

Durham E-Theses

Ecological Changes in the British Flora

KEVIN JOHN WALKER

How to cite:

WALKER, KEVIN JOHN (2009) Ecological Changes in the British Flora. Doctoral thesis, Durham University.

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a <https://etheses.durham.ac.uk/id/eprint/121/> is made to the metadata record in Durham E-Theses
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full Durham E-Theses policy](#) for further details.

Ecological Changes in the British Flora

Kevin John Walker B.Sc., M.Sc.

School of Biological and Biomedical Sciences

University of Durham

2009

This thesis is submitted in candidature
for the degree of

Doctor of Philosophy

Dedicated to

Terry C. E. Wells (1935-2008)

With thanks for the help and encouragement so generously
given over the last ten years



Plate 1

Pulsatilla vulgaris, Barnack Hills and Holes, Northamptonshire
Photo: K.J. Walker

Contents

List of tables	vi
List of figures	viii
List of plates	x
Declaration	xi
Abstract	xii
1. An introduction to ecological changes in the British flora	1
Introduction	1
Change in the British flora	2
<i>Extinct species</i>	2
<i>Declining species</i>	9
Availability of plant trait information for the British flora	13
Attributes of extinct and declining species	13
Objectives and outline of the thesis	19
2. Using local floras to assess floristic change	21
Summary	21
Introduction	21
Methods	22
Results	23
<i>The publication of local floras, 1660-2002</i>	23
<i>The aims of local floras</i>	24
<i>Local floras as historical baselines</i>	25
<i>Perceptions of change</i>	27
<i>County extinction</i>	28
<i>Comparisons between time periods</i>	30
<i>Habitat studies</i>	32
Discussion	34
<i>Assessing change using data on extinction</i>	34
<i>Assessing change using historical data</i>	36
Conclusions	36
3. One species lost every year? An evaluation of plant extinctions in selected British vice-counties since 1900	39
Summary	39
Introduction	39
Methods	41

<i>Sources of data</i>	41
<i>Assessment of native/alien status</i>	41
<i>Assessment of dates of extinction</i>	42
<i>Selection of species</i>	42
Results	43
<i>Extinct species in Northamptonshire</i>	43
<i>Changes to the Gent & Wilson (1995) list of “presumed extinctions”</i>	43
<i>Extinction rate</i>	45
<i>Extinction in other British vice-counties</i>	45
<i>One species lost every year?</i>	48
Discussion	49
<i>Definition of native taxa</i>	50
<i>Reliability of last date</i>	50
<i>Is extinction forever?</i>	51
<i>County area</i>	52
<i>The history of botanical recording</i>	53
Conclusions: One species lost every year?	54
4. Ecological predictors of extinction risk in the flora of lowland England	56
Summary	56
Introduction	56
Study region	58
<i>History of botanical recording</i>	59
Compilation of data on extinction	60
<i>Identification of native and extinct native species</i>	60
<i>Ecological characteristics of native and native extinct species</i>	61
<i>Land use</i>	62
Data analysis	62
Results	64
<i>Extinct species</i>	64
<i>Timing of extinctions</i>	64
<i>Hypothesised relationships between plant traits and extinction</i>	66
<i>Extinction risk</i>	69
Discussion	70
<i>Rarity</i>	70
<i>Habitat specialisation</i>	71
<i>Competitive ability</i>	72
<i>Dispersal ability</i>	72
<i>Position in range</i>	73
<i>Predictions of extinction risk</i>	73
<i>Extinction, land use change and eutrophication</i>	75
<i>Limitations</i>	78
Conclusions	79

5. Fifty years of change in an area of intensive agriculture: plant trait responses to habitat modification and conservation	81
Summary	81
Introduction	81
Methods	84
<i>Habitat studies</i>	84
<i>Habitat change 1949-2004</i>	84
<i>Species' trends 1949-2004</i>	84
<i>Plant trait responses to habitat modification and conservation</i>	85
Results	87
<i>Habitat change</i>	87
<i>Species' trends</i>	90
<i>Plant trait responses</i>	90
Discussion	93
<i>Habitat change</i>	93
<i>Plant trait responses to habitat modification</i>	96
<i>Effectiveness of conservation</i>	97
Conclusions	98
6. Change at the local scale: assessing the status of <i>Trifolium ochroleucon</i> Huds. (Fabaceae) in Huntingdonshire	101
Summary	101
Introduction	101
Materials and methods	102
<i>Study species</i>	105
<i>Collation of records and field survey</i>	104
<i>Habitats and management</i>	104
Results	105
<i>Number and size of populations</i>	105
<i>Habitats</i>	107
<i>Management</i>	109
<i>Change in distribution since the 1960s</i>	110
Discussion	111
Conclusions	113
7. Reduced grazing and the decline of the threatened grassland herb <i>Pulsatilla vulgaris</i> Mill. (Ranunculaceae) in England	115
Summary	115
Introduction	115
Materials and methods	118
<i>Study species</i>	118
<i>Study populations</i>	119

<i>Vegetation composition and structure</i>	119
<i>Above-ground competition</i>	120
Results	121
<i>Population details</i>	121
<i>Changes in the number and size of populations</i>	125
<i>Changes in vegetation composition and structure</i>	125
<i>Effects of shading on survival and flowering performance</i>	127
Discussion	128
<i>Overall population changes</i>	128
<i>Causes of population declines</i>	130
<i>Causes of population increases</i>	131
<i>Genetic and conservation considerations</i>	132
Conclusions	133
8. Conclusions	134
Using local floras to assess floristic and ecological change	134
What has been the scale of localised extinction over the past 350 years?	134
Was extinction random across different habitats?	135
What environmental and land use drivers have caused species loss?	136
What life-history attributes make a plant species more prone to localised extinction?	136
Which species face the greatest risk of extinction in the future?	137
Effectiveness of conservation	138
Limitations and future prospects	138
Acknowledgements	140
List of papers published	141
Appendices	143
Bibliography	170

List of tables

1.1	Species thought to be extinct in Britain and the Isle of Man with the year and vice-county in which they were last recorded.	3
1.2	Species known to be (a) extinct in southeast England or (b) having displaying a marked decline and now present in five or fewer hectads.	4
1.3	Studies which have attempted to quantify (a) the rate and scale of extinction and (b) overall floristic changes by comparing contemporary and historical records at a variety of temporal and spatial scales.	7
1.4	Hypothesised relationships between plant traits and trends (winners versus losers) within intensively managed landscapes.	14
2.1	The number of (a) local floras, (b) second editions and supplements and (c) checklists published for the British and Irish counties, 1660-2002.	23
2.2	The period in which first county floras were published for British and Irish vice-counties (the total number of vice-counties are given in parentheses).	26
2.3	The recording units used to describe species distributions in local floras, including second editions, supplements and checklists, in British and Irish vice-counties, 1780-2002.	27
2.4	Species with high rates of localised extinction in the southeast England.	29
2.5	Local or county floras that have included samples of fixed-plots (“habitat studies”) used to describe typical vegetation assemblages of the county.	32
2.6	Changes in the flora of Bedfordshire recorded between 1949 and 1976 as a result of John Dony’s (1953, 1976, 1977) resurveys of fixed plots (‘habitat studies’) and the flora as a whole.	33
3.1	Marren’s (2001) ‘league table’ of twentieth century plant extinctions in 15 English vice-counties. Extinction rates (per year) were calculated by dividing the number of apparent extinctions by the number of years included in the recording period.	40
3.2	Enumeration of the revisions to the Gent & Wilson (1995) list of extinct species in Northamptonshire (v.c. 32) with indication of recording period.	42
3.3	The number of extinctions and extinction rates for 25 British counties. Figures exclude introductions to the UK and the vice-county, hybrids, critical, subspecies (where another subspecies is extant) and dubious taxa and species last recorded before 1900. The 15 counties included in Marren’s (2001) study are denoted with an asterisk. Marren’s original figures for extinction, extinction rate and recording period are given where different from the ones presented in this chapter. The reasons for these differences are enumerated in Table 3.4.	46
3.4	Reasons for revisions to Marren’s (2001) figures (‘Original list’) for the numbers of extinctions in British counties. The table includes all 12 counties for which revised figures are presented in Table 3.3. The sign indicates whether the number should be deleted or added to the figure given in the column marked ‘Original list’.	47
4.1	Plant traits used in the study of localised extinction in Bedfordshire and Northamptonshire.	63
4.2	A comparison of the numbers of extinct and surviving species in Bedfordshire (v.c. 30) and Northamptonshire (v.c.32).	64
4.3	The number of plant extinctions and the rate per decade since 1700 in Bedfordshire and Northamptonshire.	64
4.4	Results of the chi-square (χ^2) test showing the significance of the relationship between %	66

	of extinct species and trait categories.	
4.5	Results of the binary logistic regression between extinction and the six main plant traits for Bedfordshire, Northamptonshire and both counties combined including both full and reduced models.	69
4.6	The most vulnerable species in both counties ranked in order of the predicted extinction risk calculated using the reduced binary logistic regression model for both counties (see Table 4.5).	74
5.1	Summary of broad habitats and plots included in this study.	85
5.2	Plant traits used to study the change in the frequency of species in fixed plots in Bedfordshire, 1949-2004.	86
5.3	Change in broad habitats and soil pH between 1949 and 2004 ($n = 107$).	88
5.4	The 34 vascular plants displaying significant increases in range/abundance between 1949 and 2004.	91
5.5	The 63 common vascular plants displaying significant declines in range and/or abundance between 1949 and 2004.	92
5.6	Results of the multiple binary logistic regression between species trends, colonisation and extinction rates and plant traits.	94
6.1	Details of 35 site-populations of <i>Trifolium ochroleucon</i> in Huntingdonshire.	106
6.2	The habitats of <i>Trifolium ochroleucon</i> in Huntingdonshire.	107
6.3	National Vegetation Classification communities in which <i>Trifolium ochroleucon</i> occurs in Huntingdonshire.	107
6.4	Species associated with <i>Trifolium ochroleucon</i> (in >40% of quadrats) in roadside verges ($n = 6$) and meadows ($n = 7$) in Huntingdonshire.	108
6.5	Reasons for the loss of <i>Trifolium ochroleucon</i> populations in Huntingdonshire.	110
6.6	Species of ancient grasslands, woodland edges and road verges that have been shown to decline in Huntingdonshire and adjacent counties.	111
7.1	Changes in the status of <i>Pulsatilla vulgaris</i> in English counties, 1968-2006: (a) number of populations recorded, (b) trend in abundance, and (c) current population size.	122
7.2	Changes in (i) composition and structure and (ii) cover of common species in grassland containing <i>Pulsatilla vulgaris</i> in relation to overall population trends, 1968-2006.	124
7.3	Management of <i>Pulsatilla vulgaris</i> populations in relation to trends in abundance, 1968-2006.	125

List of figures

1.1	Relationship between percentage loss of plant species and the area studied for 19 studies of floristic change ($R^2 = 71\%$).	6
2.1	The publication of local floras, second editions, supplements and checklists produced for British and Irish vice-counties, 1660-2002.	24
2.2	The number of local floras, including second editions, supplements and checklists, published for English, Scottish, Welsh and Irish vice-counties, 1660-2002.	26
2.3	The recording units used to record species distributions in local floras, 1780-2002.	28
2.4	The number of British and Irish local floras which include lists of extinct species.	29
2.5	The relationship between the abundance of Cyperaceae ($n = 59$) and Orchidaceae ($n = 22$) in Northamptonshire in 1930 and 1995 ($R^2 = 63\%$, $F_{79} = 135$, $P < 0.001$).	30
2.6	The relationship between the abundance of species in Northamptonshire in 1995 and 1930 ($R^2 = 64.4\%$, $F_{680} = 1233$, $P < 0.0001$; abundance categories are the same as for Fig. 2.5).	31
2.7	The number of first records in relation to extinction rate per year in (a) Cambridgeshire and (b) Bedfordshire.	35
3.1	Average (± 1 S.E.) twentieth century extinction rates (per year) for the 25 vice-counties included in this chapter (Table 3.3).	48
3.2	The number of extinct species in Cambridgeshire (v.c. 29) and Northamptonshire (v.c. 32) since 1620.	49
3.3	The relationship between the number of extinctions since 1900 and area of the 25 counties included in this chapter (linear regression = $58.54 - 0.003894$ area; $R^2 = 14.6\%$; $P = 0.059$).	53
3.4	The discovery of new species in Northamptonshire (v.c. 32) (within 20 year categories) in relation to extinction rate (calculated for 20 year categories before 1980).	53
4.1	The number of first (---) and last recorded dates (\square) for species in (a) Bedfordshire and (b) Northamptonshire in each 20 year interval, 1600-2000.	60
4.2	The proportion of species in Bedfordshire (grey bar) and Northamptonshire (open bar) that are extinct in relation to a range of plant trait and phytogeographical categories (see Table 4.1 for details).	65
4.3	The proportion of extinct species in relation to broad habitat type (see Appendix 4 for details).	67
4.4	The average English Change Index values (Preston et al. 2002a) for extinct and extant species in both counties (Bedfordshire, $F_{1,786} = 18.76$, $p < 0.001$; Northamptonshire, $F_{1,759} = 33.25$, $p < 0.001$).	70
4.5	Changes in proportion of arable, permanent grassland and non-agricultural land in (A) Bedfordshire and (B) Northamptonshire, 1870-2000.	76
4.6	Changes in livestock (A) and human population densities (B) in Bedfordshire and Northamptonshire.	77
5.1	Map showing the location of the study sites included in this study. The inset shows the 1 km square-level distribution of habitat studies in Bedfordshire with land above 150 m superimposed.	83
5.2	(a) The main causes of floristic change in plots where % similarity scores were $\leq 40\%$ ($n = 79$). (b) Differences in % similarity scores between 1949 and 2004 for unprotected sites and sites with conservation designations in relation to broad habitat type (acid grassland,	88

	arable, waste and river are excluded as none of the sites included in this study were protected). ** $p < 0.01$; NS not significant.	
5.3	Habitat change at three contrasting sites included in this study.	89
5.4	Relationship between (a) the number of plots occupied in 1949-51 and 2003-04; (b) the number of plots occupied in 1949-51 and colonisation rate; (c) colonisation rate and English range, (d) specialism index, (e) Ellenberg <i>N</i> and (f) plant height; (g) extinction rate and the number of plots occupied in 1949, (h) Ellenberg <i>L</i> and (i) plant height.	95
6.1	(A) The hectad distribution of <i>Trifolium ochroleucon</i> in southeast Britain showing post-1986 (red circles), 1970-1986 (green circles) and pre-1970 records (yellow circles). Introductions are represented by a ×. (B) The 1 × 1 km distribution of <i>T. ochroleucon</i> in Huntingdonshire (v.c. 31).	105
6.2	Changes in the proportion of land used for arable (including temporary grass), permanent grassland and rough grazing in Huntingdonshire and the Soke of Peterborough since 1860.	112
7.1	The distribution of <i>Pulsatilla vulgaris</i> in the British Isles in 10-km grid squares.	117
7.2	Changes in the number and size of populations of <i>Pulsatilla vulgaris</i> in England, 1960-2006.	123
7.3	(a) Sward height (cm), (b) species diversity and (c) % cover of <i>Bromopsis erectus</i> (± 1 S.E.) on extant <i>Pulsatilla vulgaris</i> sites in England ($n = 14$) grouped in relation to population trends in the period 1968-2006	127
7.4	The effects of shading on the (a) survival and (b) flowering performance of <i>Pulsatilla vulgaris</i> .	128
7.5	The decline of <i>Pulsatilla vulgaris</i> in England since 1750.	129

List of plates

1. *Pulsatilla vulgaris*, Barnack Hills and Holes, Northamptonshire. Photo: K.J. Walker. i
2. The title page of Charles Babington's 1860 *Flora of Cambridgeshire*, the first county flora to have environmental changes as a major theme. 20
3. Four species that are now extinct in Northamptonshire, one of the counties with the highest rates of extinction in lowland England: (a) *Ajuga chamaepitys* (1712), (b) *Orchis ustulata* (1956), (c) *Epipactis palustris* (1956) and (d) *Gentianella campestris* (1882). All four species have suffered widespread declines in lowland England. Photos: K.J. Walker. 38
4. Species with a high predicted risk of extinction in lowland England based on life history traits (see text for explanation): (a) *Baldellia ranunculoides*, (b) *Littorella uniflora*, (c) *Schoenus nigricans* and (d) *Carex ericetorum*. Photos: Carl Farmer (A-C) & K.J. Walker (D). 55
5. One of the maps from John Dony's (1953) *Flora of Bedfordshire* showing the location of three "habitat studies" re-recorded in 2003-04 as part of this study 80
6. *Trifolium ochroleucon*, Brampton Meadow, Huntingdonshire. Photo: K.J. Walker. 100
7. *Pulsatilla vulgaris* growing at Knocking Hoe, Bedfordshire, one of only five sites in Britain where it is still abundant. Photo: K.J. Walker. 114

Declaration

The material contained within this thesis has not been previously submitted for a degree at the University of Durham or any other university. The research reported within this thesis has been conducted by the author unless reported otherwise (see pages 141-142). It should be noted that fieldwork for the 'shading' experiment described in Chapter 7 (see pp. 120 & 127-128) was carried out by the late Terry Wells in the 1970s. The author computerised and analysed these data for the first time, and with permission, for the sole purpose of this thesis.

© The copyright of this thesis rests with the author. No quotation from it should be published in any format, including electronic or the internet, without the author's prior written consent. All information derived from this thesis must be acknowledged appropriately.

Abstract

1. In Britain the long tradition of botanical recording at the local (county) scale provides a unique observational record from which to assess floristic change. In this study I utilise historic and contemporary datasets to assess localised extinction at a variety of spatial and temporal scales.

2. One way to quantify floristic change is to calculate county extinction rates: in lowland England this approach revealed a loss of 0.5 species per year since 1900, and not one species a year as previously thought, with northern counties having a lower rate (0.4 species year⁻¹) than those in the south and east (0.6 species year⁻¹).

3. In lowland counties (Bedfordshire and Northamptonshire) the most important predictors of extinction risk were rarity, habitat specialisation and competitive ability, with short species of open, nutrient-poor habitats having declined the most.

4. A resurvey of fixed plots in Bedfordshire first visited in 1949-1951 gave similar results with tall nutrient-demanding species increasing at the expense of small habitat specialists. Losses were greatest in arable, waste and neutral to acid grassland habitats. Woodlands and calcareous grasslands showed little change and, remarkably, conservation designation had no significant effect on the magnitude of change in most habitats.

5. Population changes of the two short grassland specialists, *Trifolium ochroleucon* and *Pulsatilla vulgaris*, reinforced these results. Over the last 40 years, half the populations of both have been lost at the county (*Trifolium ochroleucon*) and national (*Pulsatilla vulgaris*) scale, initially due to habitat loss but more latterly due to reduced management (cutting and grazing) of isolated nature reserves and linear fragments of grassland.

6. *Synthesis and conclusions:* These findings, which parallel national trends, indicate that habitat loss and eutrophication have been the primary drivers of localised extinction in lowland regions over the past 350 years. Lack of management now appears to be a more pervasive threat to habitat specialists isolated in otherwise intensively managed lowland landscapes. Good regenerative ability or conservation designation are unlikely to buffer these species from further extinction, unless management or habitat restoration is undertaken to expand existing populations and promote dispersal and gene-flow.

Chapter 1

An introduction to ecological changes in the British flora

Introduction

Over the last three centuries profound habitat changes associated with a rapid rise in human population are thought to have had a major impact on local floras throughout northwest Europe (Hodgson 1986b; McKinney & Lockwood 1999; Thompson 1994; Vitousek et al. 1997a). However, opportunities to study in detail the patterns of local extinction that accompany human settlement and habitat modification are rare because it is difficult to find historical records of plant species that once occurred in a given locale (Stehlik et al. 2007). In the few cases where comprehensive historical records are available, comparisons with contemporary species lists can be used to estimate local extinction rates, elucidate the primary causes of extinction and to identify the ecological and life history traits that predispose plant species to extinction. In the UK at least, such an approach is now possible for lowland areas where comprehensive surveys of local (county) floras, habitats and species have been undertaken in successive time periods, in some cases extending over three centuries (Marren 1999a). In addition, information on the ecological demands and life history traits of virtually the entire British native and archaeophyte flora are now available (e.g. Fitter & Peat 1994; Hill, Preston & Roy 2004; Grime, Hodgson & Hunt 2007).

The use of these historical “baselines” to measure floristic changes has many benefits. First, in well recorded areas or for well recorded species they can considerably extend the period over which floristic changes can be observed, thereby allowing an assessment of the timing of change in relation to historical events. Second, because they provide information for a large number of species from many different habitats they can be used to test the pervasiveness of interacting drivers of change across a range of environmental conditions and plant trait syndromes (Schaffer et al. 1998; Smart et al. 2006). Detailed revisitation studies for individual habitats or species provide independent tests of the generality of these findings.

Finally, by comparing the ecological characteristics of successful and unsuccessful species the results can be used to predict which species are likely to succeed (or fail) in the future.

This introduction provides a brief review of the evidence for localised extinction and decline in the British flora, the approaches that have been used to investigate them and the traits often associated with “failure” in intensively managed modern landscapes. Species that have increased over recent centuries are beyond the scope of this thesis and are therefore excluded. The term extinction is used synonymously with localised or regional extinction as with one possible exception, none of the species mentioned in this thesis has become globally extinct. Nomenclature follows Stace (1997) for higher vascular plants and Smith (2004) for mosses.

Change in the British and Irish flora

Extinct species

For relatively immobile organisms such as vascular plants, natural changes in a species' distribution, such as range expansion or retreat, may take many millenia (Huntley 1991) and are therefore unlikely to be observed within historical time periods. In contrast, a decline from rarity to extinction at a local scale (e.g. population, site, grid square, county) due to human activity can be relatively rapid and is often well recorded (Lawton 1991). Therefore, localised extinctions provide an observable, albeit conservative measure of floristic change that can be indicative of more widespread environmental and ecological changes.

In Britain as a whole, only 23 species have become nationally extinct since detailed records were first made by herbalists in the sixteenth century (Table 1.1) and, with the possible exceptions of *Bromus interruptus* and *Senecio eboracensis*, both of which may be recently evolved neo-endemics (Rich & Lockton 2002; Lowe & Abbott 2003), none have become globally extinct. Furthermore, many are either ancient introductions (archaeophytes), of dubious native or taxonomic status or are likely to have been over-looked (e.g. *Epipogium aphyllum*). Interestingly, an equivalent number of species (30) were discovered as new to the British Isles in the twentieth century (Stace 2002); of these far fewer are of questionable origin, although notable exceptions include possible introductions (*Crassula aquatica*, *Cystopteris diaphana*, *Fumaria reuteri*, *Schoenoplectus pungens*, *Serapias parviflora*, *Teucrium chamaedrys*, *Vulpia unilateralis*) and *Epipactis youngiana*, which is now considered to be a recently evolved ecotype of *E. helleborine* (Hollingsworth et al. 2006).

Table 1.1. Species thought to be extinct in Britain and the Isle of Man with the year and vice-county in which they were last recorded. The list was adapted from Stace (2002) and excludes genera that include microspecies that are difficult to identify and have been confused taxonomically in the past (*Alchemilla*, *Euphrasia*, *Hieracium*, *Limonium*, *Rubus*, *Sorbus* and *Taraxacum*).

Species	Year	Vice-county	Status
<i>Trichophorum alpinum</i>	1804	Angus	Native
<i>Carex davalliana</i>	1831	N Somerset	Native
<i>Rubus arcticus</i>	1841	East Perthshire	Uncertain, no confirmed record in wild
<i>Carex trinervis</i>	1869	East Norfolk	Hybridisation with <i>C. nigra</i> suspected
<i>Cystopteris alpina</i>	1881	MW Yorkshire	Native in Teesdale only
<i>Dryopteris remota</i>	1894	Dunbartonshire	Uncertain
<i>Tephrosia palustris</i>	1899	East Norfolk	Native
<i>Pinguicula alpina</i>	1912	East Ross-shire	Single site, possibly introduced
<i>Holosteum umbellatum</i>	1930	Surrey	Neophyte associated with habitation
<i>Otanthus maritimus</i>	1936	Scilly Isles	Native
<i>Euphorbia peplis</i>	1949	East Cornwall	Native
<i>Filago gallica</i>	1955	North Essex	Archaeophyte. Re-introduced
<i>Spiranthes aestivalis</i>	1959	S Hampshire	Native. Illegally re-introduced
<i>Bupleurum falcatum</i>	1962	South Essex	Neophyte. Re-introduced
<i>Arnoseris minima</i>	1971	Bucks	Archaeophyte. Re-introduced
<i>Bromus interruptus</i>	1972	Cambridgeshire	Neo-endemic. Re-introduced
<i>Schoenoplectus pungens</i>	1972	South Lancashire	Only native on Jersey. Re-introduced
<i>Galeopsis segetum</i>	1975	Caernarvon	Archaeophyte
<i>Saxifraga rosacea</i> subsp. <i>rosacea</i>	1978	Caernarvon	Native. Still occurs in Ireland
<i>Crepis foetida</i>	1980	East Kent	Archaeophyte. Re-introduced
<i>Epipogium aphyllum</i>	1986	Berkshire	Unconfirmed records since 1990
<i>Neotinea maculata</i>	1986	Isle of Man	Temporary colonist. Still occurs in Ireland
<i>Senecio eboracensis</i>	2000	SE Yorkshire	Neo-endemic. Possibly extinct?

Notes: *Luzula pallidula* was included by Stace (2002) but there are a number of confirmed records from Holme Fen in Huntingdonshire (v.c. 31) since 1992. *Sagina boydii* was once thought to be extinct, having been collected only once by William Boyd from Ben Avon near Breamar in 1878, although he had no recollection of collecting the plant in Scotland. Recent genetic work has shown it to be a form of *S. procumbens*, *Sagina procumbens* 'Boydii' (Rich et al. 2005). A more complete list that includes the whole of GB and Ireland is given by Rich (2001).

In contrast to these rather modest changes at the national level, there has been a dramatic loss of species at the regional scale since the nineteenth century. Using information on the loss of *Nationally Scarce* species since 1970 (i.e. species recorded in between 16-100 10 km squares; Stewart, Pearman & Preston 1994) Thompson and Jones (1999) showed a strong positive relationship between localised extinction in British vice-counties and human population density. Although not thought to be a direct cause, human population density was interpreted as a crude measure of human impact on the landscape combining a range of drivers such as intensive agriculture, urbanisation and eutrophication. In the most intensively populated region of lowland England, Walker (2007) calculated that 23 native species have gone regionally extinct since records began and that an equivalent number were on the verge of extinction following dramatic declines (Table 1.2).

Table 1.2. Species known to be (a) extinct in southeast England or (b) having displaying a marked decline and now present in five or fewer hectads.¹ ‘Extinct hectads’ is the number of 10-km squares from which a species was recorded prior to 1987 but has not since been recorded and ‘Extant/extinct’ is the number remaining over the number lost. For (b) a further 65 species are present <5 hectads but are not thought to have declined. These species are listed below the table.

(a) Extinct	Extinct hectads	(b) Marked decline ²	Extant/extinct
<i>Tephrosia palustris</i>	26	<i>Gastridium ventricosum</i>	5/71
<i>Huperzia selago</i>	24	<i>Potamogeton praelongus</i>	5/55
<i>Gymnocarpium Dryopteris</i>	13	<i>Damasonium alisma</i>	3/46
<i>Genista pilosa</i>	7	<i>Gentianella campestris</i>	5/46
<i>Pseudorchis albida</i>	7	<i>Antennaria dioica</i>	1/34
<i>Schoenoplectus triquetus</i>	6	<i>Lactuca saligna</i>	3/33
<i>Elatine hydropiper</i>	5	<i>Cynoglossum germanicum</i>	3/30
<i>Listera cordata</i>	4	<i>Teucrium scordium</i>	1/20
<i>Epipogium aphyllum</i>	3	<i>Atriplex pedunculata</i>	1/17
<i>Selaginella selaginoides</i>	3	<i>Utricularia intermedia</i> sens. lat.	1/17
<i>Asplenium viride</i>	2	<i>Liparis loeselii</i>	2/16
<i>Luronium natans</i>	2	<i>Orchis militaris</i>	3/16
<i>Orobancha alba</i>	2	<i>Alchemilla glabra</i>	4/14
<i>Scheuchzeria palustris</i>	2	<i>Leersia oryzoides</i>	3/14
<i>Asplenium obovatum</i>	1	<i>Viola persicifolia</i>	3/14
<i>Cirsium tuberosum</i>	1	<i>Campanula patula</i>	3/13
<i>Diphasiastrum alpinum</i>	1	<i>Vicia bithynica</i>	5/13
<i>Diphasiastrum complanatum</i>	1	<i>Carex limosa</i>	3/12
<i>Mertensia maritima</i>	1	<i>Erodium maritimum</i>	3/10
<i>Pyrola media</i>	1	<i>Potentilla neumanniana</i>	5/10
<i>Trientalis europaeus</i>	1	<i>Lotus angustissimus</i>	5/9
<i>Vaccinium vitis-idaea</i>	1	<i>Salicornia nitens</i>	3/9
<i>Vicia orobus</i>	1	<i>Hypochaeris maculata</i>	5/8

Notes: ¹ SE England includes all vice-counties to the east of a line running from Poole in Dorset to Goole in SW Yorkshire (vcs 10-32 & 53-56). ² A further 65 species occur in ≤5 10-km squares in SE England but are not thought to have suffered marked declines: *Alisma gramineum*, *Allium scorodoprasum*, *Apium repens*, *Artemisia campestris*, *Asplenium marinum*, *Atriplex longipes*, *Blysmus rufus*, *Bupleurum baldense*, *Calamagrostis stricta*, *Carex depauperata*, *Carex filiformis*, *Carum verticillatum*, *Cephalanthera rubra*, *Clinopodium menthifolium*, *Cyperus fuscus*, *Dactylorhiza purpurella*, *Eleocharis parvula*, *Equisetum variegatum*, *Eriophorum gracile*, *Euphorbia portlandica*, *Festuca altissima*, *Fumaria purpurea*, *Gentianella ciliata*, *Gnaphalium luteoalbum*, *Goodyera repens*, *Gymnocarpium robertianum*, *Hymenophyllum tunbrigense*, *Juncus acutus*, *Juncus filiformis*, *Lavatera arborea*, *Lobelia urens*, *Ludwigia palustris*, *Luzula pallidula*, *Maianthemum bifolium*, *Melica nutans*, *Najas marina*, *Ophioglossum azoricum*, *Ophrys fuciflora*, *Orchis simia*, *Orobancha artemisiae-campestris*, *Orobancha caryophyllea*, *Petrorhagia nanteuillii*, *Phegopteris connectilis*, *Pilosella peleteriana*, *Phyteuma spicatum*, *Polygala amarella*, *Polygonum maritimum*, *Potamogeton nodosus*, *Pulmonaria obscura*, *Rosa mollis*, *Rubus saxatilis*, *Salicornia obscura*, *Salix myrsinifolia*, *Scleranthus perennis*, *Scilla autumnalis*, *Selinum carvifolia*, *Senecio paludosus*, *Seseli libanotis*, *Sibthorpia europaea*, *Sparganium angustifolium*, *Stachys germanica*, *Stellaria nemorum*, *Thlaspi perfoliatum*, *Thymus serpyllum*, *Veronica spicata*, *Veronica verna*.

