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National-scale vegetation change across Britain; an analysis of sample-based surveillance data from the Countryside Surveys of 1990 and 1998

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Abstract

Patterns of vegetation across Great Britain (GB) between 1990 and 1998 were quantified based on an analysis of plant species data from a total of 9596 fixed plots. Plots were established on a stratified random basis within 501 1 km sample squares located as part of the Countryside Survey of GB. Results are primarily conveyed in terms of a classification of national land-cover into 22 mutually exclusive Broad Habitat types. Each of the fixed vegetation plots could be assigned to the Broad Habitat in which they were located in either year. Two types of analysis are reported, both based on changes in plant species composition within monitoring plots. The first examined turnover and net change between Broad Habitat types. The second quantified more subtle changes that had occurred within each Broad Habitat using a series of condition measures that summarized multivariate plant species data as a single scalar value for each plot at each time. There are major difficulties in using uncontrolled, large-scale surveillance data to unravel causal linkages and no attempt was made to quantitatively partition variation among competing causes. However, it was clear that results were broadly consistent with environmental drivers known to have operated prior to and during the survey interval. Large-scale vegetation changes could be summarized in terms of shifts along gradients of substrate fertility and disturbance. Changes implied increased nutrient availability across upland and lowland ecosystems while, in lowland landscapes, linear features and small biotope fragments saw a marked shift to species compositions associated with greater shade and less disturbance.

Keywords: Vegetation survey; Biodiversity; Monitoring; Surveillance; Large-scale; Indicators; Condition measures

1. Introduction

Recent developments in European and international policy have recognized the importance of long-term environmental surveillance in tracking the response of biodiversity to ongoing drivers of negative change as well as the progress of abatement measures (Coates, 1992; Wascher, 2000). Biodiversity surveillance contributes to the measurement of change in so-called free goods and services. Since these are typically externalized and uncosted in traditional economic systems, changes in their abundance are not reflected in market price fluctuations (van der Straaten, 1995; Simpson, 1998). Ecosystems, species and the services they provide are however valued by people (Wackernagel and Rees, 1996). Therefore ecological surveillance is required if environmental and land-use policies are to be based on sound assessments of the ecological consequences of human actions.

Without national surveillance of land-cover and biodiversity it is impossible to know what has changed and where, and to ask whether observed change matters. Because the answers to this last question are inevitably negotiable and value-laden (Lawton, 1997; Zeide, 1997), environmental surveillance programs should at least strive to provide objective and statistically based estimates of the quantities to be evaluated. In addition, long-term environmental surveillance data can also be used to characterise reference points in time and can therefore help to counterbalance the increasing imprecision with which previous ecological and landscape baselines are defined as humans age and social memory fades (Dayton et al., 1998). Surveillance data provide reliable descriptions of previous states of nature against which change at larger or smaller scale can be compared (Magnuson, 1990; Smart, 2000; ten Brink et al.,1990).

In recognition of the need for data on large-scale change in biodiversity and land-cover, many nation states have designed and implemented national ecological recording programs (Shear, 1995; Bischoff and Dröschmeister, 2000). The target ecosystems or biological features differ widely among existing schemes (see the numerous examples in (McKenzie et al., 1992; Celedinio 1995). Spatial scale and survey design also differ greatly: for example, so-called sentinel site systems (Sykes and Lane, 1996; Jassby, 1998) allow a high frequency of monitoring of detailed biotic and abiotic data, but on relatively few sites. Other large-scale recording programs survey less intensively but on more sites so that changes in biota and land-cover maybe estimated for the whole statistical population with varying levels of precision. Recording can be carried out as a census of the area of interest (Spencer and Kirby, 1992) or by sampling (Rich and Woodruff, 1996; Solly et al., 1999).

Long-term and large-scale surveillance data can also be used to explore possible links between distal environmental drivers and observed changes in state variables (Firbank et al., 2000; Petit et al., 2001). However, partitioning spatial and temporal variation between the independent effects of known drivers using large-scale surveillance data faces a number of problems. These include a lack of interspersion, replication and crossing of effects, which by definition are not known and designed into the sampling domain prior to the first survey or after a control survey (Stow et al., 1998). Despite considerable technical challenges, ways of estimating the importance of competing causes of large-scale ecosystem change are urgently required.

In Britain, quantitative estimates of stock and change in land-cover and biodiversity have been generated by the sample-based countryside surveys (CS) of 1978, 1984, 1990 and 1998. These data play a developing role in addressing the importance and causes of large-scale change in land-cover and plant species diversity and composition (Barr et al., 1993; Bunce et al., 1999a; Firbank et al., 2000; Haines-Young et al., 2000). In this paper the results are presented of a national scale analysis of change in plant species composition between 1990 and 1998 sampled by CS vegetation plots located within a stratified, random series of 1 km squares across Britain. The spatial co-location of vegetation sample plots within areas mapped for land-cover allow measurements of change in areas and lengths of mapped land-cover features (Howard et al., 2003; Petit et al., 2003) to be augmented by detailed analyses of change in the plant species composition of those features.

The choice of methods used for analysis of vegetation change reflects the objective of quantifying patterns and inferring processes, rather than a need to model variation in species composition in terms of spatial environmental gradients or independent data on potential drivers of vegetation change. Since comprehensive and well-understood classifications of the land-cover and vegetation recorded in the CS already exist, their units are used to define subsets of vegetation plots for analysis (Bunce et al., 1999a; Howard et al., 2003). The two major floristic gradients in the existing vegetation classification have shown strongest correlations with vegetation indices of substrate fertility (primary gradient) and light availability at ground level (secondary gradient). Changes in plant species data are therefore summarised as scalar indicator variables that convey shifts along these two principal environmental gradients. Vegetation change is also conveyed in terms of species richness in plots. The advantage of this measure is its simplicity but it is also simplistic and interpretation needs to take careful account of the likely position of floristic starting points along the hump-backed diversity versus productivity curve.

2. Methods

2.1. Vegetation recording

The CS sample design consists of a series of stratified, randomly selected 1 km squares. Stratification of sample squares was based on predefined strata referred to as ITE land classes. These have been derived from a classification of all 1 km squares in Britain based on their topographic, climatic and geological attributes obtained from published maps (Bunce et al., 1996). For the 1990–1998 analysis, a modification of these land classes was undertaken to allow estimates of stock and change to be calculated by individual countries (England, Wales and Scotland) as well as by aggregations of land classes into Environmental Zones (Firbank et al., 2003).

