Engulfed by suburbia or destroyed by the plough: the ecology of extinction in Middlesex and Cambridgeshire

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ABSTRACT

Middlesex (v.c. 21) has lost 18% of the recorded native vascular plant species through extinction; the corresponding loss in Cambridgeshire (v.c. 29) is 13%. If species which became extinct before 1750 are excluded, this amounts to the loss of one species every 1·7 years in Middlesex and one every 2·0 years in Cambridgeshire. The extinct species share many ecological similarities: they tend to be small, to grow in open habitats and to be characteristic of environments with low fertility. A disproportionate number of calcifuge species has been lost in both areas; in Middlesex, where calcareous soils are rare, many marked calcicoles have also been lost. In both counties the percentage extinction in the small Boreal and Oceanic groups has been greater than that in the larger phytogeographical elements. The peak periods of extinction in Cambridgeshire have been those characterised by major agricultural change; in Middlesex they coincide with the spread of the London conurbation. The overall totals suggest that, judging by the number of extinctions, agricultural intensification is almost as damaging to the native flora as urbanisation.

KEYWORDS: Life-form, Ellenberg values, phytogeography.

INTRODUCTION

One of the many ways to study the changes in the native flora of Britain during recent centuries is to look at extinctions at a local level. Over a century ago, West (1898) suggested that no counties had lost more native species than Middlesex (v.c. 21) and Cambridgeshire (v.c. 29), two areas where the landscape had been drastically modified by agricultural and urban change. A comparison of the nature of the species which have become extinct in these counties ought therefore to be particularly illuminating. The aim of this paper is to investigate whether the vascular plant species which disappear when an area undergoes major environmental change have anything in common either ecologically or phytogeographically, or whether they approximate to a random sample of the species present in the area.

Middlesex (734 km^2) is only a third the size of Cambridgeshire (2124 km^2), but the counties share important geographical similarities*. Both areas are exclusively lowland: the highest point in Middlesex scarcely exceeds 150 metres and nowhere in Cambridgeshire reaches even this altitude. Neither county has a coastline, though a few coastal species penetrate into Cambridgeshire along the tidal portions of the River Nene and reach Middlesex along the tidal Thames. There are, however, important differences in the superficial geology of the two areas. Middlesex is made up of the predominantly acidic clays, sands and gravels of the London Basin with a small area of chalk at the edge of the county near Harefield. In Cambridgeshire calcareous soils predominate; acidic ground is rare. Southern Cambridgeshire is dominated by chalk and calcareous boulder clay, with only small areas of acidic, sandy soil over the Lower Greensand near Gamlingay at the western edge of the county and on the fringe of Breckland to the east. The extensive Fenland of northern Cambridgeshire, which falls below sea-level in places, has no parallel in Middlesex.

A comparison of extinctions in Middlesex and Cambridgeshire is particularly appropriate because of certain similarities of botanical history. Most importantly, the counties share a long tradition of field study, sustained in Middlesex by the presence of London with its metropolitan population and institutions and in Cambridgeshire by the University of Cambridge. In Cambridgeshire the first thorough investigation of the flora was Ray's *Catalogus plantarum circa*

* Like Kent (1975), I have taken the area of the Watsonian vice-counties from the Agricultural Returns for 1873, the year of publication of Watson's *Topographical botany*. In this paper the names Middlesex and Cambridgeshire refer to the Watsonian vice-counties unless the administrative counties are explicitly referred to.

Cantabrigiam nascentium of 1660, followed by another detailed Flora, Relhan's *Flora Cantabrigiensis* (1785). Rather surprisingly, there was no Flora of Middlesex in this period but very many records from sites in Middlesex were published in national works from those of Turner (1548) onwards, and these are augmented by local publications (e.g. Blackstone 1737) and specimens in the London herbaria. The botanical history of the two counties subsequently converged, with the publication in the mid-19th century of Floras which included both historical records and the results of recent fieldwork (Babington 1860; Trimen & Dyer 1869). In the 20th century, Floras of the two counties were again published little more than a decade apart, Cambridgeshire (Perring *et al.* 1964) again preceding Middlesex (Kent 1975). These have been supplemented by updated checklists (Crompton & Whitehouse 1983; Kent, in press). Kent's book *The historical flora of Middlesex* (1975) was especially notable for its thorough coverage of the voluminous historical records available from the county.

IDENTIFICATION OF NATIVE AND EXTINCT NATIVE SPECIES

In investigating the characteristics of the extinct species, I have attempted in this paper to characterise the native flora of each county as a whole with respect to each ecological or phytogeographical factor, then to compare this overall pattern with that shown by the species which are regarded as extinct. Lists of native and of extinct native species for each county were drawn up from published and unpublished sources, namely Kent (1975 and in press) for Middlesex and Perring *et al.* (1964), Crompton & Whitehouse (1983), Crompton & Wells (1996) and Preston (1997) for Cambridgeshire. These draft lists were then submitted to the vice-county recorders, R. M. Burton (v.c. 21) and Mrs G. Crompton & D. A. Wells (v.c. 29) for vetting. Nomenclature follows Stace (1997).

DEFINITION OF NATIVE SPECIES

The list of British native species provided by Preston & Hill (1997) was used as the basis of the study. Where there is doubt about whether or not a species is native in Middlesex or Cambridgeshire, the species was accepted as native if its history, habitat and distribution in the county is similar to that in those areas of Britain where it was assumed native by Preston & Hill (1997). Kent (1975) classifies Middlesex plants as native, denizen, colonist, alien or introduced, and the list of native species accepted here is very similar to the combined list of natives, denizens and colonists. The Cambridgeshire Floras pay less attention to the question of whether or not species are native.

IDENTIFICATION OF EXTINCT SPECIES

Species were regarded as extinct if they had not been reported from the county from 1970 onwards, or had been seen between 1970 and 1989 but were known to have disappeared subsequently. No species seen from 1990 onwards was regarded as extinct, on the grounds that such a judgement would be premature. Critical segregates which have been recognised recently from herbarium material collected before 1970 (e.g. *Erophila majuscula*) were not regarded as extinct if there has not yet been time to search for them in the wild. In compiling the list for Cambridgeshire an unpublished list of extinct species prepared by Crompton & Wells (1996) was particularly helpful, but this needed considerable modification as it includes both native and alien taxa. The last year in which a species was recorded was noted for each species. By convention, species which were known in Cambridgeshire to Relhan (1785, 1802, 1820) and Babington (1860) but not to later authors were regarded as having been last recorded in 1820 and 1860 respectively in the absence of an exact date for the last record.

In some cases species are extinct as natives but survive as aliens or introductions. These have been treated as extinct, with the date of extinction the year when a native population was last recorded. A particular difficulty in Middlesex was the treatment of a number of arable weeds which are extinct as natives but persist as casuals. The species in this category were treated as extinct (*Anchusa arvensis*, *Anthemis cotula*, *Chrysanthemum segetum*, *Scandix pecten-veneris*, *Silene noctiflora*, *Stachys arvensis*). The last record as a persistent weed of cultivated land has been taken as the last native record, though this is difficult to establish with certainty.

The extinct natives in Middlesex and Cambridgeshire are listed in Appendix 1, with the date of the last native record.

NUMBER AND RATE OF EXTINCTIONS

A total of 146 native species have become extinct in Middlesex since records began, representing 18% of the 816 species recorded. For Cambridgeshire the number of extinct native species is 120, 13% of the 897 species recorded. There are 45 species which have become extinct in both counties (Table 1).

The number of species last recorded in successive 30-year intervals from 1750 is shown in Table 2. The rate of extinction, as measured by the number of species lost per decade, can be calculated on the assumption that a species became extinct in the period when it was last recorded. The year 1750 has been chosen rather arbitrarily as the starting point for these calculations. From 1750 to 1809 the rate of extinction was low, with 2·3 species lost from Middlesex per decade and 1·5 from Cambridgeshire. In the next 30 years the rate of extinction increased dramatically in Cambridgeshire, with a species lost on average every 1·3 years. By contrast the rate actually fell in Middlesex during this period. This pattern was reversed between 1870 and 1929, when extinctions in Middlesex were almost twice as numerous as those in Cambridgeshire. Extinctions continued at approximately the same rate in Middlesex until 1989; in Cambridgeshire the rate increased from 1900 to 1959 to match that in Middlesex.

From 1750 onwards 5·8 species have been lost per decade from Middlesex and 4·9 from Cambridgeshire; the rates for the 20th century (1900–1989) are 8·4 and 7·3 respectively. One species has been lost from Middlesex every 1·7 years and from Cambridgeshire every 2·0 years since 1750.

TABLE 1. A COMPARISON OF EXTINCT AND SURVIVING SPECIES IN MIDDLESEX (V. C. 21) AND CAMBRIDGESHIRE (V.C. 29)

	Extinct in v.c. 21	Never recorded in v.c. 21	Still present in v.c. 21	Total
Extinct in v.c. 29	45	43	32	120
Never recorded in v.c. 29	39	-	28	67
Still present in v.c. 29	62	105	610	777
Total	146	148	670	964

TABLE 2. RATE OF EXTINCTION OF SPECIES IN MIDDLESEX (V.C. 21) AND CAMBRIDGESHIRE (V.C. 29)

Species are assumed to have become extinct during the period when they were last recorded. The overall rate of extinction is calculated for the period 1750–1989, and excludes species last recorded before 1750.

Time period	Number of extinct species		Rate of extinction (species per decade)	
	v.c 21	v.c. 29	v.c. 21	v.c. 29
pre-1750	8	2	-	-
1750–1779	3	3	1·0	1·0
1780–1809	11	6	3·7	2·0
1810–1839	6	24	2·0	8·0
1840–1869	14	10	4·7	3·3
1870–1899	27	9	9·0	3·0
1900–1929	23	18	7·7	6·0
1930–1959	24	27	8·0	9·0
1960–1989	29	21	9·7	7·0
Date unknown	1	0	-	-
Total	146	120	5·8	4·9

ECOLOGICAL CHARACTERISTICS OF EXTINCT SPECIES

In this section seven ecological characteristics of the extinct species are examined. Data on plant height and life-form are derived from the Ecological Flora Database (see Fitter & Peat 1994) with appropriate additions and corrections. The light, moisture, pH and nitrogen requirements of the species studied and the typical vegetation in which they grow are assessed by Ellenberg's indicator values (Ellenberg 1988; Lindacher 1995). Ellenberg values are available for a maximum of 778 (95%) species in Middlesex and 870 (97%) species in Cambridgeshire, and the results are therefore based on these species. The values refer to the behaviour of species in central Europe. Species which have a different habitat in central Europe from that in eastern England will be misclassified from a British perspective but there are relatively few examples of such differences (some are discussed in the section on vegetation below). A modified set of Ellenberg indicator values, corrected where appropriate and applied to all British and Irish species, has recently been prepared and will be available for future analyses (Hill *et al.* 1999).

