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Prediction of plant diversity response to land-use change on Scottish agricultural land

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Abstract

Surveys of 87 sites within nine locations on Scottish agricultural land, during 1995–1997, recorded 335 species of vascular plants and 95 bryophyte species, within 31 recognisable plant communities. Multivariate analysis placed the vegetation into five main vegetation types, with differing plant species richness (S : number of species per 100 m²). These were upland grassland (mean $S = 37$); mesotrophic semi-improved grassland (mean $S = 25$); mire/heath vegetation (mean $S = 22$); intensive grassland (mean $S = 12$); and arable land and weed communities, including set-aside (mean $S = 9$).

Management intensity was a good predictor ($R^2 = 0.729$) of vegetation type, with low intensity being typical of upland grassland, and high intensity typical of arable vegetation. The data were used to develop and test a set of minimal linear models of plant diversity response to land-use changes, operating at field scale, under the agro-geo-climatic conditions of mainland Scotland. The models utilised predictor variables drawn from a suite of functional vegetation attributes, environmental data, and management information. All-plant-species S was well predicted at quadrat level (i.e. within field, excluding margins) by three models with high R^2 values (0.82–0.93) utilising management variables such as crop-type, livestock density, time since last cultivation; vegetation state variables such as bryophyte cover, sward height, litter cover; and environmental variables such as soil P content. Bryophyte S was well predicted by four models with high R^2 values (0.83–0.92). Bryophyte percentage cover was the most important predictor variable in these models. Vascular plant species S was less well predicted than either all-plant-species or bryophytes-only models. The models can be used to assess the implications of land-use change scenarios, and to aid management decisions to help to maintain plant diversity within the Scottish agricultural landscape.

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1. Introduction

This paper outlines the findings of a study aimed at developing a suite of models using land-use and agricultural management variables, plus functional attributes of the vegetation, as predictors of plant biodiversity response to changing agricultural land-use in

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Scotland. The study was part of a larger project to model the diversity responses of plants, selected invertebrate groups and birds to agricultural change in Scotland (Abernethy et al., 1996). Results for the animal groups are presented elsewhere (e.g. Foster et al., 1997; Downie et al., 1998, 1999, 2000).

A major task in applied ecology is to predict the impacts of different scenarios of human impact (including land management) on the plant and animal communities of ecosystems (Scheffer and Beets, 1994; Murphy and Hootsmans, 2002). Attempts to model whole-ecosystem response to such impacts have had limited success (e.g. the International Biological Program approaches used in the 1970s: Rigler, 1982), although some recent progress has been made (e.g. Straskraba, 2001). More success has been gained with models which use applied response variables (such as biodiversity measures) as indicators of changes occurring at ecosystem level, within a defined envelope of environmental conditions. Such minimal linear models (Scheffer and Beets, 1994) have proved to be useful tools to understand the functioning of ecological communities within a range of different ecosystem types (e.g. Hilton et al., 1992; Scheffer, 1992; Wilson et al., 1996; Willby et al., 1998; Ali et al., 1999, 2000; Murphy et al., 2002).

Biodiversity may be measured at levels from genome to biome (Colwell and Coddington, 1994; Roy and Foote, 1997; Hawksworth, 1995). Measurement of number of species present (S) within a defined target area is one of the simplest measures of biodiversity. Other diversity indices, e.g. Simpson's index (Ghent, 1991), were found in this study to be highly significantly ($P < 0.001$) correlated with S , and provided no advantage over the simpler measure for modelling purposes, though such indices can be useful where equitability of species occurrence needs to be taken into account (Hawksworth, 1995; Bini et al., 2001). Once baseline values of S are established for the type of ecosystem under consideration, change in S can provide a measure of ecosystem response to altered land-use, e.g. resulting from policy decisions affecting management of the agricultural landscape (Fry, 1991). In particular, loss of diversity often signals ecosystem degradation (Prance, 1991; Murphy, 2002; Robinson and Sutherland, 2002).

The variables measured in this study were considered to be potentially useful predictors of change in

Table 1
Changes in Scottish agricultural land-use (ha) between 1995 and 1997

Land-use	1995	1997	Change	%
Total combine-harvested crops	479910	538520	58610	12
Oilseed rape	52120	59340	7220	14
Winter wheat	108380	108650	270	0
Spring barley	231930	265210	33280	14
Set-aside	80420	40180	-40240	-50
Crops for stock feed, e.g. turnips, fodder beet	28240	27150	-1090	-4
Total improved grass	1112310	1104660	-7650	-1
Grass under 5 years old	346440	325250	-21190	-6
Rough grazing	3303020	3212700	-90320	-3
Woodland	140410	154260	13850	10

plant diversity. The study took place within a land-use envelope ranging from upland sheep-grazed grasslands to lowland intensive arable systems. A multiple regression approach was used to model change in S resulting from land-use and agricultural management changes, which had shown substantial change in Scotland, in the years during which this study was undertaken (Table 1). The model outcomes are only valid for predictive purposes within the envelope of overall applicability of the models. However, the range of agro-geo-climatic conditions prevailing at the input data sites makes the models applicable over most of Scottish agricultural land. There is a reasonable probability that they would also be applicable to other areas of the British Isles having comparable conditions.

2. Methods

During 1995–1997, field sampling was conducted at 87 sites, within nine locations on Scottish agricultural land (Fig. 1). Input data for model construction were collected from sites sampled during 1995–1996. Data from 21 sites, sampled during 1997 were used for model testing. A subset of 15 of the 1995–1996 sites was also sampled during 1997, giving a run of 3 years data for some sites.