The majority of these extinctions are of Northern (Boreal) species at the southern edge of their range in southeast England that declined following the widespread loss of lowland heath and bog (e.g. *Diphasiastrum* spp., *Huperzia selago*, *Gymnocarpium dryopteris*, *Listera cordata*, *Pseudorchis albida*, *Pyrola media*, *Scheuchzeria palustris*, *Trientalis europaeus*, *Vaccinium vitis-idaea*). Other common reasons included drainage of fenland (*Tephrosia*

palustris), habitat modification followed by hybridisation (*Schoenoplectus triquetus*), ploughing of calcareous grassland (*Cirsium tuberosum*) and changes to aquatic habitats (*Elatine hydropiper*, *Luronium natans*). Species which have suffered dramatic declines show a similar pattern with the majority of species associated with rivers and wetlands (*Damasonium alisma*, *Leersia oryzoides*, *Potamogeton praelongus*, *Teucrium scordium*), infertile grasslands and heaths (*Antennaria dioica*, *Gentianella campestris*, *Orchis militaris*, *Potentilla neumanniana*) and lowland bogs and mires (*Carex limosa*, *Liparis loeselii*, *Veronica persicifolia*, *Utricularia intermedia*).

The publication of numerous county floras over recent decades (>30 including checklists since 1990) that include lists of extinct species has provided a fascinating picture of the scale and rate of plant losses at the local scale in England (Marren 2000, 2001). Using data from 15 modern floras, Marren (2000) showed that British vice-counties lost between 0.3 and 1.4 species per year during the twentieth century (average 0.7 species yr⁻¹). A similar rate of loss has been reported for equivalent sized rural areas in the USA and Europe (0.2-0.5 species yr⁻¹) (Marks, Wesley & Gardescu 2008; Van Calster et al. 2008) whereas much higher rates (0.7-2.9 species yr⁻¹) have been recorded for smaller urban areas (Drayton & Primack 1996; Duncan & Young 2000; DeCandido 2004).

In England, Preston (2000) has extended analyses of localised extinction as far back as 1750 for Middlesex and Cambridgeshire and has shown that rates of extinction vary depending on the dominant type of land use. In Middlesex, the peak period of extinction (> 7 species per decade) coincided with the spread of the London conurbation after 1870 whereas in Cambridgeshire two peaks coincided with the main period of parliamentary enclosure between 1810 and 1830 and the introduction of mechanised agriculture after 1930. Dony (1977) carried out a more limited analysis in Bedfordshire and showed that 66% (71 species) of the total native extinctions in the county occurred prior to the publication of Abbott's (1798) *Flora Bedfordiensis* in 1798. Similarly, 70% of extinctions (up to 1989) in the adjacent county of Huntingdonshire occurred before 1900, mainly due to the drainage of Whittlesea Mere and adjacent bogs which was completed by 1852 (Wells 1989). Other local studies that have taken a similar approach are listed in Table 1.3.

Local studies have also revealed marked variation in the magnitude of local extinction at different spatial scales. In a comparison of 19 studies that used complete historical floras, the

percentage loss of species was negatively related with log-transformed size of the study area regardless of landscape type ($F = 41.3$, $P < 0.001$, $R^2 = 71$, Fig. 1.1). Studies at the smallest scales included moderate sized cities, peri-urban areas and rural parishes and reported a loss of over 20% of their respective floras over the last century (e.g. Duncan & Young 2000; Preston et al. 2003; DeCandido 2004). In comparison, moderately sized English counties lost between 10-20% (e.g. James 1997; Preston 2000, Van Calster 2008; Chapter 4) whereas losses in largest regions (Sheffield, Cayuga) were between 5-8% (Hodgson 1986a; Marks et al. 2008).

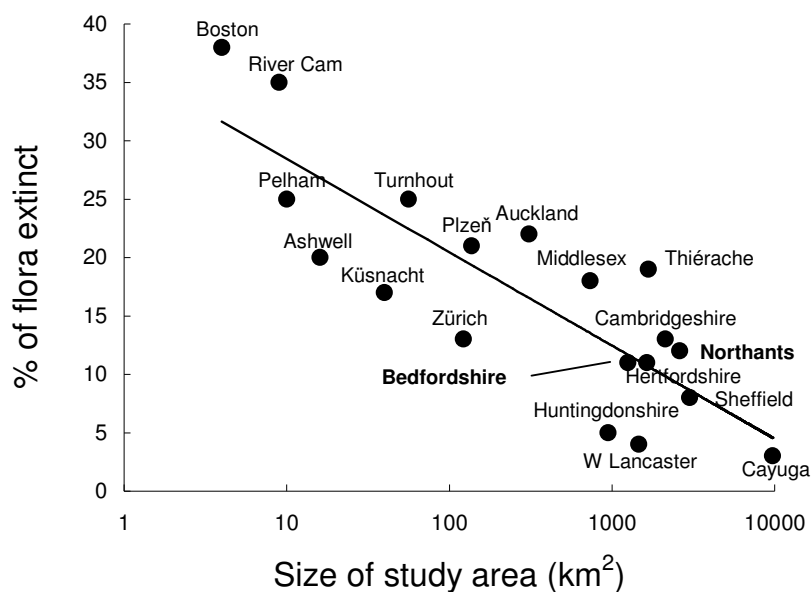


Figure 1.1. Relationship between percentage loss of plant species and area for 19 studies of floristic change ($R^2 = 71\%$). Sources are as follows: Boston (Drayton & Primack 1996), River Cam (Preston et al. 2003a), Pelham (DeCandido 2004), Ashwell (James 1992), Künsnacht (Stehlik et al. 2007), Turnhout (Van der Veken et al. 2004), Zürich (Landolt 2001), Plzeň (Chocholoušková & Pyšek 2003), Auckland (Duncan & Young 2000), Middlesex (Preston 2000), Huntingdonshire (Wells 1989), Bedfordshire (this study, Chapter 4), W Lancaster (Greenwood 2003), Hertfordshire (James 1997), Thiérache (Van Calster et al. 2008), Cambridgeshire (Preston 2000), Northamptonshire (this study, Chapter 4), Sheffield (Hodgson 1986a), Cayuga (Marks et al. 2008).

Table 1.3. Studies that have attempted to quantify (a) the rate and scale of extinction and (b) overall floristic changes in an area by comparing complete contemporary and historical records at a variety of temporal and spatial scales.

Study	Time period	Yrs	Recording unit	Area (km ²)	Method used	Source
(a) Studies utilizing historical records to quantify rate and scale of localized extinction (listed in order of area covered):						
Jura Mountains, Switzerland	1950-1985	35	100m ² plots	26 sites	Resurvey of calcareous grassland plots	Fischer & Stöcklin (1997)
Middlesex Fells, Boston USA	1894-1993	119	City	4	Comparison of historical and contemporary records	Drayton & Primack (1996)
Pelham Park, New York, USA	1947-1998	51	City park	11	Comparison of historical and contemporary records	DeCandido (2004)
Ashwell, Hertfordshire, UK	1800-1990	190	Parish	16	Comparison of historical and contemporary records	James (1992)
Küsnacht, Switzerland	1839-2003	164	Municipality	40	Comparison of historical and contemporary records	Stehlik et al. (2007)
Turnhout, Belgium	1880-1999	119	City	56	Comparison of historical and contemporary records	Van der Veken et al. (2004)
Auckland, New Zealand	1871-1985	114	City	308	Comparison of historical and contemporary records	Duncan & Young (2000)
Middlesex, UK	1750-2000	250	County	734	Comparison of historical and contemporary records	Preston (2000)
Huntingdonshire, UK	1949-1989	50	County	948	Comparison of historical and contemporary records	Wells (1989)
West Lancaster, UK	1907-2001	94	County	1462	Comparison of historical and contemporary records	Greenwood (2003)
Hertfordshire, UK	1924-1997	73	County	1640	Comparison of historical and contemporary records	James (1997)
Thiérache, N France	1891-2005	114	Region	1673	Comparison of historical and contemporary records	Van Calster et al. (2008)
Cambridgeshire, UK	1750-2000	250	County	2124	Comparison of historical and contemporary records	Preston (2000)
Sheffield, UK	Unknown	NA	Region	3000	Comparison of historical and contemporary records	Hodgson (1986a)
Hérault, S France	1886-2001	115	Region	6250	Comparison of historical and contemporary records	Lavergne et al. (2005)
Cayuga Region, Ithaca, USA	1886-2005	119	Region	9700	Comparison of historical and contemporary records	Marks et al. (2008)
English grazing marshes, UK	1840-1994	254	3 wetland areas	Unknown	Comparison of historical and contemporary records	Mountford (1994)
Howardian Hills, Yorkshire, UK	1794-1988	194	AONB	Unknown	Comparison of historical and contemporary records	Gulliver (1990)

Table 1.3. Continued.

Study	Time period	Yrs	Recording unit	No. samples	Method used [†]	Source
(b) Studies utilizing complete historical baselines to quantify change at a variety of scales:						
British & Irish flora	1930-1999	70	Hectad	c.2500	Resurvey of hectads in GB & Ireland	Preston et al. (2002a)
BSBI Monitoring Scheme	1930-1987	57	Hectad	264	Resurvey of every 9th hectad in E, W & S	Rich & Woodruff (1996)
BSBI Local Change	1987-2004	17	Tetrad	635	Resurvey of 3 tetrads in 1/10 hectads in E, W & S	Braithwaite et al. (2006)
Dutch flora	1902-2000	98	Monad	National	Resurvey of monads	Tamis et al. (2005)
Druce's abundance, Northants	1930-1995	65	Pentad	120	Comparison of 1930 abundance with modern pentads	McCollin et al. (2000)
Bunce's Woodland Survey	1971-2001	30	200m ² plot	103	Resurvey of 16 fixed plots per site in E, W & S	Kirby et al. (2005)
Countryside Survey	1978-2007	29	10-200m ² plot	1538	Resurvey of fixed plots in 1 km squares in E, W & S	Smart et al. (2005)
Dony's Habitat Studies, Beds	1951-1976	25	65m ² plot	111	Resurvey of fixed plots in range of habitats	Dony (1977)
Perring's calc. grassland plots	1952-2003	51	50m ² plot	263	Resurvey of grassland stands in England	Bennie et al. (2006)
Good's Dorset heathlands	1931-1993	62	Plot	390	Presence of 41 species in fixed "stands"	Byfield & Pearman (1994)
Good's Dorset hedgerows	1931-2001	70	Plot	358	Resurvey of a sample of fixed hedgerow "stands"	DERC (2003)
Oxon/Berks arable survey	1962-1997	35	Margin	156	Resurvey of field margins recorded in 1960s	Sutcliffe & Kay (2000)
River Cam, Cambridge	1660-2000	340	River	1	Comparison of historical and contemporary records	Preston et al. (2003a, 2008)
Judith's Hedge, Huntingdon	1971-1998	27	Hedgerow	1	Resurvey of ancient hedgerow	Garbutt & Sparks (2002)
Plzeň, Czech Republic	1880-2000	120	City	137km ²	Comparison of historical and contemporary records	Chocholoušková & Pyšek (2003)

[†] E, England; W, Wales; S, Scotland.

Although the overall scale of losses in lowland areas appears similar, there are a number of limitations in using extinction as a surrogate measure of floristic and ecological change. First, as noted above, area buffers against extinction and therefore more species are likely to be lost from smaller areas (e.g. May et al. 1995). Second, species-rich areas can be expected to lose more species than species-poor areas (other things being equal). Third, counties vary dramatically in the timing of extinction events, as Preston's (2000) analysis clearly shows. Finally, and probably most important, extinction is seldom forever and often remarkably difficult to prove. Many species thought to be extinct either persist in seed banks or are overlooked because they are rare, difficult to record or occur in under-recorded habitats. Indeed, studies on localised extinction in Switzerland have shown that rates of pseudo-turnover (non-detection reported as extinction) can be as high as 19% (Fischer & Stöcklin 1997) and consequently repeated revisits are required to allow the separation of extinction from simple non-detection for some species (Kéry et al. 2006). Because uncommon species tend to have much higher rates of pseudo-turnover (Fischer & Stöcklin 1997) some studies have excluded rarer species from analyses of changes on fixed plots where the exact location of the original survey location is unknown (e.g. Bennie et al. 2006). Pseudo-turnover may be accentuated at the county scale because of the difficulties of censusing species over large areas. For example, in Hertfordshire nearly half the species presumed extinct by Edward Salisbury in the 1920s (Salisbury 1924) had been re-found by the time John Dony published his flora of the county in 1967 (Dony 1967; James 1997). Preston (2000) adds a sensible note of caution in suggesting that species which have been seen at some point within the last decade should not be considered extinct as "such a judgement would be premature" (p.60). A more detailed account of the approaches used to study localised extinctions and their limitations is presented in Chapter 3.

Declining species

Because rare species tend to be confined to protected sites they can be poor indicators of environmental changes occurring in human modified ecosystems (Thompson & Jones 1999). Consequently more widespread species are more useful as indicators of floristic and ecological changes. Unfortunately there are few datasets available that provide repeatable baselines for these species over more than a few decades (Stehlik et al. 2008) and even where these do exist, differences in recorder effort and behaviour can make comparisons between surveys difficult to interpret (Rich & Woodruff 1992; Rich & Smith 1996; Rich 2001; Rich &

Karran 2006). Despite these limitations, many studies comparing complete contemporary and historic datasets to quantify change have been published in recent years (Table 1.3b).

Early county floras and maps in the first *Atlas of the British flora* (Perring & Walters 1962) showed that many species had already suffered marked contractions in range by the early part of the twentieth century (e.g. *Drosera rotundifolia*, *Lycopodiella inundata*, *Myosurus minimus*, *Orchis ustulata*, *Torilis arvensis*). Some of these species were discussed in detail by Perring (1970) who was in no doubt that although “some may be due to subtle biological causes...the vast majority are due to man, and the evidence is that his destructive effect on the flora is accelerating” (pp.130-131). More recent recording projects, most notably the *New Atlas of the British and Irish Flora* (Preston, Pearman & Dines 2002a), have shown the full extent of these declines up to 1999. For each species (excluding the rarest and the majority of alien species) a measure of change was calculated. This *Change Index* (CI) is based on a comparison of the results of the nationwide surveys of British plant distribution at the 10 × 10 km (hectad) scale (1930-1969 and 1987-1999) and takes into account differences of recording intensity (Telfer, Preston & Rothery 2002). For an individual species a CI refers to the change in frequency of occurrence compared to that of an “average species”. The indices of all species sum to zero. When summarised by habitat the results showed a dramatic decline of species of unproductive arable, dwarf shrub heaths and calcareous grasslands and an increase in the occurrence of species of improved grasslands and urban areas (Preston et al. 2002b). Relatively stable habitats included neutral grassland, fens, marshes, swamps and broad-leaf woodland. Using a different scale and statistical approach, remarkably similar results were recorded for the Dutch flora over the same period, with a marked decline in vegetation types of nutrient-poor sites, particularly those on circum-neutral soils (Tamis et al. 2005).

The re-survey of every ninth hectad in 1987 and 1988 as part of the Botanical Society of the British Isles (BSBI) *Monitoring Scheme* (Rich & Woodruff 1996) and more recently as part of the BSBI *Local Change* project (Braithwaite, Ellis & Preston 2006) have provided more detailed assessments of change in the British flora during the latter part of the twentieth century. By comparing the results of the *Monitoring Scheme* with data collected for the first Atlas, Rich & Woodruff (1996) were able to provide lists of species that had changed significantly in frequency since 1960. In order to account for variations in recording effort, frequency data for the original *Atlas* survey were corrected to a relative value for comparison with the frequency in the *Monitoring Scheme*. This included a correction for country effort

(constant) which ensured that the total number of *Atlas* database records equalled the total number of *Monitoring Scheme* records. The results showed that 24% of the species recorded in England displayed significant changes in distribution between the two surveys with a dramatic decline of species associated with grassland, heathland, aquatic and swamp habitats and arable weeds whilst many introduced species had increased.

The BSBI *Local Change* project, carried out between 2003 and 2004, aimed to re-survey three 2×2 km squares (tetrads) in each hectad originally visited during the *Monitoring Scheme* (“A, J, W” tetrads using the 25 letter ‘DINTY’ naming convention for the 25 tetrads in each hectad) to assess changes over the intervening period (see Braithwaite et al. 2006). This provided comparable information for 635 tetrads and 860 species found in 15 or more of the sample tetrads. A change statistic was calculated in the same way as for the *New Atlas* (i.e. a residual from a linear regression of net change divided by range plotted against range). However, for *Local Change* this was weighted to take into account the extent to which a species was under-recorded (see Appendix 2 in Braithwaite et al. 2002 for further details). Again the results showed an overall loss of species of infertile habitats, particularly calcareous grassland and dwarf shrub heath, with the overall causes thought to be increased fragmentation, eutrophication and both under and over grazing.

In comparison to these large scale surveys the UK’s *Countryside Survey* has, since 1978 attempted to assess the fate of common species located in over 1000 small, fixed plots (10-200 m²) located within a random national sample of over 250 1 km squares (Smart et al. 2003, 2005). Re-recording of plots in 1978, 1990, 1998 and 2007 has shown trends consistent with the impact of increased nutrient availability amongst unproductive habitats and secondary succession on linear habitats and habitat fragments in the lowlands (Smart et al. 2003). In addition, plant communities became functionally more similar over the same period as different communities became dominated by a more restricted suite of successful species (Smart et al. 2006).

Two national sample surveys of specific habitats have utilised historic data from sample plots in broadly the same way as *Countryside Survey*. Between 2000 and 2003 Kirby et al. (2005) resurveyed fixed plots within 103 woodlands throughout Britain in order to assess changes at both the plot and site level since they were first surveyed in 1971. The results showed that although the broad composition and structure had not changed dramatically there was overall

increase in soil pH and decline in specialist woodland ground flora diversity. This was taken to represent a deterioration in the quality of woods as a result of diffuse pollution and the management of adjacent land. Bennie et al. (2006) assessed long term vegetation changes on 17 British chalk grassland sites in four regions originally surveyed by Franklyn Perring in 1952-53. A re-survey of 92 plots in 2003 showed a dramatic decrease in species-richness and a shift in composition from calcareous to mesotrophic grassland consistent with the predicted effects of habitat fragmentation and nutrient enrichment.

In Britain at least, only a handful of studies have attempted to quantify floristic changes at more restricted spatial scales (Table 1.3b). In Dorset re-surveys of stands of vegetation recorded by Professor Ronald Good (1948) during the 1930s have shown a dramatic decline in the numbers of threatened heathland species (Byfield & Pearman 1994) and in the diversity of hedgerows (DERC 2003). A similar approach was taken in Bedfordshire where John Dony (1953) recorded over 100 fixed plots in a range of habitats (“habitat studies”) to enable “field botanists of a future generation to determine with some degree of accuracy changes which may occur in the flora” (Dony 1953, p. 54). A partial re-survey of these plots in 1976 revealed dramatic changes on acid grassland, heathland, marsh and water meadow plots whereas those in woods and on calcareous grassland were relatively unchanged (Dony 1977). The results of a complete re-survey of these plots, carried out in 2003-04, are presented in Chapter 5. Surveys of arable field margins first recorded in the 1960s have also shown the dramatic decline of certain arable species as a result of increased use of herbicides and fertilisers and more intensive cropping regimes (Sutcliffe & Kay 2000). In Northamptonshire McCollin et al. (2000) used a novel approach to quantify floristic changes since the publication of George Claridge Druce’s flora of the county in 1930 (Druce 1930). By converting Druce’s historical abundance classes into an ordinal scale they were able to plot the historic abundance against the numbers of modern 5 × 5 km grid squares (pentads). The residuals from a linear regression were then used to assess the degree of change for each species across the two survey periods. The comparison of historical abundance classes with contemporary records has also been used to assess floristic changes in Auckland, New Zealand (Duncan & Young 2000) and in the Thiérache region of France (Van Calster et al. 2008).

Availability of plant trait information for the British and Irish flora

The previous section has shown that a range of approaches have been used successfully to quantify floristic changes at a range of spatial and temporal scales over the last 30 years. However, our ability to interpret these changes in relation to major environmental drivers has been limited in the past by the availability of trait information. Although databases of ecological attributes have been available for some British species since the late 1980s (e.g. Grime, Hodgson & Hunt 1988, 2007; Fitter & Peat 1994) their use has been limited by the lack of information for some species. This led to the development of more comprehensive datasets that could be used to analyse changes in botanical characteristics at a national level (e.g. Hill et al. 1999, 2000; Hill, Preston & Roy 2004). As a consequence, the approaches used have changed markedly over the last 20 years from simple correlations with habitat (e.g. Rich & Woodruff 1996) to more sophisticated modelling approaches that attempt to differentiate the impacts of multiple drivers using functional types (e.g. Smart et al. 2006). Although the use of these traits has greatly increased our ability to analyse and interpret floristic changes, new traits may be required to provide ‘signals’ of more pervasive pressures such as climate warming or atmospheric pollution.

Attributes of extinct and declining species

The hypothesised relationships between plant traits and the localised extinction of plant species within intensively managed lowland landscapes is presented in Table 1.4. Each trait group is discussed in detail below.

Habitat

Habitat is often the strongest predictor of extinction risk as they differ markedly in the extent to which they have been affected by recent land use changes. For example, James (1997) showed that the majority of extinctions since the middle of the seventeenth century in Hertfordshire occurred in acid grassland (19%), marshes (21%) and arable habitats (17%). Similar results have been reported for Cambridgeshire, Bedfordshire and Northamptonshire, which have all lost a high proportion of species associated with open grasslands (especially on acid soils), wetlands and cultivated land (Robertson 1982; McCollin et al. 2000; Preston 2000). These changes support national findings and the decline of species associated with arable land, wetlands and unproductive grasslands and heaths (Rich & Woodruff 1996; Preston et al. 2002a,b; Braithwaite et al. 2006). Studies from other countries have shown that species associated with the most fragmented habitats are more likely to suffer localised

extinctions than those occurring in less affected habitats (e.g. Duncan & Young 2000; Sthelik et al. 2007). In comparison, some habitats appear to have lost relatively few species, presumably because they have been less susceptible to modern land use changes. Woodlands, for example, appear to have remained relatively stable in composition throughout Europe over recent decades indicating a flora that is largely resistant, or only responding very slowly, to past or current changes in land-use and atmospheric pollution even in urban or peri-urban areas (e.g. Rackham 1980; Preston 2000; DeCandido 2004; Kirby et al. 2005; Stehlik et al. 2007; Van Calster et al. 2008). However, in the UK changes in management (coppicing, ride management etc.), increased deer grazing and deposition of atmospheric pollutants is predicted to cause changes, particularly to the composition of the ground flora, in the near future (Kirby et al. 2005).

Table 1.4. Hypothesised relationships between plant traits and trends (losers versus winners) within intensively managed landscapes.

Trait group	Plant trait	Losers	Winners	Potential drivers
Habitat	Habitat type	Unproductive	Productive	Habitat loss, fragmentation, eutrophication
	Habitat specificity	High	Low	
	Resource requirements	Specialised	Generalist	
Competitive ability	Plant height	Small	Tall	Eutrophication, succession (i.e. reduced disturbance)
	Life-history	Short-lived	Long-lived	
	Lateral spread	Non-clonal	Clonal	
Dispersal ability	Seed size	Large seed	Small seeds	Habitat loss, fragmentation, changing agricultural practices
	Specialised dispersule structures	Absent	Present	
	Seed bank longevity	Transient/short	Long	
Reproductive strategy	Breeding system	Out-crossing	Mixed mating	Habitat loss, fragmentation
	Regeneration	Seed only	Seed & vegetative	
Range	Range size	Restricted	Widespread	Habitat loss, fragmentation, eutrophication, succession, climate change
	Position in range	Range margin	Core	
	Abundance	Rare	Abundant	

A positive correlation between niche breadth and range size is predicted because species which can exploit a wide range of resources will be able to survive in more places and hence over a larger area (Brown 1984). Indeed, in Central England habitat specialisation was found to be one of the most important predictors of range size (Thompson et al. 1998) even when

combined with other factors believed to control abundance (Thompson et al. 1999). Consequently habitat specialists are predicted to decline to a much greater extent than generalists as a result of habitat loss and fragmentation. Although relatively few studies have tested this hypothesis explicitly there seems to be a strong positive correlation of increasing specialisation with higher rates of localised extinction and decline (e.g. Fischer & Stöcklin 1997; McCollin et al. 2000).

Competitive ability

An inability to tolerate competition is predicted to be a major determinant of species loss within intensively managed landscapes as poor competitors are unlikely to persist within increasingly disturbed and fertile man-made habitats. Conversely, competitive species are predicted to become much more widespread and abundant across a range of human-modified habitats (Thompson 1994). Plant height provides a direct measure of above-ground competitive dominance (Weiher et al. 1999) and has been related to rarity and extinction in a number of studies. Thompson (1994) demonstrated a marked correlation between low canopy height and a tendency to decline in England and Preston (2000) showed that the majority of extinct species in Middlesex and Cambridgeshire were of very low stature. Similarly, short species were more likely to be extinct or rare in Auckland, New Zealand, following 114 years of European settlement (Duncan & Young 2000).

Although life-history provides a measure of longevity and therefore of the ability of a species to survive unfavourable conditions, it is not yet clear how a short or long life cycle relates to extinction risk. High extinction rates have been biased towards short-lived species in some studies presumably because of dramatic declines of annual arable species relative to other life-forms (e.g. Stehlik et al. 2007; Van Calster et al. 2008) and succession on isolated grassland sites promoting the increase of taller phanerophytes (e.g. Fischer & Stöcklin 1997). However, Thompson (1994) showed that short-lived species with a high R- radius (the extent to which a species is adapted to disturbance) had fared much better in England and the Netherlands, presumably because this study included many short-lived aliens that are able to exploit disturbed man-made habitats. Likewise, the extent to which clonality (lateral spread) can buffer a species from population declines as a result of seed or pollination failure is not clear (Bond 1995; Fischer & Stöcklin 1997). Although McCollin et al. (2000) reported a limited capacity for lateral spread for declining species in Northamptonshire other studies have shown it to be unimportant (e.g. Thompson 1994; Duncan & Young 2000).

Competitive ability combines a measure of a species' resource requirements and in particular soil nutrients vital for plant growth. As a consequence of recent land-use changes, which have led to an increase in the fertility and therefore productivity of many habitats, we would expect species with high nutrient requirements to increase and species of unproductive habitats to decline (McKinney & Lockwood 1999; Thompson 1994; Vitousek et al. 1997a,b; Stevens et al. 2005). Ellenberg's indicator values for fertility (N), moisture (F), light (L) and reaction (R) provide the most widely used metrics to test this hypothesis and N in particular has been shown to be one of the most consistent predictors of localised extinction risk across a wide range of both spatial and temporal scales in northwest Europe (e.g. Preston 2000; McCollin et al. 2000; Preston et al. 2002a; Smart et al. 2005; Tamis et al. 2005; Braithwaite et al. 2006). A modified version of this scale, developed by Landolt (1977), has been used in Europe, giving very similar results, with species adapted to the most nutrient-poor soils displaying the highest levels of local extinction risk (e.g. Stehlik et al. 2007).

Dispersal ability

Metapopulation theory asserts that regional survival of species requires that local populations are connected by sufficient rates of dispersal (Hanski 1998). In contrast to mobile animal species, plants depend for their dispersal on external vectors, including water, wind, birds and large animals. With the breakdown of this "dispersal infrastructure" following habitat modification and fragmentation (Poschlod & Bonn 1998; Ozinga et al. 2004), a positive relationship between dispersal ability and declining range size might be expected, as species with poor dispersal abilities cannot attain distant suitable sites (Harrison & Bruna 1999; Ozinga et al. 2009). However, the majority of recent studies have revealed only a weak relationship between seed dispersal and declining range size in seed plants (e.g. Thompson 1994; Duncan & Young 2000). Furthermore, comparisons of common and rare species have shown that dispersal characters only account for a small amount of the variance (2-4%) within local distributions, none of the variation in national range and that, most surprisingly of all, species with limited dispersal ability were more widespread (Thompson, Gaston & Band 1999). The reasons for this weak relationship is far from clear but may relate to the simplistic distinction between well (wind) and poorly (not-wind) dispersed species in many studies which fails to take into account other potentially important mechanisms, such as zoochory (Thompson & Hodgson 1996; Thompson et al. 1999). Using a more sophisticated approach, Ozinga et al. (2009) showed that differences between species in adaptations to various dispersal vectors, in combination with changes in the availability of these vectors,

contributed significantly to explaining declines in plant species across Northwest Europe in recent decades. Species with water- or fur-assisted dispersal had declined to a much greater extent than bird or wind dispersed species suggesting that a degraded “dispersal infrastructure” is likely to be as important as eutrophication in explaining plant diversity losses during the twentieth century.

It is often assumed that species with heavier seeds will be poorly dispersed and therefore are likely to suffer more severe declines as a result of habitat loss and fragmentation. However, no correlation has been found between seed weight and range size (Thompson et al. 1999), the degree of aggregation of scarce species (Quinn et al. 1994) or changes in species status at the national scale (Thompson 1994). Conversely, McCollin et al. (2000) found heavier-seeded species had actually increased in abundance in Northamptonshire over the last 70 years whereas in New York species with fleshy fruits were no more likely to have gone extinct than other species (DeCandido 2004). The reason for this is not clear but may partly be explained by the dispersal of large fruits and seeds by birds and mammals which has been shown to be more effective than wind for many tree species (e.g. Walker, Swetnam & Sparks 2000).

A persistent seed bank is expected to buffer species against local extinction because it enables populations to survive unfavourable periods below ground. However, the findings of recent studies are equivocal. Stöcklin & Fischer (1999) reported lower extinction rates for species with longer lived seed banks (>5 years), and Ozinga et al. (2009) showed that species with the ability to accumulate a soil seed bank have fared better than species with transient seed banks in the Netherlands, Great Britain and Germany over recent decades. However, in earlier analyses no relationships were found with the changing status of species in Britain and the Netherlands (Thompson 1994) or distribution of scarce species in Britain (Thompson & Hodgson 1996). Most surprisingly, McCollin et al. (2000) found that species with the largest seed banks had declined the most in Northamptonshire.