Within each 1 km sample square a series of vegetation plots were located using a restricted randomization procedure designed to reduce clumping in each square. Plots were also constrained to sample either linear features (road verges, watercourse banks, hedges and field boundaries) or areal features (fields, unenclosed land and small seminatural biotope patches). Plots differed in size depending upon their type (Table 1). The types and total numbers of plots has increased over time from 1978 to 1998 along with the total number of CS 1 km squares surveyed (257 in 1978 rising to 508 in 1990 and 569 in 1998). The locations of all plots were mapped and in some cases permanently marked when first recorded. The same plot locations were then located in subsequent surveys by means of compass bearings, sketch maps and plot location photographs.

In each vegetation plot a complete list of all vascular

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Table 1
Descriptions of the different types of vegetation plots recorded in fixed locations within Countryside Survey 1 km sample squares in 1990 and again in 1998, distinguishing between plot space located in areal and in linear features

Plot type	Number per square	Size (m^2)	Location
X (areal)	5	200	Restricted random sample of fields and unenclosed land
Y (areal)	5	4	Random sample from plant communities in each 1 km square not represented by the other plot types. In highly modified landscapes these plots therefore often sample remnant fragments of semi-natural biotope
B (linear)	5	10	Field boundaries paired with the nearest X plot
H (linear)	2	10	Restricted random sample of hedgerows in each 1 km square. Woody canopy as well as ground layer recorded
R (linear)	2	10	Restricted random sample of road verge vegetation (first established in 1978)
V (linear)	3	10	Additional, restricted random sample of road verges (first established in 1990)
S (linear)	2	10	Restricted random sample of vegetation on river, stream and ditch banks (first established in 1978)
W (linear)	3	10	Additional, restricted random sample of river, stream and ditch banks (first established in 1990)

plants and a selected range of the more easily identifiable bryophytes and macro-lichens was made. Predetermined combinations of species were recorded as amalgams reflecting known difficulties in their separation in the field. Cover estimates were made to the nearest 5% for all species reaching a least an estimated 5% cover. Canopy cover of overhanging trees and shrubs was also recorded even if individuals were not rooted within the plot. All plant species recorded were used in the analyses presented here with no downweighting of rare taxa.

2.2. *Classification of vegetation plot data by plant species composition*

Analyses of vegetation change were carried out on subsets of plots grouped by their type ie. areal or linear, as well as by geographic location, i.e. country or environmental zone. In addition, repeat plots could be classified into similar plant community types, thus minimising variation in species composition and potentially adding sensitivity to the detection of change particular to specific vegetation types. The plant community classes used in this analysis were taken from the countryside vegetation system (CVS), a multivariate classification of CS vegetation plot data. The classification consists of 100 minor classes and eight larger units called Aggregate Classes. Full descriptions of each class and the construction of the classification are given in Bunce et al. (1999a,b). Briefly, the classification was constructed as follows. 100 minor units were derived from a TWINSPAN (Hill, 1979a) classification of all plant species by plot data recorded for the survey years of 1990 and 1978. A small number of outlying groups were rejected including vegetation plots located on bare, ploughed soil and in saltmarsh, an under-represented habitat in CS data. These 100 vegetation classes were aggregated into eight Aggregate Classes using Ward's (1963) method of cluster analysis by maximising the ratio of between- to within-class variance of plot scores on the first four rescaled DECORANA axes (Hill, 1979b). These eight Aggregate Classes provided an ecologically meaningful division of the vegetation data, while maximising sample sizes available for analyses of change (Table 2; Fig. 1).

Environmental interpretations of the major gradients across the classification units were based on correlation between plot scores for ordination axes and mean Ellenberg indicator scores for each plot (see below). Ordination axes 1 and 2 were most strongly correlated with Ellenberg fertility and light scores. Thus changes in plot membership between classes can be interpreted as shifts along these two axes, in turn implicating changes in nutrient availability and disturbance in vegetation change (Fig. 1).

2.3. *Classification of vegetation plots by Broad Habitat*

The Broad Habitat classification for Britain (Jackson, 2000; Howard et al., 2003) provides a framework of 22 generalised land cover types designed to allow the whole land surface to be mapped. During the field survey the total land area within each 1 km square was mapped to Broad Habitat (Howard et al., 2003). However, areas mapped as one type of Broad Habitat can contain considerable floristic variation within them. This follows partly from the scale of the mapping exercise and partly from the generalised definitions of the Broad Habitats (Howard et al., 2003). It applies particularly to the Boundaries and Linear Features and the Rivers and Streams Broad Habitats since they are defined primarily by landscape feature rather than by species composition. While information on dominant plant species forms a part of some definitions, detailed floristic data are not used to determine the identity and mapped extent of Broad Habitat areas on the ground. Hence, CS vegetation data were recorded independently of the

Table 2
Summary descriptions of the eight Aggregate Casses which together form a coarse classification of plant species assemblages represented in Countryside Survey vegetation plots across Britain. For full descriptions see Bunce et al. (1999a)

Aggregate class	Code	Description
Crop/weeds	1	Communities of cultivated and disturbed ground. Includes land under arable cultivation
Tall grassland/herb	2	Most typical of road verges and infrequently disturbed patches of herbaceous vegetation. Includes 'old field' communities of spontaneous, fallow grassland. Usually dominated by tussock-forming perennial grasses and tall herbs
Fertile grasslands	3	Improved and semi-improved grasslands very common across Britain. Usually with a long history of high macro-nutrient inputs and cut more than once a year for silage
Infertile grasslands	4	Unimproved and semi-improved communities in wet or dry and basic to moderately acidic vegetation. Lowland, species-rich mesotrophic grassland is represented here
Lowland wooded	5	Tree and shrub dominated vegetation of hedges, woodland and scrub in lowland Britain
Upland wooded	6	Includes upland semi-natural broadleaved woodland and scrub plus conifer plantation. Also includes established stands of Bracken (*Pteridium aquilinum*)
Moorland grass/mosaics	7	Extensive, graminaceous upland vegetation, usually with a long history of sheep grazing
Heath/bog	8	Ericaceous vegetation of wet or dry ground most extensive in upland areas of Britain. Includes raised and blanket bog vegetation

definition and mapping of the linear or areal Broad Habitat patches in which plots were located. However, because each plot location has a mapped Broad Habitat context, subsets of plots can be grouped by Broad Habitat as well as by plot type, Aggregate Class within the Broad Habitat and geographic location (i.e. country or Environmental Zone) (Table 3).