2.1. Vegetation

At each sampling site vegetation data were collected from a permanent 10 m × 10 m quadrat located within

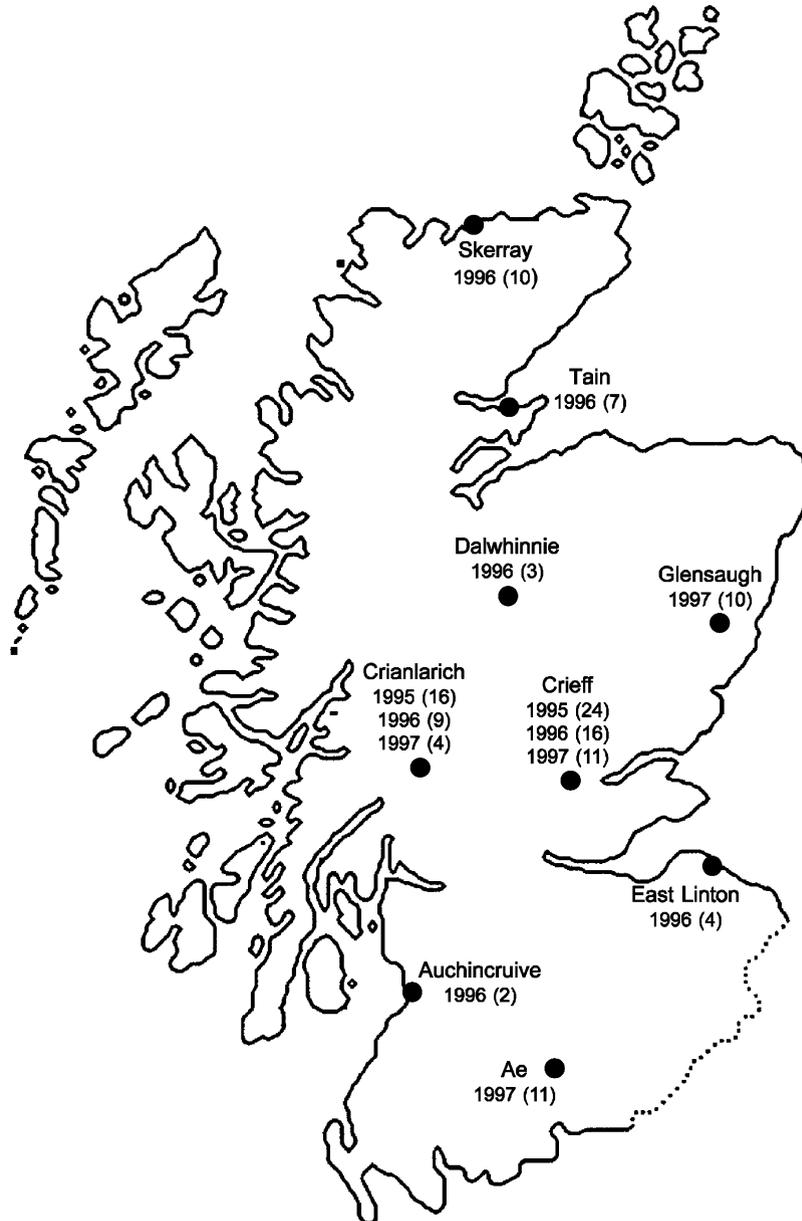


Fig. 1. Location of sampling areas in Scotland, with number of sites in each area (in brackets) and the year(s) of sampling.

a field or other target area (e.g. open moorland). Data were collected three times during the plant growth season (June–September) at approximately a monthly sampling interval. Species abundance was assessed as percentage cover on a continuous scale (except in 1995 when Domin scale values were recorded, and the

data subsequently transformed to percentage cover using median values of the Domin scale cover intervals). Plant biodiversity at the whole-field level (including field (IF) margins) was recorded at each site by spending 20 min searching an area to approximately 100 m around the permanent quadrat (but without

Table 2
Vegetation state variables used 1995–1997

Variable	Measurement	Subset in 1997
Biomass (20 cm × 20 cm) in 0–5 cm vertical layer	g dry weight	Yes
Biomass (20 cm × 20 cm) in 5–10 cm vertical layer	g dry weight	–
Biomass (20 cm × 20 cm) in 10–20 cm vertical layer	g dry weight	–
Biomass (20 cm × 20 cm) in 20–40 cm vertical layer	g dry weight	–
Biomass (20 cm × 20 cm) in 40–80 cm vertical layer	g dry weight	–
Biomass (20 cm × 20 cm) in >80 cm vertical layer	g dry weight	–
Biomass (20 cm × 20 cm) total	g dry weight	Yes
Bare ground	% estimate	Yes
Stem density	In 10 cm × 10 cm quadrat	Yes
Average canopy height	Five random measures (cm)	Yes
Number of flowering or fruiting plants	In 100 cm × 100 cm quadrat	Yes
Seed production	Biomass of seeds (g: in 20 cm × 20 cm quadrat) ^a	Yes
Bryophyte cover	% estimate	Yes
Tussock cover	% estimate	–
Litter cover	% estimate	Yes
Sward-type (categorical)	1: natural/semi-natural 2: sown/improved, now reverted 3: grass mixture 4: ryegrass ley	– – – –

^a In 1995, a 10 cm × 10 cm quadrat was used.

crossing field boundaries). Species were recorded as presence/absence only. Plant species nomenclature follows [Stace \(1991\)](#) for vascular plants, [Smith \(1978\)](#) for mosses and [Smith \(1991\)](#) for liverworts.

