null
TS	<i>Pinus sylvestris</i>	0.42	0.06	0.07	null
f	<i>Hypochoeris radicata</i>	0.06	0.11	0.08	null
f	<i>Polygala serpyllifolia</i>	0.03	0.05	0.04	null
g	<i>Carex binervis</i>	0.03	0.03	0.05	null
DSH	<i>Ulex gallii</i>	0.02	0.02	0.02	null
N	<i>Senecio erucifolius</i>	0.01	0.04	0.03	null
DSH	<i>Erica cinerea</i>	0.01	0.01	0.03	null
TS	<i>Rubus fruticosus agg.</i>	0.86	0.15	0.11	0.40
N	<i>Epilobium montanum</i>	0.43	0.07	0.05	0.28
N	<i>Digitalis purpurea</i>	0.42	0.05	0.05	0.21
TS	<i>Cytisus scoparius</i>	0.44	0.08	0.07	0.19
N	<i>Urtica dioica</i>	0.24	0.14	0.09	0.17
DSH	<i>Vaccinium myrtillus</i>	0.23	0.05	0.05	0.11
f	<i>Galium saxatile</i>	0.24	0.05	0.05	0.11
TS	<i>Prunus spinosa</i>	0.20	0.40	0.40	0.07
N	<i>Cirsium arvense</i>	0.06	0.24	0.21	0.04
N	<i>Cirsium vulgare</i>	0.07	0.42	0.43	0.04
N	<i>Rumex obtusifolius</i>	0.07	0.51	0.53	0.04

N	<i>Juncus effusus</i>	0.04	0.06	0.06	0.03
N	<i>Ranunculus acris</i>	0.05	0.19	0.18	0.03
N	<i>Ranunculus repens</i>	0.05	0.19	0.18	0.03
N	<i>Juncus squarrosus</i>	0.04	0.04	0.04	0.02
g	<i>Festuca rubra</i>	0.04	0.08	0.06	0.02
g	<i>Agrostis stolonifera</i>	0.04	0.08	0.05	0.02
g	<i>Agrostis capillaris</i>	0.04	0.06	0.05	0.02
g	<i>Carex ovalis</i>	0.04	0.16	0.16	0.02
g	<i>Festuca ovina</i>	0.03	0.06	0.05	0.02
g	<i>Nardus stricta</i>	0.03	0.03	0.03	0.01
f	<i>Potentilla erecta</i>	0.04	0.04	0.05	0.01
g	<i>Danthonia decumbens</i>	0.04	0.08	0.06	0.01
N	<i>Senecio jacobaea</i>	0.02	0.07	0.05	0.01
f	<i>Galium verum</i>	0.03	0.09	0.07	0.01
f	<i>Rumex acetosella</i>	0.03	0.03	0.03	0.01
g	<i>Carex pilulifera</i>	0.03	0.04	0.04	0.01
f	<i>Lotus corniculatus</i>	0.03	0.10	0.07	0.01
N	<i>Senecio aquaticus</i>	0.02	0.04	0.03	0.01
DSH	<i>Erica tetralix</i>	0.01	0.01	0.03	0.00
g	<i>Molinia caerulea</i>	0.01	0.01	0.03	0.00
N	<i>Senecio vulgaris</i>	0.00	0.15	0.14	0.00

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## **NI 1& 2: Linked soil and vegetation model application to two ASSI in Northern Ireland**

### Summary

- Local model predictions of past and future change in nitrogen and sulphur deposition were used in combination with measured soil chemistry to simulate changes in soil water pH and soil C/N in lowland meadow and raised bog vegetation at two ASSI in northern Ireland.
- Projections of soil change were in turn used to predict change in habitat suitability for the species present in 2005 plus selected CSM indicators.
- Predictions were made for the interval 2005 to 2050 assuming constant canopy height (ie. management intensity) and constant soil moisture content.
- The unimproved lowland meadow vegetation at Dromore Motte is expected to show a small, ongoing reduction in soil C/N to 2050. This would tend to result in increased fertility but changes are predicted to be so small that effects on current species composition are negligible.
- Predictions are however, uncertain because MAGIC did not calibrate well to observed soil pH. Also the species composition of the vegetation appears to reflect a much less fertile system than indicated by actual measurement of soil C/N. This reflects the significant uncertainty in the calibration equation used to translate soil C/N into mean Ellenberg fertility values for the purposes of predicting plant species changes.
- At Dead Island Bog, soil and vegetation were sampled from a lagg area of quaking mire that appeared to be influenced by calcareous groundwater discharge.
- At this location soil C/N is predicted to have decreased historically at a faster rate than at Dromore Motte and this is expected to continue until 2050.
- Again though, MAGIC did not calibrate well to the measured pH in 2005 however no significant change in soil water pH is expected over the next 45 years.
- Predicted soil changes translated into small predicted changes in habitat suitability for the species present and for CSM indicators for raised bog. This is hypothesised to reflect the constraint on the species composition imposed by continued waterlogging and high pH. The situation might therefore be destabilized by succession and dewatering so that conditions rapidly become more favourable for atypical species.

## Introduction

Two sites were employed for model testing. Dromore Motte comprised lowland unimproved meadow vegetation present over the surfaces of an iron age hill fort. At this site soil and vegetation were recorded on the western side of the central mound. Dead Island Bog comprised a large raised bog complex. Soil and vegetation were sampled in a lagg area on quaking ground. The species present indicated a minerotrophic, topogenous mire while the high observed pH of 6.3 suggested flushing by calcareous groundwater.

Table 1. NVC matching of botanical plot data from the two sites based on the cover-weighted species composition of a 4m<sup>2</sup> plot recorded in each site. The MAVIS software was used for NVC matching ([www.ceh.ac.uk/products/software](http://www.ceh.ac.uk/products/software)). The top three best fitting sub-communities are shown.

### Dromore Motte

<b>NVC unit</b>	<b>% similarity</b>
MG5c <i>Cynosurus cristatus</i> – <i>Centaurea nigra</i> grassland	41
MG1c <i>Arrhenatherum elatius</i> grassland, <i>Filipendula ulmaria</i> sub-community	40
MG3 <i>Anthoxanthum odoratum</i> – <i>Geranium sylvaticum</i> grassland	40

### Dead Island Bog

<b>NVC unit</b>	<b>% similarity</b>
M6d <i>Carex echinata</i> – <i>Sphagnum recurvum/auriculatum</i> mire, <i>Juncus acutiflorus</i> sub-community	31
M23a <i>Juncus effusus/acutiflorus</i> – <i>Galium palustre</i> rush-pasture, <i>J.acutiflorus</i> sub-community	31
M25c <i>Molinia caerulea</i> – <i>Potentilla erecta</i> mire, <i>Angelica sylvestris</i> sub-community	30

The criteria for selection were that a) the Priority Habitats raised bog and lowland meadow should be present, b) sites should have a time-series of vegetation monitoring data, c) sites should have accurate local measurements of total N deposition.