Seven Broad Habitats were omitted from the analyses because of small sample sizes reflecting their rarity in the CS survey squares. The coastal and marine Broad Habitats were

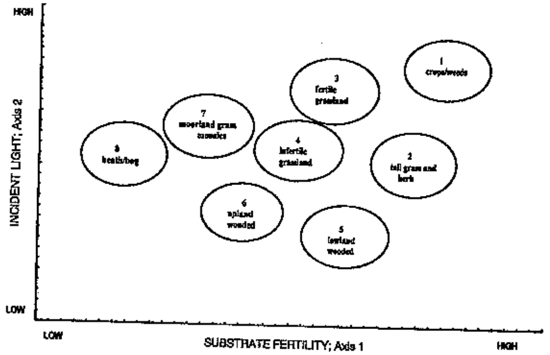

Fig. 1. Countryside Survey vegetation plot data for 1978 and 1990 ($n = 13\,853$) were classified by TWINSPAN to form 100 units. Cluster analysis of their mean DCA scores (axes 1–4) produced eight Aggregate Classes (Bunce et al., 1999a). The diagram shows ellipses which surround the approximate location of the centroids of each Aggregate Class in two dimensions defined by the mean DCA scores of their constituent minor classes. The dimensions of each ellipse are illustrative only and are not intended to represent the range of variation within each class. The Aggregate Classes fall along two primary gradients. Axis 1 is a gradient of substrate fertility and axis 2 a gradient of field layer light availability, which is therefore also correlated with disturbance regime and canopy height. Changes in species composition over time within a plot can result in shifts in Aggregate Class membership and hence the plot may move along the two axes. The direction and magnitude of such shifts can be interpreted as indications of changes in disturbance regime, succession (natural or managed) or eutrophication.

Table 3
Numbers of Countryside Survey vegetation plots recorded in the same locations in 1990 and again in 1998 in 1 km sample squares. The total number of available repeat plots are here divided up by: (a) plot type and Aggregate Class; (b) plot type and mapped Broad Habitat unit. Numbers refer to the membership of plots in each unit in 1990: (a) gives the actual number of plots; (b) has an element of double-counting because plots located in the 'Boundaries and Linear Features' Broad Habitat are also classified on the basis of their nearest adjacent areal Broad Habitat. See Table 1 for descriptions of plot types. In analyses of change R and V plots have been combined as RV. S and W plots have been combined as SW. Rows in italics indicate Broad Habitats with too few plots for meaningful analysis to be carried out

Aggregate class	Plot type						
	Code	B	H	RV	SW	X	Y
(a) *Plot type and Aggregate Class*							
Crops/weeds	1	34	2	42	1	368	25
Tall grassland and herb	2	547	139	594	460	53	282
Fertile grassland	3	202	4	585	120	397	173
Infertile grassland	4	300	41	376	354	371	526
Lowland wooded	5	242	274	28	129	67	176
Upland wooded	6	50	14	47	203	122	164
Moorland grass and mosaics	7	73		105	390	213	345
Heath/bog	8	15		16	171	379	295
Total		1463	474	1793	1828	1970	1986

Broad Habitat name	Plot type					
	B	H	RV	SW	X	Y
(b) *Plot type and Broad Habitat unit*						
Broadleaved woodland	97	18	150	245	147	389
Conifer woodland	32	3	69	68	108	86
Boundaries and linear features	1468	475	1801		3	44
Arable and horticultural	501	171	435	270	358	117
Improved grassland	567	225	510	410	602	267
Neutral grassland	58	15	92	132	59	250
Calcareous grassland	4		7	1	13	23
Acid grassland	63	11	51	146	129	167
Bracken	16	2	15	48	42	59
Dwarf shrub heath	19		29	103	161	131
Fen, marsh and swamp	31		25	134	55	140
Bog	15		18	199	231	180
Open water				*14*		*10*
Rivers and streams				1837		3
Montane				*1*	*3*	*1*
Inland rock			*2*	*3*	*1*	*12*
Urban	*20*	*12*	*70*	*17*	*13*	*39*
Supralittoral rock	*1*		*3*	*5*	*4*	*22*
Supralittoral sediment	*1*				*3*	*5*
Littoral sediment	*2*		*1*	*4*	*10*	*17*
Sea	*1*					*1*
Total	2896	932	3278	3637	1942	1963

under-represented because the limit of field survey was set at the mean high water mark. The urban Broad Habitat was also under-represented since CS, being a survey of the British countryside, deliberately avoided 1 km squares with >75% built land.

2.4. Static and dynamic strata

Subsets of vegetation plots can be classified for analysis of change by strata that cannot change over time. These include plot type and geographic location. In contrast, subsets of plots defined by their Aggregate Class and the Broad Habitat in which they are located can be grouped according to how their Broad Habitat and Aggregate Class changed between the two surveys. This leads to four types of possible analysis, each of which answers a different question about vegetation change by focusing on different aspects of turnover and net change (Fig. 2). In this paper results from two types of analysis are presented; an 'inclusive' analysis of change in Aggregate Class membership within each Broad Habitat type and a 'staysame' analysis of change in indicator scores within each Broad Habitat. These analyses are described in more detail below.

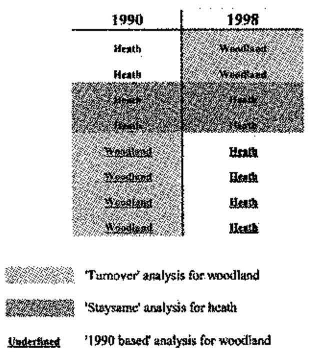

Fig. 2. CS vegetation plots can be grouped for analysis of change by their membership of dynamic strata in each year. In this example, eight plots recorded in the same locations in 1990 and 1998 are shown where vegetation change has resulted in movement between habitat types. The 'inclusive' analysis would involve testing change over all the plots. In this simplistic example, there are only shifts between woodland and heath so that inclusive analyses for each vegetation type would yield the same results. The 'turnover' analysis requires a test of differences in unpaired plots while a '1990-based' analysis includes plots defined by their habitat membership in 1990 irrespective of their plot membership in 1998. A 'staysame' analysis would examine change only in plots that were members of the same habitat type in both years.

2.4.1. Analysis 1: an 'inclusive' analysis of change in Broad Habitat and Aggregate Class membership over time

Statistical tests of net change in membership of each Aggregate Class were carried out on inclusive plot groups for each Broad Habitat. For any plot to be included in this analysis it had only to have been located within the relevant Broad Habitat in either 1990 or 1998 (Fig. 2). This type of analysis provides the broadest possible picture of change between Broad Habitats and Aggregate Classes within each Broad Habitat, since all plots could have changed in either direction over time. This type of analysis is sensitive to net recruitment into and out of a particular vegetation unit from a range of different starting points and can therefore capture relatively large changes in land-cover and plant species composition, for example afforestation of upland bog or cultivation of established grassland. The response variable tested was the net change in numbers of plots in each Aggregate Class between 1990 and 1998 by each Broad Habitat.