Vegetation state variables (field-measured functional attributes of the plant community as a whole) were collected within three 1 m² quadrats (randomly placed within the 10 m × 10 m permanent quadrat area) at each site on each sampling visit. The suite of variables ([Table 2](#)) measured in the first two seasons was reduced to a smaller subset in the third field sampling season (1997) in the light of model development outcomes. Derived variables were calculated for mean biomass and average canopy height over the three sampling occasions.

2.2. Environmental data

During the first visit to each site, four soil cores were taken from within each permanent quadrat area, and returned to the laboratory for analysis of pH, organic and moisture contents, available P and K, and texture. Further cores were taken from the 17 repeat sites sampled during 1997. Data on a range of landscape, land-use, and agricultural management variables were

collected in the field, from farmers' records, and from map records. These variables were compiled once for each site (the repeat-sampled sites only had landscape data collected in 1995). Data were acquired as appropriate from farmers and a range of other sources on the management regime in operation at each site ([Table 3](#)).

A management intensity index (MII) was constructed from the dataset as a summary variable indicating the overall intensity of agricultural management at each site. Eight land management variables were scored at each site for pre-assigned categories (see [Table 3](#)). The sum of the variable scores was then banded as follows: MII band: 1, ≤6; 2, 7–8; 3, 9–11; 4, 12–15; 5, 16–19; 6, ≥20.

2.3. Classification and ordination

Sites were first classified into groups of high internal similarity in terms of flora. Two approaches were followed, the first utilising the broad framework of the UK National Vegetation Classification (NVC) ([Rodwell, 1991–1995](#)). The second method used fuzzy clustering procedures ([Bedzek, 1981](#); [Equiha, 1990](#)) in conjunction with ordination by detrended correspondence analysis (DCA) ([Hill, 1979](#)).

Table 3
Environmental variables used 1995–1997

Variable	Units/categories	Source of data
Hedge length	m/ha	Field/map
Hedge quality	% gaps	Field
Boundary wall (categorical)	1: absent 2: present	– –
Open ditches	m/ha	Field/map
Broad leaved trees	ha	Field
Vegetation layers	Number per 100 m ²	Field
Headland width	m	Field
Altitude	m above sea level (a.s.l.)	Map
Available K	mg/g	Soil analysis
Available P	mg/g	Soil analysis
Sward-type ^a (categorical)	1: natural/semi-natural 2: sown/improved, now reverted 3: grass mixture 4: ryegrass ley	Field/farm records – – –
Age ^a (time since cultivation): categorical	1: uncultivated 2: >10 years 3: 5–10 years 4: <5 years	Farm records – – –
Cutting intensity ^a : categorical	1: no cutting 2: low (topping only) 3: moderate (one complete cut) 4: high (2 or more cuts)	Farm records – – –
Soil disturbance ^a : categorical	1: no disturbance 2: low (only harrowed in past 3 years) 3: moderate (ploughed once in last 3 years) 4: high (ploughed > once in last 3 years)	Farm records – – –
Soil pH		Soil analysis
Grazing ^a : cattle	Number of cattle grazing units	Farm records
Grazing ^a : sheep	Number of sheep grazing units	Farm records
Inorganic input (fertiliser) ^a : categorical	kg/ha of NPK fertiliser 1: none 2: low (<50) 3: moderate (50–100) 4: high (>100)	Farm records – – –
Organic input ^a —organic fertiliser used/not used: categorical	1: not used 2: used	Farm records –
Pesticide input ^a —pesticide(s) applied/not applied: categorical (includes fungicides, herbicides and insecticides)	1: not applied 2: applied	Farm records –
Soil loss—organic content lost on burning	% loss on ignition	Soil analysis
Soil moisture	% water content	Soil analysis

Note that grazing did not distinguish sheep and cattle in calculation of MII.

^a Variables used in calculation of management intensity index (MII).

2.4. Modelling

The input data collected for the vegetation, landscape, management and environmental variables measured at each site were used to develop a suite of multiple regression predictive models for biodiversity response variables (i.e. values of S for each plant group: bryophytes, vascular plants and all-plant-species combined). The main features of the modelling process were as follows.

1. Models were progressively built up using generalised linear modelling (GLIM) procedures (Crawley, 1993), first from 1995 data. Outputs were used this to predict 1996 values of S , then re-analysed on the basis of combined datasets for the 2 years. Principal components analysis (PCA) was used to generate start points for the modelling process, but PCA ordinate values were not used as modelling variables themselves (Robertson et al., 1993). This process would be repeated using the two most significant variables from each of the four most significant PCA axis. If no interesting results were generated then alternate start points would be used. These included using the two most significant variables from other PCA axis, or using every variable within the pool as an individual start point.
2. The modelling procedure was hierarchical, using a sub-routine technique, with models initially built at the level of the data groups. The data were subdivided into three groups: vegetation state variables, management variables, and landscape variables. Each sub-routine included five response variables randomly selected from the group's total pool. Generation of sub-routines was complete when each response variable was represented within a minimum of three sub-routines. For each sub-routine non-significant variables were deleted until a minimal model was generated, then each variable from the total pool was re-added to the minimal model and the significance of the added variable checked by removal. The generation of models from each sub-routine was continued until options were exhausted. Thus, if a variable from the pool was found to be significant, it would be added to the minimal model and the re-addition process iterated. Using this approach, each sub-routine could generate several models for further consideration.
3. On completion of the initial round of sub-routine modelling, the entire process was iterated with the variables selected as significant in the first round acting as the pool for selection of sub-routines in the second round. This would lead to the generation of a series of minimal models from which no further variables could reasonably be deleted from the pool. To these 'final' minimal models, all variables in the original pool would be individually re-added and tested for significance, thereby generating a selection of final models. If the addition of a new variable caused a variable already in the model to become insignificant, then one of two paths would be followed. Either the new variable would be rejected and modelling continued using the old variable, or the model would be built using the new variable (the old variable being rejected).
4. All tests on the significance of explanatory variables included in the models were by backwards deletion (Crawley, 1993). The statistical validity of models was assessed by residual testing: residuals were examined for normality, randomness against fitted values, randomness against all variables in the minimal model, and randomness against farm (location). Failure of any part of the residual testing process led to culling of that model. Jackknifing procedures (which entailed removal of each site individually from the model, and re-fitting of the model to the input data) were a final check. Gradients and intercepts of the regressions were examined to ensure that they remained within the original standard error for the model. Again, failure at this stage would ensure rejection of the model.
5. On completion of the residual and jackknife testing procedures, a substantial number of candidate models had been generated for each of the target response variables. Including models rejected for imperfect residuals the total number of candidate models generated for was: all plants (AP): 21; bryophytes (B): 27 + 1 composite model; vascular plants (V): 12. Optimal predictive models were subsequently selected from the candidate set on the basis of the following criteria.
 - (i) R^2 value: indicating how well the model performs in predicting actual values for the response variable;