Breeding system

Out-breeding, insect pollinated plants are predicted to have more restricted distributions than self-fertilising species because they are limited by the distribution and ecological requirements of their associated pollinators (Baker 1953). As a consequence, we might expect obligate out-crossing species to be more susceptible to the effects of land-use change, and in particular isolation, as fragmentation will reduce their chance of reproductive success (Kunin

1992). Indeed Beiswenger et al. (2006), showed parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands suggesting a causal connection between the local extinction of both functional groups. Furthermore, Quinn et al. (1994) showed that, for scarce species, obligate out-crossing species have much more strongly aggregated distributions than all other species. However, I am not aware of any studies that have attempted to relate localised extinctions to breeding systems at more local scales.

Range

The rarity of a species is predicted to be a strong predictor of decline as smaller populations are more vulnerable to localised extinction as a result of genetic, demographic or environmental problems (Lande 1988; Schaffer 1987). Studies at a variety of scales have shown this to be the case, with rare species suffering much higher localised extinction than species that were more common or widespread (e.g. Fischer & Stöcklin 1997; Duncan & Young 2000; Preston 2000; Van Calster et al. 2008). The position within a species' overall range will also have a strong influence on localised extinction because species tend to be rarer nearer range margins. In addition, recent increases in mean temperature are expected to result in a poleward shift in the distributions of some species (Roy & Sparks 2000) thereby causing declines of northern plant species at their southern range margins in the UK. The predicted increase in the oceanicity of the British climate might also result in an eastward shift in the range of more continental species (Crawford 1997). By assigning species to biogeographic elements based on latitudinal and longitudinal range extents, recent classifications of the British flora (Preston & Hill 1997; Preston 2007) provide the information required to test these hypotheses. However, in the southeast of England, there appears to be little evidence to support these shifts, with the main changes being a reduction in phytogeographic diversity and the increasing predominance of species already in the dominant major biomes (Boon 1998; Preston 2000). Indeed, in Northamptonshire increasing species tended to belong to more continental (eastern) categories (i.e. Eurosiberian, Euroasian) (McCollin et al. 2000).

Objectives and outline of the thesis

The main objective of this thesis is to utilise the wealth of historical data available for the British flora in order to quantify the floristic changes that have taken place since botanical recording began over 350 years ago. By comparing historic and modern datasets at a range of spatial and temporal scales I address the following five questions:

- (1) What has been the scale of localised extinction over the past 350 years?
- (2) Has extinction been random across different habitats?
- (3) What underlying environmental and land use drivers have caused species loss?
- (4) What life-history attributes make a plant species more prone to localised extinction?
- (5) Which species face the greatest risk of extinction in the future?

In Chapter 2 I review the production of local floras produced for British and Irish counties and provide an assessment of the ways in which they can be used to study floristic change. In Chapter 3, published lists of localised extinctions are analysed to assess the rate and scale of extinction at the county scale in England. The problems associated with the use of these data are discussed. Chapter 4 provides a more detailed analysis of localised extinction in the lowland counties of Bedfordshire and Northamptonshire in relation to plant traits which are modelled to identify the most important predictors of extinction risk. In Chapter 5, changes in the flora of Bedfordshire are further analysed using a revisitation survey of small fixed plots in 1949-51 and 2003-04. Overall changes are related to habitat, plant traits and the main drivers of change. In Chapters 6 and 7, documentary records and field survey are used to assess population changes for two declining grassland specialists, *Trifolium ochroleucon* and *Pulsatilla vulgaris*, at the county and national scale respectively. Population trends are related to changes in community composition and management. In Chapter 8, the wider implications of the study are discussed and suggestions made for further research.

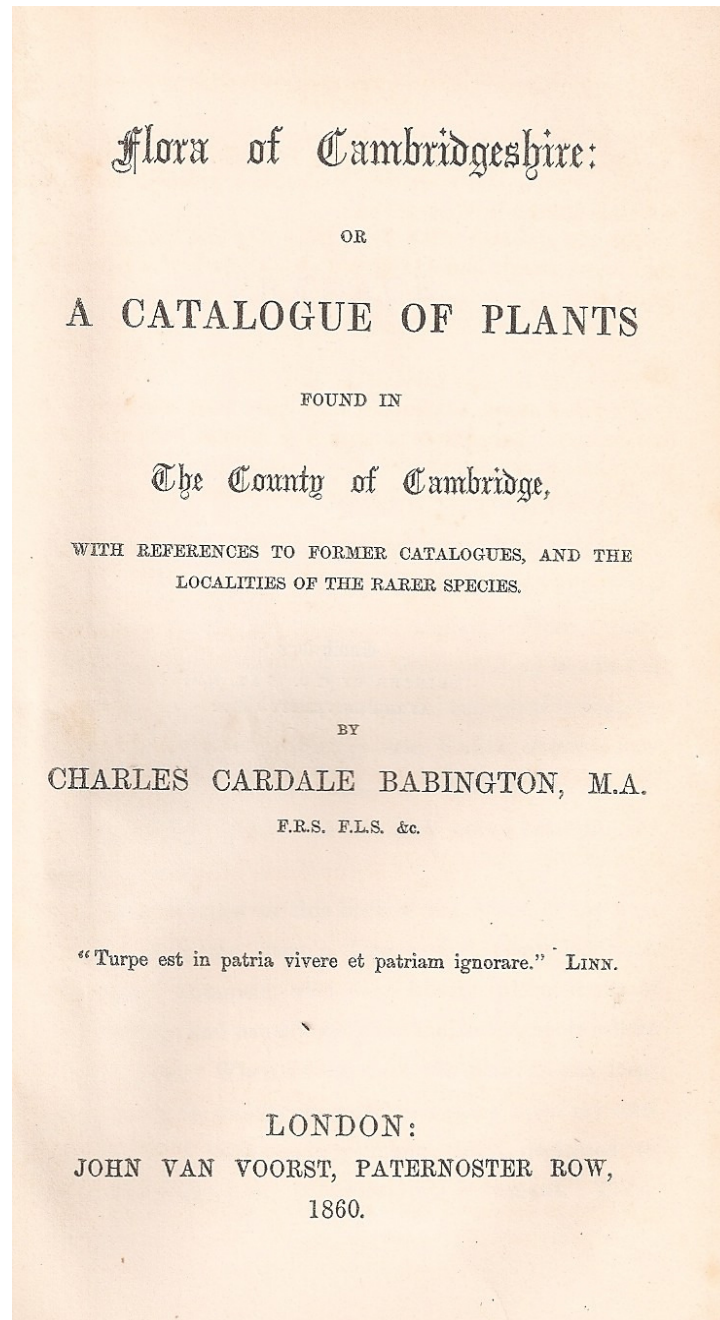


Plate 2

The title page of Charles Babington's 1860 *Flora of Cambridgeshire*, the first county flora to have environmental changes as a major theme

Chapter 2

Using local floras to assess floristic change

Summary

Local floras provide valuable historical baselines which have seldom been used to measure floristic change. This is due to the lack of historical data for most counties but also because of changes in recording behaviour over the past 350 years. One of the simplest ways to assess change is to calculate extinction rates: in English counties at least, this method has shown an average loss of 0.5 species per year during the last century. In contrast, quantitative assessments of increase/decline have proven more difficult because of the nature (or lack) of historical data. In order to overcome this problem regression analyses have been used to calculate *relative* changes in species' distributions. This approach is particularly useful because it takes into account differences in recording intensity between surveys. In contrast, *absolute* floristic changes have only been recorded from sample sites ("habitat studies") in two counties (Bedfordshire and Dorset).

Introduction

Although seldom acknowledged, an important role of the local flora is to provide a baseline from which to measure change (Allen 1963). This is now possible for many counties where a long history of botanical recording has resulted in the publication of two or more detailed floras (e.g. Killick et al. 1998; Beckett & Bull 1999; French et al. 1999; Bowen 2000; Crawley 2005). Yet with a few notable exceptions, flora writers have seldom attempted to use earlier floras in order to measure floristic change. In some areas this is understandable: many counties, particularly in the remoter parts of the British Isles, lack an early flora. For example, the Scottish parish of Assynt, which has long been a mecca for British botanists, was not adequately recorded until after 1990 (Evans et al. 2002). Compare this with Nottinghamshire for which three major floras had already been published by 1900 (Deering 1738; Ordoyno 1807; Howitt 1839).

The ways in which botanists have recorded species' distributions has also limited the number of studies which have been carried out. Over the past 350 years these have changed from county checklists with localities for the rarer species (e.g. Ray 1660), to entries under botanical divisions (e.g. Babington 1860) and latterly to "dot" atlases based on grid systems of different sizes (e.g. Dony 1976; Gent & Wilson 1995). This shift to a more systematic approach, and the increase in recorder effort which it demands, has made modern authors reluctant to compare their datasets with those collected for earlier works (e.g. Jermyn 1974; Killick et al. 1998).

The aim of this chapter is to assess the extent to which local floras can be used to quantify the floristic changes which have taken place in the British Isles over the last 350 years. More specifically: (1) to what extent do local floras provide adequate baselines from which to measure change and (2) how have these been used in studies of floristic change? Some of the problems associated with these approaches are discussed, specifically in relation to extinction and the detection of broad scale changes between surveys, and possible solutions suggested.

Methods

For the purposes of this chapter I have attempted to include all local floras (including second editions, supplements and detailed checklists) which provide complete coverage for British or Irish vice-counties or works that cover parts of different vice-counties where there is at least some tradition of botanical recording (e.g. Baker 1863; King 1891; Lavin & Wilmore 1994; Halliday 1997). The following works were excluded: species lists published in general studies (e.g. Victorian County Histories), book chapters or journal papers (e.g. Druce 1922), or works dealing with smaller geographical areas, such as individual parishes (e.g. Evans et al. 2002), islands (e.g. Campbell 1945) and cities (e.g. Bristol, London, Liverpool, Edinburgh). The floras included were compiled by consulting earlier lists of local floras (e.g. Perring 1971; McCosh 1988) as well as those listed in Simpson (1960) and are summarised in the Table 2.1.

For each local flora the following information was noted: (1) Is the provision of a baseline mentioned as an aim in the introductory chapter? (2) How do the authors record the abundance and distribution of species (e.g. sites, parishes, botanical districts, grid-squares)? (3) Do the authors provide a list of extinct species with the year of the last record? (4) Are

there detailed lists of species for individual sites (e.g. “habitat studies” sensu Dony 1953)? (5)
If so, have these data been utilised to quantify floristic change?

Table 2.1. The numbers of (a) local floras, (b) second editions and supplements and (c) checklists published for the British and Irish counties, 1660-2002.

Period	England	Wales	Scotland	Ireland	Total
(a) Local floras					
1660-1800	5	0	0	0	5
1800-1860	14	0	3	0	17
1860-1900	30	3	7	3	43
1900-1960	21	3	10	3	37
1960-2002	42	7	11	6	66
Total floras	112	13	31	12	168
(b) Second edition/supplement					
1660-1800	0	0	0	0	0
1800-1860	0	0	0	0	0
1860-1900	3	0	0	0	3
1900-1960	8	1	3	1	13
1960-2002	13	0	0	4	17
Total 2 nd ed./supp.	24	1	3	5	33
(c) Checklist					
1660-1800	0	0	0	0	0
1800-1860	0	0	0	0	0
1860-1900	0	0	0	0	0
1900-1960	0	1	1	0	2
1960-2002	6	3	16	2	27
Total checklist	6	4	17	2	29
Total	142	18	51	19	230

Results

The publication of local floras, 1660-2002

The first local floras differed from earlier herbals (e.g. Gerarde 1597) in providing a comprehensive list of plants for their own sake and not their potential usefulness (Marren 1999a). The earliest examples, which attempted to cover entire counties, included the works of Ray (1660) and Relhan (1785) in Cambridgeshire, Deering (1738) in Nottinghamshire, Abbott (1798) in Bedfordshire, and Sibthorp (1794) in Oxfordshire. In contrast the nineteenth century saw a dramatic increase in botanical activity culminating in the publication of 43 major floras in as many years (30 of which covered English vice-counties; Fig. 2.1). Of these the works of Babington (1860), Druce (1886, 1897) and Trimen & Dyer (1869) were particularly influential in both style and content. This peak in botanical activity was then

followed by a gradual decline during the first half of the twentieth century and reached its nadir between 1940 and 1959 when only six floras were published, the lowest number since the early 1800s (Good 1948; Riddelsdell et al. 1948; Brunner 1951; Dony 1953; Grose 1957; Lloyd & Rutter 1957). However, the publication of the first *Atlas of the British flora* in 1962 (Perring & Walters 1962) led to renewed recording activity and an unprecedented increase in the number of floras published followed (66 in 42 years).

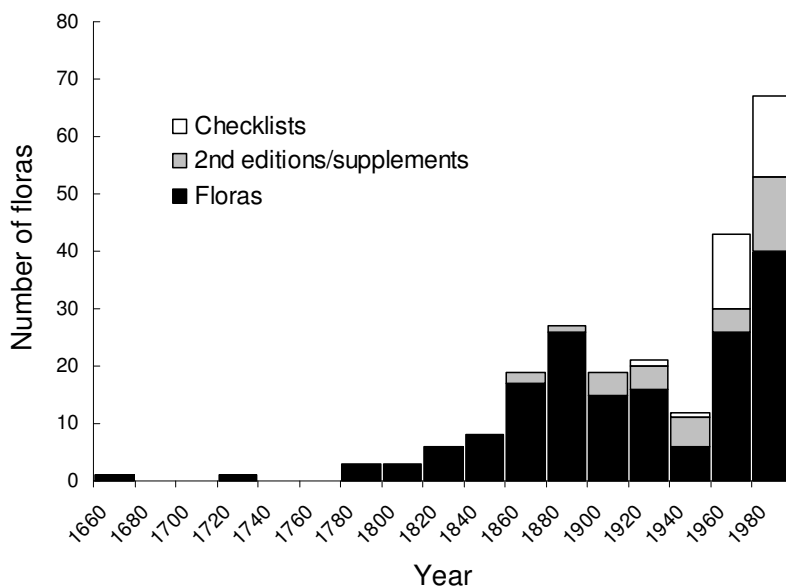


Figure 2.1. The publication of local floras, second editions, supplements and checklists produced for British and Irish vice-counties, 1660-2000. Each bar represent a twenty year interval, thus ‘1980’ covers all works published between 1980 and 2000.

The aims of local floras

The stated aims of local floras have changed dramatically since the seventeenth century when botany was viewed as a sobering pursuit intended to distract “men of university standing” from “ball-games...drinking, gambling, money-making, popularity-hunting” (Ray 1660, translated by Perring et al. 1964, p.v). Although similar sentiments are expressed in a number of eighteenth (e.g. Deering 1738), nineteenth, and even some twentieth century floras (e.g. Perring et al. 1964) introductory statements became increasingly scientific after 1800 as authors attempted to provide their counties with a comprehensive flora or fill the gaps left by previous works (Gilmour 1963). At its height, in the late nineteenth century, this led to a number of very detailed floras, including Trimen and Dyer’s (1869) *Flora of Middlesex* which was intended “to give a complete and accurate catalogue of the plants which have at any time been recorded to grow in Middlesex”. As a consequence, the length of introductory chapters

increased dramatically. For example, the introductions to Druce's (1886, 1897, 1926, 1930) Thames series of floras ran to over 150 pages, including chapters on physiognomy, land use, mini-biographies of major recorders (botanologia) and phytogeographic comparisons with adjoining counties. Despite 'creeping inflation' in the length of county floras (Preston & Walker 2003) no modern account, with the possible exception of Crawley's (2005) *Flora of Berkshire*, has attempted to deal with introductory material in such glorious detail as Druce did.

The potential use of local floras to measure floristic change was only recognised after the publication of the 1962 *Atlas*. Edward Salisbury was one of the first authors to acknowledge this, suggesting that the maps produced in the *Flora of Hertfordshire* (Dony 1967) "should be regarded, not merely as a summary of past records, but as a basis for further observations on distribution and the process of never-ceasing change that the plant population evinces". Perring (1979) said much the same in the *Ecological flora of Breckland* (Trist 1979) and in Cornwall Margetts & David (1981) acknowledged that their work would not only "take stock of the work of the generation that succeeded that of Davey, Vigurs and Thurston"^[1] but also "...provide a baseline for the further investigations that are now likely to proceed vigorously". Similar statements appear in many subsequent local floras (e.g. Stace 1990; Swan 1993; Killick et al. 1998; Mabey 1999; Bellamy 2000).

Local floras as historical baselines

Our ability to measure floristic change depends on the availability of historical data to which we can compare modern records for a given locale. As Figure 2.2 shows, this is unlikely to be a limiting factor for the majority of English vice-counties as all have at least one local flora or checklist, and 85% have two or more. Indeed, the best recorded British county, Cambridgeshire, has five major floras as well as a recent checklist (Crompton & Whitehouse 1983). However, this is not the case for the majority of Scottish, Welsh and Irish vice-counties. Of these 14 %, 20% and 61% respectively lack even a single flora or checklist and only 47%, 46% and 16% respectively have more than one. In comparison to England no Scottish, Welsh or Irish vice-county has more than three local floras.

¹ Davey (1909); Vigurs & Thurston (1922).

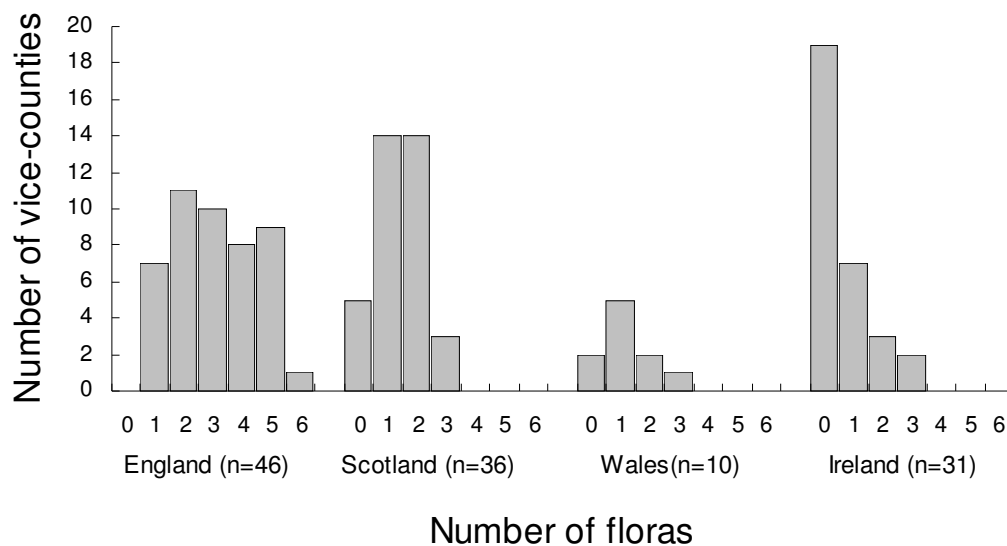


Figure 2.2. The number of local floras, including second editions, supplements and checklists, published for English, Scottish, Welsh and Irish vice-counties, 1660-2002. The numbers of vice-counties are given in parentheses.

The length of time since the first published flora for a vice-county will also influence our ability to measure change as counties with the longest tradition of recording will tend to be better studied. Once again English vice-counties are favoured in this respect as the majority of local floras were published between 1850 and 1899 (46%; Table 2.2). In contrast only 28%, 23% and 10% were published before 1900 in Scotland, Wales and Ireland respectively.

Table 2.2. The period in which first county floras were published for British and Irish vice-counties (the total number of vice-counties are given in parentheses).

Period	England (n=46)	Scotland (n=36)	Wales (n=13)	Ireland (n=31)	Total (n=126)
1650-1699	1	0	0	0	1
1700-1749	1	0	0	0	1
1750-1799	2	0	0	0	2
1800-1849	6	3	0	0	9
1850-1899	21	7	3	3	34
1900-1949	9	8	2	2	21
1950-2002	6	13	6	7	32
Before 1900	31	10	3	3	47
Total	46	31	11	12	100

Notes: The total number of vice-counties in England, Scotland, Wales and Ireland are 58, 41, 13 and 40 respectively. The figures quoted here differ because a number of vice-counties have been combined within floras. These include vice-counties 1 & 2, 3 & 4, 5 & 6, 7 & 8, 11 & 12, 13 & 14, 15 & 16, 18 & 19, 25 & 26, 27 & 28, 33 & 34, 53 & 54, 62 & 65, 63 & 64, 67 & 68 and 69 & 70 in England, 79 & 80, 87-89, 91 & 92 and 107 & 108 in Scotland, and H1 & H2, H3-5, H7 & H10, H15 & H17, H26 & H27, H34 & H35, H38-40 in Ireland. Four additional areas have also been included: Scillies (1b), Jersey (S), Guernsey (S), Breckland (part 26 & 28).

The methods used to record distribution have changed dramatically over the past 350 years (Fig. 2.3; Table 2.3). For example, the majority of early floras contain nothing more than a list of species recorded from a county, with localities for the rarer plants (e.g. Ray 1660). With the development of road and rail links during the nineteenth century, however, botanists were able to visit the remoter corners of their counties. This led to the division of counties into “botanical districts” in order to ensure a more even coverage of recording effort. This approach, pioneered by Webb and Coleman (1849) in *Flora Hertfordiensis*, was adopted by many Victorian botanists and remained the preferred method until the advent of grid-based recording schemes during the 1960s (e.g. 10 × 10 km, Perring et al. 1964; 5 × 5 km, Bowen 1968; 2 × 2 km, Dony 1967). Since then over 60 grid-based floras have been published, of which 44 have been for English vice-counties (Table 2.3).

Table 2.3. The recording units used to describe species distributions in local floras, including second editions, supplements and checklists, in British and Irish vice-counties, 1780-2002.

Recording unit	England	Scotland	Wales	Ireland	Total
Sites	37	25	9	8	79
Botanical ‘districts/divisions’	61	13	4	9	87
10 × 10 km (hectad)	12	9	1	1	23
5 × 5 km (pentad)	5	2	2	0	9
2 × 2 km (tetrad)	25	2	2	1	30
1 × 1 km (monad)	2	0	0	0	2
Total	142	51	18	19	230

Perceptions of change

The simplest way to assess floristic change is to see how perceptions of change have been reported in the text of floras (Preston 2003). One of the earliest examples are Edward Salisbury’s revealing comments on the changes that took place in the flora of Hertfordshire during his lifetime (Dony 1967), in particular the “decline or disappearance of many marsh plants such as Grass of Parnassus, *Triglochin palustris* and *Pulicaria vulgaris*” due to “the neglect of many ponds, upon which the watering of stock once depended”, and how on commons the abrasive effects of footwear “have depressed or eliminated many of the smaller open habitat species” (Salisbury 1967). In recent floras these comments have been replaced by whole chapters devoted to the impacts of land use change (e.g. Bowen 1968; Lousley 1976; Best 1995; Killick et al. 1998; Bowen 2000; Crawley 2005) or accounts of the species which have increased or declined (e.g. Dony 1976; Newton 1971; Kent 1975; Hall 1980; Primavesi & Evans 1988; Halliday 1997; French et al. 1999). Despite their historical value,

such accounts are often selective and reliant on the author's experience. In the remainder of this chapter I review the approaches used to quantify the floristic change in a more objective way.

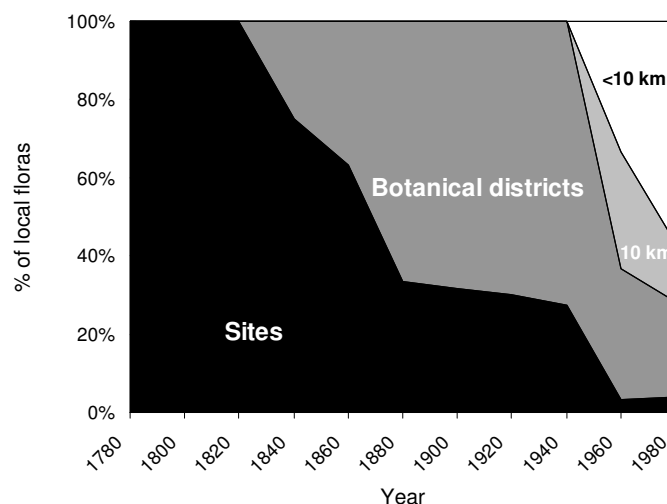


Figure 2.3. The recording units used to record species distributions in local floras, 1780-2002.

County extinction

Over the last 40 years the number of floras which include lists of extinct species has risen markedly (Fig. 2.4). As a result there have been a number of attempts to use these data to calculate extinction rates for individual counties (e.g. Marren 2000, 2001; Preston 2000; Chapter 3). These suggest that British vice-counties have lost one species every two years since 1900, with, on average, southern and eastern counties having lost more (0.6 species a year) than those in the north and west (0.4 species a year; Chapter 3). In addition, these data have also been used to identify periods of heightened extinction. For example, in Cambridgeshire Preston (2000) showed that the peak periods of extinction coincided with the first main wave of parliamentary enclosure during the early part of the nineteenth century whereas in Middlesex they occurred soon after 1870 as a result of the spread of the London conurbation.

Information on county extinctions can also be used to identify which species have declined the most and thus the habitats which have suffered the greatest changes in recent decades. For example, Table 2.4 lists those species which have been lost from more than half the best recorded counties in southeast England. Five of these species have a predominantly northern distribution in the British Isles but have undergone severe declines as a result of drainage and

habitat loss (*Antennaria dioica*, *Carex dioica*, *Lycopodium clavatum*, *Parnassia palustris*, *Utricularia minor*), four were formerly rare plants of cultivated land (*Arnosseris minima*, *Lythrum hyssopifolium*, *Melampyrum arvense*, *Valerianella rimosa*), and six were localised species of acid grasslands and bogs (*Anagallis minima*, *Hammarbya paludosa*, *Hypochaeris glabra*, *Lycopodiella inundata*, *Mentha pulegium*, *Pulicaria vulgaris*).

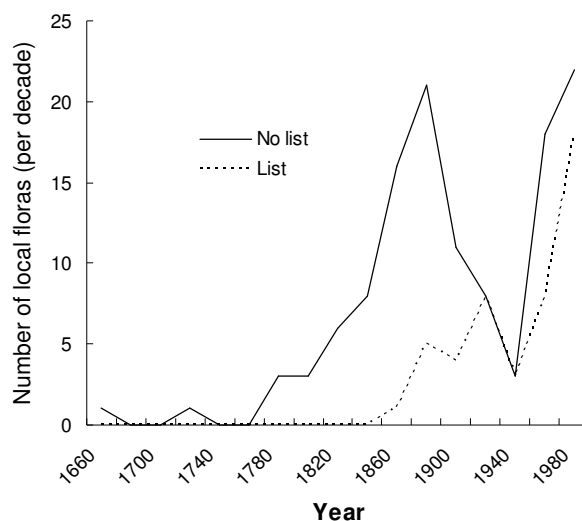


Figure 2.4. The number of British and Irish local floras which include lists of extinct species.

Table 2.4. Species with high rates of localised extinction in the southeast England. The species listed are those which have been lost from over half of the following counties: Bedfordshire (v.c. 30), Cambridgeshire (v.c. 29), Dorset (v.c. 9), Kent (v.cc. 15 & 16), Lincolnshire (v.cc. 53 & 54), Middlesex (v.c. 21), Norfolk (v.cc. 27 & 28), Northamptonshire (v.c. 32), Oxfordshire (v.c. 23), Suffolk (v.c. 25 & 26) and Surrey (v.c. 17).

Species	Status ^a	Broad habitat	Counties recorded	Counties extinct	% counties extinct
<i>Arnosseris minima</i>	Extinct ^b	Arable	9	9	100
<i>Pulicaria vulgaris</i>	Red Data	Acid grassland	9	8	89
<i>Antennaria dioica</i>	Not scarce	Calcareous grassland	8	7	88
<i>Lycopodiella inundata</i>	Scarce	Bog/heath	9	7	78
<i>Melampyrum arvense</i>	Red Data	Arable	9	7	78
<i>Hammarbya paludosa</i>	Scarce	Fen, marsh, swamp	8	6	75
<i>Mentha pulegium</i>	Red Data	Standing water	11	7	73
<i>Valerianella rimosa</i>	Red Data	Arable	11	8	73
<i>Carex dioica</i>	Not scarce	Fen, marsh, swamp	10	7	70
<i>Lythrum hyssopifolium</i>	Red Data	Arable	9	6	67
<i>Parnassia palustris</i>	Not scarce	Fen, marsh, swamp	9	6	67
<i>Anagallis minima</i>	Not scarce	Acid grassland	11	7	64
<i>Utricularia minor</i>	Not scarce	Fen, marsh, swamp	10	6	60
<i>Hypochaeris glabra</i>	Scarce	Acid grassland	11	6	55
<i>Lycopodium clavatum</i>	Not scarce	Bog/heath	11	6	55

Notes: ^a Red Data (Wigginton 1999), Scarce (Stewart et al. 1994). ^b Last recorded in the British Isles in 1971.

Comparisons between time-periods

There have only been a few attempts to quantify floristic changes using data collected for earlier floras. This is unsurprising and reflects the predisposition of many flora writers to the compilation of records rather than analyses. Furthermore, most counties lack detailed historical baselines to which modern records can be compared and, even where they do exist, differences in recording intensity have made direct comparisons difficult to interpret (e.g. Primavesi & Evans 1988). For example, even extremely thorough recorders, such as Druce and Gibson, did not always cover the various parts of the county with equal intensity (Jermyn 1974; Killick et al. 1988) and as a consequence their qualitative statements of abundance are likely to be biased (Perring 1963; Rich & Smith 1996).

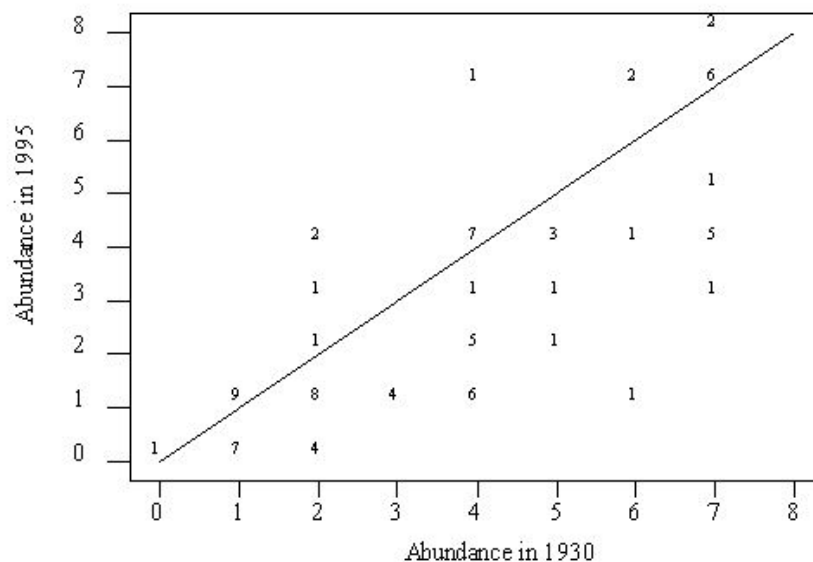


Figure 2.5. The relationship between the abundance of Cyperaceae ($n = 59$) and Orchidaceae ($n = 22$) in Northamptonshire in 1930 and 1995 ($R^2 = 63\%$, $F_{79} = 135$, $P < 0.001$). The number of species within each abundance category are shown in relation to a 1:1 line. Categories are as follows: 0 – ‘extinct’, 1 – ‘very rare’, 2 – ‘rare’, 3 – ‘very local’, 4 – ‘local’, 5 – ‘locally common’, 6 – ‘locally abundant’, 7 – ‘frequent/common’, 8 – ‘very common’ (see McCollin et al. 2000 for details). Abundance scores were taken from Druce (1930) and Gent & Wilson (1995).