Results are presented for analyses of change in areal plots only, thereby focussing on fields, woodland and unenclosed land away from the linear landscape network.

2.4.2. Analysis 2: a 'staysame' analysis of change in mean indicator scores in CS plots that remained in the same Broad Habitat over time

In this analysis, tests of change in mean values of indicator scores were carried out on 'staysame' subsets of vegetation plots that remained in the same Broad Habitat between 1990 and 1998 (Fig. 2). By holding Broad Habitat constant, this analysis is sensitive to more subtle vegetation changes that were not so dramatic as to have resulted in a change Broad Habitat of the parcel of land in which the plot was located.

Tests were carried out on subsets of staysame plots defined by all combinations of country, Environmental Zone, plot type and Broad Habitat. Counts of the outcomes of significant tests are reported for each plot type and Broad Habitat based on tests across plots grouped by the six Environmental Zones, two country divisions and an overall test for GB with no geographic subdivisions, resulting in a total of nine levels of tests. The total numbers of vegetation plots available for analyses of change between 1990 and 1998 are shown in Table 3.

2.5. Derivation of indicator scores

Analyses of vegetation change were based on three indicator variables. Firstly, species richness was calculated for each plot, based only on native species according to Stace (1997) and a standard list of taxa that were considered to have been reliably identified by field surveyors. These filters were used to achieve comparability with previous analyses of 1978–1990 data (Bunce et al., 1999b). The interpretation of changes in species richness is not straightforward because the measure takes no account of the identity of the species concerned. In addition, if a wide enough range of plant communities is sampled, the direction of change in richness is typically not monotonic along either substrate fertility or shade/disturbance gradients (Waide et al., 1999). However, species richness remains an attractive indicator precisely because of its simplicity and appears to be most useful when the floristic starting point is clearly stated since this gives an expectation of the direction of change. In these analyses we interpret species richness changes with reference to the position of plots representing each areal Broad Habitat along inferred gradients of fertility and light availability. Linear Broad Habitats were not treated in this way because they classify land cover on the basis of landscape feature rather than dominant vegetation cover. The remaining indicators were the mean Ellenberg values per plot for fertility and light, used to convey implicit shifts along the two primary gradients of substrate fertility and incident light (Ellenberg et al., 1991). Robust correlations between Ellenberg values and environmental measurements have been found in a range of vegetation types across Europe (Hill and Carey, 1997; Ertsen et al., 1998) and these indicator values are being increasingly used in a range of vegetation change studies (McCollin et al., 1999; Smart, 2000). Mean Ellenberg scores for CS plots used the range of values recently re-estimated for the British flora (Hill et al., 1999, 2000). To achieve comparability with analyses of 1978–1990 data (Barr et al., 1993; Bunce et al., 1999b), none of the indicator scores used were weighted by species cover. Being based on plant species composition the mean plot scores only provide an indirect indication of change in ecological conditions. With this caveat in mind, we hypothesise actual change in ecological conditions from detected change in mean scores over time.

2.6. Analyses of change

2.6.1. Shifts between Aggregate Classes

Changes in plot membership over time were established by allocating 1998 plots to one of the 100 minor vegetation classes. Membership of one of the eight Aggregate Classes then followed from the fact that each of the 100 classes is also an exclusive member of an Aggregate Class. Plot membership of the 1998 data was determined by applying the weightings generated previously for every species during the original TWINSPAN classification of CS data for 1990 and 1978. This algorithm has been implemented as a software tool available free on the World Wide Web at www.ceh.ac.uk/products_services/software.

Two-way matrices of change were formed giving the number of plots in each Aggregate Class i in 1990 and Aggregate Class j in 1998 $(i, j = 1, \dots, 8)$. Net changes from Aggregate Class i to Aggregate Class j were then calculated. McNemar's test (Siegel and Castellan, 1988) for net change among paired data could not be used because vegetation plots within the same 1 km square were more likely to change in the same way and hence were not independent observations. Instead, valid confidence limits and appropriate statistical tests for net change were obtained using the bootstrap data re-sampling technique (Efron and Tibshirani, 1993). Specifically, the matrices of plot changes for each 1 km square (the basic top-level sampling unit) were re-sampled with replacement separately to generate a bootstrap estimate of the overall matrix of change. This re-sampling was repeated 1000 times to generate the bootstrap distributions of the uncertainty in the matrix of change, from which confidence limits and statistical tests of no real change between any particular pair (i, j) of Aggregate Classes were obtained.

2.6.2. Change in mean indicator scores per plot

Significance tests of change in mean indicator scores between 1990 and 1998 were carried out using Student's t-tests for paired data, as the differences were approximately normally distributed. To take account of the potential correlation and hence lack of independence between CS plots within the same 1 km square, the variance of the difference in mean scores was adjusted to take account of contributions from both the within-square and between-square variances estimated by random effects analysis of variance (Searle, 1971). The correct degrees of freedom, allowing for the differing variance components, were calculated using the approximation method of Satterthwaite (1946). No adjustments of table-wide p values were carried out. Instead the total number of tests expected by chance was noted.

3. Results

3.1. Analysis 1: tests of change in Aggregate Class membership between 1990 and 1998 by Broad Habitat

Sufficient repeat plots were available in ten of the 22 Broad Habitats for statistical tests of net change to be carried out between at least one pair of Aggregate Classes. All tests were based on plots located on areal rather than features. Of the ten Broad Habitats analysed, no significant patterns of net recruitment or loss between Aggregate Classes were found in Conifer, Improved Grassland, Acid Grassland, Bracken or Fen, Marsh and Swamp. However, statistically significant net change was detected between at least one pair of Aggregate Classes in Broadleaved Woodland, Arable and Horticultural, Neutral Grassland, Dwarf Shrub Heath and Bog (Table 4).

Net shifts within the Broadleaved Woodland Broad Habitat saw gains to the later successional, tree and shrub dominated vegetation of Aggregate Class 5 away from the mid to late-successional tall grassland and herb vegetation of Aggregate Class 2 (Table 4). In addition, a significant recruitment to the more fertile and usually more intensively managed vegetation of Aggregate Class 3 occurred at the expense of the more species-rich infertile grassland of Aggregate Class 4 (Table 4).

Areal plots located in the Arable Broad Habitat saw a net increase in tall grass and herb vegetation of Aggregate Class 2 at the expense of the highly disturbed communities of the crops/weeds Aggregate Class (Table 4).