PLANT HEIGHT

Data on the typical maximum height of a species have been used to group terrestrial species into eight height categories. (Submerged and floating aquatics are excluded from this analysis.) These categories are those defined for canopy height by Grime *et al.* (1988). In both Middlesex and Cambridgeshire the proportion of short species which have become extinct greatly exceeds the proportion of taller species (Table 3, Fig. 1).

TABLE 3. EXTINCT SPECIES IN MIDDLESEX (V.C. 21) AND CAMBRIDGESHIRE (V.C. 29) RELATED TO PLANT HEIGHT AND RAUNKIAER LIFE FORM

The totals for plant height exclude aquatic species. Species which occur as two Raunkiaer life-forms are scored as 0·5 under each.

	Middlesex (v.c. 21)			Cambridgeshire (v.c. 29)		
	no. spp.	no. extinct	% extinct	no. spp.	no. extinct	% extinct
Plant height (cm)						
0–10	17	5	29	16	5	31
11–29	78	24	31	88	21	24
30–59	204	46	23	234	42	18
60–99	209	30	14	224	22	10
100–300	220	28	13	243	19	8
301–600	15	1	7	15	0	0
601–1500	13	0	0	12	0	0
>1500	16	0	0	16	0	0
Total	772	134	17	848	109	13
Life form						
Bulbous geophytes	8	3	38	8	2	25
Other geophytes	52	12	23	64·5	15	23
Hemicryptophytes	337·5	47	14	370·5	35	9
Chamaephytes	37	8	22	46	7·5	16
Nanophanerophytes	32	7	22	32	5	16
Larger phanerophytes	38·5	0	0	37·5	0	0
Epiphytes	1	0	0	1	0	0
Therophytes	197	43	22	211·5	30	14
Helophytes	52	12	23	61·5	12	20
Hydrophytes	61	14	23	64·5	13·5	21
Total	816	146	18	897	120	13

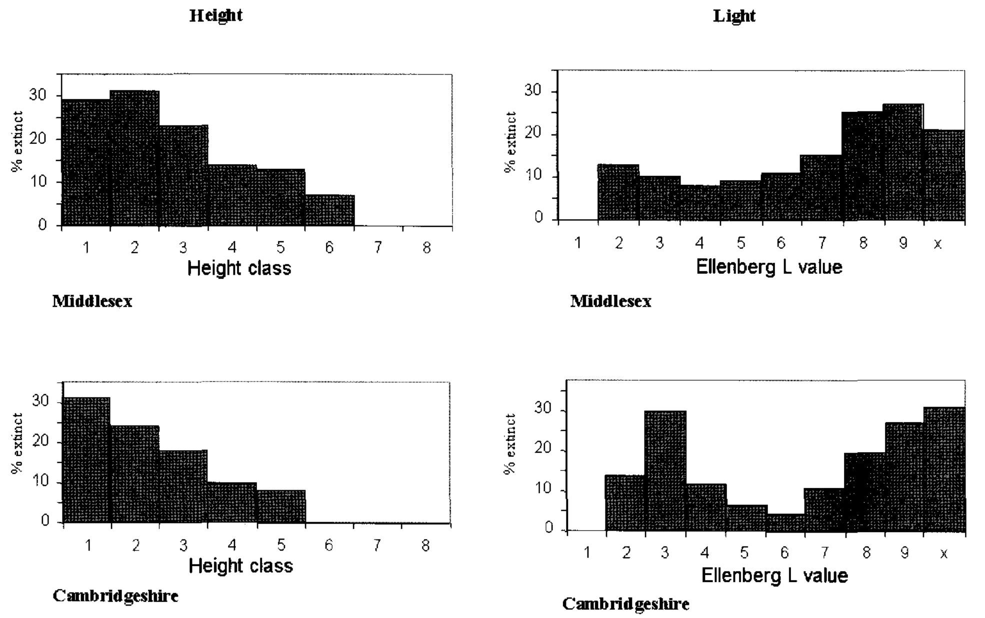

FIGURE 1. The proportion of extinct species in Middlesex and Cambridgeshire in relation to typical maximum plant height classes and to Ellenberg light values. Plant height increases from class 1 to 8 (see Table 3) and light requirements increase from value 1 to 9 (see Table 4). In both cases x represents species with a wide amplitude.

LIFE-FORM

The Raunkiaer life-form system classifies species by the height of the winter buds rather than the summer foliage (Clapham *et al.* 1987). Geophytes have resting buds below ground level, hemicryptophytes at ground level, chamaephytes up to 25 cm above the soil surface and phanerophytes over 25 cm above the ground. For the purposes of this analysis, nanophanerophytes (with resting buds 25 cm to 2 m above soil level) are separated from larger phanerophytes (which have resting buds more than 2 m above the ground). In the Raunkiaer system annuals (therophytes) form a separate category, as they pass through the unfavourable season as seeds. Marsh plants (helophytes), water plants (hydrophytes) and epiphytes are also treated separately. The overall life-form spectrum and the proportion of species in each life-form which have become extinct are very similar in the two counties (Table 3). A disproportionate number of geophytes, chamaephytes and nanophanerophytes have become extinct, and in Middlesex therophytes show a greater extinction than average. Extinctions in the wetland groups also exceed the overall average. The proportion of extinctions is below average for the hemicryptophytes, the preponderant life-form in both counties, and there have been no extinctions amongst the larger phanerophytes in either county. The single epiphyte, the hemiparasitic *Viscum album*, has survived in both areas.

LIGHT

Ellenberg L values for light range from 1 (plants of deep shade) to 9 (plants only found in full light); there is also a category for species with a wide amplitude (x). The values for species in Middlesex and Cambridgeshire (Table 4, Fig. 1) show that the light-loving species in categories 8 and 9 have suffered a disproportionate number of extinctions. In Cambridgeshire there is also a high level of extinction in one group of shade plants (category 3), attributable to the extinction of five woodland species (*Blechnum spicant*, *Carex strigosa*, *Equisetum sylvaticum*, *Lathraea squamaria*, *Polystichum aculeatum*) in this small group. Rather surprisingly, the small group of species of wide amplitude (x) has also lost a disproportionate number of species. This group includes ecologically tolerant species such as *Anemone nemorosa*, *Festuca rubra* and *Urtica dioica* which have survived in both counties, but also parasitic or hemiparasitic species such as *Cuscuta epithymum*, *Melampyrum pratense* and *Orobanche rapum-genistae* which contribute almost all the extinctions.

TABLE 4. EXTINCT SPECIES IN MIDDLESEX (V.C. 21) AND CAMBRIDGESHIRE (V.C. 29) RELATED TO ELLENBERG VALUES FOR LIGHT, WATER, pH AND NITROGEN

Ellenberg value	Middlesex (v.c. 21)			Cambridgeshire (v.c. 29)		
	no. spp.	no. extinct	% extinct	no. spp.	no. extinct	% extinct
Light						
1 Deep shade	1	0	0	1	0	0
2	8	1	13	8	1	13
3 Shade	20	2	10	18	5	28
4	38	3	8	37	4	11
5 Half shade	47	4	9	49	3	6
6	122	14	11	123	5	4
7 Partial shade/full light	275	40	15	313	30	10
8 Light-loving	202	51	25	237	43	18
9 Full light only	51	14	27	69	17	25
x Wide amplitude	14	3	21	14	4	29
Total	778	132	17	869	112	13
Water						
1 Extremely dry	0	0	-	0	0	-
2	16	4	25	20	1	5
3 Dry	46	14	30	66	4	6
4	143	27	19	166	18	11
5 Moist	168	15	9	169	13	8
6	68	4	6	73	12	16
7 Damp	58	15	26	65	12	18
8	78	16	21	87	12	14
9 Wet	66	20	30	80	24	30
10 Occasionally flooded	36	6	17	39	6	15
11 Emergent or floating	19	4	21	21	2	10
12 Submerged	24	5	21	28	7	25
x Wide amplitude	54	2	4	54	2	4
Total	776	132	17	868	113	13
pH						
1 Extremely acid	8	5	63	8	7	88
2	24	5	21	24	9	38
3 Acid	51	18	35	52	21	40
4	46	11	24	48	6	13
5 Fairly acid	48	7	15	53	7	13
6	71	8	11	77	7	9
7 Weakly acid or weakly basic	210	32	15	237	24	10
8	126	24	19	160	18	11
9 Calcareous	15	4	27	26	3	12
x Wide amplitude	176	16	9	183	10	5
Total	775	130	17	868	112	13
Nitrogen						
1 Nitrogen-poor	33	11	33	37	13	35
2	87	29	33	122	35	29
3 Prefers nitrogen-deficient	89	24	27	104	17	16
4	90	13	14	96	10	10
5 Average	109	17	16	128	13	10
6	107	8	7	110	8	7
7 Prefers nitrogen-rich	105	13	12	113	7	6
8	71	5	7	70	3	4
9 Extremely nitrogen-rich	21	3	14	21	3	14
x Wide amplitude	59	7	12	61	3	5
Total	771	130	17	863	112	13

WATER

Ellenberg F values for water range from 1 (indicators of extreme dryness) to 12 (submerged plants); there is also a category for species with a wide amplitude (x). The values for species in Middlesex and Cambridgeshire are set out in Table 4. None of the species are classified as indicators of extreme dryness. In Middlesex more extinctions than average have taken place in a wide range of groups, especially those of dry-site (values 2, 3) and damp- or wet-site (7, 8, 9) species. Extinct species of dry sites include some calcicoles (e.g. *Helianthemum nummularium, Scabiosa columbaria*) but most are calcifuges (e.g. *Potentilla argentea, Teesdalia nudicaulis*). The extinct species in groups 7–9 (e.g. *Anagallis minima, Carex binervis, C. dioica, Cicuta virosa, Cirsium dissectum, Drosera rotundifolia, Mentha pulegium, Oenanthe lachenalii, Parnassia palustris*) would have been found in a wide range of damp or wet habitats. The lowest rates of extinction are in the species of moist sites (5, 6), large categories which include many woodland species, and those with a wide amplitude (x). In Cambridgeshire, as in Middlesex, there is a particularly high proportion of extinctions in the wet-site species (9) and a particularly low proportion in the species of wide amplitude (x). However, few species in the driest sites (2, 3) have become extinct.