The sites selected did not meet the second criteria. New botanical plot data were recorded from a single 4m<sup>2</sup> plot on each site in Spring 2005. Fresh soil (0-10cm excluding litter) was also sampled from the same location at the same time and subsequently analysed for soil chemistry parameters required to initialise the MAGIC model.

## Case study application

The dynamic soil model MAGIC was used to predict pH and soil C/N ratio from 2005 to 2050 based on measured soil chemistry in 2005. These predictions were then used to generate changes in indices of habitat suitability for two groups of plant species; firstly those present in plot samples in 2005 and second, Common Standards Monitoring indicator species for raised bog and lowland meadow that were not present in plots but were recorded in the local 10km square species pool or seen on each site.

MAGIC predictions of C/N and soil pH were also used in combination with observed soil moisture content and canopy height to generate a prediction of change in species richness per 4m<sup>2</sup> plot over the time period.

Results are evaluated in terms of the values of habitat suitability for plant species and their rate and direction of predicted change to 2050.

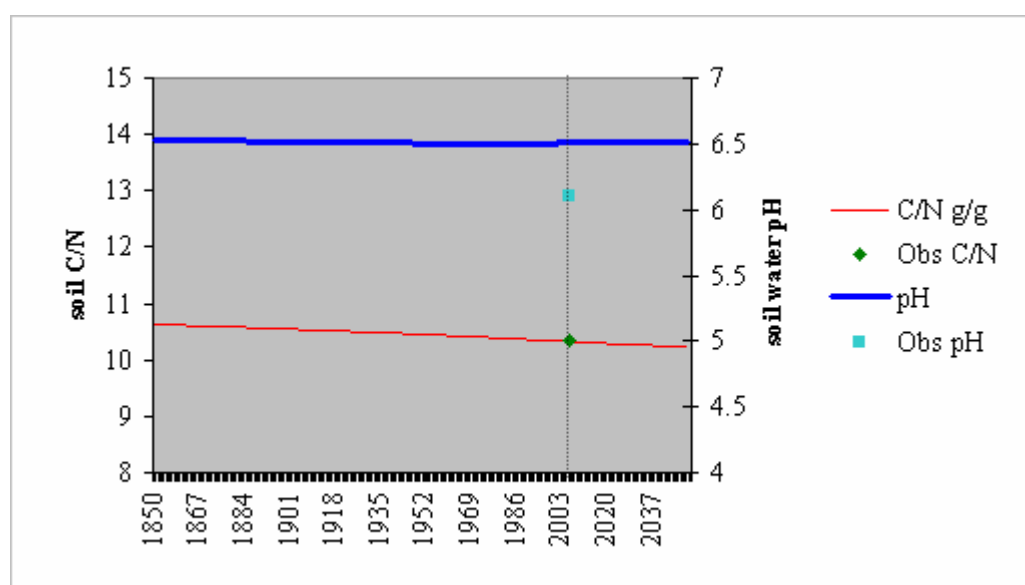
### **SITE 1 - Dromore Motte**

Scenario: Prediction based on constant soil moisture and canopy height with changes in soil C/N and pH driven by FRAME/GANE predictions of change in total N and S deposition for the local 5 kilometre square.

#### Results:

At Dromore Motte, MAGIC calibrated well to the observed C/N value but not to soil water pH (Fig 1). However, since future trends are considered reliably predicted, the rate of predicted change in pH per year was applied to the observed value to yield pH values as input to the plant species models.

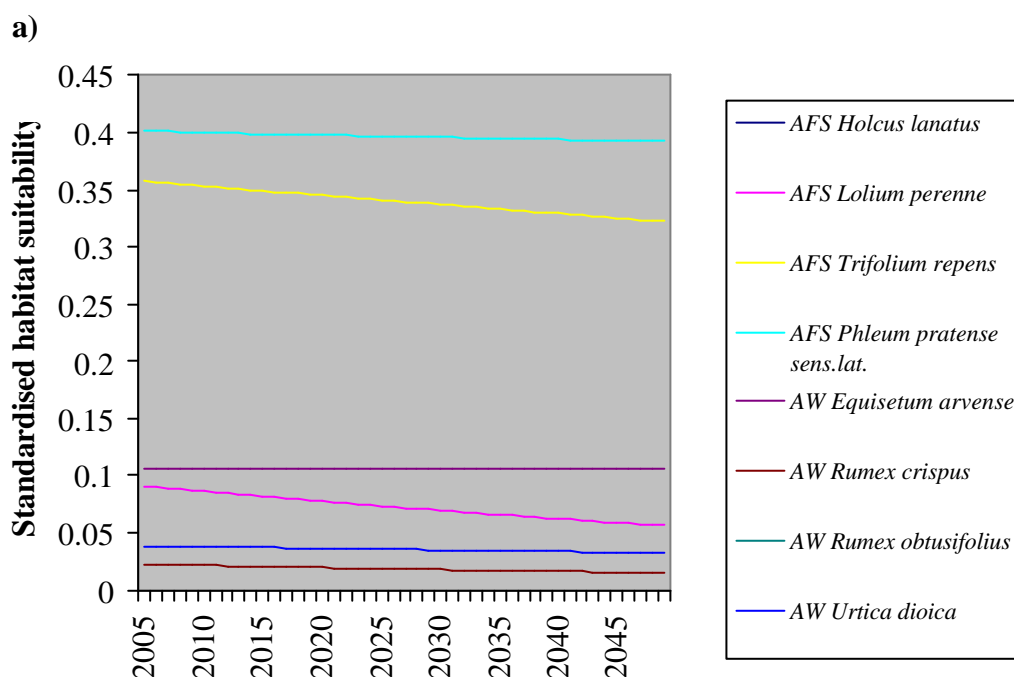
Figure 1. MAGIC prediction of change in soil water pH and soil C/N at Dromore Motte. The interval between the vertical dashed line and the right axis indicates the time period over which plant species changes were predicted.