The Neutral Grassland Broad Habitat comprises a range of semi-improved as well as unimproved and often species-rich mesotrophic grasslands. Within this Broad Habitat two significant net shifts in Aggregate Class occurred. In the targeted (Y) plots an increase in the much more productive and less disturbed vegetation of Aggregate Class 2 occurred at the expense of the unimproved, mid-successional vegetation of Aggregate Class 4 (Table 4). In the same Broad Habitat but in field situations more likely to be under direct agricultural management (X plots), the change was again to tall grassland and herb vegetation but from the intensively managed fertile grassland of Aggregate Class 3 (Table 4).

Changes within the Dwarf Shrub Heath and the Bog Broad Habitats were similar. In both, the more graminaceous vegetation typical of Aggregate Class 7 gained at the expense of the heather-dominated Aggregate Class 8 (Table 4).

Table 4

Analysis 1: changes in Aggregate Class membership of vegetation in CS fixed plots sampled in 1990 and again in 1998. Column and row numbers indicate Aggregate Class identity (Fig. 1). Numbers in the body of the tables indicate plot counts. * indicate the location of statistically significant net shifts between Aggregate Classes over time. Analyses were carried out on inclusive plots within each Broad Habitat mapping unit in either 1990 or 1998 (Fig. 2). Only matrices that contained at least one statistically significant net shift are shown

		98										90	98	Net Change
		1	2	3	4	5	6	7	8					
(a) *Broad Habitat 1; broadleaved woodland-Y plots*[a]														
90	1		1		**1**					2	1	2	1	−1
	2		**54**	5	5	25*	3			92	2	92	91	−1
	3		8	**9**	*	2	1			20	3	20	20	0
	4		8	6*	**55**	3	9	2		83	4	83	74	−9
	5	1	11*		1	**112**	8			133	5	133	148	15
	6		8		8	6	**43**	3	1	69	6	69	68	−1
	7		1		4		2	**11**	1	19	7	19	18	−1
	8						2	2	**9**	13	8	13	11	−2
		1	91	20	74	148	68	18	11	**431**				
(b) *Broad Habitat 4; Arable-X plots*[b]														
90	1	**255**	28*	39	3					325	1	325	309	−16
	2	12*	**4**	4	2					22	2	22	36	14
	3	38	4	**20**	3					65	3	65	68	3
	4	4		5	**1**					10	4	10	9	−1
	5									0	5	0	0	0
	6									0	6	0	0	0
	7									0	7	0	0	0
	8									0	8	0	0	0
		309	36	68	9	0	0	0	0					
(c) *Broad Habitat 6; Neutral grassland-Y plots*[c]														
90	1	**2**	2	3						7	1	7	4	−3
	2	2	**45**	9	5*	4				65	2	65	82	17
	3		15	**21**	11					47	3	47	46	−1
	4		17*	12	**110**		7	2		148	4	148	132	−16
	5		1			**2**	1			4	5	4	6	2
	6		2	1	4		**6**			14	6	14	15	1
	7						1	**7**	1	11	7	11	10	−1
	8							1	**3**	4	8	4	5	1
		4	82	46	132	6	15	10	5					
(d) *Broad Habitat 6; Neutral grassland-X plots*[d]														
90	1	**3**		3						6	1	6	6	0
	2		2	*						2	2	2	11	9
	3	2	6*	**5**	6					19	3	19	12	−7
	4	1	3	4	**52**					60	4	60	60	0
	5						1			1	5	1	0	−1
	6						**3**			3	6	3	5	2
	7				2		1	**4**		7	7	7	4	−3
	8									0	8	0	0	0
		6	11	12	60	0	5	4	0					
(e) *Broad Habitat 10; Dwarf Shrub Heath—X plots*[e]														
90	1									0	1	0	0	0
	2									0	2	0	0	0
	3									0	3	0	0	0
	4				1			1		2	4	2	2	0
	5									0	5	0	0	0
	6				1		3	4		8	6	8	9	1
	7						4	**37**	6*	47	7	47	62	15
	8						2	20*	**107**	129	8	129	113	−16
		0	0	0	2	0	9	62	113					

Table 4 (*continued*)

		98												
		1	2	3	4	5	6	7	8			90	98	Net Change
(f) *Broad Habitat 12; Bog—X plots*[f]														
90	1									0	1	0	0	0
	2									0	2	0	0	0
	3									0	3	0	0	0
	4				1			1		2	4	2	1	−1
	5									0	5	0	0	0
	6							1	1	2	6	2	2	0
	7						1	**26**	3*	30	7	30	46	16
	8						1	18*	**192**	211	8	211	196	−15
		0	0	0	1	0	2	46	196					

[a] Increase in 3 from 4; $P = 0.040$. Increase in 5 from 2; $P = 0.030$.
[b] Increase in 2 from 1; $P = 0.017$.
[c] Increase in 2 from 4; $P = 0.019$.
[d] Increase in 2 from 3; $P = 0.040$.
[e] Increase in 7 from 8; $P = 0.010$.
[f] Increase in 7 from 8; $P = 0.002$.

3.2. Analysis 2: changes in indicator variables within plots that stayed in the same Broad Habitat between 1990 and 1998

Mean Ellenberg light scores decreased in tests across all linear plot types except hedgerows (Table 5) where no significant changes were detected. Decreased scores indicate a shift toward a species composition associated with more shaded and less disturbed conditions. Away from linear features most tests conveyed decreases in indicator scores, the only exception being Acid Grassland (Table 5). Of those Broad Habitats with sufficient plots for analysis, no significant change was seen in Bog, Dwarf Shrub Heath, Conifer Woodland, Bracken, Urban or Calcareous Grassland.

Tests of change in mean Ellenberg fertility scores were also remarkably consistent. All statistically significant changes but one were increases indicating a shift toward species compositions associated with higher nutrient availability. Increases were seen on the linear network as well as in areal plots (Table 5). No significant changes were detected for Conifer Woodland, Calcareous Grassland, Bracken, Bog or Dwarf Shrub Heath.

Species richness changes were also highly convergent, with 34 out of 37 significant changes being decreases (Table 5). Again, linear and areal plots showed similar changes. Only in areal plots in Acid Grassland and on road verge plots in the Boundaries and Linear Features Broad Habitats were increases detected (Table 5). No significant changes were detected in Calcareous Grassland, Bracken, Fen, Marsh and Swamp, Conifer Woodland or Urban Broad Habitats.