pH

Ellenberg R values for pH range from 1 (indicators of extreme acidity) to 9 (always found on calcareous soils); there is also a category for species with a wide amplitude (x). Both in Middlesex and more especially in Cambridgeshire (Table 4, Fig. 2) there has been a massive loss of species which indicate extreme acidity (value 1). The same eight species were originally present in both counties. *Calluna vulgaris* is the only one to survive in Cambridgeshire, whereas *Juncus squarrosus* and *Pedicularis sylvatica* have also survived in Middlesex; *Carex binervis, Drosera rotundifolia, Erica tetralix, Teesdalia nudicaulis* and *Trichophorum cespitosum* are extinct in both. The extinctions in the other acidic categories (2, 3) are also well above the mean, especially in Cambridgeshire. In Middlesex the species of basic habitats (9) also show a high level of extinction, but this is not the case in Cambridgeshire. In both counties the lowest proportion of extinct species is in the wide-amplitude category (x).

NITROGEN

Ellenberg N values for nitrogen range from 1 (indicators of sites poor in available nitrogen) to 9 (in extremely rich situations such as areas where cattle congregate); there is also a category for species with a wide amplitude (x). The proportion of extinct species in Cambridgeshire and Middlesex (Table 4, Fig. 2) is highly correlated with nitrogen value, especially in Cambridgeshire: 33–35% of the indicators of sites poor in available nitrogen (value 1) have become extinct, compared to 4–7% of species characterised by value 8. The exception to this trend is the small group of species characteristic of extremely rich situations (value 9), which show a higher proportion of extinctions than those species of somewhat less rich soils. The extinct species are *Beta vulgaris*, a coastal plant, and *Bidens cernua, Chenopodium glaucum* and *C. vulvaria.*

VEGETATION

Ellenberg's (1988) classification of species by the characteristic vegetation in which they grow is based on phytosociological categories, with each species classified by its occurrence in one of eight major groups. The proportion of extinct species in each vegetation type is again similar in the two counties (Table 5). The marked losses of coastal and wetland species in both counties is evident, whereas species of wide tolerance, broadleaved woods and (in Cambridgeshire) scrub and woodland edges show the least losses. The tiny group of conifer woodland species shows the highest percentage loss, but of the four species which fall into this category only one (*Pyrola minor*) appears from a British perspective to be correctly classified; two of the other three (*Blechnum spicant, Monotropa hypopitys*) could equally well be classified as species of broadleaved woodland and the fourth, *Carex ericetorum*, is a continental species which in Britain is confined to calcareous grassland. As both counties have lacked native conifer woodland in historic times they would not be expected to possess native species typical of this habitat. *Pyrola minor* may have colonised the county naturally by wind-borne seed, but failed to persist.

In Table 5 the species in the three largest vegetation types are subdivided by phytosociological class. This shows marked variation in the proportion of extinct species in different aquatic and wetland classes. The few species of bogs (Oxycocco-Sphagnetea) are all extinct in both counties and the larger groups typical of acidic mires (Scheuchzerio-Caricetea nigrae) and shallow, acidic

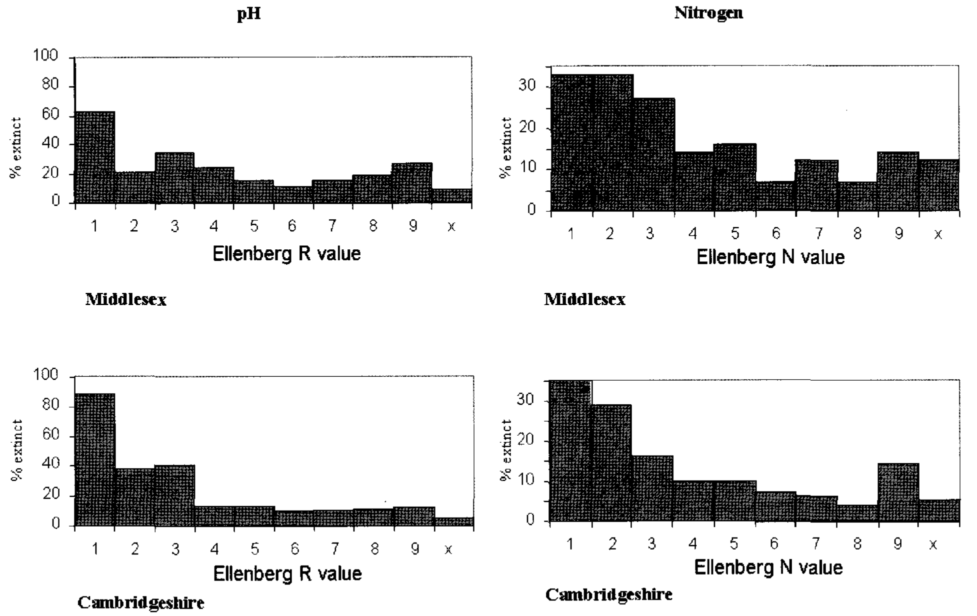

FIGURE 2. The proportion of extinct species in Middlesex and Cambridgeshire in relation to Ellenberg pH and nitrogen values. As Ellenberg pH values increase the species become increasingly characteristic of base-rich soils; nitrogen requirements increase from Ellenberg value 1 to 9 (see Table 4). In both cases x represents species with a wide amplitude.

waters (Littorelletea) also show disproportionate extinction. In contrast, species in communities characteristic of more basic and more eutrophic waters (Potamogetonetea, Phragmitetea) tend to have survived. There are no marked differences between the two counties. The disturbed ground community which has lost most species is the Isoëto-Nanojuncetea, found on seasonally flooded terrain. Otherwise the different communities of disturbed ground show less variation in the proportion of extinct species within each county. The main differences between counties are the higher percentage of species in the Secalietea (arable weeds) and Agrostietea stoloniferae (pioneer plants of damp or flooded sites) which have become extinct in Middlesex. There are also marked differences between the two counties in the plants of heaths, meadows and pastures. In Cambridgeshire the greatest losses have been amongst the calcifuge plants in the Nardo-Callunetea, whereas in Middlesex the calcicolous Festuco-Brometea has lost most species. Losses in the Molinio-Arrhenatheretea, which contains many species characteristic of moister and often more nutrient-rich soils, have been low, especially in Cambridgeshire.

DISTRIBUTION AND PHYTOGEOGRAPHY OF EXTINCT SPECIES

DISTRIBUTION WITHIN THE COUNTIES

Have the species which have become extinct in Middlesex and Cambridgeshire always been rare, or have more widespread species become extinct as well? Answering this question is not straightforward, as distributional data are presented in different ways in the Floras of the two counties. In Middlesex, Kent (1975 and in press) followed Trimen & Dyer (1869) in dividing the county into seven divisions. In Cambridgeshire, Perring *et al.* (1964) and Crompton & Whitehouse (1983) list records in 10-km squares. To make the Cambridgeshire data comparable to those available for Middlesex, seven divisions based on blocks of 5 to 6 10-km squares were defined (Appendix 2). These were broadly based on the eight divisions defined by Babington (1860), with two of the smaller divisions amalgamated and the areas redefined in terms of 10-km squares. Details of the number of divisions in which the native and extinct native species have been recorded are provided in Table 6. If a species is recorded as a native in some divisions and as an alien in others, only the native occurrences have been counted, if possible. However, the introduced or even casual occurrences of some species are not separable from the native records.

In Middlesex over 50% of extinct species were recorded from only 1–2 divisions and over 80% from 1–4 divisions. In Cambridgeshire the tendency of rarer species to become extinct is even more marked, with over 50% of extinct species recorded from a single division and over 80% from 1–3 divisions. Despite this clear general trend some widespread species have become extinct, especially in Middlesex. Seven of the nine species which were recorded from all seven divisions in v.c. 21 but are now extinct are arable or other weeds (*Anchusa arvensis*, *Anthemis cotula*, *Chenopodium vulvaria*, *Chrysanthemum segetum*, *Lithospermum arvense*, *Ranunculus arvensis*, *Scandix pecten-veneris*), the exceptions being *Ranunculus hederaceus* and *Spiranthes spiralis*. The only extinct Cambridgeshire species to have been recorded from all divisions is *Marrubium vulgare*.