Little change in pH was predicted between 2005 and 2050 while soil C/N was predicted to decrease slightly from 10.32 to 10.23. Overall, the site showed relatively little predicted impact of acidification or eutrophying N deposition on soil conditions but cautious interpretation is required because of the poor model calibration to current soil water pH.

Predicted soil C/N and pH values resulted in very low habitat suitability indices for the species actually recorded at Dromore Motte in 2005 (Fig 3 and Table 2). This reduces the level of confidence in the predictions of species changes since high habitat suitability should be predicted for species growing *in situ*. The low values reflect the apparent mismatch between measured C/N ratio and above-ground species composition. Thus, a much more fertile assemblage would be expected than in fact occurs.

Figure 3. Predicted changes in habitat suitability for the CSM indicator categories Agriculturally Favoured species and Agricultural Weeds as listed in JNCC habitat guidance for lowland meadows. Habitat suitability ranges between 0 and 1 with higher values indicating more favourable conditions for growth.



All species modelled were expected to see conditions become increasingly unfavourable over time including the agricultural indicators. Because habitat suitability indicators were mainly low in 2005 however, the actual size of these reductions will be very small (Fig 3 and Table 2) hence overall stability is expected among the species present with no major increases in favourability of conditions for negative indicators. It should be noted though, that soil conditions appear to be inconsistent with above-ground species composition resulting in a mismatch between species present and their predicted habitat suitability. This reduces confidence in the prediction.

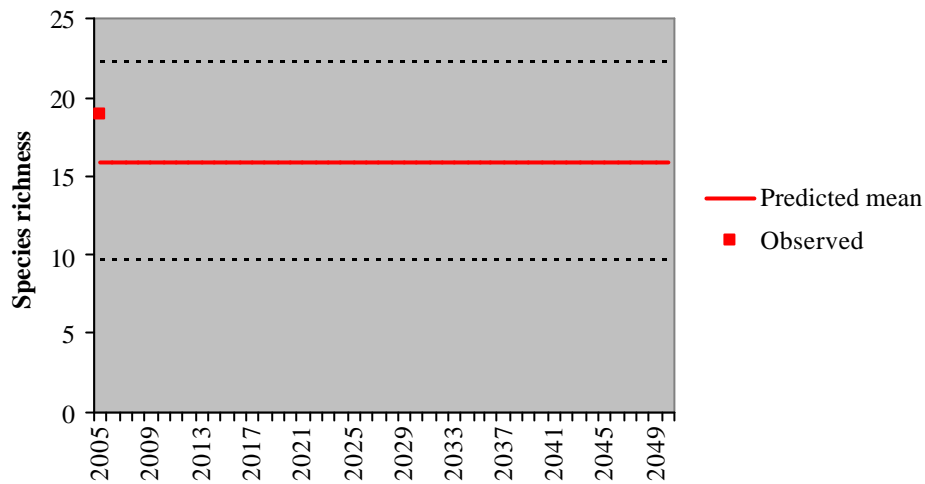
The only species with reasonably large habitat suitability indices were *Taraxacum* agg., *Conopodium majus*, *Phleum pratense sens lat* and *Trifolium repens* (Table 2).

Table 2. CSM indicator table for Dromore Motte. MG5 indicator species are denoted 1. CSM categories follow those listed in JNCC habitat guidance for the Priority Habitat as follows; P=positive, AW=Agricultural Weeds, AFS=Agriculturally Favoured Species. Predicted habitat suitability values are listed in column Hs 2005. Values range between 0 and 1 with a higher value indicating more favourable conditions for growth. % change in Hs indicates the size of the predicted reduction or increase in Habitat suitability index as a percentage of the starting value in 2005.

MG5	Present in 2005	CSM category	Species	Hs 2005	% change in Hs 2005 to 2050
	1		<i>Taraxacum</i> agg.	0.98	-6
1	1	P	<i>Conopodium majus</i>	0.262263	-1
	1		<i>Cynosurus cristatus</i>	0.023318	-38
	1		<i>Agrostis capillaris</i>	0.004458	-38
	1		<i>Hyacinthoides non-scripta</i>	0.000979	-28
	1	AW	<i>Senecio jacobaea</i>	0.000705	-35
	1		<i>Plantago lanceolata</i>	2.5E-05	-55
1	1	P	<i>Centaurea nigra</i>	1.61E-06	-57
	1		<i>Festuca rubra</i> agg.	7.5E-07	-65
	1		<i>Anthoxanthum odoratum</i>	3.43E-07	-64
	1		<i>Vicia sepium</i>	2.75E-08	-69
1	1	P	<i>Lathyrus pratensis</i>	3.83E-10	-75
	1		<i>Potentilla sterilis</i>	2.01E-10	-71
1	1	P	<i>Potentilla erecta</i>	1.73E-10	-72
	1		<i>Luzula campestris</i>	1.49E-12	-78
	1		<i>Helictotrichon pubescens</i>	1.76E-16	-80
		AFS	<i>Phleum pratense sens.lat.</i>	0.401498	-2
		AFS	<i>Trifolium repens</i>	0.358062	-10
		AW	<i>Equisetum arvense</i>	0.106844	0
		AFS	<i>Lolium perenne</i>	0.091853	-37
		AW	<i>Urtica dioica</i>	0.039132	-15
		AW	<i>Rumex crispus</i>	0.02331	-33
		AFS	<i>Holcus lanatus</i>	0.000215	-54
		AW	<i>Rumex obtusifolius</i>	5.43E-05	-71

Given modelled changes in soil conditions between 2005 and 2050, no significant trends in species richness are expected. Again however, the mismatch between soil conditions and above-ground vegetation suggests the prediction should be cautiously interpreted.

Figure 4. Predicted species richness change per 4m<sup>2</sup> at Dromore Motte. The dashed line indicates the 95% prediction interval.