Given these caveats there is no reason why qualitative datasets should not be used to provide some indication of the overall floristic changes which have taken place. This is illustrated by plotting Druce’s (1930) personal observations of the abundance of orchids and sedges in Northamptonshire against abundance categories reported in a recent flora of the county (Fig. 2.5; Gent & Wilson 1995). Although rather crude this approach shows that, despite the increase in recording activity since the turn of the century, 49 species (61 %) appear to have declined (e.g. *Orchis morio* and *Luzula pilosa* decreased by 5 and 4 categories respectively),

whereas only eight species (10 %) appear to have increased (e.g. *Carex remota*, *C. ovalis* and *Juncus compressus* increased by 3, 3 and 2 categories respectively).

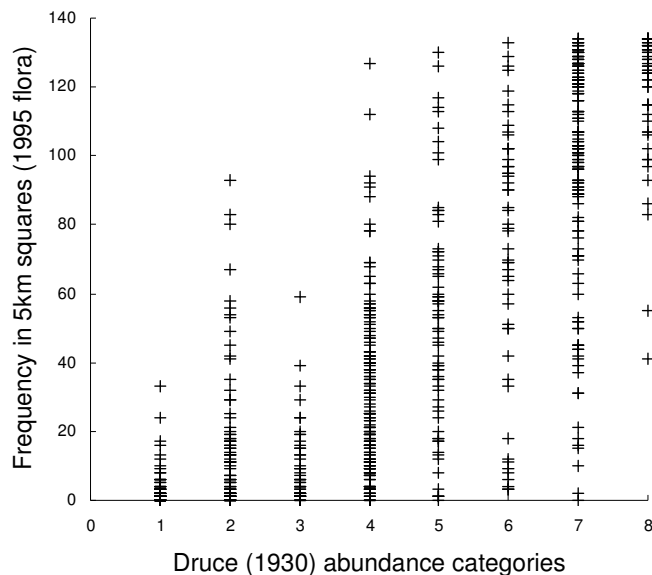


Figure 2.6. The relationship between the abundance of species in Northamptonshire in 1995 and 1930 ($R^2 = 64.4\%$, $F_{680} = 1233$, $P < 0.0001$; abundance categories are the same as for Fig. 2.5). Data for 1995 are 5×5 km grid squares (pentads) and for 1930, abundance scores assigned to species by Druce (1930) in his flora of the county. Graph taken from McCollin et al. (2000) and reproduced by kind permission of the authors and Elsevier Press.

Given the subjectivity involved in assigning species to abundance categories a more statistically meaningful approach is to compare quantitative measures between time periods. However, despite some counties having had grid-based floras since the 1960s (Table 2.2) no comparison has yet been published. An alternative approach is to compare earlier qualitative measures with modern grid-based data. For Northamptonshire Druce's (1930) qualitative assessments of abundance (eight categories) have been compared to modern pentad (5×5 km) distributions (Fig. 2.6; McCollin et al. 2000). Changes during the intervening period were then calculated as standardised residuals from the linear regression line for the whole dataset ($R^2 = 64.4\%$, $F_{680} = 1233$, $P < 0.0001$). Thus differences between the observed and predicted values (standardised residuals) provided an indication of the *relative change* in distribution since 1930: those species which deviated most from the predicted distribution were assumed to have changed the most and vice versa. Using this method species which had apparently declined the most included seven arable plant species (*Agrostemma githago*, *Anthemis cotula*, *Legousia hybrida*, *Ranunculus arvensis*, *Sison amomum*, *Torilis arvensis* and *Veronica polita*), five species associated with semi-natural grassland (*Astragalus danicus*,

Helianthemum nummularium, *Orchis morio*, *Rhinanthus minor* and *Thymus polytrichus*) and three aquatics (*Hottonia palustris*, *Oenanthe fluviatilis* and *Spirodela polyrhiza*).

A similar approach was used to measure change in the distributions of species included in the *New Atlas of the British and Irish flora* (Telfer et al. 2002). As in Northamptonshire (McCollin et al. 2000) the measure of change for each species (*Change Index*) was based on the standard deviation from the regression line for the entire dataset, i.e. the extent to which a species' 10 × 10 km distribution has changed *relative* to the 'average species' between 1930-1969 and 1987-1999. This is a powerful technique because it takes into account recorder biases caused by differences in the geographical coverage and the greater intensity of recorder effort in the latter survey period.

Habitat studies

A small number of floras include "habitat studies" which provide lists of species for individual sites as well as, in some cases, information on soil type, pH, aspect, topography, etc. (Table 2.5).

Table 2.5. Local or county floras that have included samples of fixed-plots ("habitat studies") used to describe typical vegetation assemblages of the county.

County	Plot size and shape	Number of plots	Number revisited	Source(s)
Bedfordshire	5 yard radius circle	128	107	Dony (1953, 1977); Chapter 5
Breckland	Variable	26	0	Trist (1979)
Derbyshire	Variable	84	0	Clapham (1969)
Dorset	Variable	7500	390	Good (1948); Byfield & Pearman (1994)
Flintshire	2-20 m ²	49	0	Wynne (1993)
Hertfordshire	5 yd radius circle	109	0	Dony (1967)
Leicestershire	Whole site	107	0	Primavesi & Evans (1988)
Wiltshire	c.250-350 square yrd	5000	0	Grose (1957)

The first author to use this approach was Professor Ronald Good (1948) who recorded the vegetation of 7500 sample plots ("stands") in Dorset (Poole Basin) during the 1930s. The precise locations were marked on Ordnance Survey maps to allow relocation and an assessment of changes in composition (e.g. Byfield & Pearman 1994; DERC 2003). A decade later, John Dony carried out a similar survey of sites in Bedfordshire (Dony 1953) and Hertfordshire (Dony 1967). Although more limited in coverage Dony used a standard area (a

circle of 5 yards radius) and attempted to survey a representative sample of vegetation types rather than just the richest. A handful of flora writers have adopted this approach (Clapham 1969; Trist 1979; Primavesi & Evans 1988; Wynne 1993) although surprisingly few have attempted to use a standardised method or sample area (Table 2.5).

In 1976 Dony (1977) re-recorded the original Bedfordshire “habitat studies” in order to assess the changes which had taken place during the intervening 26 years (a resurvey in 2003-04 is described in Chapter 5). The results of this survey were extremely revealing (Table 2.6): overall c.13 % of the sites had been converted to other land uses, whereas a further 28 % had deteriorated to a greater or lesser extent. Some habitats had fared much worse than others: in particular, wet grasslands, heathlands and calcareous grasslands had suffered the greatest losses whereas woodlands had remained largely unaffected. Overall, the percentage of recorded extinctions was comparable to the losses for the county as a whole (Table 2.6).

Table 2.6. Changes in the flora of Bedfordshire recorded between 1949 and 1976 as a result of John Dony’s (1953, 1976, 1977) resurveys of fixed plots (‘habitat studies’) and the flora as a whole. For habitat studies percentages are given in parentheses.

Broad habitat	Habitat studies			Extinct species (%)	
	Number destroyed	Number deteriorated	Number unchanged	Habitat studies	Bedfordshire flora
Woodland	2 (8)	2 (8)	20 (83)	4.6	5.3
Calcareous grassland	1 (13)	3 (38)	4 (50)	4.3	6.1
Acid pasture and heath	1 (9)	4 (36)	6 (55)	16.2	19.0
Marshes and meadows	4 (22)	8 (44)	6 (33)	22.8	35.3
Total	8 (13)	17 (28)	36 (59)	-	-

In Dorset a more restricted re-survey of Professor Good’s plots was undertaken in order to assess the changes in the distribution of 41 specialist heathland species (Byfield & Pearman 1994). In this study 390 of the original stands were relocated, using Good’s original maps and the presence of target species noted. Of these 35% had been converted to agriculture (22 %) or forestry (7 %). More importantly, there had been a 75% decline in the number of populations of target species. For example, eleven species which were fairly widespread in Good’s day (present in more than 20 sites) had declined by more than 50% (*Anagallis minima*, *Chamaemelum nobile*, *Filago vulgaris*, *Genista anglica*, *Lycopodiella inundata*, *Potentilla palustris*, *Pinguicula lusitanica*, *Radiola linoides*, *Rhynchospora fusca*, and *Veronica scutellata*).

Discussion

Assessing change using data on extinction

Although figures for extinction provide an indication of the nature and scale of environmental changes over recent decades there are a number of problems associated with their use (see Chapter 3). In many cases extinction at the local (county) scale is rarely forever: some species will be overlooked because they are difficult to find or identify, occur in habitats which are difficult to study (e.g. water bodies) or have been traditionally ignored by botanists (e.g. arable plants). On the other hand some species may well re-appear because they have unpredictable or transient life-histories (e.g. arable weeds). For example, in Hertfordshire over 20 species deemed extinct by Salisbury (1924) in the 1920s have been refound (Dony 1974; James 1997). A similar scale of rediscovery has been found in Cheshire (14 %; Newton 1971, 1990), Norfolk (12 %; Petch & Swan 1968; Beckett & Bull 1999), Lincolnshire (8 %; Gibbons 1975; Gibbons & Weston 1985) and Northamptonshire (5 %; Chapter 4). On the contrary, the ultimate demise of a species may take many years to be acknowledged and often long after it actually disappeared from a local area. As a consequence, the perceived rate of extinction may well differ markedly from the *actual* rate within a given area.

Secondly, smaller areas tend to have higher extinction rates because the area of suitable habitat is reduced thereby increasing the likelihood of localised extinction (May et al. 1995). As a consequence, smaller counties, such as Middlesex, have higher extinction rates when compared to larger counties such as Cornwall or Norfolk (Chapter 3). A similar argument applies to the latitudinal position of a county: southern and eastern counties tend to have more species, and so are likely to lose more species regardless of the environmental changes which have taken place.

Finally, the apparent rate of extinction is influenced by the history of plant recording in the county, with concentrations around periods of intensive recording (Preston 2000). For example, in Bedfordshire (Fig. 2.7b) peaks in extinction coincide with the publication of major works (e.g. Abbott 1798).

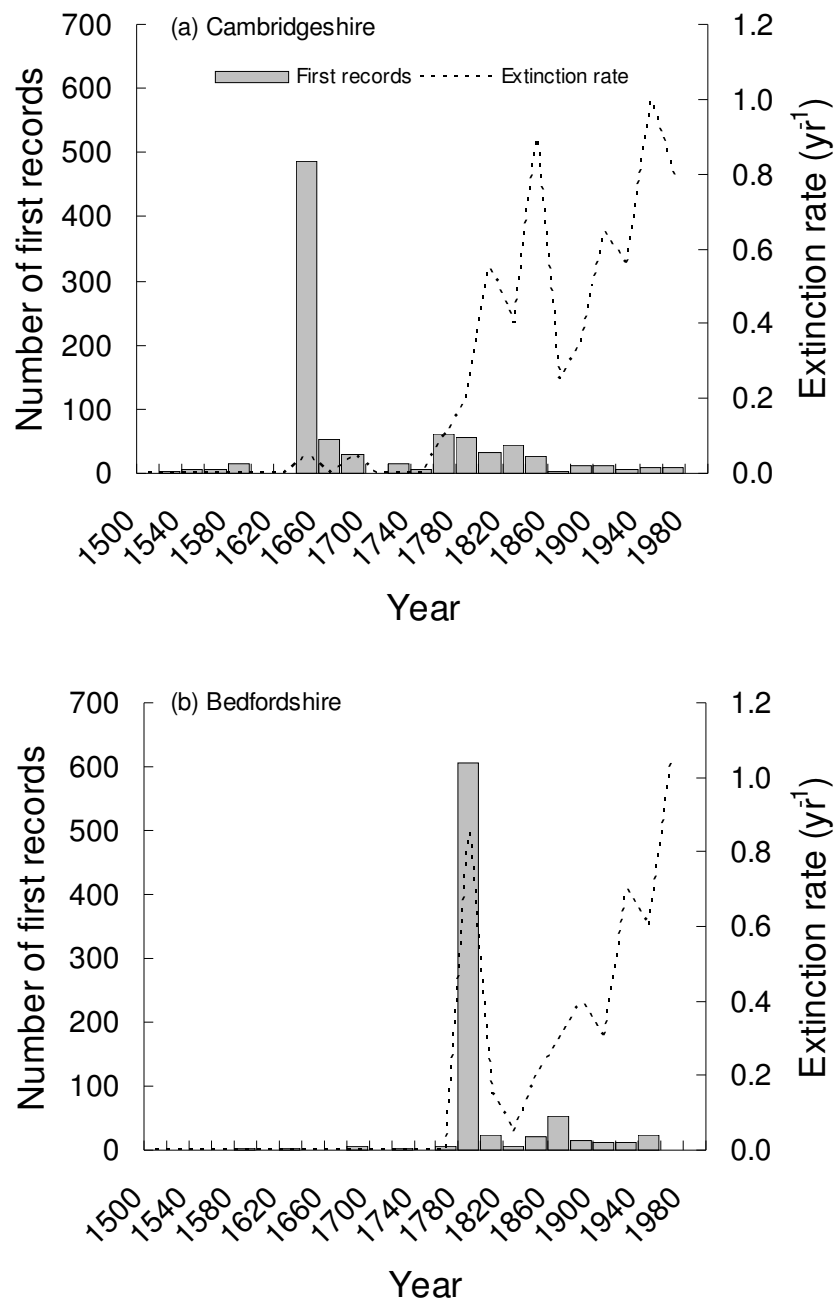


Figure 2.7. The number of first records in relation to extinction rate per year in (a) Cambridgeshire and (b) Bedfordshire. Figures for both are summarised within 20 year intervals. For Cambridgeshire last recorded dates were taken from Preston (2000) and first dates from Perring et al. (1964) and Crompton (2001). For Bedfordshire first recorded dates were taken from Dony (1953, 1976) and figures for last records supplied by the vice-county recorder (C. Boon, pers. comm., 2001).

Prior to this, few extinctions had been recorded, not necessarily because environmental changes had been slight, but because so few species were known to earlier botanists. In contrast, the peak periods of extinction in Cambridgeshire (Fig. 2.7a) appear unrelated to

recording activity, presumably because the majority of its species were well known by the time of the major agricultural changes in the eighteenth and nineteenth centuries (Preston 2000).

Assessing change using historical data

Despite the publication of over 200 local floras few attempts have been made to assess floristic changes in the British flora. As the results show this is primarily due to a lack of historical baselines for many areas (Fig. 2.2). Whilst the majority of English counties possess at least one modern flora, much of Wales and Scotland has to make do with checklists, while most of Ireland has not even got that (Marren 1999a). This problem is exacerbated by the nature of the historical data available (Fig. 2.3; Perring 1963; Rich & Smith 1996): due to changes in recording methods and behaviour, particularly the increase in recording intensity in later surveys, few counties are likely to possess historical datasets which are directly comparable to modern data. Furthermore, increasing knowledge of the taxonomy and biogeography of difficult, critical or cryptic taxa may mean that apparent changes in the distributions of some species are likely to be an artefact of recording (Rich & Woodruff 1992; Rich & Smith 1996; Rich 1998).

Studies which focus on the nature, rate and scale of extinction avoid many of these problems because they are less affected by recording behaviour. However, such studies provide very *conservative* estimates of change for a small sample of a local flora. In comparison, quantitative assessments of change which utilise a historic baseline allow us to take stock of *all* the species in an area and gauge the relative magnitude of the changes which have taken place during the intervening time period. As such they often highlight changes in the distribution of formerly “common” species which may have become increasingly localised or threatened during the intervening period. Regression analyses that provide a measure of *relative change* between surveys are preferable because they take into account the differences in recording intensity between surveys. Similarly, the effects of recorder bias are minimised in resurveys of fixed plots if there is precise information on when, how and where the original survey was carried out.

Conclusions

As the results of this chapter have shown, many counties in Britain and Ireland lack adequate baselines from which to measure floristic change. As a consequence, a priority for botanists

over the coming decade should be to complete baseline floras for these counties, as well as repeat grid-based surveys for counties where detailed baselines already exist (in particular earlier tetrad surveys). With this in mind, recorders should attempt to collect their data in ways which will be of use to future botanists, who will inevitably look back at our floras, as we have done with Ray, Babington, Druce, and Dony, in order to assess the floristic changes which have taken place. Anyone currently embarking on a local flora project would do well to bear this in mind before they begin.

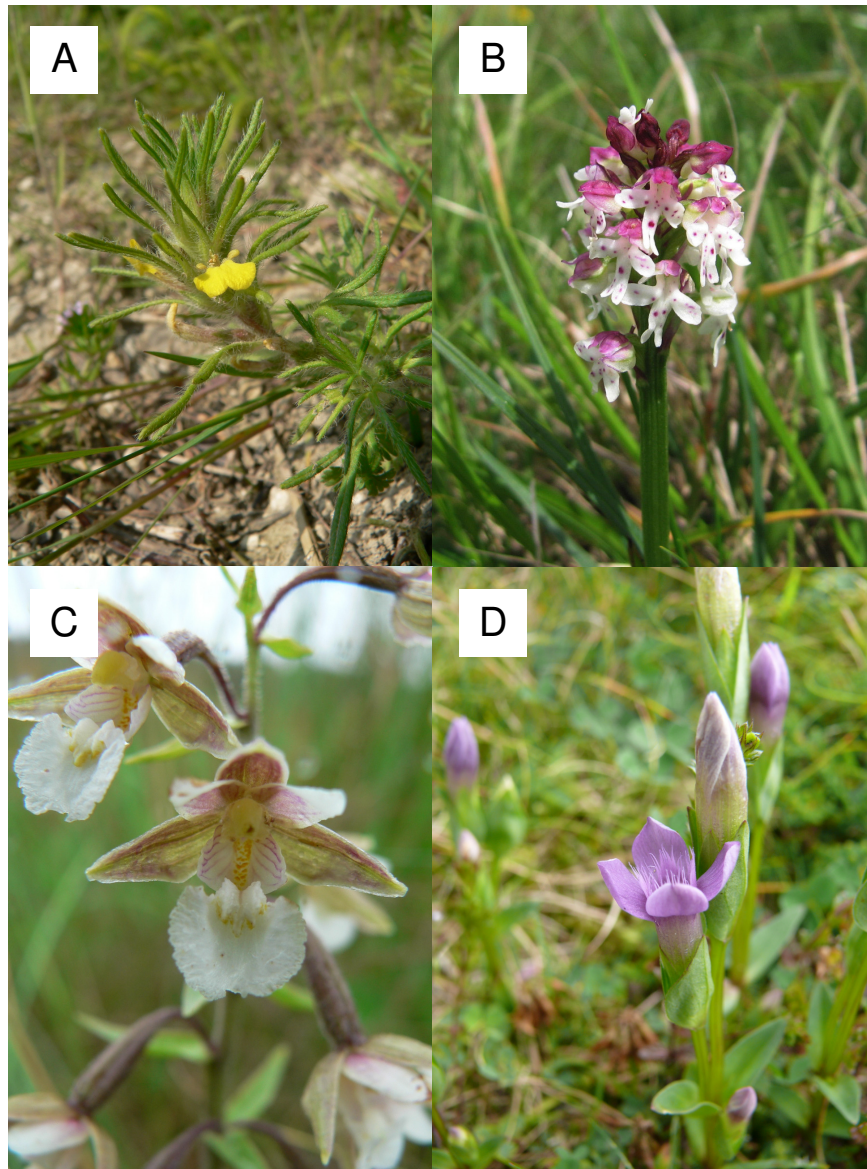


Plate 3

Four species formerly present in Northamptonshire, one of the counties with the highest rates of extinction in lowland England: (a) *Ajuga chamaepitys* (1712), (b) *Orchis ustulata* (1956), (c) *Epipactis palustris* (1956) and (d) *Gentianella campestris* (1882). All four species have suffered widespread declines in lowland England. Photos: K.J. Walker.

Chapter 3

One species lost every year? An evaluation of plant extinctions in selected British vice-counties since 1900

Summary

A review of local extinctions since 1900 was carried out for 25 British counties. Previous rates of extinction were revised to exclude species that went extinct before 1900 and non-native species. The average rate of extinction was 0.5 species a year with northern and western counties having lost fewer species (0.4 species a year) than those in the south and east (0.6 species a year). These losses suggest a period of heightened extinction during the twentieth century as a result of major environmental changes. However, they should be treated with caution as extinction rates are influenced by the size of the county, the history of botanical recording and the degree of certainty with which a species can be recorded as extinct.

Introduction

Peter Marren's study of county extinctions provides a dramatic indication of the loss of species in England over the last century (Marren 2000, 2001). Using lists of localised plant extinctions published in county floras, as well as Preston's (2000) study of extinctions in Middlesex (v.c. 21) and Cambridgeshire (v.c. 29), he calculated an average loss of 0.7 species per year since 1900, with figures ranging from 0.3 species per year in Norfolk (v.cc. 28 & 27) to 1.4 species per year in Northamptonshire (v.c. 32). His 'league table of extinctions' (Table 3.1) indicated geographical variation in rates of decline: southern and eastern counties, which occupy the top ten positions, have suffered the worst, with an annual loss of around 0.8 species per year, as opposed to around 0.6 in the north and west (Fig. 3.1).

These figures, which suggest a loss of almost 'one species every year' in the worst counties, were publicised by conservationists to highlight the extent of declines (Vines 2000; Frankland 2001). However, they present a number of intriguing irregularities. Most surprisingly, twice as many species appear to have gone extinct in Northamptonshire (v.c. 32), which tops the

table, than in rural Cambridgeshire or suburban Middlesex. This is surprising given the rather unexceptional nature of the flora and landscape of v.c. 32. Due to its rather uniform geology (Sutherland 1995) the flora of the county is not unduly rich and lacks many of the localised heathland and grassland species present in adjacent counties. Recent environmental changes do not appear to have been any more extreme than in surrounding lowland counties. For example, only 22% of land is classed as “non-agricultural” and the area of cultivation increased by just 25% between 1928 and the 1990s (661-1214 km²) to around half the area of the county (McCollin et al. 2000).

Table 3.1. Marren’s (2001) ‘league table’ of twentieth century plant extinctions in 15 English vice-counties. Extinction rates (per year) were calculated by dividing the number of apparent extinctions by the number of years included in the recording period. Counties are listed in the descending order of extinction rate.

Vice-county (number)†	Number extinct	Extinction rate (yr ⁻¹)	Recording period	Number of years	Source(s)
Northamptonshire (32)	93	1.43	1930-95	65	This chapter
Lincolnshire (53/54)	77	0.91	1900-85	85	Gibbons (1975); Gibbons & Weston (1985)
Gloucestershire (33/34)	78	0.91	1900-86	86	Holland et al. (1986)
Middlesex (21)	76	0.84	1900-90	90	Preston (2000)
Durham (66)	68	0.77	1900-88	88	Graham (1988)
Cambridgeshire (29)	66	0.73	1900-90	90	Preston (2000)
Leicestershire (55)	59	0.67	1900-88	88	Primavesi & Evans (1988)
Surrey (17)	51	0.67	1900-76	76	Lousley (1976); Lesley (1987)
Essex (18/19)	68	0.61	1862-74	112	Jermyn (1974)
Suffolk (25/26)	50	0.61	1900-82	82	Simpson (1982)
Cheshire (58)	49	0.54	1900-90	90	Newton (1971, 1990)
Westmorland (69)	56	0.58	1900-97	97	Halliday (1997)
Cumberland (70)	48	0.49	1900-97	97	Halliday (1997)
South Lancashire (59)	50	0.49	1860-63	103	Greenwood (1999)
Norfolk (27/28)	33	0.33	1900-99	99	Beckett & Bull (1999)

† Marren’s original study included Ashdown Forest (Rich et al. 1996) but this has been excluded from this as it only covers a small area of East Sussex (v.c. 14).

The aim of this chapter is to assess the rate of extinction for a selection of British counties using a standardised approach which excludes introduced species and those lost before 1900. Additionally, due to its comparatively high rate of extinction, a detailed re-evaluation of localised extinctions in Northamptonshire is presented which takes into account the recent rediscovery of “extinct” species. Factors likely to have influenced these figures are suggested and the implications for conservation discussed.

Method

Sources of data

Twenty five counties are included in this study, including the 15 originally analysed by Marren (2001) plus an additional ten for which there is a recent flora and/or a list of extinctions (Table 3.3). Eighteen of these floras, including Northamptonshire, provide a list of extinctions with the year in which they were last recorded. Where no list was provided, information was either taken from the species accounts of floras (Cornwall, Dorset and Oxfordshire) or from published studies of floristic change. The latter included Bedfordshire (Boon 1998), Cambridgeshire (Preston 2000), Middlesex (Preston 2000) and South Lancashire (Greenwood 1999).

Because of its high rate of extinction Northamptonshire was treated in greater detail. Initially the list of extinctions was taken from the most recent flora of the county (Gent & Wilson 1995; hereafter referred to as the 1995 Flora). This includes 96 species which were last recorded before the publication of George Claridge Druce's (1930) flora of the county (hereafter referred to as the 1930 Flora), or between 1930 and 1970, but not since, despite deliberate searching at former sites (Gent & Wilson 1995). This list was subsequently revised in the light of more recent survey data collected in preparation for the *New Atlas of the British and Irish flora* (Preston et al. 2002a).

Assessment of native/alien status

In calculating extinction rates Marren accepted taxa as native if the author of the flora had done so, as well as non-native species so well-established in wild places that they can be categorised as permanent members of semi-natural communities (Marren 2000). The approach taken in this study differs in excluding species which are not considered native by Preston & Hill (1997), or British native species (*sensu* Preston & Hill) which have obviously been introduced to the county. For Northamptonshire this approach excludes many species classified in the 1930 Flora as “denizen”, “colonist”, “alien” or “exotic” and in the 1995 Flora as “British”, “adventive” or “introduction”. It also excludes a number of long-established introductions with naturalised ranges in the British Isles, such as *Centaurea cyanus*, which is considered to be native by some authorities (e.g. Stace 1997) but classified as a long-established alien (archaeophyte) by Preston, Pearman & Hall (2004).

For all counties where there is doubt over whether a British native species is native or not, the species is accepted as native if its habitat, history and distribution in the county is similar to those areas of Britain where it is assumed to be native. In this study a number of atlases (e.g. Perring & Walters 1962; Stewart et al. 1994; Preston & Croft 1997; Wigginton 1999) and monographs (e.g. Graham & Primavesi 1993; Page 1997) were very helpful in assigning county status.

Assessment of dates of extinction

The year in which a species was last recorded was taken from the most recent published work for the county. Consequently, the accuracy of some of the figures presented, particularly those for counties with older floras (e.g. Essex, Lincolnshire, Suffolk) could well be revised in the light of more up to date information. For Northamptonshire last dates were taken from the *Vascular Plants Database* used to produce the maps in the *New Atlas of the British and Irish flora* (Preston et al. 2002a). This allowed species which have been rediscovered since the 1995 Flora to be included.

For 20 species recorded in the 1930 Flora of Northamptonshire, but not since, no last date is given, presumably because Druce considered the species to be extant or because no last date was known to him. For these species approximate dates were derived from herbarium sheets in the Druce-Fielding herbarium in Oxford (**OXF**) and plant records published by Druce in preparation for the 1930 Flora (Druce 1880-81 et seq.). For six species (*Eleogiton fluitans*, *Galium tricornerutum*, *Mentha suaveolens*, *Oenanthe lachenalii*, *Thelypteris palustris* and *Valerianella carinata*) no last date could be traced. As a consequence, these are treated as having been last seen in 1930. Similarly, for species which were known to Morton (1712) and Notcutt (1843) but no later authors the dates of extinction are given as 1712 and 1843 respectively.

Selection of species

In this chapter the lists of extinctions used to calculate rates for British counties exclude the following species; those species last recorded before 1900, critical species and hybrids, species not considered to be British natives by Preston & Hill (1997), British native species which had obviously been introduced, species of dubious county status and those which had subsequently been re-found since the publication of the flora.

Results

Extinct species in Northamptonshire

For Northamptonshire, changes to the list of “presumed extinctions” given in the 1995 Flora are summarised in Table 3.2. Of the original 96 localised extinctions 24 were excluded because they were either obvious errors, introductions to Britain or v.c.32, or have subsequently been re-discovered. Conversely, 32 localised extinctions have been added to this list as a result of subsequent fieldwork and historical research. In total, 103 species have apparently been lost from Northamptonshire since records began, representing 13% of the 810 species recorded in the county. The revised list of extinctions is given in Appendix 1 with the year of the last known record. The full list of revisions is given in Appendix 2.

Table 3.2. Enumeration of the revisions to the Gent & Wilson (1995) list of extinct species in Northamptonshire (v.c. 32) with indication of recording period.

Breakdown of revisions	Recording period				Total
	Before 1900	1900-1930	1930-1970	After 1970	
Extinctions listed in the 1995 Flora ^a	35	16	36	9	96
Species excluded (reason given below):	8	3	4	9	24
Rediscovered since 1970 ^b	-	-	-	5	5
Subspecies (<i>species extant</i>)	-	1	-	-	1
Not native ^c	1	-	-	2	3
Dubious record or error ^d	4	-	-	-	4
British natives, introduced to v.c.32 ^e	3	2	4	2	11
Extinctions since 1995 Flora ^f	2	6	10	13	31
Revised number for v.c. 32	29	19	42	13	103

Notes: ^a Some dates have been re-determined as a result of historical research and are therefore different from those given in Gent & Wilson (1995). ^b Rediscovered as a result of fieldwork for the New Atlas. ^c Native status follows Preston & Hill (1997). Two species excluded on this basis (*Centaurea cyanus* and *Prunus cerasus*) have been rediscovered in recent years. ^d This figure does not include *Eriophorum gracile* which has recently been confirmed for the county (Walker 2003). ^e Not considered native in v.c. 32 given their native distribution and habitats elsewhere in the UK. ^f These figures are based on recent recording data, herbarium material and correspondence with local botanists.