TABLE 5. EXTINCT SPECIES IN MIDDLESEX (V.C. 21) AND CAMBRIDGESHIRE (V.C. 29) RELATED TO TYPICAL VEGETATION TYPE

Vegetation type	Middlesex (v.c. 21)			Cambridgeshire (v.c. 29)		
	no. spp.	no. extinct spp.	% extinct spp.	no. spp.	no. extinct spp.	% extinct spp.
1 Freshwater and mires	133	33	25	155	37	24
1.1 Lemnetea	*6*	*1*	*17*	*8*	*1*	*13*
1.2 Utricularietea	*1*	*1*	*100*	*2*	*2*	*100*
1.3 Potamogetonetea	*35*	*6*	*17*	*35*	*3*	*9*
1.4 Littorelletea	*11*	*6*	*55*	*10*	*6*	*60*
1.5 Phragmitetea	*48*	*6*	*13*	*52*	*2*	*4*
1.6 Montio-Cardaminetea	*7*	*1*	*14*	*7*	*2*	*29*
1.7 Scheuchzerio-Caricetea nigrae	*21*	*9*	*43*	*35*	*15*	*43*
1.8 Oxycocco-Sphagnetea	*3*	*3*	*100*	*5*	*5*	*100*
2 Saltwater and sea coasts	5	2	40	28	10	36
3 Frequently disturbed sites	225	37	16	237	24	10
3.1 Isoëto-Nanojuncetea	*14*	*4*	*29*	*13*	*5*	*38*
3.2 Bidentetea	*19*	*2*	*11*	*19*	*3*	*16*
3.3 Chenopodietea	*52*	*5*	*10*	*53*	*2*	*4*
3.4 Secalietea	*34*	*9*	*26*	*45*	*5*	*11*
3.5 Artemisietea	*59*	*9*	*15*	*57*	*3*	*5*
3.6 Agropyretea	*6*	*1*	*17*	*6*	*1*	*17*
3.7 Plantaginetea	*7*	*0*	*0*	*7*	*1*	*14*
3.8 Agrostietea stoloniferae	*24*	*7*	*29*	*27*	*3*	*11*
4 Stony sites and walls	8	1	13	8	1	13
5 Heaths and grasslands	189	35	19	215	23	11
5.1 Nardo-Callunetea	*25*	*6*	*24*	*27*	*11*	*41*
5.2 Sedo-Scleranthetea	*36*	*8*	*22*	*40*	*4*	*10*
5.3 Festuco-Brometea	*30*	*11*	*37*	*48*	*3*	*6*
5.4 Molinio-Arrhenatheretea	*89*	*10*	*11*	*91*	*5*	*5*
6 Scrub and wood edges	27	4	15	32	2	6
7 Conifer woods and allied heaths	2	1	50	3	2	67
8 Broadleaved woods	120	11	9	124	9	7
x Wide amplitude	64	6	9	63	3	5
Total	773	130	17	855	111	13

TABLE 6. EXTINCT SPECIES IN MIDDLESEX (V.C. 21) AND CAMBRIDGESHIRE (V.C. 29) RELATED TO THE NUMBER OF DIVISIONS OF THE COUNTY FROM WHICH THEY WERE RECORDED

Number of divisions	Middlesex (v.c. 21)			Cambridgeshire (v.c. 29)		
	no. spp.	no. extinct spp.	% extinct spp.	no. spp.	no. extinct spp.	% extinct spp.
1	71	54	76	109	61	56
2	36	20	56	56	22	39
3	37	22	59	71	18	25
4	66	25	38	72	11	15
5	58	7	12	88	6	7
6	83	9	11	93	1	1
7	465	9	2	408	1	<1
Total	816	146	18	897	120	13

For details of the divisions, see Kent (1975) for Middlesex and Appendix 2 of this paper fc Cambridgeshire.

TABLE 7. EXTINCT SPECIES IN MIDDLESEX (V.C. 21) AND CAMBRIDGESHIRE (V.C. 29) RELATED TO NATIONAL RARITY

National rarity	Middlesex (v.c. 21)			Cambridgeshire (v.c. 29)		
	no. spp.	no. extinct spp.	% extinct spp.	no. spp.	no. extinct spp.	% extinct spp.
Extinct	1	1	100	3	3	100
Rare	22	20	91	31	13	42
Scarce	46	29	63	67	23	34
Other	747	96	13	796	81	10
Total	816	146	18	897	120	13

There are two reasons why these results should be treated with some caution. It is doubtfı whether recording of species in the 17th, 18th and early 19th centuries was sufficiently thorough ı ensure that species which became extinct at an early date were recorded in all the districts in whic they grew. There may therefore be a tendency for extinct species to appear to have been le: widespread than they were, although the habitat requirements of many of the extinct speci(suggest that they would always have been rare and restricted. In any case, the pattern in bo counties is so clear that one has to conclude that the rarer a species was originally, the more like it is to have become extinct. The species which appear to have been widespread are mainly weed and the records in some divisions may have been only casual occurrences.

RARITY OF SPECIES IN BRITAIN

Three terms are conventionally used to describe the rarest species in Britain: extinct, rare (prese in 1 to 15 10-km squares) and scarce (present in 16 to 100 squares). The native and extinct nati species in the two counties are classified in these categories in Table 7; details of the nation status are taken from Stewart *et al.* (1994) and Wigginton (1999). One species formerly record in Middlesex (*Arnoseris minima*) and three formerly found in Cambridgeshire (*Arnoseris minim Bromus interruptus*, *Tephroseris palustris*) are now extinct in Britain as a whole. Of 22 ra species which have been recorded from Middlesex only two survive (*Arabis glabra*, *Cyper fuscus*) and over 60% of the scarce species have been lost. A smaller proportion of nationally ra and scarce species has been lost in Cambridgeshire, although even in Cambridgeshire losses these species have been much greater than those of species which are more frequent in Britain as whole.

Whereas the analysis of the rarity of species within the counties is based on all records of the species, this analysis is based on *current* national status. It therefore contains an element of circularity, as species may be rare or scarce because they have declined in counties such as Middlesex and Cambridgeshire. However, it does at least demonstrate these changes at the local scale.

PHYTOGEOGRAPHY

Preston & Hill (1997) classify native species according to their latitudinal and longitudinal distribution in the northern hemisphere. The extinct flora of both counties is analysed in relation to these phytogeographical elements in Table 8.

There is a clear relationship between the phytogeographical elements and the proportion of extinct species in both counties. The greatest proportion of extinctions has taken place in the small Boreal and Oceanic elements. A single Boreo-arctic species (*Carex dioica*) occurred in both counties, but has now been lost. In Middlesex five out of six Boreal species have been lost; *Vaccinium myrtillus* survives but is reduced to a single plant on Hampstead Heath (R. M. Burton, *in litt.* 1999). Similarly eight of the 13 Boreal species in Cambridgeshire have become extinct; the surviving species are *Carex lasiocarpa*, *Coeloglossum viride*, *Potamogeton alpinus*, *P. praelongus* and *Salix myrsinifolia.* Although less severe, losses of Oceanic and Suboceanic species are also much greater than the average values.

TABLE 8. EXTINCT SPECIES IN MIDDLESEX (V.C. 21) AND CAMBRIDGESHIRE (V.C. 29) IN RELATION TO PHYTOGEOGRAPHICAL AFFINITIES

The percentage of extinct species in each phytogeographical group is given. The values for groups containing less than 11 species in total are bracketed. For details of the phytogeographical classification, see Preston & Hill (1997).

	Eastern limit category						
Major biome category	1 Oceanic	2 Suboceanic	3 European	4 Eurosiberian	5 Eurasian	6 Circumpolar	Total
Middlesex							
1 Arctic-montane	-	-	-	-	-	-	-
2 Boreo-arctic Montane	-	-	-	-	-	(100)	(100)
3 Wide-boreal	-	-	-	-	(0)	(20)	(18)
4 Boreal-montane	-	-	(100)	(0)	-	(100)	(80)
5 Boreo-temperate	(100)	(67)	14	12	19	16	17
6 Wide-temperate	-	-	(0)	0	(0)	(0)	0
7 Temperate	57	30	16	18	14	6	18
8 Southern-temperate	(20)	35	17	16	0	(10)	18
9 Mediterranean	(44)	8	-	-	-	-	20
Total	50	28	16	15	13	16	18
Cambridgeshire							
1 Arctic-montane	-	-	-	-	-	-	-
2 Boreo-arctic Montane	-	-	-	-	-	(100)	(100)
3 Wide-boreal	-	-	-	(0)	(0)	25	21
4 Boreal-montane	-	-	(100)	(0)	-	64	62
5 Boreo-temperate	(50)	(50)	19	5	16	24	16
6 Wide-temperate	-	-	-	0	(0)	17	17
7 Temperate	33	39	9	7	10	13	11
8 Southern-temperate	(60)	26	8	8	0	0	11
9 Mediterranean	(33)	17	-	-	-	-	21
Total	39	27	10	6	10	23	13

EXTINCTIONS AND LAND-USE CHANGE

Although the ecological and phytogeographical characteristics of the extinct species of Cambridgeshire and Middlesex are broadly similar, the above analysis revealed marked differences in the timing of the extinctions. The differences are particularly marked in the 19th and early 20th centuries: extinctions in Cambridgeshire exceeded those in Middlesex between 1810 and 1839, whereas the rate in Middlesex was markedly greater from 1870 to 1929. There is no obvious explanation of these figures in terms of recording intensity: the recording history of both counties is broadly similar, and a major Flora of each was published in the 1860s. It is therefore worth seeking an explanation of these differences in terms of the land-use history of both counties.

CAMBRIDGESHIRE

Cambridgeshire has always been a predominantly agricultural county, and the land-use history which is most relevant to the botanist is the history of its agriculture. The county lies in one of the areas of Britain which are most suitable for cereal growing, and, once drained, the fenland soils support a range of arable crops. Only the clays of the west were once more marginal as agricultural land.

The period of just over a century from 1640 to 1750, the first for which numerous detailed botanical records are available, was one in which agriculture was in relative decline in Britain. Agricultural output increased much more rapidly than did the population. Agricultural prices, which had increased six-fold between 1500 and 1640, increased by only 2% between 1640 and 1750 (Jackson 1985; Thirsk 1984). Farmers attempted to compensate for this by growing new crops, and there was a boom in 'alternative agriculture' (Thirsk 1997). It was during this period that drainage of the 'Great Level' of the Fens was accomplished in Cambridgeshire (Darby 1956; Taylor 1973). The Bedford Level was declared drained in 1652 and Soham Mere, a large Fenland lake, was drained, enclosed and brought into cultivation in 1664. The fact that 'alternative' crops such as flax, hemp, rapeseed and vegetables could be grown in the newly drained fenland perhaps encouraged these schemes for agricultural improvement. Continued technical problems resulted in the deterioration of some of the drained land, especially in the first half of the 18th century when the incentive for capital investment was low, but these problems were eventually solved by the application of steam power to pumping engines.

From 1750 onwards the growth in agricultural output in England and Wales slowed, whereas population grew rapidly, from 6 million in 1750 to 18 million in 1850. Improvements in transport made it easier for farmers to get their products to the growing urban centres (Mingay 1989). Consequently there was a prolonged agricultural boom. As agriculture prospered, farmers brought more and more 'waste' into intensive cultivation. At first the increase in the area of cultivated grassland exceeded that of arable, but after 1800 arable expanded more rapidly and by 1840 the acreage of arable in England and Wales actually exceeded that of pasture (Prince 1989). Interest in alternative crops waned as the rewards of mainstream farming increased.