If species richness change occurred as a consequence of change to more fertile and more shaded conditions then direction should depend upon starting point along the gradient of substrate fertility or disturbance versus species richness. Following increases in substrate fertility and shade, reductions in richness ought to occur in Broad Habitats situated to the right of the modal fertility or incident light level, and in the absence of species pool constraints, increases ought to occur in Broad Habitats situated to the left. In fact, the best separation of Broad Habitats and the most pronounced hump-backed relationship was along the indirectly measured fertility gradient (Fig. 3). When Broad Habitats were arranged along this curve it was apparent that those to the right of the mode, which saw significant changes in mean richness, all showed reductions (Fig. 3(a) and Table 5) and were therefore consistent with observed increases in fertility score (Table 5). However, out of the five Broad Habitats situated to the left of the modal fertility score (Fig. 3(a)) only Acid Grassland showed local increases in mean species richness (X plots only—Table 5). Both Dwarf Shrub Heath and Bog Broad Habitats saw reductions in mean richness but with no apparent parallel changes in either Ellenberg fertility or light scores. Species richness changes seem therefore to be rather loosely coupled with changes in Ellenberg scores over the same period.

4. Discussion

4.1. Patterns and processes of large-scale vegetation change between 1990 and 1998

The two types of analysis carried out indicate different aspects of vegetation change across Britain between 1990 and 1998. Analyses of net movement of plots between Aggregate Classes and Broad Habitats are sensitive to relatively large changes in plant species composition. These shifts need not involve large numbers of species but are more likely to reflect the appearance or disappearance of taxa characteristic of markedly different plant communities. Also, since movement between classes can be interpreted as movement along light availability and substrate fertility gradients, observed changes imply processes such as change in disturbance regime and eutrophication. Analyses of change in Ellenberg indicator scores also implicitly convey changes in light availability and substrate fertility by summarising species compositional change in terms of the known associations between plant species and different parts of these two gradients in British vegetation (Hill et al., 2000).

Table 5
Analysis 2: 'Staysame' analysis if change in three indicator variables between 1990 and 1998 based on CS vegetation plots that were in the same Broad Habitat in each year of survey. Counts summarise the number of statistically significant changes detected out of nine tests carried out for each Broad Habitat. Tests were based on plots grouped by plot type, country (England with Wales and Scotland) and six Environmental Zones that further subdivided each country (Firbank et al., 2003)

Broad Habitat	Plot type	Number of significant test results	
		−	+
(a) *Ellenberg light score*[a]			
Broadleaved woodland	X	3	
Broadleaved woodland	Y	4	
Boundaries and Linear	B	4	
Boundaries and linear	RV	3	
Arable and horticultural	X	2	
Arable and horticultural	Y	2	
Improved grassland	X	3	
Neutral grassland	Y	2	
Acid grassland	Y		3
Fen, marsh and swamp	X	1	
Rivers and streams	SW	5	
Total		29	3
(b) *Ellenberg fertility score*[b]			
Broadleaved woodland	X		3
Broadleaved woodland	Y		1
Boundaries and linear	B		6
Boundaries and linear	H		3
Boundaries and linear	RV		4
Rivers and streams	SW		7
Improved grassland	Y		4
Neutral grassland	Y		3
Acid grassland	Y		1
Fen, marsh and swamp	Y		1
Urban	X	1	
Total		1	33
(c) *Species richness*[c]			
Broadleaved woodland	X	3	
Broadleaved woodland	Y	4	
Boundaries and linear	B	4	
Boundaries and linear	RV	4	1
Arable and horticultural	Y	4	
Improved grassland	Y	4	
Neutral grassland	Y	3	
Acid grassland	X		2
Dwarf shrub heath	Y	3	
Bog	Y	1	
Rivers and streams	SW	4	
Total		34	3

[a] Total of 135 possible tests were carried out. 2 ×, 3 × and 22 × as many significant results were detected at $P = 0.05$, 0.01 and 0.001 respectively, than expected by chance.

[b] Total of 135 possible tests were carried out. 1 ×, 2 × and 37 × as many significant results detected at $P = 0.05$, 0.01 and 0.001 respectively, than expected by chance.

[c] Total of 135 possible tests were carried out. 1.5 ×, 3 × and 74 × as many significant results detected at $P = 0.05$, 0.01 and 0.001, respectively, than expected by chance.

Changes in species richness are perhaps more difficult to interpret since decreases or increases maybe positively or negatively valued depending upon position along the diversity versus productivity and disturbance curves as well as on the identity of the species that changed (Huston, 1979; Grime, 1979; Waide et al., 1999; Mittelbach et al., 2001). For these reasons we have considered changes in species richness as outcomes hypothesised to be consistent with detected changes in Ellenberg indicator scores given the position of each areal Broad Habitat on the hump-backed richness versus Ellenberg light and fertility curves.

Analyses of change in indicator scores also focussed on changes in the vegetation of linear as well as areal features and, by holding Broad Habitat constant over time, concentrated on floristic changes not influenced by major shifts in the mapped Broad Habitat type. In the next sections results from the two analysis types are used to jointly assess vegetation change across Broad Habitats in the context of recent land-use change in the British countryside.

4.2. Vegetation change in larger areas of Broad Habitat; 1990–1998

The overall pattern of changes among larger areas of British Broad Habitats is summarised in Table 6 based on analytical results for vegetation change among X plots. Patterns of net change between Aggregate Classes by Broad Habitat saw later-successional classes recruit plots at the expense of earlier-successional vegetation while more fertile classes gained from less (Table 6). These patterns are also broadly consistent with changes in Ellenberg indicator scores, although only Broadleaved Woodland saw increased fertility scores in the larger area (X) plots (Table 6). This pattern of results implies that vegetation change, particularly in lowland Broad Habitats, has been driven by reduced disturbance and/or increasing nutrient availability. Also, given their starting positions along the richness versus inferred fertility curve, the local decreases in mean species richness seen in Broadleaved Woodland and the local increases in Acid Grassland were consistent with the