Changes to the Gent & Wilson (1995) list of “presumed extinctions” in Northamptonshire

Five native species have been refound since the publication of the 1995 Flora and so are excluded from the revised list. In addition, *Polygala vulgaris* subsp. *collina* is excluded because subsp. *vulgaris* is still extant in the county and *Filago gallica*, which was last recorded near King’s Cliffe in 1838, *Centaurea cyanus* and *Prunus cerasus* (both of which have been refound since the 1995 Flora) are all excluded as they are not considered native by Preston & Hill (1997).

Four species recorded as extinct in the 1995 Flora are likely to have been recorded in error. These include *Scleranthus perennis* subsp. *perennis* which was recorded by Morton sometime before 1712 (Druce 1930), and possibly on a wall near Wellingborough in 1974 (Gent & Wilson 1995). These records seem very doubtful given the rarity of *S. perennis* in Britain: subsp. *perennis* has only ever been confirmed from Doloritic rocks at one site in Radnorshire (Slater 1999) whereas subsp. *prostratus* is confined to a handful of sandy heaths in East Anglia (Leonard 1999). The Northamptonshire plants are more likely to be referable to overwintering or biennial forms of *S. annuus* which occurs on sandy ground in the county or possibly subsp. *polycarpus* which appears to be more widespread than previously thought (Preston et al. 2002a). Similarly, Morton's record for *Crepis foetida*, which is now a very rare native plant in the British Isles, is more likely to have been an early record for *Crepis vesicaria* subsp. *taraxacifolia*, which was first recorded in Britain in 1713 (Clapham et al. 1987). Other doubtful species include *Galium sternerii*, which has its most southerly English station in the Peak District (Lusby & Slack 1994) and *Sagina subulata* which has a predominantly northern and western distribution in England (Perring & Walters 1962). In contrast, *Eriophorum gracile*, which was collected by Druce from Hornstocks Wood near Wittering in 1867 has recently been confirmed from herbarium specimens held at the Druce-Fielding herbarium in Oxford (OXF) (Walker 2003).

Eleven British native species are considered to have been introduced into Northamptonshire. All these species occur outside their native range in the county (e.g. *Impatiens noli-tangere*, *Gymnocarpium robertianum*) or were recorded from artificial or disturbed habitats which suggest accidental introduction. In addition, both *Eryngium campestre* and *Daphne mezereum* were recorded in semi-natural habitats where they were presumably planted (grassland adjacent to garden and copse respectively).

Thirty-one native species which were not included in the list of "presumed extinctions" in the 1995 Flora are considered extinct in this chapter. Twenty-three of these have not been recorded since 1989, despite fieldwork for the *New Atlas*, and so are assumed to be extinct. However, a number of these are likely to have been overlooked and may well reappear in future years (e.g. *Anagallis minima*, *Aphanes australis*, *Rosa* spp.). Of the remaining eight species, six were classified as extinct in the main text of the 1995 Flora but not in the main list, and two are critical segregates (*Erophila majuscula* and *Euphrasia arctica*).

Extinction rate

Marren's extinction rate for Northamptonshire is based on the list of "presumed extinct" species given in the 1995 Flora, and is calculated by dividing the number of extinctions (96, excluding doubtfully present species) by 65, the number of years between the two floras. This gives an average loss of 1.4 species per year, or 14 species a decade, since 1900. However, this is a significant overestimate because it assumes that all the species on this list were last recorded *after* 1930. As a result Marren includes 52 species, italicised in the Gent & Wilson list, which were last recorded *before* 1930 and in many cases before 1900. When these pre-1900 extinctions are removed from the analysis then this gives a loss of 74 species since 1900 or 0.82 species a year (Table 3.3).

Extinction in other British vice-counties

The revisions presented in this study show that Marren over-estimates the rate of extinction for at least nine other vice-counties (Table 3.3). For example, the figure of 0.91 species a year for Lincolnshire (v.cc. 53 & 54) appears to be significantly higher than the revised rate because he includes 31 species last recorded before 1900. If non-native and rediscovered species (Gibbons & Weston 1985) are excluded from the list given in the 1975 Flora (Gibbons 1975) then 64 native species have apparently become extinct in Lincolnshire, 38 of which were last recorded after 1900. This gives a probable rate of extinction of around 0.45 species per year since 1900 which interestingly is comparable to similar sized counties such as Norfolk (v.cc. 27 & 28) and Cornwall (v.cc. 1 & 2).

The revised rate for Gloucestershire (v.cc. 33 & 34) is also different because he includes all 79 (Marren actually cites 78) species listed as probably extinct in the supplement to the Flora of the county (Holland et al. 1986). However, this includes 17 species which have never been satisfactorily confirmed for the county (all recorded before 1948), three ancient introductions and 14 species which were last recorded before 1900. When these figures are taken into account the overall rate declines from 0.91 to 0.52 species per year.

Table 3.3. The number of extinctions and extinction rates for 25 British counties. Figures exclude introductions to the UK and the vice-county, hybrids, critical, subspecies (where another subspecies is extant) and dubious taxa and species last recorded before 1900. The 15 counties included in Marren's (2001) study are denoted with an asterisk. Marren's original figures for extinction, extinction rate and recording period are given where different from the ones presented in this chapter. The reasons for these differences are enumerated in Table 3.4.

Vice-county (number)	Region	Number extinct species	Marren (where different)	Extinction rate (yr ⁻¹)	Marren (where different)	Recording period	Marren (where different)	No. of years	Source(s)
Bedfordshire (30)	SE	55		0.61		1900-1990		90	Boon (1998) amended by C. Boon
Bristol Region (6/pt 34)	SE	64		0.64		1900-2000		100	Green et al. (2000)
Cambridgeshire (29)*	SE	66		0.73		1900-1990		90	Preston (2000)
Cheshire (58)*	NW	41	49	0.46	0.54	1900-1990		90	Newton (1971, 1990)
Cornwall (1/2)	NW	36		0.36		1900-1999		99	French et al. (1999)
Cumberland (70)*	NW	36	48	0.37	0.49	1900-1997		97	Halliday (1997)
Dorset (9)	SE	32		0.32		1900-2000		100	Bowen (2000)
Durham (66)*	NW	55	68	0.63	0.77	1900-1988		88	Graham (1988)
Essex (18/19)*	SE	68		0.61		1862-1974		112	Jermyn (1974)
Gloucestershire (33/34)*	SE	45	78	0.52	0.91	1900-1986		86	Holland et al. (1986)
Kent (15/16)	SE	28		0.34		1900-1982		82	Philp (1982)
Leicestershire (55)*	SE	60	59	0.68	0.67	1900-1988		88	Primavesi & Evans (1988)
Lincolnshire (53/54)*	SE	38	77	0.45	0.91	1900-1985		85	Gibbons (1975); Gibbons & Weston (1985)
Middlesex (21)*	SE	76		0.84		1900-1990		90	Preston (2000)
Norfolk (27/28)*	SE	37	33	0.37	0.33	1900-1999		99	Beckett & Bull (1999)
Northamptonshire (32)*	SE	74	93	0.82	1.43	1900-1990	1930-1995	90	This chapter
Northumberland (67/68)	NW	23		0.25		1900-1993		93	Swan (1993)
Oxfordshire (23)	SE	39		0.40		1900-1998		98	Killick et al. (1998)
Radnor (43)	NW	38		0.41		1900-1993		93	Woods (1993)
Shropshire (40)	NW	33		0.37		1900-1990		90	Sinker et al. (1985) amended by A. Lockton
South Lancashire (59)*	NW	48	50	0.50	0.49	1900-1996	1860-1963	96	Greenwood (1999)
Suffolk (25/26)*	SE	46	50	0.56	0.61	1900-1982		82	Simpson (1982)
Surrey (17)*	SE	29	51	0.34	0.67	1900-1986	1900-1976	86	Lousley (1976); Lesley (1987)
Sussex (13/14)	SE	69		0.78		1900-1988		88	Hall (1980); Briggs (1990)
Westmorland (69)*	NW	37	56	0.38	0.58	1900-1997		97	Halliday (1997)

For Surrey Marren includes all 51 species listed as extinct in Lousley's (1976) flora of the county despite the fact that 14 of these species were last recorded before 1900. In addition, he includes three species which are not considered native by Preston & Hill (1997), four species which have been subsequently rediscovered and one species (*Carex diandra*) which has never been satisfactorily confirmed (Leslie 1987). When these figures are taken into account 43 native species are considered to have disappeared, of which 29 were last recorded after 1900. Taking these figures into account the rate of extinction declines from 0.67 to 0.34 species a year (Table 3.3).

Table 3.4. Reasons for revisions to Marren's (2001) figures ('Original list') for the numbers of extinctions in British counties. The table includes all 12 counties for which revised figures are presented in Table 3.3. The sign indicates whether the number should be deleted or added to the figure given in the column marked 'Original list'.

	Original list	Difficult taxa	Pre-1900	Alien GB	Native - alien	Dubious	Re-found	List error	Revised list
Cheshire	49			-2			-6		41
Cumberland	48	-10						-2	36
Durham	68	-6		-5	-1	-1			55
Gloucestershire	78		-14	-3		-17		+1	45
Leicestershire	59							+1	60
Lincolnshire	77		-31	-2	-1		-6	+1	38
Norfolk	33							+4	37
Northamptonshire	93	-1	-35	-2	-8		-5	+32	74
South Lancashire	50							-2	48
Suffolk	50			-3				-1	46
Surrey	51		-14	-3		-1	-4		29
Westmorland	56	-17						-2	37

Notes on categories: Difficult taxa – includes critical genera and hybrids; Pre-1900 – species last recorded before 1900; Alien GB – not native in any British vice-county; Native – alien – native in the GB but thought to be introduced into the vice-county; Dubious – very unlikely to occur in the vice-county or if known to be present unlikely to be of native origin; Re-found – no longer believed to be extinct in the county; List error – discrepancy between the figure given by Marren and the number of extinct species listed in the flora (for Northamptonshire this also includes 29 species now known to be extinct following fieldwork for Atlas 2000).

For six other vice-counties the revised figures are different to those given by Marren due to the exclusion of thirteen non-native, critical and doubtful species² in Durham (Graham 1988), 17 and 10 hybrids in Westmorland and Cumberland respectively (Halliday 1997), six recently discovered species and two aliens in Cheshire (Newton 1971, 1990) and three non-native species in Suffolk (Simpson 1982). Norfolk is the only county for which the Marren

² Includes *Gymnadenia odoratissima* which has never been confirmed for the British Isles (Stace 1997).

underestimates the actual rate by excluding four species last recorded between 1900 and 1914 (*Epipactis purpurata*, *Herminium monorchis*, *Huperzia selago* and *Hypochaeris maculata*; Beckett & Bull 1999). As a consequence, Marren's figure of 0.33 species per year increases to 0.37 when these species are included.

One species lost every year?

Marren's study was admittedly based on a small and geographically biased sample of counties. However, the revisions presented in this chapter suggest that vice-counties in Britain have lost just over half a species a year during the last century (0.55), and not "one species a year" as the Marren "league table" suggests (Fig. 3.1). This figure declines further, to 0.51 species per year, when figures for all 25 counties are included.

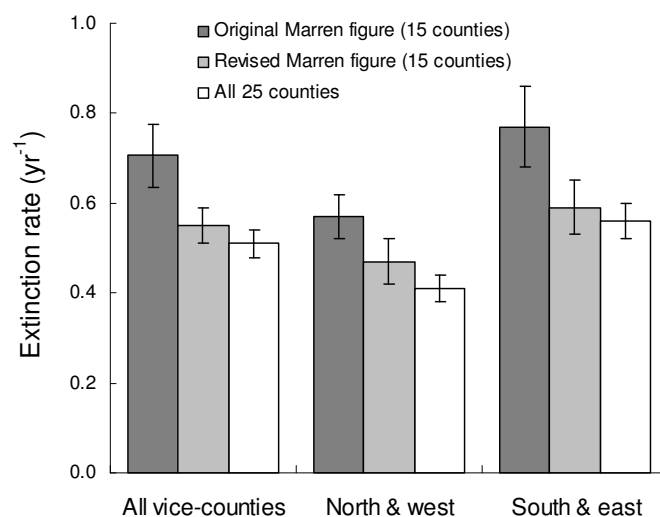


Figure 3.1. Average (± 1 S.E.) twentieth century extinction rates (per year) for the 25 vice-counties included in this chapter (Table 3.3). These were derived from the original figures for the 15 vice-counties included in Marren (2001, 2002) and the revised values which exclude introduced, hybrid, dubious and critical taxa and species last recorded before 1900. Averages are displayed for all 25 counties and by region (see Table 3.3). The difference in extinction rate between regions was significantly different for 'All 25 counties' (two-sampled *t*-test, $t = -2.6$, $P = 0.016$) but not for the 'Original Marren 15' or 'Revised Marren 15' figures.

Figure 3.1 also shows the uneven geographical distribution of extinction. Counties in the north and west have, on average, lost fewer species (0.41 species per year) than those in the south and east (0.56 species per year). Although there is a great deal of variation within this dataset the regional difference is statistically significant when all the counties shown in Figure 3.1 are included ($P < 0.05$).

Although these data suggest a much lower level of extinction than first thought, they do support Marren's original assertion that Northamptonshire has suffered more than most other counties during the twentieth century (0.82 species per year) (Marren 2000, 2001). Indeed, even when the revisions presented in this chapter are taken into account the overall loss of species in v.c.32 is comparable to suburban Middlesex (0.84), and is higher than Cambridgeshire (0.73) and Sussex (0.78). The reason for this may be related to the timing of peak periods of extinction in Northamptonshire, which appears to have occurred much later than in some other counties (Fig. 3.2). For example, in Cambridgeshire the first wave of extinction coincided with habitat destruction caused as a result of parliamentary enclosure during the early part of the nineteenth century (Preston 2000). However, in Northamptonshire twentieth century losses were much higher than in the preceding century, presumably because the majority of semi-natural grasslands were ploughed up after 1900.

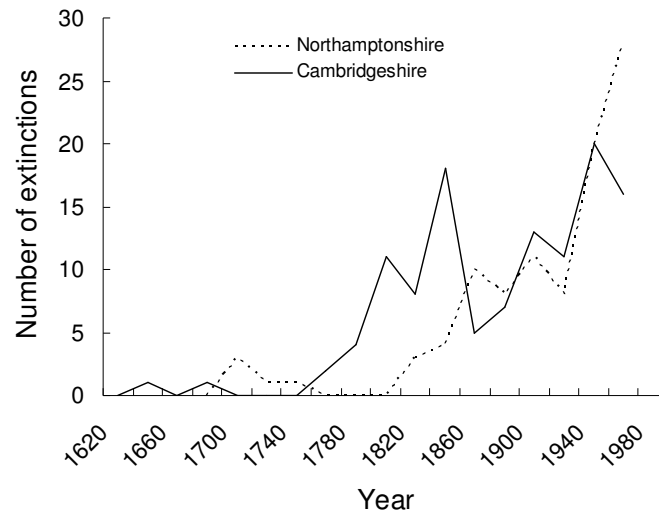


Figure 3.2. The number of extinct species in Cambridgeshire (v.c. 29) and Northamptonshire (v.c. 32) since 1620. The number of extinctions are plotted for 20 year intervals, using the assumption that a species became extinct in the period in which it was last recorded.

Discussion

The figures for plant extinction presented in this chapter reflect the pace and scale of major environmental changes which have occurred within individual counties during the twentieth century. However, they may have been influenced by a number of other factors (e.g. recording bias, county area, etc.) which may have led to the *actual* rate of extinction being over or under-estimated. Such problems are rarely acknowledged in studies on floristic

change despite the effects they are likely to have on the overall findings and conclusions. These are discussed below.

Definition of native taxa

The revised figures for extinction presented in this chapter are lower than in the Marren study, partly because of the exclusion of non-native British species (sensu Preston & Hill 1997) or British native species which have obviously been introduced outside their native range. For a sizeable proportion of these species there may be good grounds for exclusion. For Northamptonshire obvious examples include casuals imported into the county in rubble and sand (e.g. *Medicago minima*, *Potentilla argentea*, *Trifolium scabrum*) and colonists introduced by other means (e.g. *Impatiens noli-tangere*, *Gymnocarpium robertianum*). The exclusion of a number of long-established alien species, such as *Centaurea cyanus*, which were probably introduced by early farmers after the Neolithic, is more problematic. Many of these species, which were fully naturalised by the fifteenth century, are important indicators of environmental change because they have undergone dramatic declines in recent years as a result of modern farming practices (Sutcliffe & Kay 2000). Conversely, many more recent introductions are becoming increasingly widespread on highly fertile, disturbed soils associated with human activities (Thompson et al. 1995).

Reliability of last date

In the absence of more detailed information the extent to which the date of last record actually reflects the timing of extinction can vary from species to species. For example, Druce provides precise dates for the loss two species in Northamptonshire; *Diploxys tenuifolia* which was “formerly on the south-west bastion of Northampton Castle, where it was plentiful until the castle was destroyed in 1879” (Druce 1930, p.22) and *Daphne mezereum* which was “destroyed in 1909 by someone digging up the large shrub” (Druce 1930, p.202). In most cases timing of extinction is not known with certainty. Two notable examples are given in the 1930 Flora; the loss of *Stachys germanica*, from “some old quarries between Fineshade and Wakerley” which “have since been filled up, and the plant destroyed” (Druce 1930, p.184), and *Ophrys sphegodes* for which “the large planting of larch appears to have been responsible for its destruction” (Druce 1930, p.225). Often extinction follows a long period of decline during which time succession or man-made changes render a site increasingly unsuitable. In Northamptonshire, this presumably accounts for the loss of a number of heathland species (e.g. *Lycopodium clavatum*, *Juncus squarrosus* and *Moenchia erecta*) which declined as a

result of piecemeal drainage, afforestation with conifers and housing development. Similar losses must have gone unnoticed during major periods of agricultural innovation. Indeed, Druce gives the example of *Ajuga chamaepitys*, which disappeared well before his day, presumably as a result of the “extensive enclosures” which took place in the early part of the nineteenth century (Druce 1930).

These discrepancies are often exacerbated by the nature of the recorders themselves. Botanists tend to be reluctant to classify a species as extinct, even if it has not been seen for many years, and prefer to use terms such as “presumably extinct” or “almost certainly extirpated”, rather than to write it off completely (Marren 2001). Given the often arbitrary nature of this decision then it would seem sensible to accept Preston’s (2000) cut-off: a species should not be considered extinct if it has been seen in the preceding decade unless there is good evidence to the contrary.

Is extinction forever?

As Preston (2000) quite rightly states “at the vice-county level the slogan of ‘extinction is forever’ is manifestly false” as occasionally apparently extinct species reappear. This is often the case for species which form persistent seed banks. For example, in Northamptonshire *Genista anglica* was refound “springing up in newly cleared ground” at Harlestone Heath (Druce 1930, p.50) following the removal of a plantation and more recently *Agrostemma githago* flowered following ground disturbance associated with the planting of a new hedge (Gent & Wilson 1995). However, it is more common for species to reappear because they have been overlooked, either in places where they not been previously sought or in old sites where they were formerly recorded. For most species this is because their ecology or taxonomy makes them difficult to record. For example of the five species recently rediscovered in Northamptonshire two are very closely related to more common taxa (*Ulex minor* and *Pedicularis sylvatica*), one is an inconspicuous aquatic (*Potamogeton alpinus*) and one is a cornfield weed with a tendency to appear sporadically (*Papaver hybridum*).

Some species tend to be overlooked because they are inconspicuous, difficulty to identify or occur in habitats which are poorly recorded. As a result there may be an argument for excluding them from lists of localised extinctions because they are unlikely to have been recorded consistently in the past. For example, the historical distributions of *Erophila* taxa have only recently been understood through the use of herbarium material (Rich & Lewis

1999). Furthermore, the distribution of critical segregates of *Rosa*, *Rubus*, *Hieracium* and *Euphrasia* often reflect the areas where taxonomists have worked rather than the actual distribution of the individual species. As a result for these species “rediscovery” or “extinction” may well represent nothing more than a change in the intensity of recording.

Aquatic species pose a number of problems for the study of extinction. Traditionally they have been poorly recorded, largely because they occur in habitats which are difficult to examine and the major genera are taxonomically difficult (Preston & Croft 1997). Furthermore, the life histories of some species make them hard to study: most species are very mobile and adapted to the unstable conditions of water bodies. Some species are also susceptible to competition with alien waterweeds, such as *Elodea canadensis*, which spread rapidly throughout Britain in the nineteenth century. All these factors have meant a “kaleidoscopic pattern of change” in the distribution of some species making an assessment of their apparent extinction and colonisation difficult to interpret (Preston & Croft 1998). The most obvious example in Northamptonshire is *Luronium natans*, which was last recorded in the county in 1986. In Britain the extent of its distribution has only recently been fully appreciated, following the discovery that the majority of its populations occur as inconspicuous, submerged plants, with rosettes of unremarkable grass-like leaves (Ferguson et al. 1998). The variability in growth-forms of some other aquatic species (e.g. pondweeds, water-starworts) poses similar problems for the study of extinction.

Thus for Northamptonshire the rate of extinction presented in this chapter may well be an over-estimate as some species may be rediscovered, especially amongst the 23 species not recorded since 1989. For example are *Anagallis minima*, *Aphanes australis*, *Rosa obtusifolia* and *R. rubiginosa* really extinct in v.c. 32 or have they just been overlooked?

County area

Area buffers against extinction and therefore more species are likely to be lost from smaller areas (e.g. May et al. 1995; Figs 1.1 & 3.3). For example, twice as many species have gone extinct in the tiny suburban county of Middlesex (724 km²) than in rural Lincolnshire which is almost ten times as big (7200 km²). This is primarily to do with habitat availability as within smaller areas specialist habitats tend to be more restricted. However, this relationship is influenced by a number of other factors, not least regional differences in habitat destruction, climate, species-pool and habitat diversity. For example, the Shetland Islands have lost only 2

species since 1900 whereas Bedfordshire, which is roughly the same size, has lost 55 over the same period (Scott & Palmer 1987). Consequently, the overall relationship between extinction and area is relatively weak (Fig. 3.3; $R^2 = 14.6\%$; $P = 0.059$).

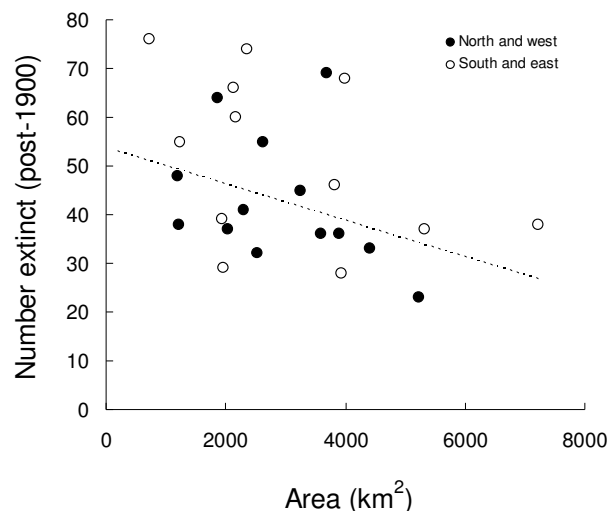


Figure 3.3. The relationship between the number of extinctions since 1900 and area of the 25 counties included in this chapter (linear regression = $58.54 - 0.003894 \text{ area}$; $R^2 = 14.6\%$; $P = 0.059$).

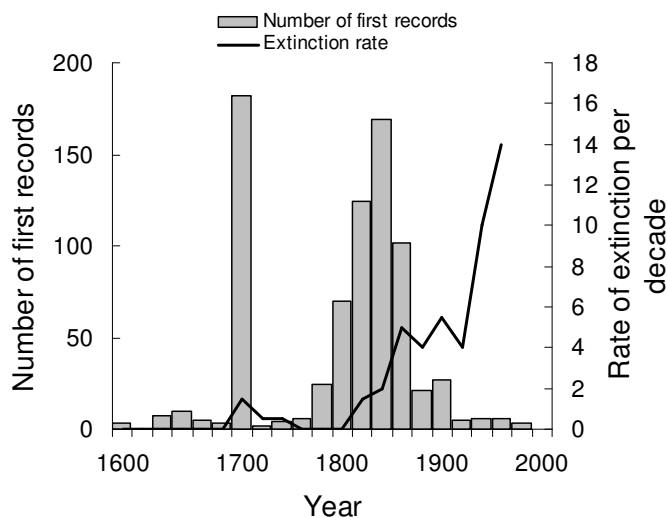


Figure 3.4. The discovery of new species in Northamptonshire (v.c. 32) (within 20 year categories) in relation to extinction rate (calculated for 20 year categories before 1980). First dates are taken from the Gent & Wilson (1995) Flora (for 35 species no first date is given). Notable botanical works, which included new plant records for the county, are: Gerarde (1597), How (1650), Morton (1712), Notcutt (1843), Druce's early published plant records (1880-81 et seq.), and Druce (1930).

The history of botanical recording

The rate of extinction may well be influenced by the history of plant recording in the county, with concentrations in periods of intensive recording (Preston 2000). This was certainly the

case in Northamptonshire where the first major period of botanical activity in the county, between 1800 and 1900, was immediately followed by a pronounced peak in plant extinction (Fig. 3.4). Prior to this few losses had been recorded, not necessarily because the environmental changes had been slight, but because so few species were known to sixteenth, seventeenth and eighteenth century botanists. For example, only around 200 species were known to Morton in 1700 whereas by 1900 Druce had recorded over 700 species in the county. As a result the number of extinctions increased markedly towards the end of the nineteenth century. Given that most species had been discovered by the time of the 1930 Flora, the second peak in extinction after 1920 is presumably a more realistic reflection of the environmental changes which were taking place in the county at that time.

Conclusions: One species lost every year?

Given the inherent problems in defining localised extinction the figures presented in this chapter should not be regarded as very precise: some species listed as extinct may well re-appear whereas others will be missing because insufficient time has elapsed for their loss to be noted or a judgement to be made as to their status. Furthermore, not everyone will agree with the exclusion of non-native species, or indeed Preston & Hill's conclusions as to the native status of some species. Although this treatment is certainly the most credible for most species, it could well be refined, particularly with regard to some introductions such as *Centaurea cyanus* which are now thought to be very long established. Furthermore, the accuracy of some of the revised figures presented could be revised in light of more up to date information, particularly with respect to the rediscoveries since the publication of the last flora.

Despite these caveats the overall figures suggest a period of heightened extinction at the local, county scale in Britain during the twentieth century, of which Northamptonshire appears to be a particularly illustrative example. Although the pace and scale of change may not be as bad as first thought, in lowland counties at least, we still appear to be "losing what is natural, particular and special" (Marren 2000). However, if these figures are to be used to highlight changes which have taken place in our native flora then we must ensure the correct use of the available data and acknowledge the inherent problems that any study of extinction necessarily entails.

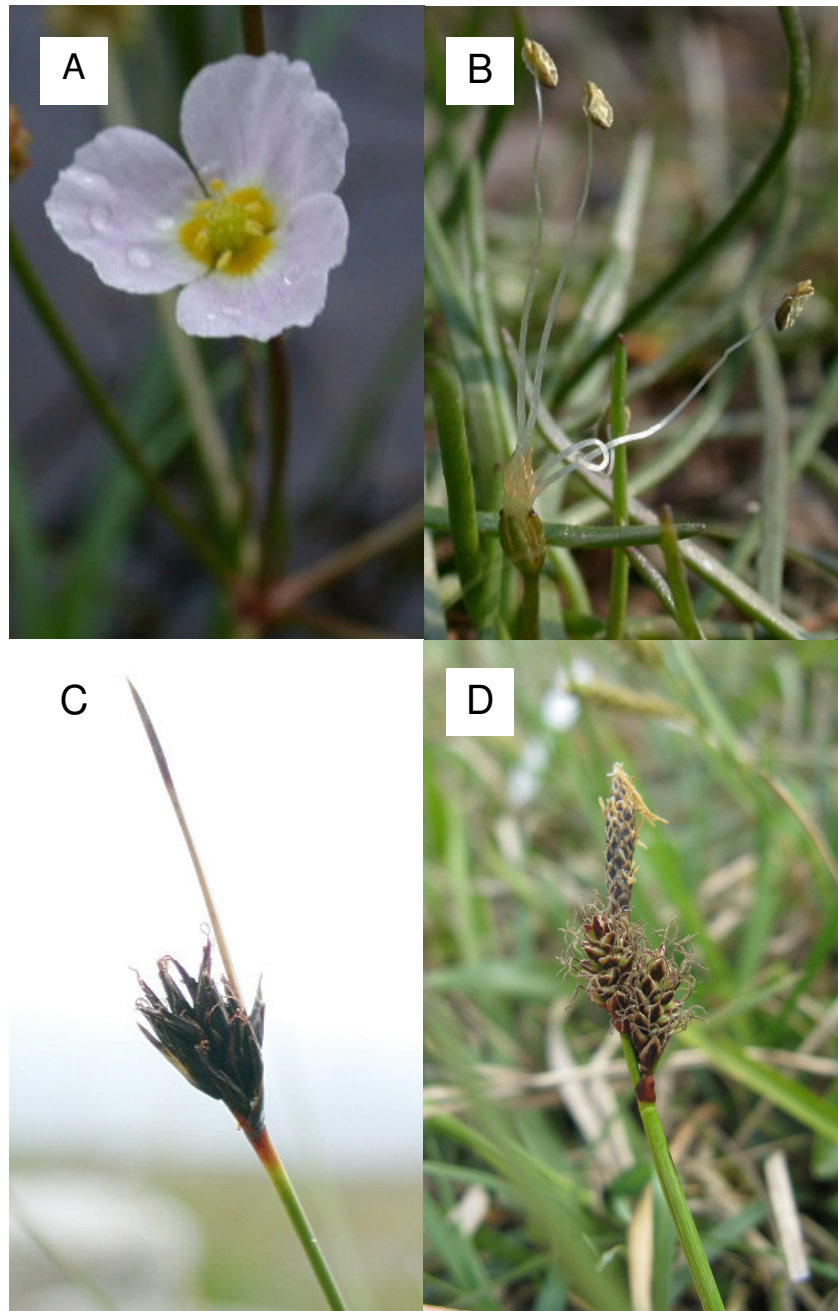


Plate 4

Species with a high predicted risk of extinction in lowland England based on life history traits (see text for explanation): (a) *Baldellia ranunculoides*, (b) *Littorella uniflora*, (c) *Schoenus nigricans* and (d) *Carex ericetorum*. Photos: Carl Farmer (A-C) & K.J. Walker (D).