In Cambridgeshire the medieval open field system survived in many parishes until the end of the 18th century. The first great wave of parliamentary enclosure in the 1760s and 1770s scarcely affected the county. However, this was not true of the second period when enclosure was "particularly rampant", between 1793 and 1815. During this period bad harvests and insecurity engendered by the Revolutionary and Napoleonic Wars led to great pressure for agricultural improvement (Turner 1980). A 'general view' of the agriculture of the county prepared by Charles Vancouver (1794) for the newly established Board of Agriculture provided detailed and forceful arguments for agricultural reform (cf. Grigg 1967). Vancouver's report was followed by a period in which many parishes were enclosed. Although the rate of enclosure slowed markedly after the end of war with France in 1815, as it did elsewhere in England, there was a period of renewed activity in the 1820s and 1830s, a feature virtually unique to the county (Turner 1980). Cambridgeshire is described by Turner as "*the* county of parliamentary enclosure". A higher percentage of land (53%) was enclosed than in any other county except Oxfordshire (54%), but the Cambridgeshire figure is reduced by the fact that there was little parliamentary enclosure in the northern, fenland areas. In the south of the county over 70% of the land was enclosed, representing "the most concentrated agricultural organisational change that there had ever been, certainly in that county and probably in any county" (Turner 1980).

The enclosures in Cambridgeshire were followed by the widespread agricultural improvement that Vancouver had recommended. Enclosure had a marked effect on the flora of the county because in its immediate aftermath semi-natural habitats were taken into cultivation: fens were drained and chalk grassland and heathland ploughed up and converted to arable land. These reforms provide an explanation of the large number of extinctions between 1810 and 1839. Corroborating evidence is not hard to find. The *Journal of Natural History* kept by the Rev. Leonard Jenyns from 1823 to 1846 reveals " a recurring concern about the effects of Parliamentary Enclosures on the extent of heathland and wetland" (Crompton 1997). Babington (1860) had no doubt why he was unable to refind some species at localities known to Relhan before 1820. *Drosera anglica* at Sawston and Hinton Moors and *D. intermedia* at Teversham and Sawston Moors had "not [been] found since these places were drained", *Pulsatilla vulgaris* and *Ulex minor* formerly grew on Barrington Hill, Linton, "a place now ploughed up", and *Vicia sylvatica* had been recorded at Hall Wood, Wood Ditton, which "does not now exist". There is no evidence from the study of extinctions to suggest that the intensification of agriculture on existing arable land had a marked effect on the flora of the county at this period.

The introductory comments in Babington's *Flora* (1860) are often cited. In reviewing the county habitat by habitat, he cited major changes which had happened to each. The Chalk Country which "until recently (within 60 years)" was "open and covered with a beautiful coating of turf...is now converted to arable land" and "even the tumuli, entrenchments, and other interesting works of the ancient inhabitants have seldom escaped the rapacity of the modern agriculturist". The plants of the Clayey District "have suffered nearly as much", and the Fens "have undergone an equally if not more destructive change than the Chalk district" as steam drainage had rendered the whole level "a pattern in farming". The statistics on extinction allow these statements to be seen in their historical perspective. They are not the exaggerations of a congenitally conservative don, but a reaction to the effects of a prolonged period of agricultural prosperity and expansion and in particular a marked increase in the proportion of arable land. This had produced effects on the native flora which no generation of botanists in Britain had hitherto experienced. Babington's *Flora of Cambridgeshire* is the first local flora in which environmental change is a major theme.

The agricultural prosperity of the 18th and 19th centuries ended relatively abruptly in the 1870s, when an increasing amount of grain and other agricultural produce became available on world markets (Perren 1995). The resulting agricultural depression lasted with minor interruptions until 1940. By 1880 the area of arable in England and Wales was again less than that of pasture, and it continued to fall so that by 1914 East Anglia was the only region in which the proportion of arable consistently exceeded that of pasture (Whetham 1978). The better land in Cambridgeshire escaped the worst of the depression, and the agriculture of the county remained overwhelmingly arable (Fig. 3). However, by the 1930s much of the permanent pasture in the western claylands was "derelict or nearly so" and the view taken of farming in the area was "necessarily gloomy" (Pettit 1941). This prolonged depression ended with the Second World War and the subsequent Agriculture Act of 1947, which guaranteed agricultural prices and markets. Further support was offered to farmers under the Common Agricultural Policy after Britain's entry into the European Economic Community in 1973. Financial prosperity was combined with technological advances to produce a prolonged period of agricultural intensification. The resulting changes in eastern England included the expansion and intensification of arable farming, with the removal of hedges to increase field sizes, a switch from spring to autumn sowing of crops, the use of more productive cereal varieties and increased applications of fertilisers, herbicides and pesticides. Remaining areas of grassland were also converted from species-rich semi-natural communities to intensively managed, heavily fertilised, species-poor swards (Stoate 1996). A detailed account of the changes in one Cambridgeshire parish during this period is given by Sell (1989).

The rate of extinction of species in Cambridgeshire was very low between 1840 and 1899. This doubtless reflects the completion of agricultural enclosure followed by the end of the long period of agricultural prosperity. It may also be influenced by the fact that there was little systematic plant recording in southern Cambridgeshire after the completion of Babington's *Flora*. The rate of extinction increased in the period from 1900 and 1929, and it further increased from 1930 onwards. The increase from 1900 to 1929 has no clear explanation in terms of national land-use history, but the later increase coincides with the post-war agricultural revolution. The two decades in the 20th century in which most species were lost were the 1950s (twelve species) and the 1960s (eleven species), although it could be argued that species which were last seen in this period are

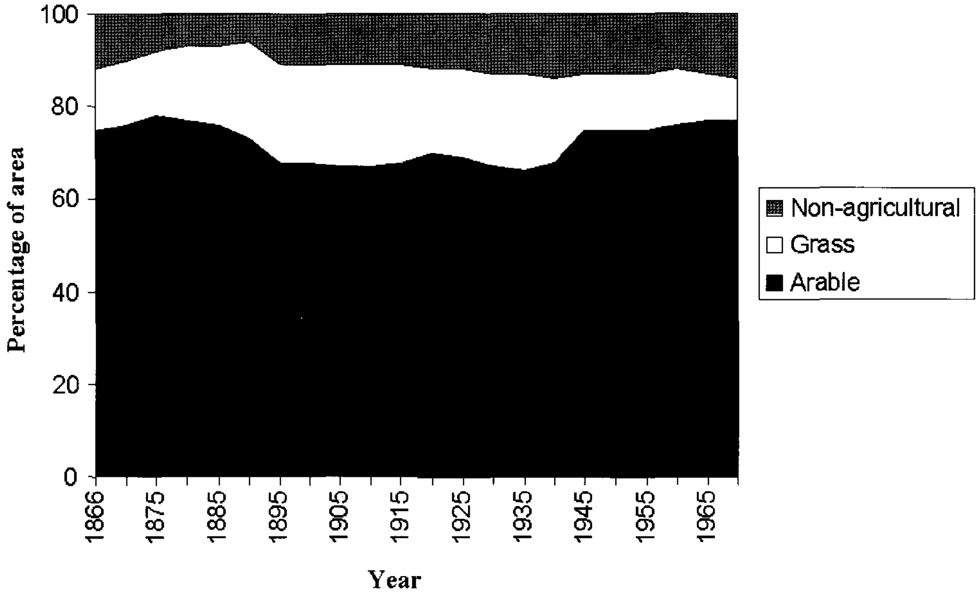

FIGURE 3. The percentage of arable land, permanent grassland (including rough grazing) and non-agricultural land in the administrative county (or counties) of Cambridgeshire and the Isle of Ely, 1866–1970. Values are plotted for 1866 and then at 5-year intervals from 1870 to 1970. They are based on official agricultural returns extracted by Stamp (1941) for the period between 1866 and 1910 and by C.D.P. from 1915 onwards. Radical revisions to the administrative county boundary took place in 1974.

more likely to be rediscovered than those last seen in earlier decades. In some cases the extinctions which have occurred since 1930 may have been the long-delayed result of earlier changes: *Potamogeton polygonifolius* was last seen at Gamlingay in 1948, for example, long after the extinction of the more exacting calcifuges there. In other cases the loss of species can be attributed directly to agricultural intensification, such as the ploughing up of the county's only site for *Cirsium tuberosum* in 1973 (Pigott 1988). However, most extinctions are probably the result of less dramatic, gradual changes brought about by factors such as eutrophication and falling water tables.

MIDDLESEX

The periods of maximum extinction in Cambridgeshire are closely related to periods of agricultural improvement. Can the same relationship between the number of extinct species and land-use history be demonstrated in Middlesex? Until it was swamped by the growth of London, Middlesex, like Cambridgeshire, was an almost exclusively agricultural county (Tanner 1911). The more fertile soils are suitable for arable cultivation, and in Elizabethan times this land, "fat and fertile and full of profite", produced "most excellent good wheate" (Norden 1593). However, although arable cultivation persisted on the best soils, agriculture in the county became predominantly pastoral between 1550 and 1750 in response to the insatiable demand for hay in London. Thus Perivale, which was praised for its wheat by Norden and in Michael Drayton's poem *Poly-Olbion* (1612), was to be remembered by John Betjeman in his poem *Middlesex* as a "parish of enormous hayfields" (Betjeman 1954). Hay was required for the city's horses and for cows kept in urban cowsheds; the name Haymarket (Piccadilly) survives from one of four new hay markets set up in the city in the 17th century. The refuse of the city provided manure which was returned to the countryside to sustain production. Close to London extensive areas of market gardens developed, so that the area west of St Martin-in-the-Fields appeared to be "a continuous garden" (Richardson 1984). Pehr Kalm, visiting London in 1748, explained that "the frightful number of people which there crawl in the streets pays the market gardeners many fold their labour and outlay" (Lucas 1892). A detailed account of the market gardens of Middlesex, and of other aspects of the changing land-use of the county, is given by Bull (1957).