- (ii) the range of predictor variables used (i.e. do different subsets of predictor variables give different outcomes for a given response variable); and
 - (iii) assessment of error pattern for the model across the range of input data for the response variable (does the model, e.g. predict low values of diversity well and higher diversity less well?).
6. The 1997 test dataset from independent sites was used to assess the accuracy of predicted values for S at these sites compared with actual measured values.

3. Results

3.1. Vegetation characteristics

In total 335 species of vascular plants and 95 bryophyte species were recorded from the target sites, together with information for the environmental variables listed in Table 3. The vegetation dataset included as follows.

- A total of 12 out of the 20 common grassland National Vegetation Classification (UK NVC: Rodwell, 1991–1995) categories known to occur in Scotland (Cooper and MacKintosh, 1996), including widespread mesotrophic (MG), upland calcifugous and montane (U), and calcicolous (CG) grassland communities. These included MG5 *Cynosurus cristatus*–*Centaurea nigra* grassland; MG6 *Lolium perenne*–*Cynosurus cristatus* grassland; MG7 *Lolium perenne*–*Trifolium repens* ley; U4 *Festuca ovina*–*Agrostis capillaris*–*Galium saxatile* grassland; U5 *Nardus stricta*–*Galium saxatile* grassland; and CG10 *Festuca ovina*–*Agrostis capillaris*–*Thymus praecox* grassland.
- Examples of all heath types (H) occurring extensively in the agricultural landscape of Scotland: H10 *Calluna vulgaris*–*Erica cinerea* heath; H12 *Calluna vulgaris*–*Vaccinium myrtillus* heath; H14 *Calluna vulgaris*–*Racomitrium lanuginosum* heath; H16 *Calluna vulgaris*–*Arctostaphylos uva-ursi* heath; plus one mire (M) community: M15 *Scirpus cespitosus*–*Erica tetralix* wet heath.
- A broad range of common arable weed communities (OV) on arable land and set-aside.

The 31 NVC categories/sub-categories of vegetation identified as present at the study sites provide a substantial coverage of vegetation types commonly present on agricultural land in Scotland (Carey et al., 1996), and hence provide an adequate envelope of vegetation conditions for the modelling process.

Ordination and classification of the vegetation assemblage data (Fig. 2) suggested that five main categories of vegetation type were represented (eigenvalues: axis 1, 0.90; axis 2, 0.5), with substantial differences in plant species richness (number of species per 100 m²). Arable crop species were excluded from the analysis.

- Group 1: mire/heath vegetation—13 sites (mean species richness $S = 22$).
- Group 2: upland grassland—14 sites (mean $S = 37$).
- Group 3: mesotrophic semi-improved grassland—13 sites (mean $S = 25$).
- Group 4: intensive grassland—24 sites (mean $S = 12$).
- Group 5: arable land and weed communities (including set-aside)—19 sites (mean $S = 9$).

There was a significant relationship between plant assemblage and diversity (measured as plant species richness, S). Assemblages of high diversity tended to occur in upland grassland and mesotrophic semi-improved grassland, whilst mire/heath, intensive grassland and arable communities had lower plant diversity. This relationship followed a humpback curve (Fig. 3), typical of vegetation diversity change across environmental stress or disturbance gradients (high diversity tends to be associated with intermediate environmental conditions rather than with extremes, e.g. Day et al., 1988; Willoughby, 1992; Murphy, 2002).

Total MII (calculated as cumulative score for a range of land management variables) was a good predictor of vegetation type within this ordination ($R^2 = 0.73$, $P < 0.01$), with low intensity being typical of upland grassland, and high intensity typical of arable vegetation. This result provides a statistical indicator of the relationship between land management intensity and vegetation type present on Scotland's agricultural land. There was a weaker ($R^2 = 0.53$, $P < 0.05$) negative relationship between vegetation diversity and management intensity: increasing intensity of