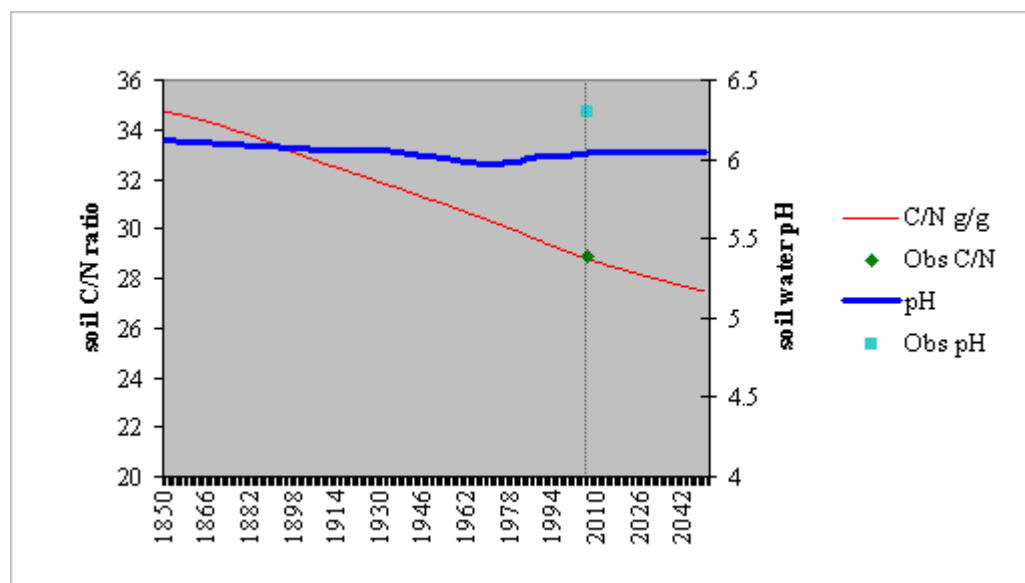
## SITE 2 – Dead Island Bog

Scenario: Prediction based on constant soil moisture and constant canopy height with changes in soil C/N and pH driven by FRAME/GANE predictions of change in total N and S deposition for the local 5 kilometre square.

### Results:

The MAGIC soil model calibrated successfully to the measured C/N value in 2005 but underestimated soil pH by 0.3 of a unit. Soil water pH is not predicted to change over the interval. Although not explicitly incorporated in the model prediction it also seems likely that the system is well buffered if the high measured pH partly reflects calcareous groundwater discharge. Soil C/N was predicted to decrease reflecting the ongoing impact of eutrophying N deposition however this did not yield predictions of significant negative changes in species composition because the continued saturation of the substrate plus high pH are likely to constrain more nutrient-demanding mesophytes (Table 3).

Figure 1. MAGIC prediction of change in soil pH and soil C/N at Dead Island Bog. The interval between the vertical dashed line and the right axis indicates the time period over which plant species changes were predicted.



Since the sampled vegetation was formed as a floating raft over waters that may comprise at least some calcareous discharge, it seems likely that the system should be well buffered against changes in soil pH and soil moisture. However, succession on such mire surfaces can see the initiation of more acidic *Sphagnum*-rich nuclei or in this case possibly the formation of a more mesophytic, drier, grassy vegetation. It is not known whether the sampled area is subject to management. If not then biomass accumulation and progressive drying of surface layers might be expected to provide conditions more favourable to mesophytes which would be exacerbated by the predicted ongoing soil response to N deposition.

Predictions of habitat suitability for species recorded in 2005 plus CSM indicators for raised bog highlight a number of points. Firstly, habitat suitability values were generally low for raised bog indicators confirming the fact that the vegetation is better classified as minerotrophic rather than ombrotrophic mire. In fact soil conditions were expected to be much more favourable for a range of rich fen indicators not actually recorded in the sample plot (Table 3). The majority of species actually present also had low predicted suitability values. This may reflect the low predicted soil water pH compared to observed and also that some of the species present are mesophytes of drier ground raising the possibility that the vegetation was characterised by vertical and horizontal variation in soil dryness and depth. Hence the soil chemistry of the rooting zone experienced by many of the more mesophytic species sampled on site might not be adequately represented by the soil sample of peat slurry taken from below the vegetation mat.

Changes in habitat suitability were predicted to be small over the 45 year period. Although percentage changes in suitability value are large for some species, the very small starting value means that the size of the absolute change is also very small (Table 3). Slowly declining soil C/N interestingly results in more favourable conditions for species such as *Sphagnum subnitens*, *Carex rostrata* and *Eriophorum angustifolium*. In parallel, increasing fertility is also predicted to favour mesophytes of

drier conditions yet their suitability values remain very low reflecting waterlogged conditions and high pH. If appreciable drying occurred habitat suitability for these less typical species could jump dramatically. Such a scenario could be simply explored by simulating reduced soil moisture alongside MAGIC predictions of change in C/N and pH, and generating new species predictions.

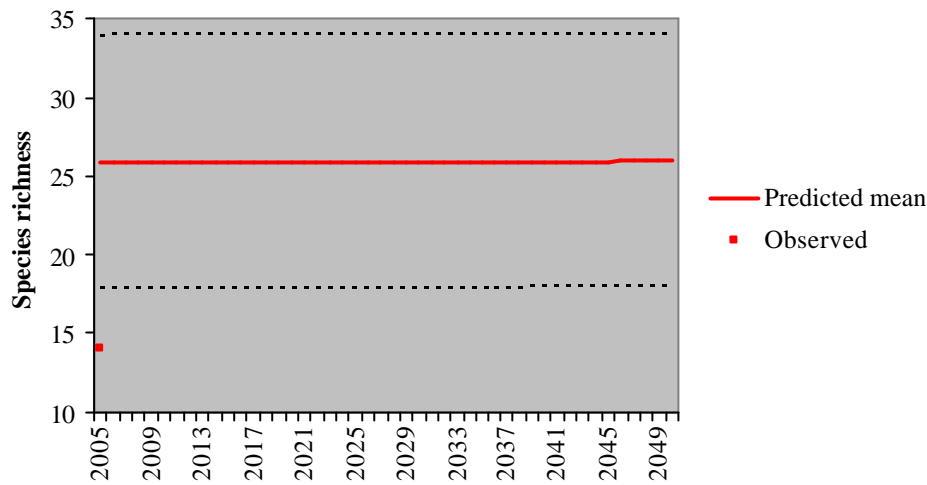
Table 3. CSM indicator table for Dead Island Bog. CSM categories follow those listed in JNCC habitat guidance for the Raised Bog Priority Habitat as follows; P=positive, N=Negative. Predicted habitat suitability values are listed in column Hs 2005. Values range between 0 and 1 with a higher value indicating more favourable conditions for species persistence. % change in Hs indicates the size of the predicted reduction or increase in Habitat suitability index as a percentage of the starting value in 2005.