Some of the open countryside of Middlesex was lost before Parliamentary enclosure to non-agricultural uses such as roads, parks and buildings. Parliamentary enclosure took place earlier than in Cambridgeshire: 28% of the total area enclosed was dealt with by 1793 and 91% by 1815, compared to 6% and 60% in Cambridgeshire (Turner 1980). The proportion of the total area of Middlesex subject to enclosure, 28%, was much less than the 53% figure for Cambridgeshire. A notable feature of the enclosure of Middlesex was the conversion of commons and wastes, including much heathland, to agricultural use. The agricultural improvers of the late 18th century regarded the presence so close to the capital of unimproved land such as Hounslow Heath as "disgraceful to the county, and insulting to the inhabitants of the metropolis" (Middleton 1798). The enclosure of these commons was the culmination of a long process of attrition that reduced the area of common land from approximately 45,000 acres in 1500 to 30,000 acres in 1760; most of these 30,000 acres had been enclosed by 1825 (Kent 1975).

After enclosure the assured profits obtained by catering for the predictable needs of London led to an agricultural regime which appears to have been relatively stable. In Trimen & Dyer's (1869) *Flora* the farmers of Middlesex bear no relationship to the rapacious agriculturalists of Babington's Cambridgeshire. Basing their account on Clutterbuck (1869), they describe the hayfields over London clay as "small and not very convenient enclosures, sometimes overgrown with timber in the hedgerows". Clutterbuck (1869) applied Norden's (1593) words to the hay farmers of the 1860s: "they only covet to maintaine their ancient course of life and observe the husbandrie of their fathers without adding any thing to their greater profit".

By 1869, however, it was apparent to Trimen & Dyer that the market gardens and orchards close to London were "giving way to the advancing wave of buildings more rapidly than they are replaced". The population of London was approximately 400,000 in 1650, 575,000 in 1700 (when it overtook Paris as the largest city in Europe), 675,500 in 1700 and 900,000 in 1800 (Wrigley 1967). But in the 19th century its population more than trebled in size, reaching 3·56 million in 1901 and growing further to 5 million by 1961. It was in the second half of the 19th century and more particularly the first half of the 20th that the large town expanded to become the "immense continuous urban area" of Greater London (Figs 4, 5).

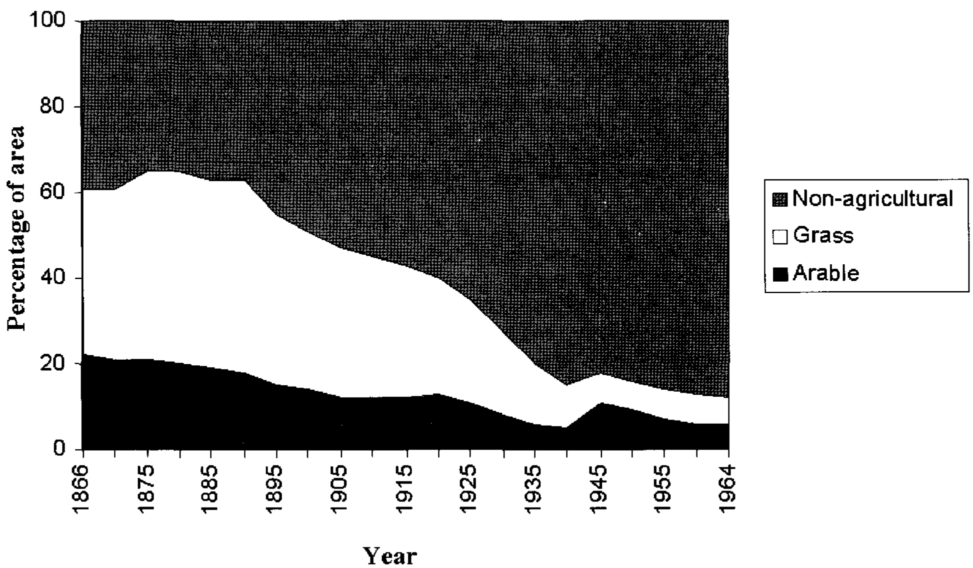

FIGURE 4. The percentage of arable land, permanent grassland (including rough grazing) and non-agricultural land in the administrative counties of Middlesex (1866–1891) and Middlesex plus London (1892–1964). Values are plotted for 1866 and then at 5-year intervals from 1870 to 1960 and finally for 1964. They are based on official agricultural returns extracted by Willatts (1937) for the period between 1866 and 1935 and by C.D.P. from 1940 onwards. From 1949 onwards the agricultural land in the county of London was apportioned between Kent, Middlesex and Surrey rather than included in the Middlesex total, but by then it represented less than 1.5% of the total area of the county of London so that the change has no appreciable effect on the diagram.

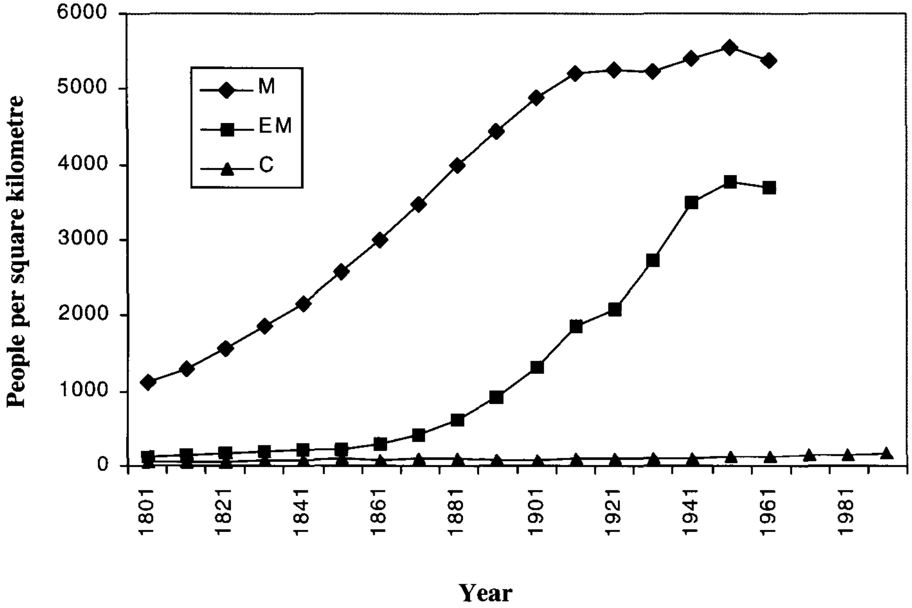

FIGURE 5. Population density (people per square kilometre) in Middlesex (M), extra-metropolitan Middlesex (EM) and Cambridgeshire (C), derived from decadal census returns from 1801 onwards. There was no enumeration in 1941 and this value was replaced by a retrospective estimate for 1939. Figures for Middlesex refer to the 'ancient geographical county', in effect the vice-county, until 1901. Subsequently the Middlesex figures are derived by adding the values for the revised administrative county of Middlesex to the figures for those areas of the county of London which were formerly in Middlesex (the City of London and 18 metropolitan boroughs). It is not possible to derive an estimate for 1939 by this method and the value plotted is therefore the mean of the 1931 and 1951 values. Extra-metropolitan Middlesex is the area of the county outside the former county of London; retrospective population estimates for extra-metropolitan Middlesex were published with the 1961 census returns. Figures for Cambridgeshire refer to the administrative county until 1971, and subsequently to four districts (Cambridge, E. Cambs., S. Cambs., Fenland) which approximate to the administrative county. The administrative and vice-counties are broadly similar (Crompton & Whitehouse 1983).

The expansion of London was made possible by improved rail and then road transport, and by the ability of engineers to solve the water supply problems which had hampered urban development on the London Clay (Smailes 1964; Willatts 1937). The growth of London "resulted in the greater part of the vice-county being virtually obliterated by a huge torrent of bricks and mortar and the creation of vast new suburbs which engulfed most of the old Middlesex villages and almost eradicated the London Clay grass plain... The rapid spread of suburbia has so reduced the agricultural areas of the vice-county that today only a minimum remains" (Kent 1975). In addition to the spread of suburbia, the county has been affected by other changes including gravel extraction from the river valleys, which has been directly responsible for the extinction of some species, and the growth of Heathrow Airport.

The land-use history of the county therefore ties in well with the statistics on extinctions. The initially higher rate of extinction when compared to Cambridgeshire is explicable in terms of early agricultural change, but during the period 1810–1839 the rate fell behind as the intense double wave of enclosures in Cambridgeshire was not matched by such radical developments in Middlesex. Thereafter the extinction rate in Middlesex picked up again, reflecting the growth of London: the primary effect of habitat destruction and all the secondary consequences of urbanisation.

DISCUSSION

ACCURACY OF THE LISTS

The analysis in this paper rests on lists of the native and extinct native species of Middlesex and Cambridgeshire. In some cases where the evidence of the occurrence of a species rests solely on old records there is an element of doubt about the correct identification of the species or its geographical location. *Limonium bellidifolium*, for example, is traditionally included in Floras of Cambridgeshire on the basis of a locality discovered by W. Skrimshire, the salt marshes below Wisbech, but three vice-counties meet in this area and there is considerable doubt as to whether the plant actually grew in Cambridgeshire (G. Crompton, in litt. 1999); the species is therefore excluded from this paper. The flora of both Middlesex and Cambridgeshire is very well-known, and the rate at which new native species are discovered is now very low. In over 20 years since the publication of Kent's Flora in 1975, *Galium constrictum* and *Salvia pratensis* have been added to the Middlesex flora as a result of the discovery of overlooked herbarium specimens, *Erophila glabrescens*, *E. majuscula* and *Juncus ambiguus* were also found in herbaria following taxonomic revisions, and two new native species were detected in the wild, the ferns *Dryopteris affinis* and *Polypodium interjectum* (Kent, in press; Rich & Lewis 1999). Similarly in Cambridgeshire the only native vascular plants to be added to those listed in the 1983 *Checklist* have been three species represented by 18th or 19th century herbarium specimens (*Eriophorum vaginatum*, *Rosa pimpinellifolia* and *Ruppia cirrhosa*, the last known previously from literature references which were misinterpreted as *R. maritima*) and a single species discovered in the wild, *Dactylorhiza maculata*. The definition of what constitutes a native species is a greater area of uncertainty than under-recording of species in the field. In this analysis the list of native species made use of that given by Preston & Hill (1997), which in turn largely followed Stace (1991), in order to maintain comparability with the national study. There are certainly changes which could and perhaps should be made to this list, but they are very unlikely to alter any of the conclusions reached in this paper.