Chapter 4

Ecological predictors of extinction risk in the flora of lowland England

Summary

Historical and contemporary records were used to determine the scale of plant extinction in Bedfordshire and Northamptonshire, and to assess whether extinct species share a range of ecological and phytogeographical traits. Since 1700 both counties have lost 94 species (11% of their native floras) with the rate of extinction increasing from 3.8-4.8 species per decade in the nineteenth century to 6-8 species per decade after 1950. The most important predictors of extinction risk were English range size and traits associated with habitat specialisation and competitive ability: poor competitors (i.e. short stress-tolerators) associated with open habitats with very low or high pH and soil moisture (e.g. lowland bogs, dwarf-shrub heath and acid and calcareous grassland) were much more likely to have become extinct in the study region than would have been expected by chance alone. Many of these species have very localised distributions and/or occur at the northern, southern or eastern edges of their range in southern England (i.e. are Northern and/or Oceanic). In contrast, there was no clear or significant relationship between extinction and dispersal ability or reproductive mode. These findings, which parallel national trends, indicate that habitat loss and eutrophication have been the main causes of population extinction in lowland England over the last 300 years. However, more fine-scaled studies are required to assess whether 'low-level' stresses, such as habitat fragmentation, climate change and atmospheric pollution, are having additional impacts on populations already severely depleted by habitat loss, as well as to quantify changes in the abundance of more widespread species which are known to have declined over the same period.

Introduction

In the UK much of the biodiversity of semi-natural habitats has been created by low intensity farming practices introduced at the start of the Neolithic period over four thousand years ago (Bignal & McCracken 1996). Since the eighteenth century, however, rapid population growth, the deliberate or accidental importation of species, and agricultural changes have resulted in dramatic changes to the composition of the British flora (Ratcliffe 1984; Thompson 1994;

Beebee 2001) most notably declines in populations of habitat specialists confined to unproductive grasslands (e.g. *Pulsatilla vulgaris*; Wells 1968). During the twentieth century further agricultural changes, increased urbanisation, road building and recreational use of the countryside, led to further declines as well as promoting the spread of tall, nutrient-demanding or recently introduced species which thrive in disturbed, eutrophic habitats created by man (Crawley et al. 1996; Williamson & Fitter 1996).

One way to study these floristic changes is to examine changes in the abundance of species within restricted geographic areas. British Watsonian vice-counties (Dandy 1969) are particularly suited to such an approach because of the long tradition of botanical recording at the county scale which began over 350 years ago (Ray 1660; Marren 1999a). All English counties now have at least one historical flora (Chapter 2) and this has allowed quantitative assessments of extinction (e.g. Dony 1974; Robertson 1982; Wells 1989; James 1997; Preston 2000; Greenwood 2003) and of changes in the abundance of species in a number of lowland counties (e.g. Dony 1977; Byfield and Pearman 1994; McCollin et al. 2000; Preston et al. 2003a). In addition, published lists of extinctions have revealed a consistent pattern of decline: since 1900 English counties have lost around five species per decade with northern and western having lost fewer species than those in the south and east (Chapter 3).

Although the ecology of declining species has received less attention, recent studies have shown that responses to environmental changes can differ significantly between species and that differences may be associated with traits associated with habitat specialisation and competitive ability. By the end of the twentieth century, species which had declined in frequency or become extinct in two English counties were biased towards short species characteristic of less fertile, semi-natural habitats (McCollin et al. 2000; Preston 2000). Changes at the national scale have been broadly similar. For example, the fate of common species in *Countryside Survey* plots between 1978 and 1998 was consistent with increased nutrient availability within vegetation types associated with hitherto low fertility (e.g. heathland, infertile grassland, bog and moorland; Smart et al. 2005). Similarly, species that declined in frequency across 10-km grid squares in the British Isles during the last century were biased toward less competitive plants of open, unproductive habitats (Preston et al. 2002a,b, 2003b). Many of these declining species occur at the southern edge of their range in lowland England (i.e. have Arctic or Boreal world distributions) suggesting that climate warming may be an additional cause of floristic change.

These results suggest that lowland landscapes are becoming increasingly inhospitable for species associated with unproductive habitats within a matrix of agricultural and urban land use (Thompson 1994). In order to test this hypothesis I assessed the extent to which vascular plants lost from two English counties (Bedfordshire and Northamptonshire) share a range of ecological and phytogeographical traits. The main factors thought to be responsible for population extinction are habitat loss and eutrophication associated with land use change. In addition, climate change and airborne pollution may contribute to overall declines, particularly where species occur at range margins (Harrison et al. 2001) or are confined to infertile habitats sensitive to increased levels of nutrient input (NEGTAP 2001). I therefore test five related hypotheses, namely that extinct species will include:

- (1) rare species, as small populations will be less resilient to land use change;
- (2) habitat specialists, adapted to low soil fertility and the extremes of soil moisture and pH;
- (3) poor competitors, because these are least likely to persist under increasing eutrophication;
- (4) poor dispersers, because these will be the most susceptible to habitat fragmentation;
- (5) species at the edges of their range in lowland England, as these are likely to be very sensitive to climatic changes.

In order to account for these losses, extinction is related to changes in land use which have taken place in both counties over the last 200 years.

Study region

The study region comprises Bedfordshire and Northamptonshire, two medium sized counties (c. 1250 and 2600 km² respectively) located in central southern England, UK³. Both areas are exclusively lowland (<250 m) with gently undulating ‘uplands’ and extensive low-lying clay vales bordering major rivers (Great Ouse and Nene). Neither county has a coastline, though a few coastal halophytes penetrate both counties along major roads (e.g. *Atriplex littoralis*, *Cochlearia danica*, *Puccinellia distans*). The climate is moderately extreme by English standards with winter temperatures a degree or two lower and summer temperatures a degree or two higher than the average for southern England (Dony 1976; Keech 1995). The coldest months are usually January and February, both with an average maximum of around 5 degrees Celsius, and July and August are usually the warmest both with maximums of around

³ Northamptonshire corresponds to the whole of botanical vice-county 32 (Dandy 1969) which includes the Soke of Peterborough now in administrative Cambridgeshire (Gent and Wilson 1995). Bedfordshire corresponds to the whole of vice-county 30 which includes small areas of adjacent administrative counties (Dony 1953, 1976).

22 degrees Celsius. Precipitation in the region close to the lowest for the country with most low-lying areas receiving less than 600 mm, increasing to around 700 mm in the 'uplands' of Bedfordshire. Because of these extremes in temperature and rainfall, a few species reach their northern (e.g. *Herminium monorchis*) and southern (e.g. *Melica nutans*) range limits in the region.

In contrast to climate, there are striking geological differences between the two counties. Bedfordshire's is rather simple with the youngest rocks (Cretaceous Chalk and Lower Greensand) forming conspicuous ridges in the south of the county separated by a low lying clay vale (Cretaceous Gault Clay). Clays (Jurassic Oxford Clay) cover much of the remainder of the county although there are isolated outcrops of Oolitic Limestone and calcareous Cornbrash (Jurassic) in the northwest. In contrast, the geology of Northamptonshire is dominated by Jurassic sedimentary rocks (e.g. Oolite, Lias) overlain by Pleistocene clays, sands and gravels (Sutherland 1995). The only acidic rocks (Jurassic Northampton Sand Formation) occur at the base of the Oolite and outcrop very locally near Northampton.

Arable farming is the dominant land cover in both counties (Northants, 53%; Beds, 59%) followed by improved grassland (Northants, 17%; Beds, 10%), broad-leaved woodland (Northants, 9%; Beds, 6%) and urban cover (Beds, 13%; Northants, 7%). In contrast, the extent of semi-natural habitat (e.g. heathlands, grasslands, bogs and mires) is extremely limited in both counties. Bedfordshire has less than 40 ha of semi-natural neutral grassland, compared to 710 ha in Northamptonshire, and both counties have around 200 ha of calcareous grassland (English Nature 1994, 1995), 35 ha of heathland (Micheals 1996), 50 ha of acid grassland (Sanderson 1998) and 15 ha of marshes, swamps and mires (Nau et al. 1987; Gent and Wilson 1995).

History of botanical recording

Botanical recording began in both counties in the sixteenth and seventeenth centuries (Gerarde 1597; How 1650; Fig. 4.1). However, the first detailed examination of the Northamptonshire flora was made by Morton (1712), who listed over 200 new species for the county (Thomas 1995), and more latterly by Notcutt (1843) and Druce (1930) who published a flora based largely on records made between 1880 and 1910 (Perring 1995). Since then only around 70 new native species have been discovered in the county (Gent and Wilson 1995). In contrast, Abbott's (1798) *Flora Bedfordiensis* listed 621 new species for Bedfordshire,

thereby leaving fewer species to be discovered by subsequent botanists. Important additions, however, were made following the formation of the Bedfordshire Natural History Society in 1870, and between 1940 and 1980 by John Dony (1953, 1976).

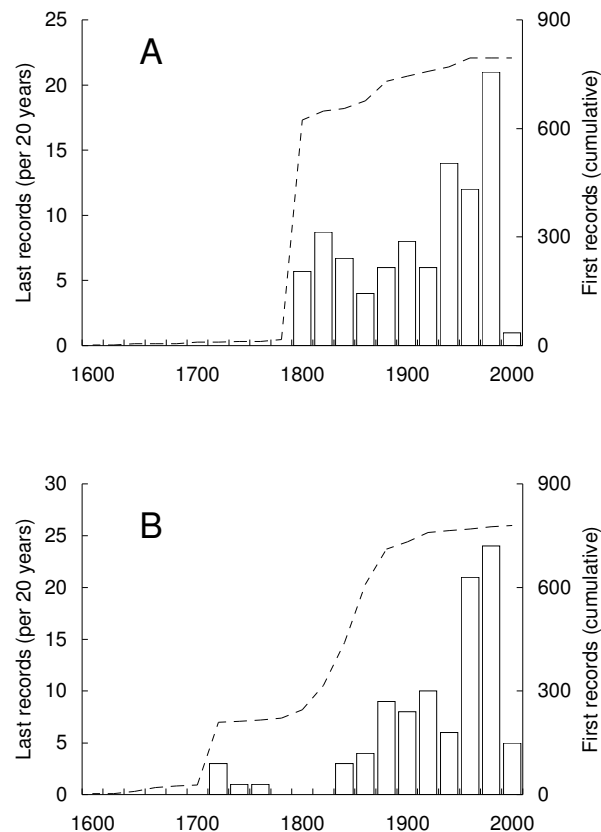


Figure 4.1. The number of first (----) and last recorded dates (\square) for species in (A) Bedfordshire and (B) Northamptonshire in each 20 year interval, 1600-2000. Note the low number of last records after 1981 due to the exclusion of species not seen since 1990.

Compilation of data on extinction

Identification of native and extinct native species

Lists of British native species recorded in each county included only those species defined as native by Preston and Hill (1997) or, where there is doubt whether a British native species is native in either county or not, only those species whose history, habitat and distribution in the county is similar to that in those areas of Britain where it is assumed to be native. These lists therefore include a number of species which are now considered to be ancient introductions (archaeophytes), plants introduced by man before AD1500 (Preston et al. 2004). Lists of extinct species, and the year in which they were last recorded, were taken from Boon (1998) for Bedfordshire and Chapter 3 for Northamptonshire, with appropriate additions and

corrections (C. Boon, R. Wilson and G. Gent, pers. comm., see Appendix 3). These treatments differ from earlier lists published for Bedfordshire (e.g. Dony 1953, 1976, 1977; Robertson 1982) and Northamptonshire (e.g. Gent & Wilson 1995; Colston et al. 1996; McCollin et al. 2000) in excluding hybrids, subspecies where another subspecies is still extant, non-native species, and British native species which were obviously introduced to the county (e.g. *Daphne mezereon*, *Impatiens noli-tangere*, *Gymnocarpium robertianum*). Species were treated as extinct if they have not been recorded from 1970 onwards, or if they had been seen between 1970 and 1987, but were known to have subsequently disappeared.

Ecological characteristics of native and native extinct species

The floras of both counties were characterised in relation to the ecological traits most likely to have determined changes in plant status over the past two centuries (Table 4.1). English range size was the total number of 10×10 km grid squares in England ($n = 1495$) from which a species has been recorded irrespective of date class or native status. Typical habitat was derived from Ellenberg (1988) and related to British Broad Habitat types (Jackson 2000; see Appendix 4) in order to allow comparisons with recent studies of floristic change. Species not classified by Ellenberg were attributed to Broad Habitat types on the basis of its known ecology. The realised ecological niche was characterised in relation to Ellenberg indicator scores (Ellenberg et al. 1991) for light (L), soil moisture (F), fertility (N) and reaction (R) recalibrated for all British higher plant species (Hill et al. 2000). Because R scores are skewed towards the acid range (i.e. R 1 to 6) the difference between R scores and neutrality ($R = 7$) were re-calculated (as R_{diff}) with R 8 and 9 being re-coded as 3 and 6 respectively (Preston et al. 2003b). Traits associated with competitive ability included plant height (as a surrogate for above-ground competitive dominance; Weiher et al. 1999) and Raunkiaer life-form (Clapham et al. 1987). Competitive ability was also measured by the main method of propagation and lateral spread (i.e. difference between vertical and horizontal extent). Traits associated with dispersal ability included seed weight and dispersal agent. The main method of fertilisation may also influence dispersal patterns because populations of cross-fertilising species appear to be more strongly aggregated than self-fertilising species (Quinn et al. 1994). Species were therefore assigned to one of four categories of sexual reproduction or to a separate category for species which reproduce asexually (i.e. vivipary or apomixis) or sexually but fail to regenerate by seed in the British Isles. Species were also examined in relation to their phytogeographical distributions in the Northern Hemisphere based on latitudinal (Major Biome) and longitudinal (Eastern Limit) range extents (Preston & Hill 1997). The

availability of attribute data was variable, ranging from around 60% for dispersal agent, seed weight and fertilisation to 100% for Ellenberg scores, plant height and phytogeographical elements (Table 4.4).

Land use

Historical data on land use (e.g. arable, permanent grassland, other) and livestock numbers were extracted from official agricultural statistics from 1866 onwards. For land use annual figures were taken from Stamp (1943a,b) for 1866 to 1939, and thereafter from official accounts of agricultural statistics. Human population figures were extracted from the decadal population returns from 1801 onwards.

Data analysis

The Chi-square statistic (χ^2) was used to test whether extinct species shared ecological traits or approximated to a random draw from the regional species-pool. To do this I characterised the entire flora of the two counties with respect to the ecological traits listed in Table 4.1, and compared this to the overall pattern shown by species which have become extinct. The χ^2 -statistic was then calculated by comparing the number of extinct and extant species within each trait category. Categories with less than five species were combined within larger categories (Table 4.4) although this was not possible for the Northern Major Biome Category in Northamptonshire as it contained only one extinct species (*Carex dioica*).

Because many traits included are related, logistic regression was used to determine the most important explanatory variables in predicting extinction risk. As species were either extinct (0) or extant (1) binary logistic regression was used including only traits identified as significant by the χ^2 analysis (i.e. English range, plant height, F, N, R_{diff} , L). Life-form, Major Biome and Eastern Limit were excluded because trait categories are not linear. Initially all significant explanatory variables were included (full model): non-significant traits were then removed sequentially in order to improve the efficiency of the regression models (reduced model). Here I report the results for both the full model and reduced models. Analysis of the residual deviance was undertaken to assess the % variation accounted for by each of these models. This analysis was carried out for both counties separately and on the entire dataset combined. The predicted probabilities generated by the reduced model (ranging from 0-1) were then used to quantify the extinction risk for each species.

Table 4.1. Plant traits used in the study of localised extinction in Bedfordshire and Northamptonshire.

Trait group	Attribute	Description	Categories	Source ¹³
Rarity	English range size ¹	10-km squares in England	<100 (1), 101-500 (2), 501-1000 (3), 1000-1495 (4)	1
Habitat specialisation	Habitat	Typical vegetation type	12 Broad Habitat types ²	2
	L	Light preference	Deep shade (1) to full sunlight (9)	3
	F	Soil moisture preference	Dry (1) to wet (9); semi- to fully aquatic (10-12)	3
	N	Soil fertility preference	Infertile (1) to fertile (9)	3
	R _{diff}	Difference from neutrality	Neutral (0) to extremely acid or basic (6)	3
Competitive ability	Height	Summer max. height (cm)	1-29 (1), 30-59 (2), 60-99 (3), 100-300 (4), 301-600 (5), 601-1500 (6), > 1500 (7)	4
	Life-form	Raunkiaer life-form ³	Geophyte (1), hemicryptophyte (2), chamaephyte (3), phanerophyte (4), therophyte (5), helophyte (6), hydrophyte (7), epiphyte ⁴ (8)	4
	Propagation	Main method	Seed (1), seed and vegetative (2), vegetative (3)	4
	Spread	Extent of physical spread	Height < width (1), height = width (2), height > width (3), other ⁵ (4)	4
Dispersal ability	Seed weight	Dry weight of seed (mg)	≤ 0.20 (1), 0.21-0.5 (2), 0.51-1 (3), 1.01-2 (4), 2.01-10 (5), > 10 (6)	4
	Dispersal agent	Main agent of dispersal	Animals ⁶ (1), water ⁷ (2), wind (3), explosive (4), unspecialised ⁸ (5)	4
	Fertilisation	Main method of fertilisation	Predominantly self (1), cross/self ⁹ (2), predominantly cross (3), obligate cross (4), other ¹⁰ (5)	4
	Dicliny	Dioecy ¹¹	Diclinous (1), hermaphrodite (2)	4
Position in range	MBC	Major Biome category ¹²	Northern (1), Temperate (2), Mediterranean (3), Widespread (4)	5
	ELC	Eastern Limit category	Oceanic (1), Suboceanic (2), European (3), Eurosiberian (4), Eurasian (5), Circumpolar (6)	5

Notes: ¹ Includes all records in England irrespective of date class or status. ² The relationship between Continental Braun-Blanquet categories published in Ellenberg (1988) and British Broad Habitats are given in Appendix 4. ³ Geophytes have resting buds below ground level, hemicryptophytes at ground level, chamaephytes up to 25cm above the soil surface and phanerophytes above 25cm. Annuals (therophytes) have a separate category as they pass through the unfavourable season as seed. Marsh plants (helophytes), aquatics (hydrophytes) and epiphytes are also treated separately. ⁴ Includes only one species (*Viscum album*). ⁵ Semi- to fully aquatic species. ⁶ Including ants, birds, mammals, eaten by birds and mammals, and man. ⁷ Includes rainwash. ⁸ No specialised dispersal structures or mechanisms. ⁹ Species which cross and self, including those that cross or automatically self. ¹⁰ Species which reproduce asexually (i.e. vivipary or apomixis) or sexually but fail to regenerate by seed in the British Isles. ¹¹ Dicliny is the extent to which individual plants (genets) are unisexual (diclinous) as opposed to hermaphrodites which bear both male and female sexual organs (Richards 1986). There are numerous forms of diclinous and hermaphrodite situations: these are summarised here simply as diclinous (dioecious, androdioecious, gynodioecious, polygamous, trioecious) or hermaphrodite (andromonoecious, hermaphrodite, monoecious, gynomoecious, gynandromonoecious). ¹² Northern = Arctic-montane, Boreo-arctic montane, Boreal-montane; Temperate = Boreo-temperate, Southern-temperate, Temperate; Mediterranean; Widespread = Wide-boreal, Wide-temperate. ¹³ Sources: 1, Preston et al. (2003b); 2, Ellenberg (1988); 3, Hill et al. (1999); 4, Fitter & Peat (1994); 5, Preston & Hill (1997).

Results

Extinct species

Both counties have lost 94 species since records began (Beds = 11.2%; Northants = 11.6%; Table 4.2). Thirty-five species have been lost from both counties whereas 28 and 29 species survive in Northamptonshire and Bedfordshire only. These losses reflect the extent of habitat loss in each county. For example, many species lost from Northamptonshire still survive on the Bedfordshire chalk (e.g. *Orchis ustulata*, *Spiranthes spiralis*, *Tephroses integrifolia*) or in acid habitats on the Greensand Ridge (e.g. *Aphanes australis*, *Filago minima*, *Jasione montana*). In contrast, many mire and wetland species which have disappeared in Bedfordshire still persist in Northamptonshire (e.g. *Apium inundatum*, *Carex hostiana*, *Pinguicula vulgaris*, *Schoenus nigricans*).

Table 4.2. A comparison of the numbers of extinct and surviving species in Bedfordshire (v.c. 30) and Northamptonshire (v.c.32).

	Extinct in v.c.32	Extant in vc.32	Not present in vc.32	Total in v.c.30
Extinct in v.c.30	35	29	30	94
Extant in v.c.30	28	659	57	744
Not present in v.c.30	31	29	-	60
Total in v.c.32	94	717	87	898

Timing of extinctions

More species were lost in Bedfordshire during the first half of the nineteenth century (Fig. 4.1a), due to the drainage of the remaining acid bogs and mires in the north of the county. However, after 1850 the rate of extinction was broadly similar, increasing from 3 and 3.8 species per decade between 1851 and 1900 to 6 and 8 species per decade between 1951 and 2000 in Bedfordshire and Northamptonshire respectively (Table 4.3).

Table 4.3. The number of plant extinctions and the rate per decade since 1700 in Bedfordshire and Northamptonshire.

	Bedfordshire		Northamptonshire	
	Extinct	Rate per decade	Extinct	Rate per decade
1700-1750	0	0	5	1
1751-1800	0	0	0	0
1801-1850	24 *	4.8	5	1
1851-1900	15	3	19	3.8
1901-1950	24	4.8	25	5
1951-2000	30	6	40	8

* 17 species were last recorded in Bedfordshire by Abbott (1798) in 1798. These were almost certainly lost in subsequent decades and have therefore been added to the total number of extinctions for 1800-50.

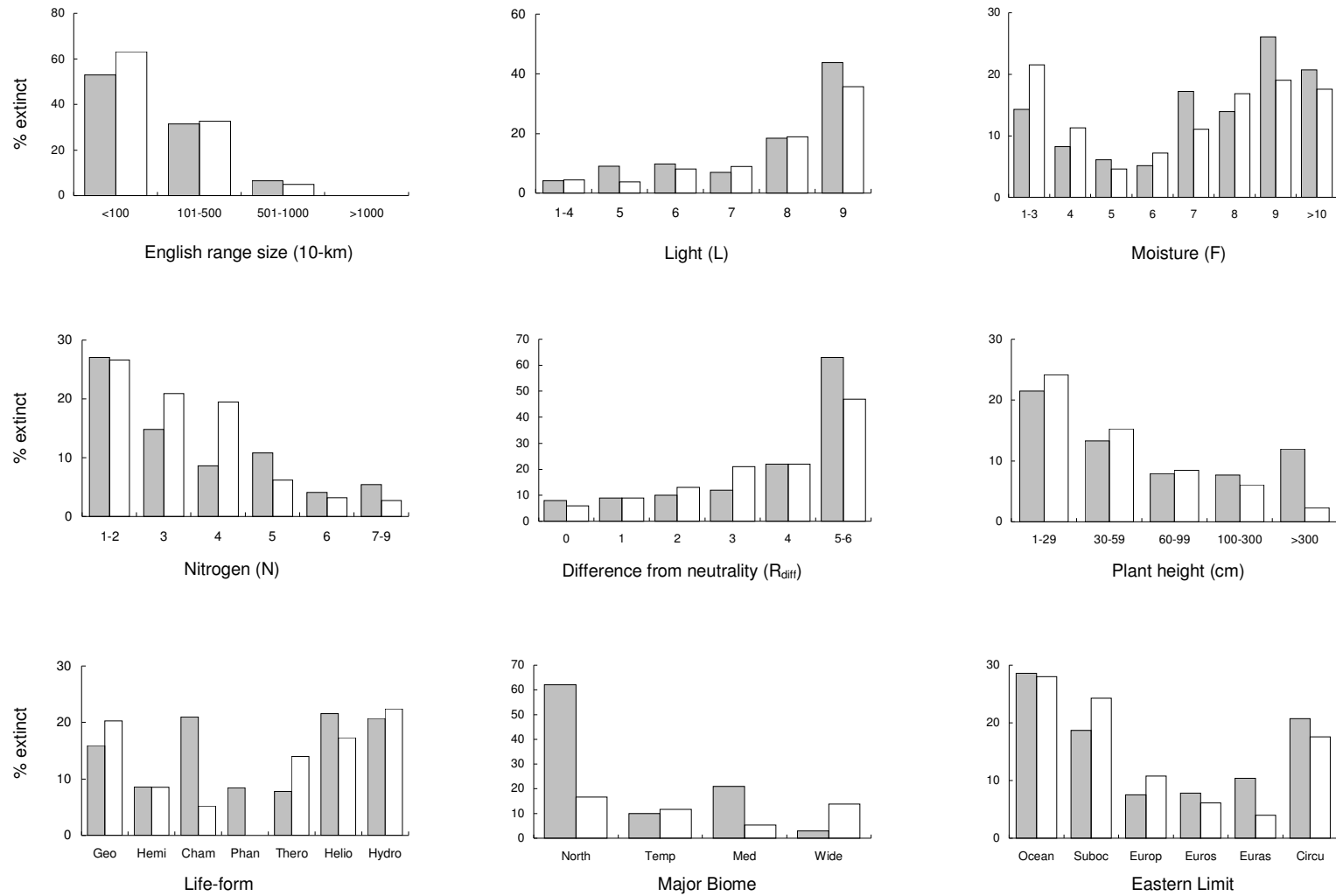


Figure 4.2. The proportion of species in Bedfordshire (grey bar) and Northamptonshire (open bar) that are extinct in relation to a range of plant trait and phytogeographical categories (see Table 4.1 for details).

Hypothesised relationships between plant traits and extinction

English range size

A significantly greater proportion of English rare species have become extinct in both counties when compared to common species (Beds $\chi^2 = 199.9$, $P < 0.001$; Northants $\chi^2 = 228.2$, $P < 0.001$; Table 4.4 and Fig. 4.2). In Northamptonshire only 14 (37%) of the 38 rare species (i.e. recorded from less than 100 10-km² in England) still occur in the county, mainly in limestone grassland in the northeast (e.g. *Carex ericetorum*, *Pulsatilla vulgaris*). A smaller proportion of scarce English species (100-500 10-km²) have been lost (33%) whereas only ten species (5%) occurring in more than 500 10-km² squares in England are extinct. A smaller proportion of English rarities have been lost in Bedfordshire (53%) although these losses have been much greater than those of species which are more frequent in England as a whole. Of the 23 rare species that have survived the majority are confined to chalk soils in the south of the county, most notably *Ajuga chamaepitys*, *Bunium bulbocastanum*, *Hypochaeris maculata*, *Pulsatilla vulgaris* and *Seseli libanotis* for which Bedfordshire still holds nationally important populations (Dony 1976).

Table 4.4. Results of the chi-square (χ^2) test showing the significance of the relationship between % of extinct species and trait categories. Asterisks denote the level of significance: * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$. The degrees of freedom, the number of trait categories used and those categories combined for analyses are also given. For 'Bedfordshire' and 'Northamptonshire', subscripts denote the number of species included in each analyses.

Attribute	Trait	Bedfordshire	Northants	df	Cate- gories	Categories combined
English range	10-km range	199.95 ₇₉₃ ***	228.22 ₇₆₆ ***	3	4	-
Habitat specialisation	L	39.29 ₈₃₆ ***	28.48 ₈₀₈ ***	5	6	1-4
	F	32.37 ₈₃₆ ***	25.23 ₈₀₈ **	7	8	1-3, 10-12
	N	46.84 ₈₃₆ ***	56.91 ₈₀₈ ***	7	8	1-2, 7-9
	R _{diff}	71.86 ₈₃₆ ***	45.61 ₈₀₈ ***	5	6	5-6
Competitive ability	Plant height	17.60 ₇₉₅ **	29.17 ₇₆₂ ***	4	5	1-2, 6-8
	Lifeform	21.89 ₈₃₇ ***	26.05 ₈₀₉ **	6	7	-
	Spread	11.58 ₇₇₂ **	7.82 ₇₄₈ *	3	4	-
	Propogation	8.29 ₅₇₆ *	3.59 ₅₄₅	2	3	-
Dispersal ability	Seed size	3.34 ₅₃₁	1.54 ₅₀₉	5	6	-
	Dispersal agent	4.16 ₄₉₇	3.40 ₄₈₃	3	4	4-5
	Fertilisation	4.47 ₅₁₂	3.30 ₄₉₅	4	5	-
	Dicliny	1.85 ₇₅₀	0.14 ₇₂₂	1	2	-
Position in range	Major Biome	39.96 ₈₃₄ ***	1.68 ₈₀₉	3	4	-
	Eastern Limit	27.88 ₈₃₈ ***	32.09 ₈₀₆ ***	5	6	-

Habitat specialisation

Bog and dwarf shrub heath habitats suffered the greatest number of extinctions in both counties (Fig. 4.3) with eight species being lost from both counties (*Botrychium lunaria*, *Carex dioica*, *Drosera rotundifolia*, *Epipactis palustris*, *Erica tetralix*, *Lycopodium clavatum*, *Nardus stricta*, *Potentilla palustris*). The proportion of losses within the wetland category was slightly lower and plants lost from both counties included two annuals of winter-saturated soil (*Anagallis minima*, *Lythrum hyssopifolium*) as well as aquatics associated with bog pools (e.g. *Myriophyllum alterniflorum*, *Utricularia* spp.) and neutral or basic water bodies (e.g. *Ceratophyllum submersum*, *Potamogeton friesii*, *P. trichoides*). In contrast, Northamptonshire lost a higher proportion of species from acid (19%) and calcareous grasslands (17%), and arable habitats (17%), whereas habitats with the lowest proportions of extinctions in both counties (<10%) included built-up, waste ground and broadleaf woodlands.

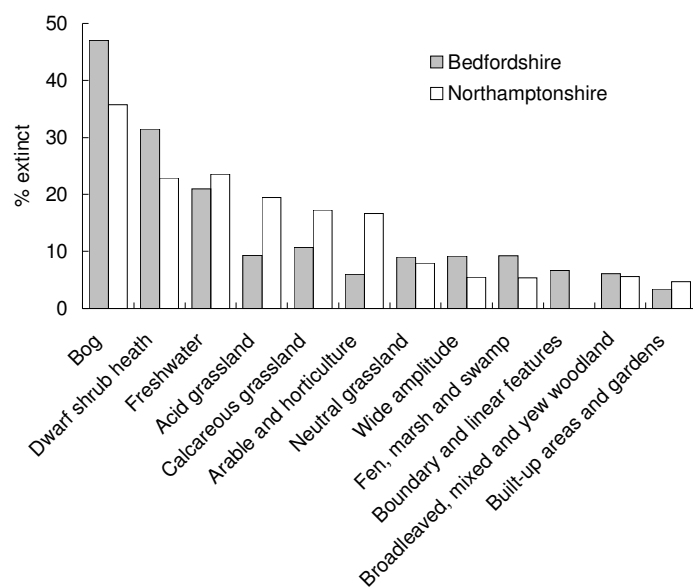


Figure 4.3. The proportion of extinct species in relation to broad habitat type (see Appendix 4 for details).