Present in 2005	CSM category	Species	Hs 2005	% change in Hs score
1		<i>Sphagnum subnitens</i>	0.758507	7
1		<i>Calliergon cuspidatum</i>	0.128934	33
1	P	<i>Eriophorum angustifolium</i>	0.043444	36
1		<i>Carex rostrata</i>	0.039313	27
1		<i>Holcus lanatus</i>	0.016294	40
1		<i>Hypnum cupressiforme sens.lat.</i>	0.015659	-15
1		<i>Hypnum jutlandicum</i>	0.015659	-15
1		<i>Festuca rubra agg.</i>	0.001134	59
1		<i>Angelica sylvestris</i>	0.000533	43
1		<i>Sphagnum recurvum</i>	0.000396	33
1		<i>Anthoxanthum odoratum</i>	5.01E-05	51
1		<i>Juncus acutiflorus</i>	4.6E-06	104
1		<i>Rumex acetosa</i>	2.34E-06	87
1		<i>Epilobium palustre</i>	7.67E-08	152
	N	<i>Phragmites australis</i>	0.344393	-4
	P	<i>Calluna vulgaris</i>	0.024667	-1
		<i>Empetrum nigrum</i>		
	P	<i>subsp.nigrum</i>	0.020845	52
	N	<i>Deschampsia cespitosa</i>	0.001586	37
	P	<i>Sphagnum capillifolium</i>	0.001527	21
	P	<i>Vaccinium oxycoccos</i>	0.001056	-1
	N	<i>Pinus sylvestris</i>	0.000574	-5
	N	<i>Picea abies</i>	0.000469	0
	P	<i>Sphagnum cuspidatum</i>	0.000417	-2
	P	<i>Drosera rotundifolia</i>	0.00037	51
	N	<i>Epilobium hirsutum</i>	0.000331	36
	P	<i>Eriophorum vaginatum</i>	0.000314	3
	N	<i>Cirsium vulgare</i>	0.000295	14
	N	<i>Picea sitchensis</i>	0.00025	-1
	P	<i>Trichophorum cespitosum</i>	0.0002	76
	P	<i>Erica tetralix</i>	0.000155	121
	N	<i>Pteridium aquilinum</i>	0.000149	9
	N	<i>Polytrichum juniperinum</i>	0.000125	-34
	N	<i>Rubus fruticosus agg.</i>	8.89E-05	25

P	<i>Sphagnum papillosum</i>	7.35E-05	-3
P	<i>Andromeda polifolia</i>	3.52E-05	-15
P	<i>Drosera longifolia</i>	3.21E-05	328
N	<i>Cirsium arvense</i>	2.79E-05	41
N	<i>Sorbus aucuparia</i>	2.11E-05	36
N	<i>Polytrichum commune</i>	1.97E-05	57
P	<i>Sphagnum magellanicum</i>	1.41E-05	-14
P	<i>Drosera intermedia</i>	9.96E-06	155
N	<i>Quercus robur</i>	9.02E-06	33
N	<i>Betula spp.</i>	5.31E-06	73
P	<i>Narthecium ossifragum</i>	2.96E-06	140
P	<i>Sphagnum pulchrum</i>	1.09E-06	-2
N	<i>Rhododendron spp.</i>	1.03E-06	11
N	<i>Polytrichum formosum</i>	3.6E-07	20
P	<i>Sphagnum tenellum</i>	1.44E-07	-4
N	<i>Polytrichum piliferum</i>	3.42E-08	-4
N	<i>Phalaris arundinacea</i>	1.99E-08	106
N	<i>Juncus effusus</i>	2.46E-10	181
N	<i>Glyceria maxima</i>	1.36E-11	191
rich fen	<i>Carex echinata</i>	0.524746	24
rich fen	<i>Primula farinosa</i>	0.524634	7
rich fen	<i>Carex panicea</i>	0.430508	13
rich fen	<i>Carex dioica</i>	0.42982	12
rich fen	<i>Carex hostiana</i>	0.339797	11
rich fen	<i>Listera ovata</i>	0.290122	-11
rich fen	<i>Molinia caerulea</i>	0.26562	11
rich fen	<i>Ranunculus flammula</i>	0.251751	-1

While no change in species richness was predicted for the interval 2005 to 2050, the observed richness in 2005 falls outside the prediction interval. Hence, the model prediction is both highly uncertain and lacks accuracy in reproducing the observation at time 1.

Figure 4. Predicted species richness change per 4m<sup>2</sup> at Dead Island Bog. The dashed line indicates the 95% prediction interval.



### Uncertainty and sensitivity

The starting C/N value at Dromore Motte was the lowest of all eleven test sites employed in the N Impacts project while the plant species composition predicted a higher soil C/N value of 12.7 when mean Ellenberg fertility was back-transformed into soil C/N. A general conclusion from the testing phase of this project is that the calibration between soil C/N and Ellenberg fertility is surrounded by very high uncertainty. Moreover, the shape of the calibration curve (an exponentially declining curve which flattens out at high mean Ellenberg fertility) means that very small changes in C/N result in large changes in Ellenberg fertility. Hence this oversensitivity coupled with high uncertainty reduces the accuracy of predictions particularly in more fertile, mesotrophic grassland systems. This is an area for further development.

In general, predictions of *change* in habitat suitability of species already present on site or as indicators in the local species pool, should be more robustly estimated than attempts to predict the entire species composition given just soil conditions and canopy height. Moreover, the degree of confidence in the predictions of changing habitat suitability can at least be readily assessed since the species actually present in soil and vegetation sample plots should have high predicted habitat suitability values. In this respect both sites performed poorly indicating species assemblages apparently inconsistent with measured soil conditions.

At Dromore Motte, measured soil water pH was consistent with that predicted by the species composition (mean Ellenberg R), but C/N was not consistent. At Dead Island Bog, measured soil water pH was closer than measured soil C/N to values predicted by the species composition of the vegetation. The mismatch between vegetation and C/N at Dead Island Bog may well be related to micro-topographic variation in soil and vegetation. It was apparent that the more mesophytic herbs and grasses such as *Holcus lanatus*, *Festuca rubra* and *Rumex acetosa* were probably rooted in drier superficial layers made up mainly of humus and litter. Hence these species may well

experience different root zone conditions than the sloppy, waterlogged and high pH peat sampled for soil chemistry beneath the quaking vegetation mat.