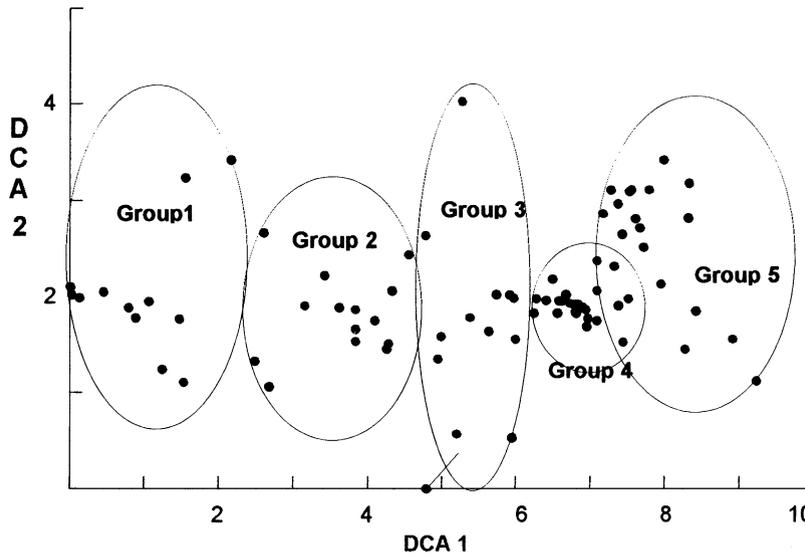


Fig. 2. DCA ordination of sites using vegetation data, overlain by fuzzy group boundaries. Units on axis 1 (DCA 1) and axis 2 (DCA 2): standard deviations of species turnover.

land management was a significant predictor of falling plant diversity.

3.2. Predictive models of plant species diversity change

For each group of plants, models are identified by the numeric codes (in subscripts) allocated to them during the development and testing procedure.

3.2.1. All-plant-species (AP) models

Three all-plant-species models (AP₂₁, AP₂₃ and AP₂₅) emerged as favourites from the selection procedure as having high R^2 (0.82–0.93) coupled with a variety of terms used within the models. From these three models, two others were generated. The first was an average of the three models (AP_{average}), the second (selection model: AP_{selection}) was generated by the following rules. If two of the three models

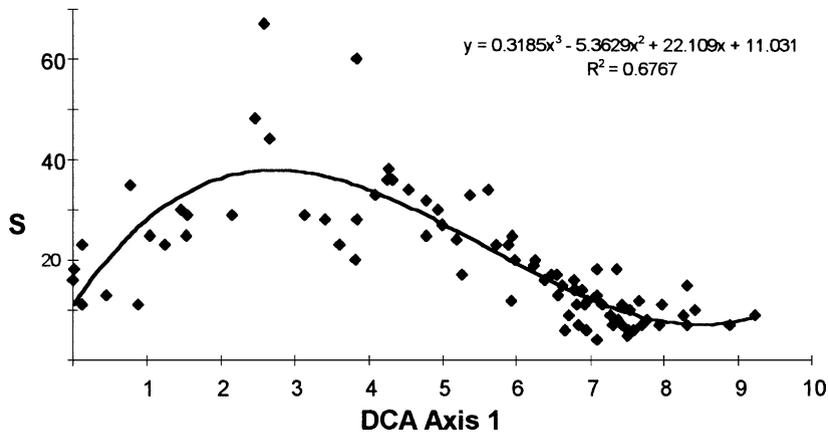


Fig. 3. Hump-backed relationship between plant diversity (S) and DCA axis 1 score (1995 and 1996 sites). Units on axis 1 (DCA 1): standard deviations of species turnover.

Table 4

All plants model (AP₂₁: $R^2 = 0.936$) for calculating species richness (S) using 1995 data

Variable	Equation
NVC ^a (UK National Vegetation Classification category)	IF(NVC = 7, 0.7743), IF(NVC ≥ 3 ≠ 7, 0.3869), IF(NVC < 3, 0)
Field ₉₅ ^a (crop-type occupying field in 1995)	IF(field ₉₅ = 5, -0.9948), IF(field ₉₅ = 9, 0.9835), IF(field ₉₅ < 4, 0), IF(field ₉₅ > 5 < 9, 0)
Age ^a (time since last cultivation)	IF(age = 4, -0.3085), IF(age < 4, 0)
Sward ^a (sward-type occupying field in 1995)	IF(sward = 4, -0.4065), IF(sward < 4, 0)
Headland (width of uncultivated headland strip, m)	0.0188 × headland
ln headland (natural log headland width)	0.3542 × ln(headland + 1)
AvailP (available soil P, mg/g)	0.003347 × availP
ln availP (natural log available P)	-0.05202 × ln(availP + 1)
Biom (change in plant biomass, g/m ²)	0.004808 × biom
Sqrt biom (square root biomass)	0.01895 × sqrt(biom + 0.5)
Cattle (livestock units ha ⁻¹)	-0.1725 × cattle
ln cattle (natural log cattle)	0.1165 × ln(cattle + 1)
Sqrt litter (square root of % litter cover)	-0.04507 × sqrt(litter + 0.5)
Bryo (% bryophyte cover)	-0.02045 × bryo
ln bryo (natural log of bryo)	0.2692 × ln(bryo + 1)
Swardht (sward canopy height, m)	-0.005728 × swardht
Calculation of S	exp(2.895 + sum(above equation outcomes) - 1)

^a For key to model categories for categorical variables, see Table 8.

predicted a value of $S > 25$ then AP₂₁ was used, if two of the three predicted S between 10 and 15 AP₂₅ was used. If the prediction was $S < 10$, AP₂₃ was used. The model for AP₂₁ is shown in Table 4.

The species richness scores of sites sampled in 1995 and re-sampled in 1997 were compared to determine an acceptable level of error for assessment of the quality of model predictions. The average between-year difference in S for this subset of sites was 4.7. The difference is probably attributable to three main factors: stochastic effects and normal sampling variation, effects caused by rotational change or other farming practices altering conditions in the fields between the years of sampling, and year-on-year seasonal differences. This provides a baseline against which to consider model predictions. In assessing the results, error values of ± 2 or ± 4 species were used when comparing predicted and actual values, thus, erring on the side of caution.