Not surprisingly, these patterns were reflected in traits associated with habitat specialisation (Table 4.4; Fig. 4.2). The most significant relationships in both counties were between extinction and N and R_{diff} with the greatest proportions of losses within the lowest fertility (Beds $\chi^2 = 46.8$, Northants $\chi^2 = 56.9$, $p < 0.001$; Fig. 4.2) and highest R_{diff} categories (Beds $\chi^2 = 71.9$, Northants $\chi^2 = 45.6$, $p < 0.001$; Fig. 4.2), indicating a significant loss of species associated with nutrient-poor, acidic or basic habitats. Similarly, a significantly greater proportion of species within the highest L categories (L 8-9) had become extinct in both

counties (Beds $\chi^2 = 39.3$, Northants $\chi^2 = 28.5$, $p < 0.001$; Fig. 4.2) indicating a greater loss of species associated with open habitats (e.g. grasslands, bogs and dwarf shrub heaths). In contrast, there was a bimodal relationship between Ellenberg F and extinction with a greater proportion of extreme dry (e.g. *Gentianella anglica*, *Salvia pratensis*, *Stachys germanica*) and extreme wet site indicators having been lost from both counties (Beds $\chi^2 = 32.4$, $p < 0.001$; Northants $\chi^2 = 25.2$, $p < 0.01$; Fig. 4.2).

Competitive ability

The relationship between extinction and competitive ability was less significant than with habitat specialisation (Table 4.4). However, a significantly greater proportion of short species have become extinct than taller species (Beds $\chi^2 = 17.6$, $p < 0.01$; Northants $\chi^2 = 29.2$, $p < 0.001$; Fig. 4.2). The results for life-form were less clear, although a greater proportion of geophytes and marsh and aquatic plants (hydrophytes, helophytes) have become extinct in both counties than taller perennials and woody species (Beds $\chi^2 = 21.9$, $p < 0.001$; Northants $\chi^2 = 26.1$, $p < 0.001$; Fig. 4.2). In contrast, the relationships between extinction and attributes associated with persistence (propagation, spread) were less significant, although spreading (i.e. height < width) and tall plants (height > width) showed a slightly greater tendency to have become extinct in both counties (Beds $\chi^2 = 11.6$, $p < 0.01$; Northants $\chi^2 = 7.8$, $p < 0.05$) whereas a greater proportion of exclusively clonal species were more likely to have become extinct in Bedfordshire ($\chi^2 = 8.3$, $p < 0.05$).

Dispersal ability

None of the attributes associated with seed dispersal (i.e. seed size, dispersal agent) or breeding system (i.e. fertilisation, dicliny) showed a clear or significant pattern in relation to extinction in either county (Table 4.4).

Position in range

Northern, and to a lesser extent Southern species at the edge of their range in the study region, suffered greater declines than either Temperate or Widespread species in Bedfordshire ($\chi^2 = 40.0$, $p < 0.001$; Fig. 4.2). Similarly, a greater proportion of species with their eastern limits in the Oceanic zone of northwest Europe became extinct in both counties (Beds, $\chi^2 = 27.9$, $p < 0.001$; Northants, $\chi^2 = 32.1$, $p < 0.001$; Fig. 4.2). In addition, a much higher proportion of Circumpolar species were lost from both counties than in the more restricted European to

Eurasian categories (e.g. *Botrychium lunaria*, *Drosera rotundifolia*, *Parnassia palustris*, *Utricularia minor*) although this may simply reflect the tendency for Northern species to be Circumpolar.

Extinction risk

The results of the binary logistic regression showed that the trait combinations accounted for around 45% of the observed variation in the six models with English range size ($Z = -12.06$; $p < 0.001$), F ($Z = 5.7$; $p < 0.001$) and N ($Z = -6.0$; $p < 0.001$) being the most important predictors of extinction risk (Table 4.5). These results were consistent for both models in Bedfordshire, whereas in Northamptonshire N was only significant within the reduced model, presumably because of the high degree of correlation between N and R_{diff} ($r = -0.5$; $p < 0.001$). In contrast, R_{diff} was also marginally significant in the full model for the combined dataset ($Z = 2.0$; $p = 0.04$) whereas N was highly significant ($Z = -6.0$; $p < 0.001$). In addition, the strength of F was less significant than in the Bedfordshire models, presumably because a greater proportion of wetland species survived in Northamptonshire.

Table 4.5. Results of the binary logistic regression between extinction and the six main plant traits for Bedfordshire, Northamptonshire and both counties combined including both full and reduced models. The standard errors of the coefficients of variation are given in italics and asterisks denote the level of significance: * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$.

	Bedfordshire		Northamptonshire		Both counties	
	Full	Reduced	Full	Reduced	Full	Reduced
Constant	-0.63 <i>1.17</i>	-0.16 <i>0.48</i>	-0.37 <i>1.20</i>	1.17 <i>0.52</i>	-0.52 <i>0.83</i>	0.47 <i>0.35</i>
English range (%)	-7.81*** <i>0.94</i>	-7.79*** <i>0.92</i>	-7.88*** <i>0.96</i>	-8.14*** <i>0.96</i>	-7.60*** <i>0.65</i>	-7.75*** <i>0.64</i>
Plant height (m)	0.04 <i>0.07</i>	-	-0.01 <i>0.02</i>	-	-0.0003 <i>0.007</i>	-
F	0.44*** <i>0.08</i>	0.44*** <i>0.08</i>	0.15* <i>0.07</i>	0.14* <i>0.07</i>	0.29*** <i>0.05</i>	0.29*** <i>0.05</i>
R_{diff}	0.05 <i>0.10</i>	-	0.23* <i>0.11</i>	-	0.14* <i>0.07</i>	-
N	-0.42*** <i>0.10</i>	-0.45*** <i>0.09</i>	-0.1897 <i>0.10</i>	-0.29*** <i>0.09</i>	-0.30*** <i>0.07</i>	-0.37*** <i>0.06</i>
L	0.03 <i>0.13</i>	-	0.09 <i>0.14</i>	-	0.05 <i>0.09</i>	-
Residual deviance	281.47	282.06	266.67	273.11	560.43	565.13
R^2	45.82	45.71	44.18	42.83	43.81	43.33

Discussion

Rarity

In this study there was a clear relationship between extinction and English range size with significantly more English rare and scarce species having become extinct than widespread species (Fig. 4.2). Although these findings contain an element of circularity, as nationally rare species are also likely to be rare in counties such as Bedfordshire and Northamptonshire, it does highlight the significant losses of rare species at the local scale in lowland England. However, because English range size includes all the 10-km grid squares from which a species has ever been recorded (irrespective of date class or native status) the analysis presented in this paper does not take into account the decline of species in England over recent decades. The extent of these recent losses, however, is clearly shown by the calculating the average Change Indices, based on the relative change in 10-km square occupancy between 1930-60 and 1987-1999 in England (Telfer et al. 2002), for species which have become extinct and those that have survived in both counties (Fig. 4.4). This shows that local scale losses do indeed reflect English trends with extinct species having a significantly lower average Change Index (CI) than those still present in both counties (Bedfordshire $F_{1,786} = 18.8, p < 0.001$; Northamptonshire $F_{1,759} = 33.2, p < 0.001$).

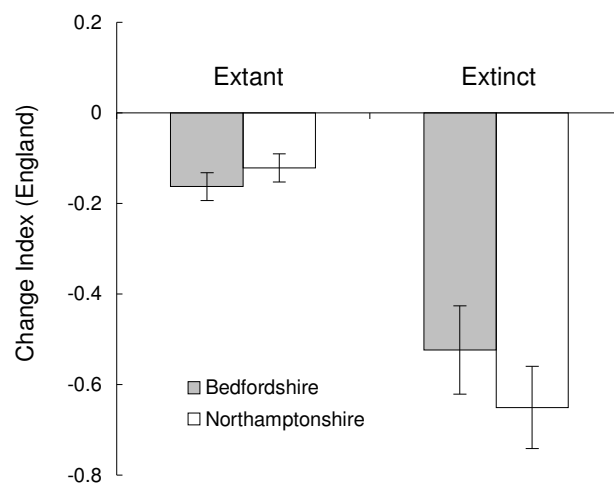


Figure 4.4. The average English Change Index values (Preston et al. 2002a) for extant and extinct species in both counties (Bedfordshire, $F_{1,786} = 18.76, p < 0.001$; Northamptonshire, $F_{1,759} = 33.25, p < 0.001$).

The disproportionate tendency for locally rare species to have become extinct has been noted in a number of studies of extinction at the local scale (Preston 2000; Preston et al. 2003a). Although I made no assessment of how widespread species were prior to extinction the fact

that 22% and 25% of extinct species were only recorded once (see Appendix 3) suggests that a large proportion of those lost were always rare in the study region or that the main period of decline predated the beginning of systematic recording during the eighteenth and nineteenth centuries (Preston 2000).

Although rarity was shown to be an important predictor of extinction it is important to note that in highly modified landscapes a species' realised niche (i.e. the extent to which it is common or rare) combines both ecology and the evolutionary and land use history of the habitats in which it typically occurs. Not surprisingly therefore English range size was highly correlated with traits associated with habitat specialisation, most notably N ($r = 0.30$; $p < 0.001$), R_{diff} ($r = -0.27$; $p < 0.001$), and L ($r = -0.19$; $p < 0.001$), thereby indicating the loss of open, nutrient-poor habitats, such as grasslands, heaths and bogs, in lowland England.

Habitat specialisation

There was a significant relationship between all traits associated with habitat specialisation and extinction in both counties, with a disproportionate loss of species associated with open habitats (L = 8-9) characterised by either very high or low pH ($R_{diff} = 5-6$) and soil moisture (F = 1-3, >7) and low soil fertility (N 1-3). Although these traits were treated separately they are clearly highly correlated with N, particularly R_{diff} , F and L ($r = -0.5, 0.2, -0.3$ respectively; all $p < 0.001$), as open habitats with low fertility generally have very low or high pH. Indeed, the results from the logistic regression suggest that N and F (plus English range size) are sufficient to account for the observed pattern of extinction in the study region, presumably because the greatest losses occurred from very wet and dry habitats (e.g. lowland bog, dwarf-shrub heath and acid and calcareous grassland; Fig. 4.3). It is important to note, however, that it is not habitat specialism *per se* that has caused the loss of species but specialisation within open, nutrient-poor habitats which have been the most susceptible to modern land use change.

Changes in adjacent counties have been broadly similar. In a separate analysis of floristic change in Northamptonshire McCollin et al. (2000) showed that overall changes in plant distribution were significantly correlated to Ellenberg et al. (1991) L and N scores with low N (i.e. low soil trophic status) being the most important predictor of a species' decline. In contrast, the relationship between relative change and R was not significant, presumably because the relationship between R and population change was not linear. The use of R_{diff} in this study overcomes this problem because it takes into account the fact that R scores are

bimodal in relation to soil fertility. National and regional trends in species' occupancy of 10-km grid squares in the UK have mirrored these trends: species with high N and low R_{diff} values have done significantly better than those with low N and high R_{diff} values in all regions of the UK except Highland Scotland, with the relative success of species which benefit from high fertility being particularly marked in southern England (Preston et al. 2003b).

Competitive ability

In this study species within the smallest height categories (<0.6 m) declined to a much greater extent than taller species. This relationship supports the findings of other studies of extinction in lowland England (e.g. Preston 2000) as well as at the national scale (e.g. Thompson 1994): less competitive species have tended to decline in 10-km occupancy over recent decades in all regions except Highland Scotland (Preston et al. 2003b). Similarly, analyses of Countryside Survey sample plots between 1978 and 1998 showed a marked reduction in short stress-tolerators on infertile grassland along linear habitats, such as roads, hedges, woodlands etc., and an increase in species with high Ellenberg fertility values (Smart et al. 2005). Using an alternative measure of competitive ability McCollin et al. (2000) also showed that species with limited powers of lateral spread (therophytes and tussock-formers) had undergone greater relative declines than strongly rhizomatous species between 1930 and 1995 in Northamptonshire. Clearly, plant height is related to life-form and as a result a significant proportion of some life-form types have become extinct in both counties. These include therophytes, which tend to be small, and marsh and aquatic plants which both suffered a high proportion of extinctions in both counties (Fig. 4.2). In addition, the high proportion of geophytes which have been lost in both counties is largely due to the loss of orchids (e.g. *Orchis ustulata*) and ferns (e.g. *Botrychium lunaria*, *Thelypteris palustris*).

Dispersal ability

The lack of a significant relationship between dispersal traits and extinction supports the findings of a number of other studies (e.g. Thompson 1994; Thompson and Hodgson 1996), and presumably reflects the very rapid declines that many species have suffered as a result of land use change. This suggests that the present distribution patterns of many species owe more to recent patterns of human habitat destruction rather than an equilibrium between local extinction and colonisation.

Position in range

A greater proportion of species at their range margins in the study region (e.g. Arctic, Boreal, Mediterranean, Oceanic elements) have become extinct. These findings are consistent with the results of earlier studies in Northamptonshire (e.g. McCollin et al. 2000), adjacent counties (Preston 2000) as well as Great Britain as a whole (Preston et al. 2003b). In contrast to the national pattern (Preston et al. 2003b), however, there was no evidence to suggest that southern (Mediterranean) species have fared better than other phytogeographic elements. Indeed, southern species showed a greater relative decline than both the Wide and Temperate elements in Bedfordshire. Despite these findings, it seems unlikely that climate change has been an important driver of floristic change in southern England. For example, the apparent retreat of northern species from southern Britain is largely due to habitat destruction which began over 200 years ago. Indeed, six of the seven Arctic or Boreal species lost from Bedfordshire were last recorded before 1900 (*Carex dioica*, *Drosera anglica*, *Hammarbya paludosa*, *Potamogeton alpinus*, *Pyrola minor*, *Trichophorum cespitosum*, *Vaccinium oxycoccus*), well before the start of the current period of climatic warming.

Predictions of extinction risk

Of 82 species with predicted probabilities of extinction greater than 0.5, 44 (54%) have become extinct within the study region whereas 38 species (46%) survive in one or more counties (Table 4.6). These therefore represent the most threatened species within the extant flora of the study region. This is reflected in their current distributions as virtually all the species listed in Table 6 are either confined to single sites (e.g. *Carex ericetorum*, *Herminium monorchis*, *Valerianella rimosa*) or to a small number of reserves where populations have been effectively 'buffered' from extinction by conservation designations (e.g. *Hypochaeris maculata*, *Pulsatilla vulgaris*). In comparison, only four species are locally abundant although both *Bunium bulbocastanum* and *Trifolium ochroleucon* are extremely localised outside the study region whereas *Oenanthe fluviatilis* has declined throughout lowland England due to water pollution and river channel 'improvements' (Preston & Croft 1997). These findings suggest that traits used to calculate the predicted probabilities (i.e. English range, plant height, F, N, R_{diff} , L) are powerful indicators of extinction risk within the study region and, given the similarity with previous studies, may help explain the extinction of species in other counties.

Table 4.6. The most vulnerable species in both counties ranked in order of their predicted extinction risk calculated using the reduced binary logistic regression model for both counties (see Table 4.5). Only extant species (in one or more county) with a predicted extinction risk greater than 0.5 are presented. Species extinct within the study region are listed below ($n = 44$).

Species	Probability of extinction	Number of sites		Species	Probability of extinction	Number of sites	
		Bedfordshire	Northants			Bedfordshire	Northants
<i>Baldellia ranunculoides</i>	0.81	Extinct	<5	<i>Melampyrum arvense</i>	0.60	1	
<i>Schoenus nigricans</i>	0.77	Extinct	2	<i>Pinguicula vulgaris</i>	0.59	Extinct	1
<i>Carex ericetorum</i>	0.75		1	<i>Ulex minor</i>	0.59	1	1
<i>Littorella uniflora</i>	0.72		2	<i>Galium parisiense</i>	0.58		1
<i>Oenanthe silaifolia</i>	0.71	Extinct	1	<i>Cerastium pumilum</i>	0.57	2	Extinct
<i>Herminium monorchis</i>	0.70	1		<i>Melica nutans</i>	0.56		1
<i>Eleocharis acicularis</i>	0.67	Extinct	c.4	<i>Monotropa hypopitys</i>	0.55	1	3
<i>Ajuga chamaepitys</i>	0.67	2	Extinct	<i>Orchis ustulata</i>	0.55	1	Extinct
<i>Antennaria dioica</i>	0.65	Extinct	1	<i>Ophrys insectifera</i>	0.53	2	4
<i>Carex curta</i>	0.65	2		<i>Oenanthe fluviatilis</i>	0.53	2	10 pentads
<i>Orobanche rapum-genistae</i>	0.64	3		<i>Aceras anthropophorum</i>	0.52	3	4
<i>Limosella aquatica</i>	0.64	1	4	<i>Calamagrostis canescens</i>	0.52		6 pentads
<i>Trifolium ochroleucon</i>	0.63	18 tetrads	1	<i>Bunium bulbocastanum</i>	0.51	20 tetrads	
<i>Phleum phleoides</i>	0.62	1		<i>Iberis amara</i>	0.51	2	
<i>Petrorhagia prolifera</i>	0.62	1		<i>Valerianella rimosa</i>	0.51	1	Extinct
<i>Carex elata</i>	0.61	Extinct	1	<i>Astragalus danicus</i>	0.51	1	4 pentads
<i>Blysmus compressus</i>	0.61	1	2	<i>Apium inundatum</i>	0.50	Extinct	c.3
<i>Hypochaeris maculata</i>	0.60	1	2	<i>Dactylorhiza incarnata</i>	0.50	1	4
<i>Melampyrum cristatum</i>	0.60	1	1	<i>Pulsatilla vulgaris</i>	0.50	4	2

Notes: 44 species with a predicted probability of extinction >0.5 are extinct within the study region: *Anagallis minima*, *Arnoseria minima*, *Bupleurum tenuissimum*, *Carex dioica*, *Cicuta virosa*, *Cirsium dissectum*, *Cladium mariscus*, *Dianthus armeria*, *Drosera anglica*, *D. rotundifolia*, *Eleocharis multicaulis*, *E. quinqueflora*, *E. uniglumis*, *Epipactis palustris*, *Eriophorum gracile*, *E. latifolium*, *Filago lutescens*, *F. pyramidata*, *Fritillaria meleagris*, *Galium pumilum*, *Gentianella anglica*, *G. campestris*, *Hammarbya paludosa*, *Himantoglossum hircinum*, *Hypericum elodes*, *Hypericum montanum*, *Linum perenne*, *Lycopodiella inundata*, *Lycopodium clavatum*, *Lythrum hyssopifolium*, *Maianthemum bifolium*, *Narthecium ossifragum*, *Ophrys sphegodes*, *Parnassia palustris*, *Platanthera bifolia*, *Pilularia globulifera*, *Pulicaria vulgaris*, *Pyrola minor*, *Rhynchospora alba*, *Teucrium scordium*, *Thelypteris palustris*, *Trichophorum cespitosum*, *Vaccinium oxycoccos*, *Vulpia unilateralis*.

Extinction, land use change and eutrophication

Changes in land use and human population density provide convincing evidence that habitat loss, as a result of agricultural intensification and urbanisation, has been the main determinant of extinction in both counties. Although I do not present direct evidence for land use changes prior to 1850, agricultural enclosure appears to have had a greater impact on grassland habitats in Northamptonshire whereas in Bedfordshire it resulted in the drainage of the remaining areas of lowland bogs, mires and marsh. Indeed 12 of the 17 species last recorded in 1798 were known to Abbott (1798) from Amptill and Potton marshes (e.g. *Drosera anglica*, *Hammarbya paludosa*, *Hypericum elodes*, *Narthecium ossifragum*, *Rhychospora alba*, *Utricularia minor*, *Vaccinium oxycoccos*) although by 1860 local botanists, such as John McLaren, were unable to find any of these species at either site (C. Boon, pers comm.). These losses coincided with the reclamation and enclosure of large areas of waste land in the county which declined from around 39% of the total area in 1800 to 7.1% by 1873 (Williams 1970). In comparison, the area of waste in Northamptonshire declined from only 1.7% to 0.4% over the same period. This suggests that by 1800 dramatic changes had already taken place in Northamptonshire, perhaps as a result of Parliamentary Enclosure and, as in Bedfordshire, these must have led to the drainage of bogs and marshes leading to the loss of *Drosera rotundifolia*, *Osmunda regalis*, *Persicaria minor* and *Pilulifera globulifera* but more importantly the enclosure and ploughing up of limestone grassland leading to the loss of *Ajuga chamaepitys*, *Juniperus communis*, *Ophrys sphegodes*, *Silene gallica*, *Spiranthes spiralis* and *Tephroses integrifolia*.

After 1850 the overall pattern of land use change was remarkably similar in both counties with the proportion of arable and grassland fluctuating markedly in response to the price of cereal crops (Fig. 4.5). With the exception of a small increase during the 1920s, the area of arable land suffered a steady decline (relative to grassland) from 1870 to 1940 due to cheap imports of grain from North America (Robinson and Sutherland 2002). As a consequence, much arable land fell into disuse or was converted to pasture as dairy and sheep farming was more profitable. From 1940 onwards and in subsequent decades the area of arable land increased dramatically as a result of government subsidies to promote mechanisation and the use of chemical fertilisers and insecticides. This led to the ploughing-up of large areas of grassland in both counties, particularly in Bedfordshire where much grassland was also lost to arable cultivation and urban development. In contrast, a greater proportion of grassland

survived in Northamptonshire because large areas, particularly in the main river valleys, were unsuitable for the cultivation of cereal crops.

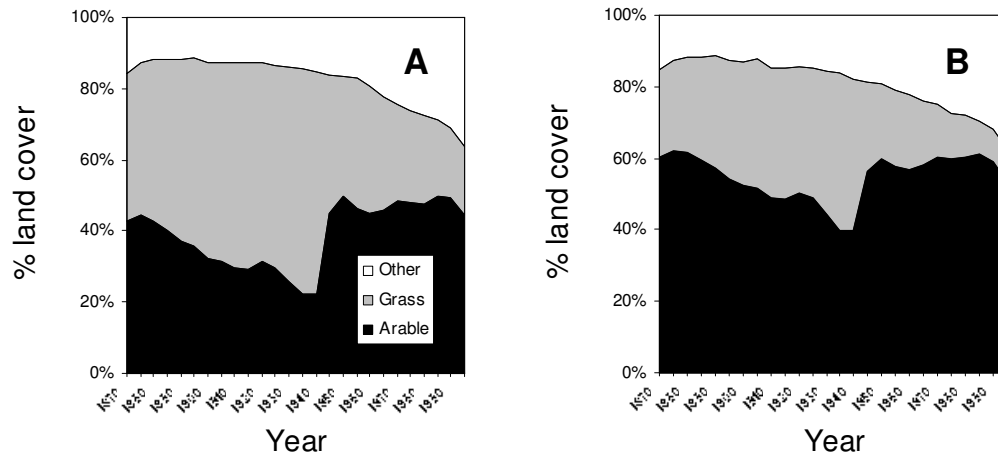


Figure 4.5. Changes in proportion of arable, permanent grassland and non-agricultural land in (A) Bedfordshire and (B) Northamptonshire, 1870-2000.

During the post-war period there was also a dramatic increase in sheep numbers in the UK (Fuller & Gough 1999) and therefore in grazing intensity on the remaining areas of grassland (Fig. 4.6a). This increase has been largely sustained through more intensive agricultural practices such as drainage, fertilisation, re-seeding and conversion from hay to silage systems on the most productive soils. At the same time the least productive grasslands on very acid or basic soils witnessed a reduction in grazing levels as sites have become smaller and more isolated, and rabbit populations have declined as a consequence of myxomatosis (Thomas 1960). This resulted in declines in the numbers of populations of downland specialists in both counties, such as *Ophrys sphegodes* and *Pulsatilla vulgaris* (see Chapter 7) where increased above-ground competition, following a cessation of grazing, has made conditions increasingly unsuitable for reproduction (Chapter 7).

Human population density conveniently unites a range of non-agricultural human activities which have negative impacts on plant populations (e.g. road-building, urbanisation, recreation pursuits) thereby providing a crude measure of human impact on the landscape (Thompson & Jones 1999). The results presented here (Fig. 4.6b) suggest that such impacts were much greater in Bedfordshire, where population density increased eightfold between 1800 and 2000, more than double the increase in Northamptonshire. This is undoubtedly a result of the spread of the Luton-Dunstable conurbation in the south of the county where housing and

industrial developments, golf-courses, wildlife parks and airports have all destroyed or encroached upon large areas of semi-natural grassland over the past 50 years causing localised declines of species associated with chalk grassland, marshes, bogs and lowland mires. However, the fact that Northamptonshire lost an equivalent number of species during the same period suggests that agricultural change has been much more important than urban pressure in causing the decline and loss of species in some counties in recent decades (Thompson & Jones 1999; Preston 2000).

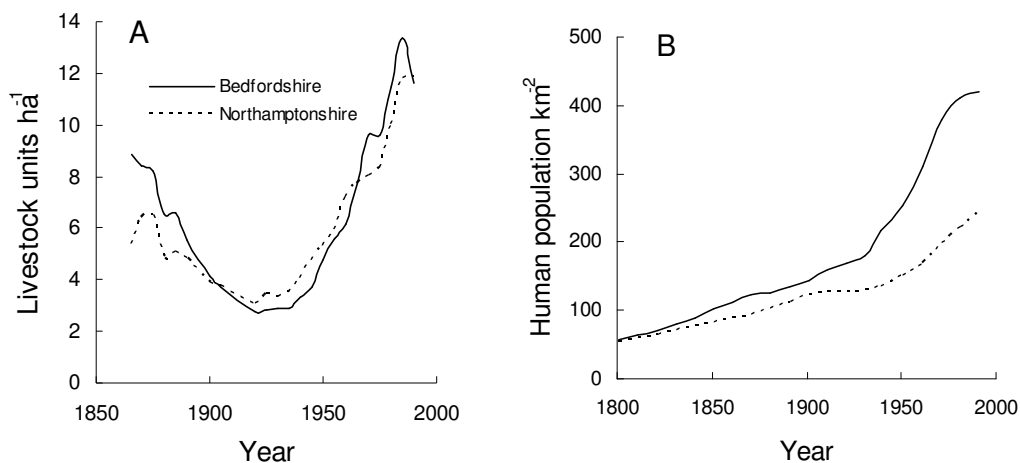


Figure 4.6. Changes in (A) livestock and (B) human population densities in Bedfordshire and Northamptonshire. ‘Livestock units’ are standardised units used to calculate grazing intensities with a single unit ranging from 0.15 (ewes, sheep, goats) to 1 (cows). Human population figures for Northamptonshire exclude the Soke of Peterborough.

Although habitat loss undoubtedly accounts for the majority of extinctions described in this study, the characteristics of the extinct species suggest that eutrophication is an important additional driver of floristic change. This includes the addition of nutrients to ‘improve’ unproductive soils for agricultural cultivation but also the indirect eutrophication of soils and water bodies as a result of diffuse deposition from a variety of sources. It is now widely accepted that food production and combustion of fossil fuels have greatly increased the availability and mobility of nutrients such as nitrogen and phosphorus over large areas of northwest Europe (Vitousek et al. 1997; Galloway & Cowling 2002). In Europe, N deposition and accumulation has increased dramatically over recent decades (e.g. NEG-TAP 2001; Peñuelas & Filella 2001) causing significant changes to the species composition of a wide range of terrestrial and aquatic ecosystems, particularly grasslands and heathlands associated with very low levels of soil fertility (Bobbink et al. 1998; Stevens et al. 2004). The disproportionate loss of small, stress-tolerant species reported in this study is consistent with a

general increase in productivity of nutrient-enriched habitats, although further work is required to assess whether such losses are independent of habitat loss. More research is also required to assess the extent to which ‘low-level’ stresses such as atmospheric deposition of pollutants and climate change place additional pressures on plant populations already severely reduced by habitat loss.

Limitations

Although the findings of this study provide convincing evidence for a period of heightened extinction over the last two centuries there are a number of factors which may have led to the overall scale of extinction being over- or under-estimated. To a large extent these figures depend on the definition of native species, as well as the exclusion of native species introduced to the county. In order to maintain comparability with other studies we used Preston and Hill’s (1997) classification of British native status although changes to this list will inevitably take place in the future, particularly with respect to arable weeds introduced to the British Isles before AD1500 (Preston et al. 2004). Many of these species suffered dramatic declines during the twentieth century (Sutcliffe & Kay 2000; Preston et al. 2002a) and as a consequence, their inclusion may have increased the proportions of extinctions within certain trait categories. The status of some British native species in the study region is also open to debate, particularly coastal species (e.g. *Medicago minima*, *Trifolium scabrum*) which may have been imported inland with sand and gravel.

Recorders may hesitate to classify the most recent disappearances as extinctions, even if a species has not been seen for many years (Shaw 2005), or conversely some may re-appear as a result of natural re-colonisation. Similarly, the ‘loss’ of critical taxa (e.g. *Rosa*, *Euphrasia*) or inconspicuous species which have been over-looked or inconsistently recorded in the past, may lead to an over-estimation of extinction rates, particularly for those species with ‘transient’ life-histories (Shaw 2005) or which occur in habitats which are poorly recorded (Walker 2003b).

Studies at the county level cannot, of course, be used to estimate the degree of extinction at the population level as species can undergo large changes in abundance but still persist within the county (Pearman 1996). For example, some species persist at critically low population levels within the study region (e.g. *Ajuga chamaepitys*, *Orchis ustulata*, *Valerianella ramosa*) although conditions are no longer suitable for sexual or vegetative reproduction at many sites.

More fine-scaled studies (e.g. population, site or tetrad level) are therefore required in order to assess the full extent of population extinction at the local scale in the UK. The results for two such species are presented in Chapters 6 and 7.

Conclusions

The results of this study confirmed four of the main hypotheses: habitat specialists, poor competitors (i.e. stress-tolerators), rarities, and species at the edge of their range in southern England, were much more likely to have become extinct in the study region than would be expected by chance alone. In contrast, there was no clear or significant relationship between dispersal ability and extinction. These findings, which parallel national trends, indicate that habitat loss and eutrophication are the main factors driving population extinction at the local scale. The perilous state of many surviving habitat specialists which combine these traits (Table 4.6) suggests that extinctions will continue to occur unless large-scale restoration programmes are implemented to reverse the loss of semi-natural habitats, increase connectivity between isolated remnants and reinstate management on sites now isolated by surrounding land uses (e.g. grazing, appropriate hydrological regimes). Similarly, eutrophication will make long-term conservation of low nutrient-status habitats difficult to sustain in some areas unless policy mechanisms intended to tackle its worst environmental effects are enforced. More fine-scaled studies are also required to quantify changes in the abundance of more widespread species at the population, site or tetrad level and to assess whether low-level stresses, such as climate change and atmospheric pollution, are having additional impacts on populations already severely depleted by habitat loss.