## **Appendix 10: Development of environmental indices (Ellenberg-style scores) for British bryophytes.**

Mark O Hill, David B Roy, Chris Preston

### **Introduction**

The indicator values of Ellenberg have been widely used in Britain and Europe to suggest causes and directions of environmental change. For example Smart *et al.* (2003) have applied the indicator values derived by Hill *et al.* (1999, 2000) to interpret changes found by CEH's Countryside Survey. At the present time, indicator values are available for a slightly extended set of British vascular plants (Hill, Preston & Roy, 2004). Bryophytes (mosses and liverworts) are thought to be more sensitive to atmospheric pollution than vascular plants (Baddeley, Thompson & Lee, 1994; Lee, Parsons & Baxter, 1993; Pitcairn, Fowler & Grace, 1995), and especially in the uplands, give a good indication of other environmental conditions.

Bryophyte indicator values have been produced for other European countries, but only the values of Düll (1991) have been fully published. Düll's values are defined for central Europe; some are definitely not right for Britain, and a few appear to be simply erroneous. A set of values was derived for the Netherlands by Siebel (1993). These accord much more closely with British habitat requirements, although the number of taxa is only 560, of which 13 do not occur in Britain or Ireland and 12 are taxa that are not recognized here. This is only about half the species that occur here, hardly surprising because the Netherlands lacks mountains. Although Siebel's values have been published as a report, they are not published on the internet. However, Dr Siebel very kindly sent them to us, and they have provided a very useful basis for comparison.

In principle, the indicator values of most plants can be inferred from their associates. In some ways, associates are better than physical measurements of the environment, because the physical meaning of indicator values varies according to habitat (Wamelink *et al.*, 2002). For species that have been recorded in a representative sample of quadrats, the mean indicator value of associated species gives a good indication of their environmental preferences. This method was formalized by Hill *et al.* (2000) in a computer program called INDEXT. When the program was applied to the British flora, it produced generally good results, though values derived for rare species were less reliable.

The aim of the present project is to produce a set of indicator values for British bryophytes. For this purpose, we have started with indicator values for vascular plants, and have used INDEXT to tie them to bryophytes. Given values calculated in this way, we have fully developed scales for pH (R values), fertility (N values) and salt tolerance (S values). Preliminary values have been calculated for light (L values) and moisture (F values) but these require further work before they can be accepted as fully developed scales.

## Data and methods

### Datasets

Dataset	Date recorded	Location	Source
Skye	1966-1969	Isle of Skye, Scotland	H.J.B. Birks (Bergen)
Grasslands	1975-1999	Wales and England	R. Alexander (EN)
Key Habitats	1990-2000	Britain	Simon Smart (CEH)
McVean & Ratcliffe	1952-1959	Scottish Highlands	D. Horsefield (SNH)
NVC	1965-1980	All Britain	I.M. Strachan (JNCC)

**Table 1.** Quadrat datasets used for calibration of bryophyte indicator values.

Taxon	Component dataset					Totals	
	Skye	Grasslands	Key Habitats	McVean & Ratcliffe	NVC	Total	Total flora
<b>Number of quadrats in dataset</b>							
<b>Number of species</b>							
Vascular	380	780	620	351	813	1267	1885
Liverwort	92	20	38	105	61	162	298
Moss	181	130	122	189	165	345	758
Lichen	18	6	39	21	8	76	1763
Other	3	2	0	1	2	7	
All species	674	938	819	667	1049	1857	
<b>Number of species with at least 5 occurrences in data</b>							
Vascular	254	531	404	239	739	1004	
Liverwort	42	8	25	57	54	107	
Moss	95	80	94	117	150	254	
Lichen	1	5	31	12	4	48	
Other	1	0	0	0	2	4	
All species	393	624	554	425	949	1417	
<b>Total number of records in dataset</b>							
Vascular	7093	321357	76374	13747	384281	802852	
Liverwort	695	281	1414	1899	9977	14266	
Moss	2688	18813	7836	6566	58759	94662	
Lichen	47	332	1296	288	373	2336	
Other	10	4	0	1	633	648	
All species	10533	340787	86920	22501	454023	914764	

**Table 2.** Records of taxa in datasets, compared with the total flora; sources for the total flora numbers are Hill *et al.* (2004) for vascular plants, Blockeel & Long (1998) for bryophytes, and the British Lichen Society website <http://www.thebls.org.uk/> for lichens.

The datasets used to link bryophytes to vascular plants came from five sources (Table 1). The Skye data have mostly been published as a book (Birks, 1973), as have the McVean & Ratcliffe data (McVean & Ratcliffe, 1962). The NVC data consists of the dataset used for compilation of frequency tables in the National Vegetation Classification (Rodwell, 1991-2000), excluding the two previous datasets. The Grasslands dataset is derived from surveys conducted by English Nature and Countryside Council for Wales. The Key Habitats dataset was also collected by survey teams of the nature conservation agencies.

Only presences and absences were used for calibration. The total number of such records, including vascular plants, was more than 900,000 (Table 2). The number of bryophyte records was 109,000, of which 14,000 were liverworts and 95,000 were mosses. Notwithstanding the large disparity in total number of records for these groups, the number of liverwort species with at least five occurrences in the total dataset was 36% for the British flora, and the proportion of moss records with this number was 34%. This is a lower proportion than for the vascular plants, for which 53% of species had at least five occurrences.

#### *Calculation of indicator values from data*

The program INDEXT was used to make an initial calibration. The program requires some initial values - in this case the indicator values for vascular plants (Hill *et al.*, 1999) together with Siebel's Dutch values for L (light), F (moisture) and R (pH). Values for N (nitrogen) were not available at the outset of the project, and were interpolated without the Dutch value. This required a two-stage process, with values calculated and readjusted to fit the original scale. Values for salt tolerance were obtained by the simpler process of reviewing the whole bryophyte flora and subjectively matching the salt tolerance of taxa to the categories defined by (Hill *et al.*, 1999). This was possible, because only a small number of bryophytes are salt tolerant or benefit from salt deposition (see below).

INDEXT is designed to remove bias, by regressing original indicator values on those derived from associates. It is not completely successful in this for the N scale, which was attempted first. For all scales, it was decided to adjust calculated values by a process designed to produce the same range of and proportions of indicator values. This process was done for the dataset including vascular plants, and then the new values were interpolated. Specifically, consider an indicator value X. Let

$zX$  be the given values there were used for INDEXT.

Values of  $zX$  were assigned using published British values (Hill *et al.*, 1999) for vascular plants, Dutch values (where available) for the L, F and R scales; the final set of bryophyte values for the N scale, and no initial bryophyte values for the S scale.