All five models gave moderately accurate predictions over the range of S actually recorded at the study sites. For AP₂₁, 26 of the 36 sites were estimated to within two species of the actual value of S . For AP₂₅, this predictive success was achieved at 16 sites, and for AP₂₃, 18 sites. Thus, for predictions within

an error value of two species, AP₂₁ provided a 72% strike rate. If the level of error is allowed to increase to 4 then AP₂₁ was only inaccurate in estimating five sites (86% strike rate).

For all five models, there were sites where predictive accuracy broke down, though the degree of breakdown was not consistent between models, suggesting that with more data, and more model subdivision according to site type, a higher level of overall accuracy could be achieved. Site DF7 (a root crop site of which only three existed in the original model, all located on a single farm) highlights the value of using several models to demonstrate the potential of this technique. At DF7, actual S was 11, AP₂₁ estimated S as 27 and AP₂₅ estimated S at 8.7. The nature of the restricted data from which the models are generated was also highlighted by DF7: more root crop samples would probably have improved the accuracy of the models for use with this crop-type.

An alternative measure of precision is to consider model accuracy in terms of the ability of the models to place sites within broad categories, rather than give precise estimates. Dividing S into four broad categories, <11, 11–20, 21–30 and over 30 species, AP₂₁ places 67% of sites in the correct category.

Table 5

Bryophytes model (B_{21} : $R^2 = 0.932$) for calculating species richness (S) using 1995 data

Variable	Equation
NVC ^a (UK National Vegetation Classification category)	IF(NVC = 6 or 10, 0.7351), IF(NVC = 4, 0.4509), IF(NVC = 5 or NVC > 6 < 10, 0.9618), IF (NVC < 3, 0)
Cut ^a (cutting intensity)	IF(cut = 1, 0), IF(cut = 2, 0.4668), IF(cut = 3, -0.4668), IF(cut = 4, -0.4594)
Layers (number of vegetation layers per plot)	$0.1274 \times \text{layers}$
ln litter (natural log litter)	$-0.1065 \times \ln(\text{litter} + 1)$
Bryo (% bryophyte cover)	$-0.0154 \times \text{bryo}$
ln bryo (natural log bryo)	$0.4801 \times \ln(\text{bryo} + 1)$
Calculation of S	$\exp(0.1006 + \text{sum}(\text{above equation outcomes}) - 1)$

^a For key to model categories for categorical variables, see Table 8.

3.2.2. Bryophyte (B) models

Four models (B_1 , B_2 , B_{17} , B_{21}) with high R^2 values (0.83–0.92) were selected to predict bryophyte S . The range of predictor variables was more limited than those used in modelling S for all-plant-species, with the most important predictor proving to be percentage bryophyte cover. The model for B_{21} is shown in Table 5.

Model B_{17} had the poorest level of performance with the remaining three models all giving similar levels of predictive accuracy. This observation, of broadly similar accuracy, is confirmed by considering the performance of the models in predicting S within a specified error range of ± 1 or ± 2 species. Generally, accuracy was quite good. The models predicted 53–69% of sites to within two species, with model B_{21} performing best.

3.2.3. Vascular plant (V) species models

Three models (V_3 , V_9 , V_{13}) were used to predict 1997 vascular plant S . The R^2 values were lower (0.72–0.78) than for the models used to predict all plant S , or bryophyte S . A further model (V_{subtr}) was calculated by subtracting the scores of the best bryophyte model (B_{21}) from the best all-plant-species model (AP_{21}). The model for V_3 is shown in Table 6.

Examination of the predictions of vascular plant S within a given error range confirmed the poorer performance of these models compared with the all plant and bryophyte models (28–31% accurate predictions for error of two species; 42–57% for error of four species). The overall picture was slightly improved when the ability of the models to place variables accurately within categories was considered. Dividing sites into high S ($S \geq 20$), medium S ($S < 20$ to

Table 6

Vascular plants model (V_3 : including all sites; $R^2 = 0.725$) for calculating species richness (S) using 1995 data

Variable	Equation
Field ₉₅ ^a (crop-type occupying field in 1995)	IF(field ₉₅ = 3 or 9, 0.8829), IF(field ₉₅ ≠ 3 or 9, 0), IF(field ₉₅ < 4, 0), IF(field ₉₅ > 5 < 9, 0)
Swardht (sward canopy height, m)	$-0.0087 \times \text{swardht}$
Wall ^a (presence of field boundary wall)	IF(wall = 1, 0), IF(wall = 2, 0.0607)
ln baregd (natural log % cover bare ground)	$-0.1497 \times \ln(\text{baregd} + 1)$
Cattle (livestock units ha ⁻¹)	$-0.1728 \times \text{cattle}$
Bryo (% bryophyte cover)	$-0.0274 \times \text{bryo}$
ln bryo (natural log bryo)	$0.3695 \times \ln(\text{bryo} + 1)$
Calculation of S	$\exp(3.068 + \text{sum}(\text{above equation outcomes}) - 1)$

^a For key to model categories for categorical variables, see Table 8.

$S > 10$), and low S ($S \leq 10$) ranges, V_3 and V_{subtr} predicted 26 of the 36 sites accurately, V_9 predicted 21 sites accurately, and V_{13} predicted 24 sites accurately. Although the ability of individual models to predict S within a given number of species appears limited, the sites where prediction errors are high are not consistent between models. Thus, 19 sites were accurately predicted to within two species in at least one of the three models. On increasing the error to within four species, 29 of the sites were accurately predicted in at least one of the three models. The results suggest that it is possible to predict S for vascular plant species (and that the level of error is not due to S being inherently stochastic), but that a single model is not adequate to cover all types of site.