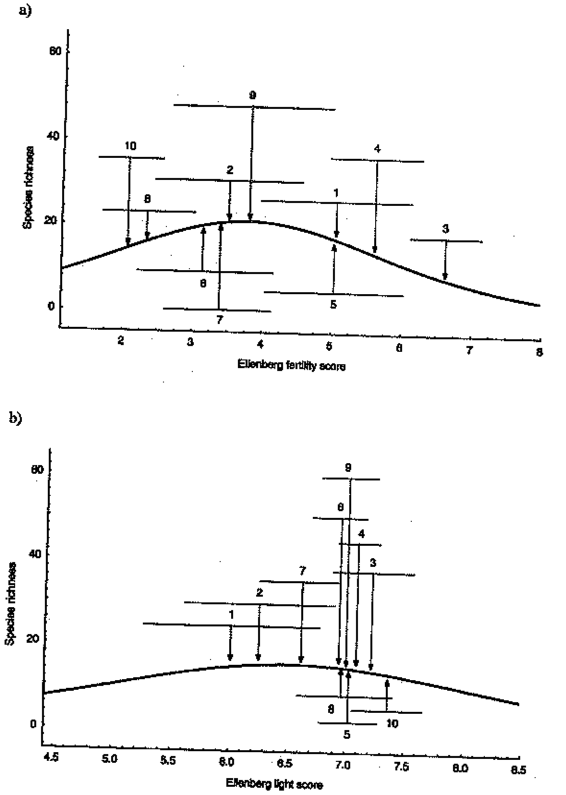

Fig. 3. The location of British Broad Habitats along two indirectly measured environmental gradients versus species richness. Each Broad Habitat is represented by fixed vegetation recording plots located in land-cover parcels that were assigned to the Broad Habitat in the Countryside of 1998. Only areal (X) plots were used because of differences in the dimensions of X and Y plots. The Rivers & Streams and Boundaries & Linear Features Broad Habitats are also excluded because they are defined by landscape feature rather than dominant vegetation. The *Y* axes are species richness per plot and the *X* axes, mean Ellenberg values for fertility (a) and light (b). The position of the mean Ellenberg value among plots in each Broad Habitat is shown plus and minus the standard deviation about the mean. HOF model IV curves (Huisman et al., 1993) were fitted to the raw scatter of plot values to produce the relationships shown. Codes for Broad Habitats are as follows: 1, Broadleaved woodland; 2, Conifer woodland; 3, Arable & Horticultural; 4, Improved grassland; 5, Neutral grassland; 6, Acid grassland; 7, Bracken; 8, Dwarf Shrub Heath; 9, Fen, Marsh & Swamp; 10, Bog.

directions of change expected following increased fertility and decreased light availability.

Net changes in Aggregate Class membership in both the Bog and Dwarf Shrub Heath, Broad Habitats saw moorland/grass mosaics gain at the expense of the heath/bog Aggregate Class, resulting in an inferred shift toward higher nutrient availability but with increased disturbance rather than less, contrary to the direction of change implied for lowland landscapes. This same type of directional change was also seen for the 12 year interval between the CS of 1978 and 1990 (Bunce et al., 1999b). For this earlier period the two most important potential drivers of this net shift were thought to be increases in sheep grazing pressure and atmospheric N deposition (Firbank et al., 2000). The 1990–1998 shift to upland grassland at the expense of Ericaceous vegetation is a continuation of the 1978–1990 pattern and there is a clear need for further attempts to estimate the contribution of competing potential causes of these changes.

Table 6
Summary of the patterns and inferred processes of change among Broad Habitats in Britain between 1990 and 1998. Inferred processes of vegetation change are shown for (a) larger areas of vegetation typically in fields and unenclosed sampled by X plots, and (b) small biotope patches sampled by targeted Y plots. All plots were recorded in the same locations in each year of survey. Changes in disturbance regime and nutrient availability are inferred from changes in species composition based on significance tests of change in Aggregate Class membership and in mean Ellenberg values for fertility and light. The inclusive analysis was based on all plots including those that changed Broad Habitat between 1990 and 1998. The staysame analysis was only based on plots that did not change Broad Habitat over time. '…' indicates that test results were not statistically significant at, at least, $P < 0.05$. Note that the lack of a detected signal can be due to low statistical power as well as absence of real change

Broad Habitat	Inclusive analysis		Staysame analysis	
	Disturbance	Nutrient availability	Disturbance	Nutrient availability
(a) *Fields and unenclosed land; X plots*				
Broadleaved woodland	…	…	Down	Up
Conifer woodland	…	…	…	…
Arable and horticultural	Down	Up	Down	…
Improved grassland	…	…	Down	…
Neutral grassland	Down	…	…	…
Acid Grassland	…	…	…	…
Bracken	…	…	…	…
Dwarf Shrub Heath	Up	Up	…	…
Fen, Marsh and Swamp	…	…	Down	…
Bog	Up	Up	…	…
(b) *Small semi-natural biotope patches; Y plots*				
Broadleaved woodland	Down	Up	Down	Up
Conifer Woodland	…	…	…	…
Arable and horticultural	…	…	Down	…
Improved grassland	…	…		Up
Neutral grassland	Down	Up	Down	Up
Acid grassland	…	…	Up	Up
Bracken	…	…	…	…
Dwarf shrub heath	…	…	…	…
Fen, Marsh and Swamp	…	…	…	Up
Bog	…	…	…	…

Four Broad Habitats showed no evidence of net change. These were Conifer Woodland, Bracken, Fen, Marsh and Swamp and Acid Grassland. The absence of marked directional shifts to Conifer Woodland from Acid Grassland was a departure from the 1978–1990 pattern where analyses of movement between Aggregate Classes, as well as change in mapped land-cover, showed a net gain to upland woodland consistent with increased afforestation in parts of upland Britain (Barr et al., 1993; Tudor and Mackey, 1995; Firbank et al., 2000).

The Arable and Horticultural Broad Habitat covers the most intensively disturbed farmland in Britain. Between 1990 and 1998 a net loss occurred from open communities of cultivated ground and a net gain to the tall grassland/herb vegetation of Aggregate Class 2. This type of change was also detected between 1978 and 1990 (Bunce et al., 1999b). Intensive arable systems in Britain can include rotation between crop and sown grass ley, and for the 1990–1998 interval this was reflected by the marked turnover seen between Aggregate Classes 1 and 3. However, the net gain to Aggregate Class 2 is inconsistent with such rotations since this vegetation type is typically dominated by common perennial herbs and perennial, tussock-forming grasses associated with high nutrient status but relatively low levels of grazing or cutting (Bunce et al., 1999a). The net gain to Aggregate Class 2 seems therefore to represent an increase in fallow grassland assembled from species recruited from the local species pool including the seedbank but especially from nearby linear features (Critchley and Fowbert, 2000). Further analyses are required to explore the relationship between this change and its possible drivers, however the increase in tall grassland/herb on arable land between 1978 and 1990 did coincide with the implementation of the EC-wide set-aside scheme. This scheme was introduced in Britain in 1988 and offered support payments for crop production on condition that a specified percentage of cultivated land was left fallow for between 1 and 5 years (Clarke, 1992).