Although the list of native species can be regarded as relatively stable, experience suggests that the list of supposedly extinct species will change. At the vice-county level, the slogan 'extinction is for ever' is manifestly false. Species may be discovered at new sites or rediscovered at sites where they have been overlooked, they may arise from seed banks after vegetation change or they may reinvade the county by natural means (although recolonisation is less likely to be a significant factor for flowering plants than for cryptogams, which have more mobile propagules). Babington (1860, pp. 314–315) listed 61 "lost plants" which had not been recorded in Cambridgeshire for many years or which, although recorded more recently, were "also probably now extirpated". Only 42 of these 61 species are natives of Cambridgeshire and, of these 42, 22 (53%) are still thought to have become extinct before 1860, 6 (14%) were rediscovered but are now regarded as extinct and 14 (33%) are still present in the county. Similarly, Trimen & Dyer (1869, pp. 345–346) reported as extinct 38 species which are accepted as natives of Middlesex in this paper. Of these 38, only 17 (45%) are still thought to have become extinct before 1869; the remaining 21 species were later rediscovered and 13 (34%) of these are still present, although 8 (21%) are again thought to be extinct. The rediscovery of supposedly extinct species has continued into modern times: 13 native species which Kent (1975) regarded as extinct had been rediscovered by the time he prepared the *Supplement* (Kent, in press). James (1997) has documented the same phenomenon in Hertfordshire. One must therefore expect some species listed as extinct in Appendix 1 to be rediscovered. There may also be species which have been seen in one or other county since 1990 and are therefore regarded as extant, but which will never be seen there again.

The extent to which the dates of the last records of extinct species reflect the actual timing of extinctions also needs to be assessed. These dates might potentially be influenced by the history of plant recording in each county. Even if the rate of extinction in a county was absolutely constant, fluctuations in the intensity of recording would nevertheless lead to an apparent concentration of last records in periods of intensive recording. It is, however, unlikely that the main fluctuations in extinction rate suggested by the data in Table 2 can be explained in this way. In Middlesex the rate in the 1840–1869 period was low despite the publication of Trimen & Dyer's Flora in 1869; subsequently the rate has been surprisingly constant. In Cambridgeshire the high rate from 1810 to 1839 cannot be explained by a subsequent falling off of recording intensity as the next period, from 1840 to 1869, was that in which Babington prepared his Flora. There is scope for a more detailed study of extinction in each county, which would attempt to estimate dates of extinction of those species which have succumbed to habitat destruction by the date of the destruction of the last site rather than by the date of the last botanical record.

Even if the date of extinction of a species is known with certainty, it will not necessarily coincide with the date of the causal event. Plants may persist for many decades after gradual changes which render sites unsuitable for the sexual or vegetative reproduction of a species but are insufficient to eradicate it completely (Summerfield 1972). However, catastrophic changes such as total habitat destruction may eliminate a species at once. Such changes were characteristic of the agricultural revolution which accompanied parliamentary enclosure in Cambridgeshire, and doubtless explain why this period stands out so strongly in the record of extinctions. In the absence of radical change, the correlation between land-use history and the rate of extinction will be less clear-cut.

ECOLOGICAL AND PHYTOGEOGRAPHICAL CHARACTERISTICS OF EXTINCT SPECIES

A high proportion of the extinct species are small, grow in open habitats, favour substrates with low pH or are characteristic of environments with low fertility. This is true of both counties, although the patterns are sharper in Cambridgeshire than in Middlesex (Figs 1, 2). Although these attributes have been treated separately, there is clearly a correlation between them. Habitats which have low pH, for example, generally have low fertility and a vegetation composed of low-growing species. Such semi-natural habitats have often been destroyed by agricultural improvement and urban expansion, and any remaining remnants have been indirectly modified by factors such as the reduction in grazing in an increasingly arable or urban landscape, eutrophication, falling water tables and increasing disturbance from a larger and more mobile population.

Twelve species combine all four attributes of the least successful species (typical maximum height <30 cm and Ellenberg L=8–9, R=1–3, N=1–2). Of these, four species are extinct in both counties (*Drosera intermedia*, *D. rotundifolia*, *Lycopodiella inundata*, *Lycopodium clavatum*), four more are extinct in the only county from which they are recorded (*Antennaria dioica*, *Drosera anglica*, *Hammarbya paludosa*, *Radiola linoides*) and two are extinct in one county but survive in the other (*Lythrum portula* extinct in Cambridgeshire and *Vicia lathyroides* in Middlesex). Surprisingly, two species in this group not only survive in both counties but even persist in central London, *Aira praecox* and *Trifolium arvense* (Kent, in press).

In an analysis of a completely different dataset, the results of the B.S.B.I. Monitoring Scheme, Thompson (1994) demonstrated a marked correlation between low canopy height and a tendency to decline in England. He pointed out that canopy height is correlated with competitive ability, so the declining species tend to be the less competitive. He commented on the "increasing restriction of slow-growing plants of infertile, relatively undisturbed habitats to fragmented islands of suitable habitat, many of them in nature reserves, surrounded by a sea of unsuitable landscape". Thompson's conclusions about the nature of the species which have declined in the modern landscape are strikingly similar to those of this survey.

In addition to these trends, there is a consistent indication in Cambridgeshire and Middlesex that wetland and coastal species have suffered more than plants in other habitats. The decrease in wetland species has been noted in other studies (e.g. Dony 1977; James 1997; Mountford 1994). The tendency of coastal species to decrease almost certainly reflects the very small area of suitable habitat for such species in these counties rather than a national trend. Judging by trends shown by nationally scarce species, the distribution of coastal species is relatively stable (Stewart *et al.* 1994). The persistence of the woodland flora of both counties is striking.

Some of the differences between Cambridgeshire and Middlesex reflect the differing geology of the two counties. Only in Middlesex do the species of basic habitats show a high level of extinction, a reflection of the small area of calcareous soil in that county. One might expect a correspondingly greater survival of calcifuge species in Middlesex, but this is only true to a limited extent. There has been massive extinction in calcifuge species and plants characteristic of plant communities of acidic soils in Cambridgeshire. However, the loss of these species has also been greater than average in Middlesex. Even though Middlesex is dominated by acidic soils, the heathland habitats of many species have been destroyed or grossly altered.

The most striking feature of the phytogeographical analysis is the loss of species from groups at the edge of their geographical range, the Boreal, Mediterranean-Atlantic and Oceanic plants. The same pattern is revealed by a recent analysis of extinctions in Bedfordshire (Boon 1999). If such changes are indeed characteristic of south-east England as a whole, they must have led to a reduction in the phytogeographical diversity of the flora and the increasing predominance of species in the already dominant major biome classes. However, it must be remembered that this applies only to native species. The increase in alien species of diverse origins is an aspect of change which has not been examined in this paper, but must be considered in an overall assessment of the phytogeographical diversity of the area.

EFFECTS OF URBANISATION AND AGRICULTURAL IMPROVEMENT

The similarities in the extent and nature of extinctions in Cambridgeshire and Middlesex are much more striking than the differences. This is remarkable in view of the differing land-use history of the counties: Middlesex has become a suburban and urban county, whereas Cambridgeshire is still rural although very intensively farmed. The fact that 18% of species have been lost from Middlesex and 13% from Cambridgeshire suggests that agricultural intensification is almost as damaging to the native flora as urbanisation. In making these comparisons it is difficult to account for the effect of the differing size of the counties. If the counties were uniform, one might expect fewer extinctions in the larger county, but the highly heterogeneous nature of Cambridgeshire with distinct areas of chalk, clay and fenland negates such a simplistic approach. Thompson & Jones (1999) found little relationship between the number of extinct scarce species and the area of a vice-county as such.

An alternative explanation for the similarity of the changes in the two counties might be that the changes in each have the same cause – that in both counties the primary cause is urbanisation. Thompson & Jones (1999) found a strong relationship between the number of nationally scarce species that have been lost from vice-counties and their current population density. They point out that population density is an indicator of many aspects of land-use (including road-building, recreation and urbanisation) which have a negative impact on plant survival. They go on to suggest that, whereas intensive agriculture "is frequently assumed to be the main cause of decline in Britain's native wildlife", these effects of population pressure may be "more pervasive and widespread than suspected" and "a major cause of local plant extinction". They conclude that a more detailed search for the proximate causes of local plant extinction would be rewarding.

The study reported in this paper differs from that of Thompson & Jones (1999) in being more limited spatially, but benefits from incorporating a temporal dimension. There has been a marked variation in the rate of extinction in differing time periods in both Middlesex and Cambridgeshire, and this provides a powerful insight into the possible causes of such extinctions. There is evidence to support Thompson & Jones' view that urbanisation has been a major cause for species loss in Middlesex (indeed, the urbanisation of that county is so extreme that no other conclusion would be credible). However, the analysis for Cambridgeshire has demonstrated the importance of agricultural change as an agent of local extinction. These variations in the rate of extinction also highlight the desirability of separating historic and recent extinctions when considering the implications of previous changes for the conservation of the modern flora. Causal factors as well as rates may have varied over time, and the fact that historic extinctions in Cambridgeshire have been primarily caused by agricultural improvement does not mean that the effects of population pressure described by Thompson & Jones (1999) are not important now, or will not become apparent in the future.

Further detailed studies of extinction at the vice-county level can be expected to throw more light on the changes which have taken place in the British flora. The vice-county is a convenient unit to use in the analysis of such changes, and such analyses are completely dependent on critical compilations of historic records such as that undertaken by Duggie Kent for *The historical Flora of Middlesex*.

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APPENDIX 1. EXTINCT NATIVE SPECIES OF MIDDLESEX AND CAMBRIDGESHIRE

The extinct species are listed below, with the date of the last record.