Let

$nX$  be the recalculated values using INDEXT, and

$iX$  be the interpolated scale.

The interpolation  $iX$  is got from  $nX$  by ensuring that the frequency of each value in  $zX$  is the same as in  $iX$ . For example, if 15 species score 4 in  $zX$ , then 15 species score 4 (rounding to the nearest whole number) in  $iX$ , excluding those species for which there was no initial value  $zX$ . Species for which  $nX$  is close to the borderline chosen for the threshold between 3 and 4 have unrounded scores approximately 3.51, and those at the upper boundary 4.49. In this way a fully-calculated interpolation is achieved.

Given an initial rescaling  $iX$ , the results for R, N and S were then reviewed and adjusted, using personal knowledge and published associates. As far as possible, calculated values were used, but for species that were rare in the sample, calculated values were often misleading. Associates were obtained especially from Paton (1999) for liverworts and Hill, Preston & Smith (1991, 1992, 1994) for mosses. Other important sources were Paton (1969) and Wigginton (1995, 1999). In a few cases of newly-reported species, the original notice in the British literature was used.

## Results

The method by which nitrogen values N were derived differed from that of the others. Initially, all bryophyte (and lichen values) were treated as unknown. The process of rescaling resulted in bryophyte-rich, nutrient-poor habitats being treated as particularly extreme. This was an artefact, which could have been eliminated by the algorithm described above, by which  $iX$  was derived from  $rX$ . The higher values of  $nN$  were reliable enough, agreeing closely with Siebel's published Dutch values. The lower ones were adjusted by a process similar to that used to derive the scales  $iX$  but this was not fully formalized. Finally, values of  $nN$  were calculated using the derived values for N. These values, and the resulting interpolated values  $iN$  have not been used, but are presented for completeness, and as a check on how reliable the process of adjustment has been.

N	1	2	3	4	5	6	7	Total
R								
1	32	1						33
2	74	87	3					164
3	45	74	24	7	1			151
4	9	66	47	12	5			139
5	3	38	49	59	25	1		175
6	2	55	32	50	36	15	4	194
7	4	89	29	59	30	30	10	251
8		36	12	23	11	1		83
9	3	17	9	4	1			34
Total	172	463	205	214	109	47	14	1224

**Table 3.** Numbers of bryophytes species in indicator-value categories of R (reaction or pH) and N (nitrogen or fertility). All taxa are shown in the totals, including varieties, subspecies, species and aggregates.

N	1	2	3	4	5	6	7	Total
S								
0	172	449	195	197	105	40	14	1172
1		10	5	5	2	1		23
2		3	3	2	1	5		14
3		1	2	3				6
4				7				7
5					1	1		2

Total	172	463	205	214	109	47	14	1224
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**Table 4.** Numbers of bryophytes species in indicator-value categories of S (salt-tolerance) and N (nitrogen or fertility). All taxa are shown in the totals, including varieties, subspecies, species and aggregates.

	L	F	R	N	S
Bryophytes	6.38	6.16	5.01	2.85	0.09
Liverworts	6.02	6.32	4.03	2.36	0.05
Mosses	6.56	6.09	5.36	3.03	0.10
Vascular plants	7.12	5.86	6.21	4.38	0.39

**Table 5.** Mean values of Ellenberg indicator scales L (light), F (moisture), R (reaction), N (fertility) and S (salt) for categories of bryophytes and vascular plants.

The resulting scales (Tables 3, 4) show very clearly that bryophytes tend to occur in low-fertility habitats. The mean N value for bryophytes (Table 5) was 2.9, and for liverworts only 2.4. This is fully 2 units lower than the mean for vascular plants. Mean R values show similar differences, the liverworts having a mean value of 4.0, whereas mosses are 5.4 and vascular plants 6.2. The average liverwort is a calcifuge of low-nutrient conditions. Bryophytes, especially liverworts, have a lower proportion of salt-tolerant species than vascular plants. Mean values for L and F are based on the calculated values iL, iF without moderation. Those for bryophyte L are undoubtedly too high, as many bryophytes are cryptic, in relatively dark parts of the ecosystem. Values for moisture indicate little difference between the major groups.

Of bryophytes with high nutrient requirements (N values of 7), only two are liverworts, the thalloid liverworts *Lunularia cruciata* and *Marchantia polymorpha* subsp. *ruderalis* which both grow in plant pots and towns. The mosses *Bryum argenteum*, *B. bicolor*, *Funaria hygrometrica* and *Leptobryum pyriforme* grow in similar places. Of the remainder, *Aphanorhegma patens* and *Physcomitrium eurystomum* grow mainly on eutrophic mud of drying ponds, while *Amblystegium humile*, *A. varium*, *Eurhynchium speciosum*, *Fissidens crassipes* and *Leptodictyum riparium* are plants of fens and eutrophic rivers.

## Discussion

The process of rescaling is designed to attach bryophyte values to a similar set of values for vascular plants. For those bryophytes such as *Sphagnum* spp. and *Racomitrium lanuginosum*, which are important components of their ecosystems, there are many records and the scaling can be done reliably. For some others, especially very small bryophytes, there may be some inaccuracy because the micro-environment does not correspond well with the meso-environment. This is certainly true of Splachnaceae, which are specialists of dung and carcasses on moorlands. It is also true of crevice plants such as *Bartramia pomiformis* and rock plants such as *Grimmia trichophylla*. These were in fact rarely sampled by the botanists recording our datasets. To get good calculated values, it would be necessary to do extensive further sampling, with much smaller recording units. Other under-recorded habitats are arable fields (a recording scheme for arable bryophytes is in progress but has yet

to report), urban habitats, and epiphytic communities. Obligate epiphytes, indeed, were hardly recorded at all.

The under-recorded groups have to be dealt with by linking them to others that are better recorded. Thus the mosses *Orthotrichum diaphanum*, *Pterogonium gracile* and *Zygodon viridissimus* occur on rocks as well as bark. There are in fact several studies of bark bryophytes in relation to pH (see Bates, Roy & Preston, 2004). These have not at this stage been incorporated, but ought to be if the results are to be more physically based in future. Instead, the links have been made by means of associates. For each species, there is a note saying how the indicator value was reached, whether because of characteristic associates or simply as a calculated value. These notes can be used as a record, to infer how reliable the derived values are.