4.3. Vegetation change in small biotope patches; 1990–1998

Net changes in Aggregate Class membership within smaller patches of semi-natural vegetation were seen in two Broad Habitats (Fig. 4b). In Broadleaved Woodland, increased shade and eutrophication were implied by net losses from less fertile grassland to woodland or to more fertile grassland. In particular, plots located in species-rich, unimproved grassland communities (Aggregate Class 4) in 1990 saw a net transfer to the more fertile and usually managed communities of Aggregate Class 3. Eutrophication was also implied by the net gain to fertile from infertile grassland seen in Y plots in the Neutral Grassland Broad Habitat (Fig. 4b). This indicates that losses of the more species-rich, mesotrophic grasslands continued through the last decade of the 20th century but appeared to affect small remnant patches rather than more extensive areas more likely to have been sampled by X plots and perhaps more likely to have already been improved. In Britain, the reduction in unimproved grassland area that occurred particularly through the last quarter of the 20th century has been well documented (Fuller, 1987; Green, 1990; Blackstock et al., 1999) but an assessment of change focussing on smaller fragmented patches has, until the availability of CS data, been impossible.

Analyses of change in indicator scores for small biotope patches (Y plots) also showed that Fen, Marsh and Swamp, Acid Grassland, Neutral Grassland and Improved Grassland saw an increase in abundance of species favoured by higher nutrient availability (Fig. 4b). Being already associated with high fertility, the Improved Grassland Broad Habitat might not be expected to show much scope for further response to increased nutrient inputs. However, mapped areas of the Broad Habitat include semi-improved swards that can respond to further agricultural improvement (Rodwell, 1992). Changes in Ellenberg light scores indicated a shift towards species compositions typical of more shaded conditions within small biotope patches in Arable and Horticultural, Broadleaved Woodland and Neutral Grassland Broad Habitats. Local Changes in Y plots in the Acid Grassland Broad Habitat implied the reverse tendency, for increased rather than decreased disturbance.

In areas of Britain where the plant species composition of the most abundant land-cover types has been shaped by intensive land management, the observed decreases in light score and increases in fertility score are consistent with aspects of the land-use history of the British countryside not just between 1990 and 1998 but also as an ecological consequence of the planned increase in inputs and agricultural outputs that accelerated throughout the post-WWII era (Green, 1990; Hopkins et al., 2000). Increasingly, evidence from Britain, as well as other northern European countries, indicates that in modern intensively farmed landscapes, remaining fragments of early and mid-successional semi-natural plant communities are vulnerable to succession since patches are more likely to be economically disconnected from the intensively farmed matrix in which they are embedded. As a result isolated fragments may experience either complete removal or lack of management (McDonald and Johnson, 2000; Agger and Brandt, 1998; Poudevigne et al., 1997). In Britain, the last half of the 20th century also saw large increases in the amount of fertilisers applied to farmed landscapes particularly in lowland regions (Potter and Lobley, 1996; Hopkins et al., 2000). Increases in nutrient loads in combination with lack of disturbance are likely to have accelerated the replacement of plant assemblages associated with less fertile conditions by species poor assemblages of potential dominants recruited from local species pools that increasingly reflect intensive land management (Hodgson, 1986; Thompson, 1994; Losvik, 1995).

For mesotrophic plant communities positioned on or to the right of the modal substrate fertility value taken across the range of Broad Habitats, the consequence of increased fertility and decreased disturbance is predicted to be a decline in species richness within sample plots. Declines were indeed seen locally across small biotope patches within Broad Habitats including Arable and Horticultural, Broadleaved Woodland, Improved Grassland and Neutral Grassland. However declining richness was also seen locally in the upland Dwarf Shrub health and Bog Broad Habitats.

4.4. Vegetation change on linear features; 1990–1998

From the limited evidence available, plant communities on linear features in lowland Britain share a common recent history of reduced disturbance with the small biotope patches sampled by the targeted Y plots. For example, although data on uptake levels is hard to find, British farmers have recently been encouraged to establish undisturbed strips along lowland stream and riverbanks to act as buffer zones for the interception of enriched run-off and pesticide drift, to prevent soil erosion and as part of conservation management plans. On roadsides, full-width cutting in Britain is now much less frequent than in the 1960s while the removal of cut biomass has become very rare (Way, 1977, 1978) often only deliberately applied to locally designated 'special' verge lengths (Cumbria County Council, 1992; Riden, 1992). Biomass accumulation in field boundaries and hedge bases may also have been favoured by a GB-wide increase in the length of fencing along these features between 1978 and 1998 (Barr et al., 1993; CS2000 unpublished data). These patterns of changing land-use are consistent with the remarkably clear tendency for increases in Ellenberg fertility scores and decreases in Ellenberg light scores within the Boundaries and Linear Features and Rivers and Streams Board Habitats. These results reflect floristic shifts towards assemblages typical of more shaded and more fertile conditions. This trajectory is also a continuation of the type and direction of change seen on linear features between 1978 and 1990 epitomised by the net gain to tall grassland/herb and lowland wooded Aggregate Classes from the mid-successional, infertile grassland Aggregate Class (Bunce et al., 1999b).

5. Conclusions

The CS of 1978, 1990 and, most recently, 1998 have revealed patterns of large-scale vegetation change that are broadly consistent with the expected effects of some of the drivers of land-use change known to have operated over the 20-year period. The most important of these are probably increased sheep grazing in the uplands, the culmination of 20th century increases in N deposition across British ecosystems, post-1945 agricultural intensification and increased under-utilisation plus eutrophication of agriculturally marginal biotopes and linear networks in the British lowlands (Firbank et al., 2000). The period from 1990 to 1998 has, however, seen subtle changes in these and other environmental drivers. For example net atmospheric N deposition may have declined in some regions of Britain (Negtap, 2001). In addition, agri-environment schemes designed to fund reduced agricultural inputs increased in coverage throughout the period (Ovenden et al., 1998). Land owner attitudes to land management may also have changed. For example, evidence from a sub-sample of land-owners in Countryside Survey squares in 1995 showed a planned decrease in activities associated with agricultural intensification between 1993 and 1998 (Potter and Lobley, 1996), while McDonald and Johnson (2000) found that the willingness of a sample of British farmers to create subsidised wildlife refugia on their land had significantly increased between 1981 and 1991.

The patterns of large-scale vegetation change reported here for the 1990–1998 interval are, however, still broadly consistent with the prolonged and widespread increase in nutrient availability that occurred across British ecosystems throughout most of the 20th century. Whether the reversal of some driving forces has resulted in locally detectable signals in 1990–1998 surveillance data will depend on the prevalence and intensity of associated impacts coupled with the responsiveness of impacted plant communities. Further analyses that attempt to more precisely estimate the role of these and other potential drivers of ecological change in British vegetation are currently underway. Perhaps the biggest challenge for current and future analyses is to find ways of detecting and partitioning out any effects of climate change since this may well prove to be the most important driver of ecosystem change over the next century.

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