MIDDLESEX (V.C. 21)

Agrimonia procera, 1874; *Alchemilla filicaulis*, 1970; *Allium oleraceum*, 1856; *Althaea officinalis*, 1760; *Anagallis minima*, 1800; *A. tenella*, 1873; *Anchusa arvensis*, 1966; *Anthemis cotula*, date not known; *Aquilegia vulgaris*, 1737; *Arnoseris minima*, 1778; *Barbarea stricta*, 1965; *Beta vulgaris*, 1887; *Blysmus compressus*, 1830; *Bupleurum tenuissimum*, 1860; *Campanula glomerata*, 1980; *Carduus tenuiflorus*, 1929; *Carex appropinquata*, 1936; *C. binervis*, 1983; *C. dioica*, 1792; *C. filiformis*, 1960; *C. laevigata*, 1830; *C. pulicaris*, 1946; *C. rostrata*, 1792; *Carlina vulgaris*, 1730; *Chenopodium glaucum*, 1953; *C. vulvaria*, 1970; *Chrysanthemum segetum*, 1978; *Chrysosplenium alternifolium*, 1838; *Cicuta virosa*, 1780; *Cirsium dissectum*, 1884; *Cochlearia anglica*, 1869; *Coeloglossum viride*, 1913; *Crepis foetida*, 1873; *Cuscuta epithymum*, 1887; *C. europaea*, 1960; *Cynoglossum germanicum*, 1710; *C. officinale*, 1955; *Damasonium alisma*, 1886; *Dianthus armeria*, 1948; *D. deltoides*, 1939; *Drosera intermedia*, 1746; *D. rotundifolia*, 1935; *Eleocharis multicaulis*, 1960; *Erica cinerea*, 1981; *E. tetralix*, 1970; *Eriophorum angustifolium*, 1980; *Euphorbia platyphyllos*, 1884; *Euphrasia arctica*, 1884; *E. confusa*, 1887; *Filago pyramidata*, 1891; *Fritillaria meleagris*, 1950; *Fumaria purpurea*, 1892; *Galeopsis angustifolia*, 1945; *Galium constrictum*, 1780; *Gentiana pneumonanthe*, 1795; *Gentianella amarella*, 1975; *G. germanica*, 1977; *Gnaphalium sylvaticum*, 1945; *Gymnadenia conopsea*, 1965; *Helianthemum nummularium*, 1907; *Hordelymus europaeus*, 1951; *Hypericum androsaemum*, 1947; *H. elodes*, 1826; *Hypochaeris glabra*, 1843; *Jasione montana*, 1935; *Juncus ambiguus*, 1842; *Juniperus communis*, 1746; *Lactuca saligna*, 1800; *Legousia hybrida*, 1914; *Leucojum aestivum*, 1845; *Lithospermum arvense*, 1888; *L. officinale*, 1914; *Littorella uniflora*, 1935; *Lycopodiella inundata*, 1869; *Lycopodium clavatum*, 1865; *Lythrum hyssopifolia*, 1778; *Maianthemum bifolium*, 1924; *Marrubium vulgare*, 1949; *Melampyrum arvense*, 1870; *Mentha pulegium*, 1871; *Myosotis secunda*, 1847; *Myosurus minimus*, 1914; *Myrica gale*, 1901; *Myriophyllum alterniflorum*, 1957; *Neottia nidus-avis*, 1946; *Nepeta cataria*, 1978; *Oenanthe lachenalii*, 1847; *Ophrys insectifera*, 1907; *Orchis militaris*, 1900; *O. ustulata*, 1737; *Orobanche elatior*, 1902; *O. rapum-genistae*, 1873; *Osmunda regalis*, 1794; *Parnassia palustris*, 1900; *Pedicularis palustris*, 1920; *Petroselinum segetum*, 1930; *Pilularia globulifera*, 1800; *Platanthera bifolia*, 1887; *P. chlorantha*, 1890; *Polystichum aculeatum*, 1965; *Potamogeton acutifolius*, 1981; *P. alpinus*, 1886; *P. compressus*, 1917; *P. polygonifolius*, 1884; *P. trichoides*, 1966; *Potentilla argentea*, 1916; *Pulicaria vulgaris*, 1908; *Pyrola minor*, 1908; *Radiola linoides*, 1890; *Ranunculus aquatilis*, 1918; *R. arvensis*, 1966; *R. fluitans*, 1977; *R. hederaceus*, 1974; *R. parviflorus*, 1885; *R. sardous*, 1912; *Rosa agrestis*, 1818; *R. micrantha*, 1910; *R. pimpinellifolia*, 1887; *Sagina nodosa*, 1906; *S. subulata*, 1783; *Salvia pratensis*, 1901; *Samolus valerandi*, 1866; *Scabiosa columbaria*, 1939; *Scandix pecten-veneris*, 1888; *Schoenoplectus triqueter*, 1887; *Scrophularia umbrosa*, 1841; *Silene noctiflora*, 1967; *Sium latifolium*, 1965; *Sonchus palustris*, 1835; *Spiranthes spiralis*, 1936; *Stachys arvensis*, 1954; *Stellaria palustris*, 1977; *Teesdalia nudicaulis*, 1932; *Trichophorum cespitosum*, 1780; *Trifolium ornithopodioides*, 1885; *T. squamosum*, 1721; *Utricularia minor*, 1746; *Valeriana dioica*, 1970; *Valerianella dentata*, 1950; *V. rimosa*, 1941; *Vicia lathyroides*, 1866; *Viola canina*, 1966; *V. lactea*, 1868; *V. palustris*, 1912; *Vulpia unilateralis*, 1969; *Wolffia arrhiza*, 1898.

CAMBRIDGESHIRE (V.C. 29)

Alchemilla filicaulis, 1953; *Alisma gramineum*, 1972; *Althaea officinalis*, 1959; *Anagallis minima*, 1820; *Antennaria dioica*, 1864; *Aphanes inexspectata*, 1977; *Armeria maritima*, 1930; *Arnoseris minima*, 1914; *Atriplex pedunculata*, 1826; *Beta vulgaris*, 1928; *Bidens cernua*, 1964; *Blechnum spicant*, 1660; *Botrychium lunaria*, 1833; *Bromus interruptus*, 1972; *Campanula latifolia*, 1852; *Carex binervis*, 1961; *C. curta*, 1853; *C. diandra*, 1860; *C. dioica*, 1841; *C. echinata*, 1954; *C. pilulifera*, 1949; *C. rostrata*, 1966; *C. strigosa*, 1795; *Catapodium marinum*, 1785; *Ceterach officinarum*, 1967; *Chenopodium urbicum*, 1837; *C. vulvaria*, 1958; *Cicuta virosa*, 1763; *Cirsium tuberosum*, 1974; *Colchicum autumnale*, 1926; *Crassula tillaea*, 1930; *Cuscuta epithymum*, 1975; *Drosera anglica*, 1840; *D. intermedia*, 1820; *D. rotundifolia*, 1913; *Eleocharis multicaulis*, 1853; *Eleogiton fluitans*, 1975; *Epilobium palustre*, 1969; *Epipactis phyllanthes*, 1987; *E. purpurata*, 1962; *Equisetum sylvaticum*, 1763; *Erica cinerea*, 1914; *E. tetralix*, 1920; *Eriophorum angustifolium*, 1960; *E. latifolium*, 1887; *Festuca filiformis*, 1964; *Frankenia laevis*, 1820; *Fritillaria meleagris*, 1820; *Genista anglica*, 1932; *Gnaphalium luteoalbum*, 1802; *Hammarbya paludosa*, 1855; *Herminium monorchis*, 1825; *Hordeum marinum*, 1881; *Hypericum elodes*, 1930; *Hypochaeris glabra*, 1964; *Jasione montana*, 1910; *Juncus squarrosus*, 1833; *Lactuca saligna*, 1953; *Lathraea squamaria*, 1889; *Lepidium heterophyllum*, 1965; *L. latifolium*, 1795; *L. ruderale*, 1831; *Limosella aquatica*, 1877; *Liparis loeselii*, 1945; *Littorella uniflora*, 1820; *Lycopodiella inundata*, 1853; *Lycopodium clavatum*, 1831; *Lythrum portula*, 1878; *Marrubium vulgare*, 1930; *Melampyrum arvense*, 1862; *M. pratense*, 1930; *Mentha pulegium*, 1903; *Misopates orontium*, 1873; *Moenchia erecta*, 1928; *Monotropa hypopitys*, 1946; *Montia fontana*, 1945; *Myriophyllum alterniflorum*, 1919; *Narthecium ossifragum*, 1833; *Ophrys sphegodes*, 1837; *Orchis ustulata*, 1955; *Oreopteris limbosperma*, 1820; *Ornithogalum pyrenaicum*, 1774; *Orobanche artemisiae-campestris*, 1935; *O. rapum-genistae*, 1913; *Osmunda regalis*, 1685; *Parnassia palustris*, 1980; *Pedicularis sylvatica*, 1912; *Pinguicula vulgaris*, 1984; *Polygala serpyllifolia*, 1954; *Polystichum aculeatum*, 1820; *Potamogeton compressus*, 1912; *P. polygonifolius*, 1948; *Potentilla anglica*, 1945; *P. palustris*, 1886; *Pulicaria vulgaris*, 1833; *Ranunculus baudotii*, 1955; *R. hederaceus*, 1900; *R. parviflorus*, 1928; *Rhynchospora alba*, 1839; *Rosa pimpinellifolia*, 1827; *R. sherardii*, 1910; *Ruppia cirrhosa*, 1795; *Sagina maritima*, 1983; *Salicornia dolichostachya*, 1959; *Silene gallica*, 1951; *Solidago virgaurea*, 1916; *Sonchus palustris*, 1843; *Stratiotes aloides*, 1960; *Teesdalia nudicaulis*, 1954; *Tephroseris palustris*, 1830; *Trichophorum cespitosum*, 1820; *Triglochin maritima*, 1930; *Ulex minor*, 1832; *Utricularia australis*, 1899; *U. intermedia*, 1898; *U. minor*, 1951; *Vaccinium oxycoccos*, 1859; *Valerianella rimosa*, 1933; *Vicia sylvatica*, 1792; *Zostera marina*, 1908.

APPENDIX 2. DIVISIONS OF CAMBRIDGESHIRE

The following seven divisions were defined to assist in comparison of data presented by Kent (1975 and in press) for seven divisons of Middlesex. They correspond very approximately to the divisions recognised by Babington (1860), which are named after each list of 10 km squares:

1: TL 54, 55, 64, 65, 75 (Cambridge); 2: TL 23, 24, 33, 34, 43, 44 (Royston); 3: TL 15, 25, 26, 35, 36, 45 (Cottenham and Wimpole); 4: TL 46, 56, 57, 66, 67, 76 (Burwell); 5: TL 47, 48, 58, 59, 68, 69 (Ely); 6: TL 29, 37, 38, 39, 49 (Chatteris); 7: TF 20, 30, 31, 40, 41, 51 (Wisbech).