Bryophytes which normally grow on rock are equally difficult to connect with the vascular plants, which do not occupy this habitat. Here, it would be particularly useful to connect them with lichens, which are more numerous and equally sensitive to rock chemistry. Data to make such a connection were not available, but it was usually possible to make an inference, as the species that are confined to basic siliceous rocks are mostly rather rare and have attracted attention because several of them are declining.

### **Future developments**

The main difficulty in using bryophytes for environmental assessment is that they are small and therefore present greater difficulties of identification than vascular plants. In grasslands and moorlands, the number of species with appreciable biomass is generally small. It is quite possible that these can be used for environmental assessment, even if only about 20 species can be identified. This possibility needs to be investigated further.

For bryophytes of trees and rocks, a connection with lichens would be useful. Here again, it may not be necessary to identify many species. A bryophyte growing with *Xanthoria parietina* is almost certainly in a eutrophic situation, whereas a bryophyte growing with *Sphaerophorus globosus* is in a nutrient-poor one.

At all events, better data from samples at a smaller scale, whether made on trees, on rocks or in the dark places under overhanging banks, would give a clearer picture of the indicator value of bryophytes. However, it is striking how well our calculated and interpolated values agree with those of Siebel (1993). This is most encouraging, because it implies that independent workers reach a similar conclusion, even for the harder cases where quadrat samples were lacking.

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## Appendix 11: Recommendations for standard soil sampling and analysis to parameterise MAGIC.

Ed Rowe, Chris Evans

MAGIC simulates the dynamics of soil pH and C/N ratio, in response to the input and loss of cations and strong acid anions. This document sets out the data essential for setting up MAGIC for a site (in bold) and the data useful but for which estimates can often be obtained (in italic). Preferred units are given.

### 1. Hydrology and deposition

Annual precipitation	m / y
Annual runoff (i.e. total water flowing out from the catchment)	m / y
Concs of cations in precipitation: Ca, Mg, Na, K, NH <sub>4</sub>	meq / m <sup>3</sup>
Concs of anions in precipitation: Cl, NO <sub>3</sub> , SO <sub>4</sub>	meq / m <sup>3</sup>

Maps are available for these parameters, but local records are preferable. Historic deposition sequences are obtained from model back-projections (GANE / CEH Bush).

### 2. Management

Removal of nitrogen from soil via hay, burning, accumulating tree biomass etc. (and changes in this removal through time)	meq N / m <sup>2</sup> / y
Removal of cations (Ca, Mg, Na, K) in hay, burning, etc.	meq / m <sup>2</sup> / y

Net N offtake from grazing can often be assumed to be zero. Other site management history should be recorded if possible e.g. type of trees planted, time of felling.

### 3. Soil

Soil parameters reported on an area basis (m<sup>2</sup>) should be calculated as the total (for amounts) or average (for concentrations) for the layers above the solution sampling depth. Depth, bulk density and moisture content measurements are simple, but are used in many of the calculations, so it is worth being accurate.

Depth / thickness	m
Bulk Density	kg/m <sup>3</sup>
Moisture content	g water / g dry soil
Cation Exchange Capacity	meq/kg
Total Carbon	%
Total Nitrogen	%
Exchangeable cations: Ca, Mg, Na, K	% of CEC
Temperature (annual average soil)	oC

Default values can be used if the soil type is known, but site-specific measurements are preferable. If more than one layer is sampled, these measurements are required separately for each layer.

#### 4. Soil solution

Cations: NH <sub>4</sub> , Ca, Mg, Na, K and Al	meq / m <sup>3</sup>
Anions: NO <sub>3</sub> , SO <sub>4</sub> , Cl	meq / m <sup>3</sup>
pH	
Dissolved Organic Carbon	mmol C / m <sup>3</sup>

Aluminium is measured in addition to the ions measured in precipitation - ionic Al is produced in soil by dissociation of minerals.

Soil solution concentrations are variable in time, and are also affected by depth, and by the size of the soil pores from which the solution is drawn. Ideally, samples of all of the active soil solution would be taken repeatedly from a defined depth, and the measurements averaged over the year. The best depth for extraction is at the base of the soil described by the other soil data, typically 30-50 cm. Coarse soil pores contain more transient water than fine pores, so it is better to sample the “matric” water from the latter. However, ionic concentrations become increasingly large as smaller pores are sampled and surface effects become stronger, so it is best to avoid sampling water from micropores, conveniently defined as those holding plant-inaccessible water at tensions below ca. -1.5 MPa.

Soil solution can be obtained by (in order of preference):

- a) Suction lysimeter e.g. Rhizon sampler. Samples coarse and fine pores. Should be left to stabilise after installation for at least 48 hours and preferably 1 month (in sandy soils) to 3 months (in clay and peaty soils) before samples are taken. Long settling-in times are necessary to sample fine rather than coarse pores.
- b) Squeezing. Samples coarse pores. On wet organic soils, squeezing out the soil by hand and filtering the solution can work.
- c) Extraction. This is not a very accurate method, since the amount of each ion that enters the extractant depends not only on the ratio of soil solution to extractant, but on the properties of each ion. Soils should be shaken with local rainwater (or a solution approximating to this, see Table 1) for 24 hours so that ions have time to equilibrate. Note that the soil water content is necessary to calculate the concentrations in the original soil solution. Dried soil should not be used, since there may be strong hystereses in ion sorption and release during drying and rewetting.

Table 1. Rainwater composition at some example sites

Ion	Moorhouse	Rothamsted	Cairngorm	Porton Down
	Conc meq/m <sup>3</sup>			
Ca	3.3	2.05	2.45	2.04
Mg	17.7	10.9	13.0	10.9
Na	77.5	47.5	56.9	47.2
K	1.63	1.00	1.19	0.99
NH <sub>4</sub>	31.8	138	8.22	151
SO <sub>4</sub>	43.6	180	61.7	61.1
Cl	67.4	55.4	66.3	55.1
NO <sub>3</sub>	28.5	106	20.1	69.4

d) Centrifuging. Samples coarse, fine and micro-pores, depending on the spin speed. Yields are small - mineral soils typically contain 0.1 to 0.2 g plant-available water g<sup>-1</sup> so 1 kg soil may be needed for a 100 ml sample. A low spin speed of 1000 rpm is recommended, for consistency and to minimise sampling of the fine pore water; increasing spin speed will not yield much more solution. Adding more solution to increase yield will change absolute and relative concentrations, as with simple extraction, thus removing any advantage of this method.

The accuracy of methods c) and d) needs further investigation.