3.3. Predicting plant diversity for land-use change scenarios

As an example, the general outcomes of using model AP₂₁ to predict the impacts (as reduction in S , no change, or increase in S) of five land-use change scenarios on within-field all plant (vascular

plants + bryophytes) diversity are shown in Table 7. For actual practical use, inputs of real values or estimates for the relevant input variables for individual fields would be used to provide values for predicted S .

Quantitative negative predictor variables in AP₂₁ were litter cover; sward height; available P; and grazing pressure. Qualitative/categorical negative predictor variables were NVC (any category except CG10, CG11, MG9, MG10, MG5, MG6, U20, U4, M15, M17, M25, H12, H14, H16: see Table 8); field-type in 1995 (wheat; other arable, except root crops or barley; ryegrass); and time since cultivation (<5 years). High values for quantitative predictor variables here are associated with low S .

Quantitative positive predictor variables in AP₂₁ were bryophyte cover; width of uncultivated headland; and change in plant biomass during growing season. Qualitative/categorical negative predictor variables were NVC categories CG10, CG11, MG9, MG10, MG5, MG6, U20, U4, M15, M17, M25, H12, H14, H16); and field-type in 1995 (root crops; barley, but no other arable crop or ryegrass; any other category). High values for these quantitative positive predictors

Table 7

Generalised outcomes of applying all-plant model (AP₂₁) for five scenarios of land-use change (for explanation of variables, see Tables 4 and 8)

Variable	Scenario 1	Scenario 2	Scenario 3 ^a	Scenario 4	Scenario 5 ^b
NVC	0	0	+	0	0
Field ₉₅	–	–	+	0	0
Age	0	0	0	0	0
Sward	0	+	+	+	0
Headland	0	0	0	0	+
AvailP	0	0	+	0	0
Biom	0	–	+	+	0
Cattle	0	–	+	+	0
Litter	0	–	–	+	+
Bryo	0	0	+	0	0
Swardht	0	+	–	–	0
Summary score	–1	–2	+5	+3	+2

Transformed variables omitted. Scenario scores: (–) probable negative impact on S ; (0) probable no impact on S (also allocated if variable does not apply in this scenario); (+) probable positive impact on S . Scenarios: 1, spring barley replaced by oilseed rape; 2, spring barley replaced by moderate-input grassland; 3, reduced inputs of fertiliser and livestock rates on sheep/beef cattle farms; 4, reduced livestock rate of sheep on hill farms; 5, increase in hedges and small woodland areas around arable fields. Summary score is the sum of all scores allocated for all variables for each scenario. A negative summary score suggests a net reduction in all-plant-species diversity is probable; positive summary score suggests a net increase in plant diversity is likely (the larger the score the bigger the likely impact on S).

^a If a shift in short-term ley to less-intensive grassland occurs as a result of this scenario, positive effect on field-type variable impact on S is predicted (shown here); if not, no probable impact on S via this variable.

^b Note that outcomes of applying AP₂₁ reflect only within-field change in S for this scenario: model does not incorporate changes due to diversity change in field margins themselves.

Table 8

Key to model categories for categorical variables used in models

Category	NVC	Age	Wall	Cut	Sward	Field ₉₅
1	Arable/root crops (OV)	Uncultivated	Boundary wall absent	No cutting	Natural/semi-natural	Barley
2	Ryegrass (MG7)	>10	Boundary wall present	Low (topping only)	Sown/improved pasture; now reverted	Grass
3	Marshy lowland grassland (MG9, MG10)	5–10	–	Moderate (one complete cut)	Grass/clover mix	Oilseed rape
4	Lowland permanent grass (MG5, MG6)	<5	–	High (two or more cuts)	Short-term ryegrass or arable crop	Set-aside
5	Bracken (U20)	–	–	–	–	Wheat
6	Upland acid grassland (U4, U5)	–	–	–	–	Gorse
7	Upland calcareous grassland (CG10, CG11)	–	–	–	–	Heath
8	Wet heath (M15, M17)	–	–	–	–	Extensive grass
9	Tussock mire (M25)	–	–	–	–	Root crops
10	Heather moor (H12, H14, H16)	–	–	–	–	–

NVC: UK National Vegetation Classification category (-ies); age: time (years) since last cultivation; field₉₅: crop-type occupying field in 1995; sward: sward-type; cut: cutting intensity (per year).

are associated with high *S*. The scenario outcomes included in Table 7 are briefly discussed as follows.

Scenario 1 (Shift from spring barley to oilseed rape). Both spring barley and oilseed rape are predicted to have low within-field (i.e. excluding margins) plant species richness. However, barley has a slight positive impact on plant *S* while oilseed rape has a slight negative effect. No other factor shifts significantly. The prediction from Scenario 1 is a slight decrease in plant diversity shifting from barley to oilseed rape. Most of the change would probably be gain or loss of a few arable weed species, with NVC category remaining unchanged (OV). Overall plant diversity would remain low.

Scenario 2 (Shifts from spring barley to moderate input grassland). Most of the changes associated with a change from arable crop to short-term grassland (ryegrass ley) are predicted to have a negative effect on plant diversity, perhaps partly offset by the predicted slight improvement associated with a shorter sward height of the grass compared with the cereal crop. The Scenario 2 prediction is a decrease in plant *S* in the ryegrass ley compared with barley. Most of the change would be gain of *Lolium perenne* (plus any associate species in the seed mix), plus gain or loss of a few

weed species NVC category would shift from OV to MG7 (ryegrass-clover) as a result of the change in crop, but both are low-diversity categories, so plant diversity would remain low.

Scenario 3 (Reduced inputs of fertilisers and stocking rates on lowland sheep/beef cattle farms). In this scenario, substantial enhancement of plant diversity is predicted, but the scale of change will be highly dependent on site-specific conditions. The prediction for Scenario 3 is, in most cases, an increase in plant biodiversity over existing moderate to high values of plant *S*; with additional grassland species colonising. The impact on plant community type (and hence diversity) would depend in part on what community was present initially, and whether the management change proved sufficiently great to alter the plant community from intensive grassland to a mesotrophic lowland grassland community (e.g. MG7 ryegrass/clover replaced by MG5/MG6 lowland permanent grassland).

Scenario 4 (Reduced livestock rates of sheep on extensive hill farms). As in Scenario 3, the net effect is likely to depend on site-specific conditions (e.g. what NVC community is initially present), but on balance a positive effect on plant diversity is likely, over and above existing moderate-high values of plant *S* typical

of this landscape type (likely to be one of CG10, CG11, U20, U4, U5, M15, M17, M25, H12, H14, H16: see Table 8). The prediction for Scenario 4 is usually an increase in plant biodiversity over existing moderate to high values of plant *S* (with additional grassland species colonising), unless bracken (*Pteridium aquilinum*) invasion occurs. In the latter case, the biodiversity increase may be reduced, or may even show a negative impact.

Scenario 5 (Increase in hedges and small woodland plots around margins of arable fields). This scenario assumes a shift involving increases in hedge/adjoining woodland, and that the grassland is a short-term ryegrass ley (note that model AP₂₁, developed for use in predicting within-field diversity, does not include field boundary predictors outside uncultivated width around edge of field). If within-field diversity alone is considered the effect of changing boundary conditions by increasing hedge or adjacent woodland probably has little net effect on plant diversity (though such changes are likely substantially to increase total site diversity, when the margins themselves are taken into account). If hedge planting results in a wider marginal uncultivated strip within the field, this may increase plant *S*. However, this may be offset by a possible increase in litter cover. The prediction is no or only a small effect on within-field plant diversity, with no change in NVC category from the original community. Plant diversity in the boundary would probably increase, but this is a separate measure, not predicted by this model and scenario.

4. Discussion and conclusions

The actual number of plant species present on an area of agricultural land, and any subsequent gain or loss, will depend on the starting point of land-use type and existing agricultural management regime, and subsequently on the intensity and precise nature of any management or land-use change. The models developed in this study can be applied either generally, or very specifically to an individual field or fields within a farm to predict changes in number of species present, and hence, the likely impact for habitat stability (measured by the biodiversity support function of the habitat) of proposed management change. Our results show

that different types of agricultural habitat support differing ranges of baseline plant diversity, so the potential changes must always be placed in the context of the actual land-use. An arable field is always likely to have a lower plant diversity than a medium intensity upland grassland area, and has only a limited number of options for management change, if it is to remain an arable field.

Several of the management and land-use regimes often considered important (e.g. Fry, 1991) in maintaining or enhancing the biodiversity of farmland ecosystems were generally confirmed by this study. Minimising inorganic and organic inputs to the land came out as important for the target plant groups examined here. This may have policy implications for both fertiliser use, and the growing practice of slurry disposal on farmland. Crop-type, management of field margins (e.g. headland width) and grazing intensity were all important, but herbicide use (within pesticide use in general) was not a significant predictive factor for plant diversity, and there is little or no evidence from this study that reducing pesticide use would have major effects in maintaining plant diversity. Herbicides are increasingly used as management tools for conservation purposes in agricultural land (e.g. to maintain heather stands in moorland systems: Marrs, 1985; Milligan et al., 1999). The use of herbicide to control bracken would, e.g. from our results be predicted to play a major role in increasing plant diversity in bracken-invaded areas (Pakeman and Marrs, 1992; Marrs et al., 1998). Other non-herbicide bracken control measures would be predicted to produce a similar result.

A factor which emerges from the study is the importance of structural diversity within the habitat for encouraging the occurrence of a wide range of plant species. While not appropriate to all types of agricultural land-use; in many situations, a more complex vegetation architecture can be encouraged by suitable management of, e.g. field margins, with benefits to biodiversity maintenance.

To conclude, biodiversity provides a good measure (though not the only one) of the health and stability of an ecosystem and the plant and animal communities which it supports (Perlman and Adelson, 1997; Dickinson and Murphy, 1998). The models produced by this study provide a tool for assessing the impacts of land-use change on plant species richness. Such

changes have been dramatic in Britain post-1945 (Robinson and Sutherland, 2002), and may be even more so in the near future, given current policy shifts in management of the UK agricultural landscape. The models developed in this study can be used to assess the likely impacts of such changes, in order to optimise land management strategies which would encourage the maintenance or enhancement of existing plant diversity. Uptake and application of models such as those developed here, for use by, e.g. policy-makers or management agencies, can be enhanced by their incorporation in Internet-based application packages, utilising relational databases and an interactive Graphic User Interface (GUI) to permit user-input of values, and to show model outcomes in a simple format. A prototype GUI for use with these models has been developed (Yelloly, 1999) and is currently undergoing further testing.

Detailed strategies for management aimed at restoring or enhancing biodiversity would require substantial additional planning, incorporating local site conditions, and taking into account likely agronomic or other constraints (e.g. Bakker and Berendse, 1999; De Graaf et al., 1998; Hutchings and Booth, 1996), together with the application of additional models where appropriate (e.g. Simpson et al., 1998) to forecast implications for attributes of the system other than just biodiversity change.

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