90

A STUDY OF THE FLORA

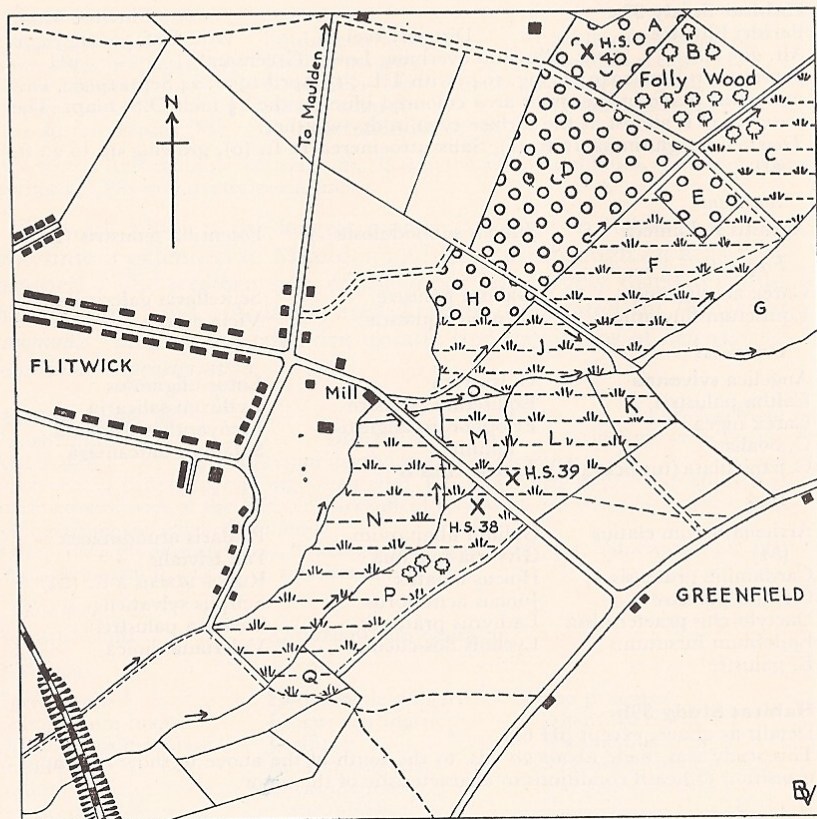


FIG. 10 FLITWICK MOOR

The area A is largely felled woodland now regenerating with birch and alder. In open parts there is a considerable amount of sphagnum-bog. B (Folly Wood) is largely alder. D, now overgrown with birch, was reputed, 50 years ago, to be the wettest part of the Moor. E is the site of the more recent and present peat-digging. F is rough meadow-land, and C and G meadow-land now regularly grazed. H, dominated by birch at its northern end, is marshy in the south. J to Q are rough meadow-land, N is regularly grazed and P very acid. M contains the wettest parts of the Moor.

Plate 5

One of the maps from John Dony's (1953) *Flora of Bedfordshire* showing the location of three "habitat studies" re-recorded in 2003-04 as part of this study

Chapter 5

Fifty years of change in an area of intensive agriculture: plant trait responses to habitat modification and conservation

Summary

I re-surveyed 107 vegetation plots recorded between 1949 and 1951 in Bedfordshire, England, UK to assess (1) the extent of habitat change, (2) quantify overall species trends, (3) relate trends to plant traits in order to identify the main causes of floristic change, and (4) assess the effectiveness of conservation protection. Many more species declined (66%) than increased (34%) indicating an overall decline in species diversity. Vegetation changes were greatest on arable, waste and neutral and acid grassland plots. The composition of woodlands, calcareous grasslands and marshes remained remarkably stable. The main causes were agricultural improvement and succession; other factors, including the spread of invasive alien species, only had very localised impacts. Shifts in plant traits were related to rarity, habitat specificity and nutrient availability with tall nutrient-demanding species increasing at the expense of small habitat specialists. These changes mirror national trends caused by the eutrophication of terrestrial and aquatic ecosystems. The increase of tall species may also reflect the cessation of woodland and grassland management. Greater regenerative abilities did not buffer species from extinction, and rather unexpectedly conservation designation had little effect in reducing habitat change in most cases. Effective conservation of habitat specialists will therefore depend on reduced nutrient enrichment of lowland habitats as well as more effective control of extrinsic as well as intrinsic factors on designated sites.

Introduction

Lowland semi-natural habitats have been fragmented and reduced in area across much of northwest Europe since the 1940s due to increasing intensity of grassland and crop management (Robinson & Sutherland 2002). There is also growing evidence that succession has occurred in some habitats due to the decline of traditional management activities (Poschlod & Bonn 1998; Nisbett & Shere, 2006) and several habitat types have displayed

shifts in species composition consistent with an increase in atmospheric deposition of macro-nutrients such as nitrogen (N) (NEGTAP 2001; Smart et al. 2003).

In Britain most assessments of floristic change have been based on changes in the occupancy of hectads (10-km squares) (Rich & Karran 2006). These lack sensitivity for two reasons. First, large changes in abundance can be masked by presence within a large recording unit such as a hectad (Pearman 1997). Second, differences in recording activity increases uncertainty over the comparability of surveys (Rich & Woodruff 1992) as well as drivers of floristic change (Smart et al. 2005). The recording of permanent plots overcomes many of these problems, providing that they can be accurately re-located and a standardised recording method is used (Chapter 2). In the UK this approach has been used to quantify species-turnover in a range of habitats (e.g. Kirby et al. 2005; Bennie et al. 2006) and since 1978, a range of plots have been used to monitor the fate of common species and broad habitats within a national series of 1-km grid squares (Smart et al. 2005).

Bedfordshire is a medium sized county (1250 km²) in central southeast England (Fig. 5.1). The county is entirely lowland (<250 m) with gently undulating chalk ‘uplands’ in the south, a ridge of acid Greensand and extensive low-lying clay vales to the north. It has no coastline, though coastal halophytes penetrate along major roads (e.g. *Cochlearia danica*, *Puccinellia distans*). The climate is moderately extreme by English standards with winter temperatures a degree or two lower and summer temperatures a degree or two higher than the average for southern England (Dony 1976; Keech 1995). The coldest months are usually January and February, both with an average maximum of around 5 degrees Celsius, and July and August are usually the warmest both with maximums of around 22 degrees Celsius. Probably only Huntingdonshire and Essex have lower precipitation than Bedfordshire (Dony 1956). Most low-lying areas receive less than 600 mm, increasing to around 700 mm in the ‘chalk uplands’ in the south of the county. Changes in land use after the Second World War appear to be representative of lowland landscapes more generally (Chapter 4) with the area of arable increasing from 40% to 59%; grassland declining to around 10% and stocking densities tripling from 4 to 12 livestock units ha⁻¹ due to improvement. The human population density increased from 150 people km⁻² to over 400 km⁻², largely due to urban growth in the south of the county. The network of major roads increased dramatically in the 1950s and there are currently over 200 mineral workings producing over two millions tonnes of aggregates per annum.

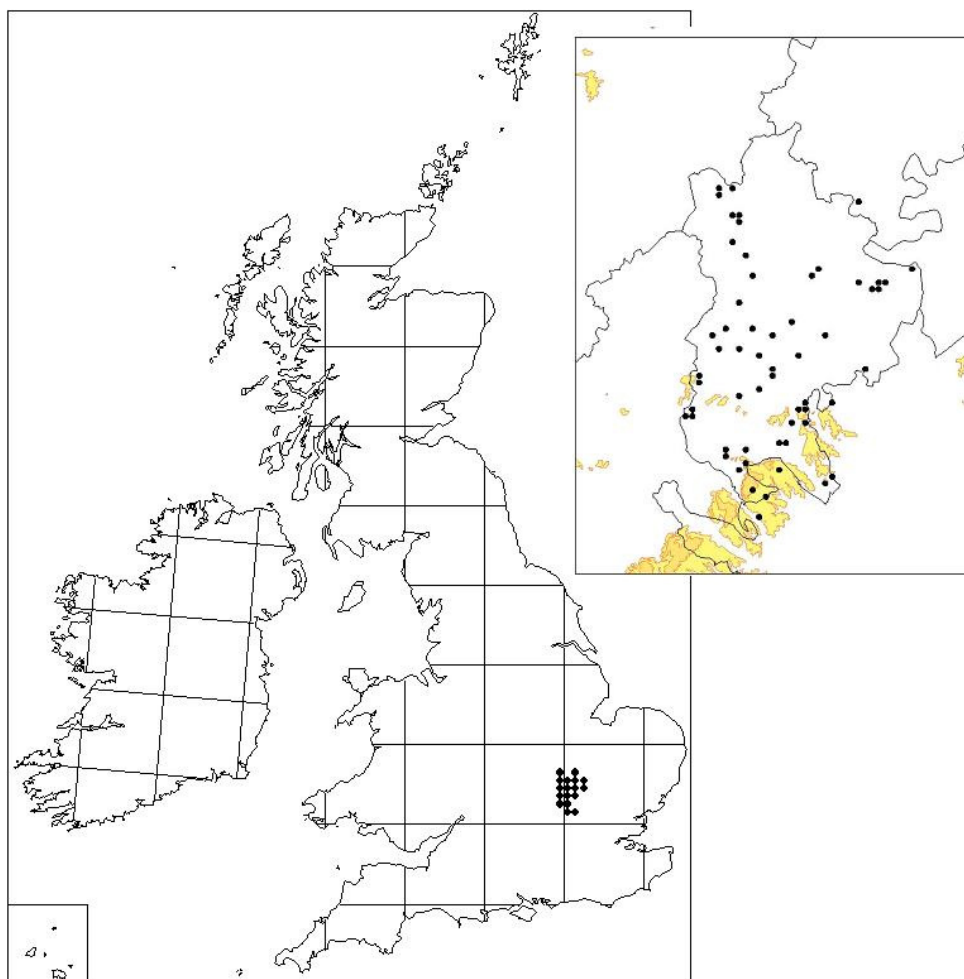


Figure 5.1. Map showing the location of the study sites included in this study. The inset shows the 1 km square-level distribution of habitat studies in Bedfordshire with land above 150 m superimposed.

In this chapter, I assess vegetation change in a series of fixed plots in Bedfordshire, originally recorded by J.G. Dony in 1949-51 and re-surveyed in 2003-04. These “habitat studies” were located in a range of “plant communities typical of the flora of the county” and were recorded to enable “field botanists of a future generation to determine with some degree of accuracy changes which may occur in the flora” (Dony 1953, p. 54). The dataset therefore provides a unique baseline from which to assess the post-war impacts of land modification and conservation on a typical lowland flora (Dony 1977). I used these data to quantify changes in (1) the composition of semi-natural habitats and (2) the frequency and abundance of plant species over the last 55 years. Changes in species’ frequency were related to plant traits associated with range size, resource specialisation, competitive ability and regenerative capacities to (3) identify the main drivers of floristic change. Finally, I assessed (4) the effect of conservation designation on changes in species composition and habitat extent.

Methods

Habitat studies

Dony's (1953) original survey included 128 fixed plots located in a range of semi-natural communities across the county. These were positioned close to permanent features to allow relocation and were recorded during several visits. They were visited again during the drought year of 1976 but the results were never published (Dony 1977). In 2003-04 all the plots were relocated using GPS and the vegetation recorded. Where locations were unclear plots were positioned in homogenous stands of vegetation with the same slope, aspect and landscape position as the original. Eighteen plots could not be relocated with confidence and were therefore excluded giving a total of 107 in this study, 22 of which were on sites with conservation designations (i.e. Sites of Special Scientific Interest and National Nature Reserves; Appendix 5). Within each plot, the abundance of all higher vascular plant species was recorded using the DAFOR scale (Dominant, Abundant, Frequent, Occasional, Rare). Each plot measured 10 yards (9.1 m) in diameter (65.6 m²) and in both surveys a 10 cm deep soil sample was taken from the centre and the pH measured in a paste of soil and de-ionised water.

Habitat change 1949-2004

To assess the extent of habitat change I assigned Dony's original plots to 11 broad habitats (Table 5.1) using TWINSpan (Hill and Šmilauer 2005). Plots were assigned to the same broad habitat in 2003-04 if their composition had not changed significantly (see below). Shifts in species composition were quantified using Czekanowski's Index of Similarity (S) after converting DAFOR values to a five point numeric scale: $S = 2 * \sum \min(x_i, y_i) / \sum (x_i, y_i) * 100$ where x_i and y_i are the abundances of species i in the consecutive surveys. These shifts in composition were also plotted using Detrended Correspondence Analysis (DCA) (Appendix 7). For plots where similarity in composition between the two surveys was < 40% a judgement was made as to the reason for observed change based on obvious aspects of change in species composition.

Species trends 1949-2004

To quantify changes in the species frequency and abundance, n_1 and n_2 were defined as the total number of plots occupied by a species in 1949 and 2004 respectively, and f_1 and f_2 the mean abundance calculated by converting DAFOR scores to a numeric five point numeric scale (Dominant = 5 to Rare = 1). The significance of the change in the number of occupied

plots was tested using Chi-square and change in the overall abundance by a two-tailed t -test. The number of plots in which the species was present in both surveys was defined as $n_{1,2}$ and the change in abundance of occupied plots assessed using a paired t -test. 233 species recorded in less than three plots in both surveys combined were excluded from these analyses.

Table 5.1. Summary of broad habitats and plots included in this study.

Broad habitat	Substrate	Mean pH	Number of plots included in study
River	Alluvium and gravels	7.2	4
Swamp	Alluvium and gravels	7.4	9
Marsh	Alluvium and gravels	6.3	13
Woodland - basic	Boulder clay	6.4	19
Woodland - acid	Lower Greensand	5.8	8
Heathland and mire	Lower Greensand	5.4	11
Acid grassland	Lower Greensand	5.5	5
Neutral grassland	Boulder clay	7.3	10
Calcareous grassland	Chalk and limestone	7.5	15
Waste (including quarries & setaside)	Light soils	6.6	5
Arable	Light soils	7.4	8

Plant trait responses to habitat modification and conservation

Thirteen plant traits were used to test hypothesized relationships between species trends and drivers of floristic change (Table 5.2). The number of plots occupied in 1949 and national range were used to assess correlation between rarity and species trends. Response to increased eutrophication was tested using traits associated with resource specialisation including habitat specificity and Ellenberg indicator values for light (L), moisture (F), fertility (N) and reaction (R) recalibrated for all British species (Hill et al. 2004) and with reaction (R) converted to differences from neutrality (R_{diff}). Measures of competitive ability included vertical and lateral spread (height and clonality). Response to habitat fragmentation was tested in relation to regenerative ability, namely a species' ability to be rescued or buffered from localised extinction by dispersal or persistence (Thompson 1994). These included longevity (i.e. perennation, seed bank persistence) and dispersal ability (assuming wind/water/animal > unspecialised/explosive). Fertilisation mode was also included as it is thought that isolation reduces reproductive success of out-crossing species (Blomqvist et al. 2003).

Table 5.2. Plant traits used to study the change in the frequency of species in fixed plots in Bedfordshire, 1949-2004.

Trait group	Trait	Description	Range/categories
Range size	Local range	No. of plots in 1949	Rare (0-5); intermediate (6-20); widespread (21-107)
	English range ¹	10-km squares in England	Rare (1-499); intermediate (500-999); widespread (1000-1495)
Resource specialization	Specialism Index ²	Habitat specificity	Generalist (8-12); intermediate (13-17); specialist (18-21)
	<i>L</i>	Light preference	Shade tolerant (2-5); intermediate (6-7); light demanding (8-9)
	<i>F</i>	Soil moisture preference	Dry (2-6); moist (7-8); wet (9-12)
	<i>N</i>	Soil fertility preference	Oligotrophic (1-4); mesotrophic (5-6); eutrophic (7-9)
Competitive ability	<i>R</i> _{diff} ³	Difference from neutrality	Neutral (0); weak acid/alkaline (1-2); strong acid/alkaline (3-6)
	Plant height	Summer max. height (cm)	1-29, 30-99, 100-299, >300
Regenerative capacity	Lateral spread	Clonality	Little/none, limited, far reaching
	Longevity	Perennation	Annual, biennial/perennial
	Seed bank longevity ⁴	Seed bank persistence	Transient (0-0.25); short-term (0.26-0.75); long-term (0.76-1.0)
	Dispersal ability	Agent of dispersal	Wind, water, animal, unspecialised/explosive
	Fertilisation	Method of fertilisation	Asexual (viviparous, apomictic), self, cross

¹ Includes all records in England irrespective of date class or status. ² The Specialism Index is based on a species' relative frequency in 11 broad habitats in 1949 and calculated using the method described by Thompson et al. (1998b). ³ Calculated as the difference in *R* from neutrality (*R* = 7) with *R* 8 and *R* 9 scored as *R*_{diff} 3 and 6 respectively. ⁴ Calculated as the number of short- or long-term persistent seed bank records for a species as proportion of all records (transient, short-term, long-term persistent) with values ranging from 0 – no persistent records, to 1 – all records persistent (Thompson et al. 1998a).

The importance of plant traits in explaining species trends was analysed using multiple binary logistic regression. The response variables were the number of plots occupied in 2004 (out of 107 plots), and the number of colonisations/extinctions (out of the plots where the species was not recorded/recorded in 1949). The explanatory variables are listed in Table 5.2: note the inclusion of the number of records in the first survey (local range). A preliminary analysis used all explanatory variables, but 349 species were excluded because of one or more missing values. In a second analysis only the statistically significant variables ($p < 0.05$) were retained (this reduced the number of excluded species to 100). For overall change, all terms in the model were statistically significant and so for comparability these variables were used for the analysis of colonisation and extinction. Previously excluded traits were then added individually to the model but none were statistically significant ($p > 0.05$). Standard errors and tests for estimated effects were adjusted to allow for overdispersion (Hosmer and Lemeshow 1989). Variation accounted for by traits included in the model and individually is summarised by the percentage deviance accounted for.

Results

Habitat change

Since 1949 acid and neutral grasslands showed the greatest change with 100 and 80% respectively of plots being lost to other Broad Habitat types. Reflecting changes in species composition, at least half of all arable, calcareous grassland and heath and mire sites were classified as other broad habitats by 2004 (Table 5.3). In comparison, 25 of 26 woodlands were still present in 2004. Of the 37 shifts in broad habitat the most frequent were to woodland ($n = 5$) and scrub ($n = 6$), improved grassland ($n = 10$) and arable ($n = 5$) and waste communities ($n = 5$). Changes in the overall species composition reflected these changes with arable, waste and neutral and acid grassland changing the most between the two surveys ($S < 20\%$) whereas marshes, calcareous grasslands and woodlands showed the least change ($S > 30\%$; Table 5.3). Changes in soil pH were only significant on basic woodland and swamp plots which became more acidic (Table 5.3).

The most frequent causes of habitat change were intensification of grassland and arable, woodland/grassland succession following the abandonment of traditional management (e.g. coppicing, extensive grazing), river works, afforestation and gravel extraction (Fig. 5.2a). With the exception of calcareous grassland, site protection did not significantly reduce

vegetation change and in three cases this was greater on protected sites where plots in the same habitat were compared (heath & mire, neutral grassland, acid woodland; Fig. 5.2b).

Table 5.3. Change in broad habitats and soil pH between 1949 and 2004 ($n = 107$). The overall change in species composition was calculated using Czekanowski's Index of Similarity (% similarity) For soil pH the significance of difference between survey periods was calculated using a paired t -test; * $p < 0.05$.

Broad habitat	Number in 1949	Same broad habitat 2004	Shift in broad habitat	Broad habitat 2004	% similarity	Change in pH
Acid grassland	5	0	1	1	15	0.4
Arable	8	4	5	9	19	-0.5
Calcareous grassland	15	8	0	8	33	<-0.1
Heath and mire	11	6	0	6	28	-0.4
Marsh	13	10	1	11	32	0.1
Neutral grassland	10	2	2	4	18	0.2
River	4	3	0	3	24	<0.1
Swamp	9	8	0	8	21	-0.3*
Waste	5	3	5	8	13	-0.2
Woodland - basic	19	18	5	23	39	-0.6*
Woodland - acid	8	8	0	8	33	-0.7
Conifer plantation	0	0	2	2	-	-
Improved grassland	0	0	10	10	-	-
Scrub	0	0	6	6	-	-
Total	107	70	37	107		

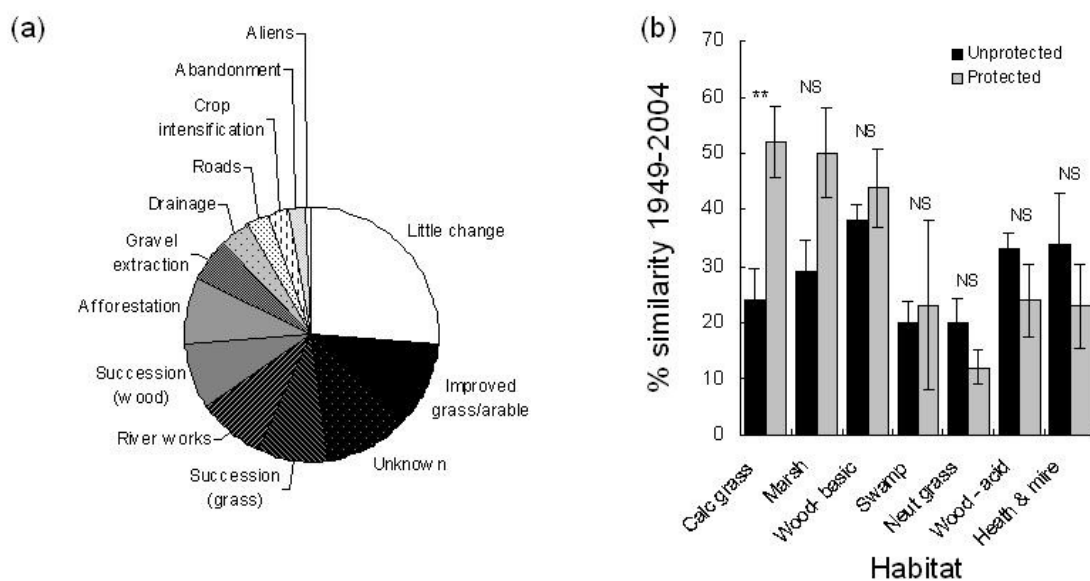


Figure 5.2. (a) The main causes of floristic change in plots where % similarity scores were $\leq 40\%$ ($n = 79$). (b) Differences in % similarity scores (± 1 SE) between 1949 and 2004 for unprotected sites and sites with conservation designations in relation to broad habitat type (acid grassland, arable, waste and river are excluded as none of the sites included in this study were protected). ** $p < 0.01$; NS not significant.

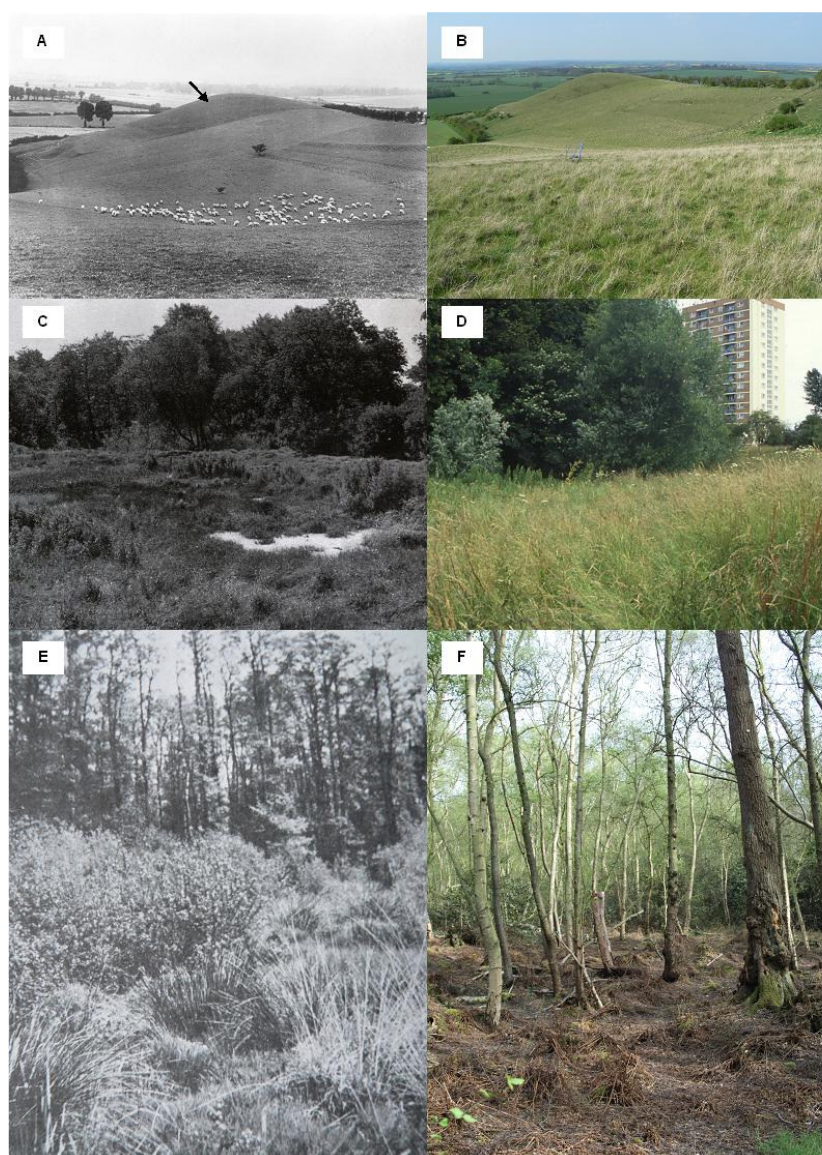


Figure 5.3. Habitat change at three contrasting sites included in this study. The photographs of Knocking Hoe (site 77) show ancient calcareous grassland in 1923 (a) and 2006 (b) and illustrate how little the site has changed over the past 80 years. The fixed plot, located on the SW-facing slope of the Hoe itself (indicated by the arrow) showed the least change in species composition of all 107 plots surveyed ($S = 66\%$; Appendix 5) and still contains many of the rare plants present in 1949 (e.g. *Hypochaeris maculata*, *Pulsatilla vulgaris*, *Tephroses integrifolia*). In comparison, Figs 5.3c and 5.3d show a small marsh adjacent to the source of the River Lea at Well Head, Luton (site 105) in 1949 and 2004 respectively. Although appearing similar, the composition of the site has changed dramatically (% similarity = 7%) from a species-rich marsh, with open pools supporting stands of *Eleocharis palustris* and *Equisetum palustre*, to a moist, species-poor grassland dominated by *Carex riparia* and the nitrophiles *Cirsium arvense*, *Galium aparine* and *Urtica dioica*. This change was caused by drainage works and eutrophication associated with the spread of adjacent urban areas. In contrast, the third habitat study shown, Folly Wood (site 56), is located on the edge of a large valley mire complex. Since 1949 drainage of the surrounding agricultural land and has caused the site to dry out. As a consequence, the vegetation has changed from a species-rich oligotrophic mire, dominated by *Carex acutiformis*, *C. rostrata*, *Hydrocotyle vulgaris* and *Molinia caerulea* with scattered shrubs to a dense birch woodland with a dense under-storey of *Dryopteris dilatata* (f) (% similarity = 8%).

Figure 5.3 shows examples of the extent of habitat change in different sites. These range from very little change on calcareous grasslands (Figs 5.3a & b), marked changes in composition in other habitats such as marshes (Figs 5.3c & d) and complete modification in the case of lowland mires (Figs 5.3e & f). Both the latter have suffered from eutrophication from adjacent land and in the case of Fig. 5.3f also succession to woodland following drainage of the surrounding land.

Species' trends

Ninety-seven species displayed significant trends in occupancy and/or abundance ($p < 0.05$). Eighteen species increased significantly in both occupancy and abundance, most notably *Urtica dioica*, *Galium aparine*, *Poa trivialis* and *Agrostis stolonifera* and sixteen species showed a significant increase in abundance only (Table 5.4). Many more species ($n = 63$) showed a significant decrease in plot occupancy indicating an overall decline in species richness (Table 5.5). *Cynosurus cristatus* was the only species showing a significant decline in both occupancy and abundance whereas six species declined significantly in abundance but not in occupancy (e.g. *Agrostis capillaris*, *Primula vulgaris*).

Plant trait responses

Seven traits were statistically significant in the regression model and explained 69.7% of the variation in species trends in the reduced model (Table 5.6). Local and English range and habitat specificity accounted for most variation followed by Ellenberg N , F and plant height. These seven traits accounted for a similar amount of variation in colonisation behaviour (65.1%): again local and English range (Figs 5.4b & c) and habitat specificity (Fig. 5.4d) were the most significant traits suggesting that widespread generalists have colonised significantly more plots than all other species over the last 55 years. Successful colonists also tended to be taller and associated with more fertile conditions (Figs 5.4e & f). For extinction, less variation was explained by the regression model (21.7%) suggesting that species were more variable in their behaviour or that better explanatory variables, for example relating to historical change in patch geometry, were missing from our analyses. Fewer traits were significant and individual traits explained less variation (all $< 10\%$). However, more localised species (Fig. 5.4g) of open habitats (Fig. 4h) and smaller plants (< 1 m) (Fig. 4i) were significantly more likely to have become extinct than other species.

Table 5.4. The 34 vascular plants displaying significant increases in range/abundance between 1949-2004 (63 species displayed negative trends, 286 species showed little or no change and 233 occurred in less than 3 plots and were excluded from the analyses). n_1 , number of plots in which a species was found in 1949-51; n_2 , number of plots in which a species was found in 2003-04; $p(\chi^2)$, significance of change in number of occupied plots (chi-square test). f_1 , mean abundance of a species in 1949-51 (numeric DAFOR-scale); f_2 , mean abundance of a species in 2003-04; t , significance of change in abundance (two-tailed t -tests); $n_{1,2}$, number of plots on which a species was recorded on both dates; $p(t)$, significance and direction of change on continuously occupied sites (paired two-tailed t -tests).

Species name	n_1	n_2	$p(\chi^2)$	f_1	f_2	t	$n_{1,2}$	$p(t)$
Increased in occupancy/abundance:								
<i>Urtica dioica</i>	18	54	< 0.001	1.8	3.4	< 0.001	13	< 0.05 (+)
<i>Galium aparine</i>	19	51	< 0.001	1.5	2.8	< 0.001	13	n.s.
<i>Poa trivialis</i>	20	42	< 0.001	2.9	4.1	< 0.05	13	n.s.
<i>Fraxinus excelsior</i>	18	43	< 0.001	2.6	2.5	n.s.	14	n.s.
<i>Rubus fruticosus</i>	27	47	< 0.01	3.5	3.8	n.s.	20	n.s.
<i>Sonchus asper</i>	10	26	< 0.01	1.6	1.8	n.s.	0	
<i>Anisantha sterilis</i>	3	13	< 0.01	1.0	2.1	-	0	
<i>Acer pseudoplatanus</i>	2	11	< 0.01	2.0	2.0	n.s.	0	
<i>Tripleurospermum inodorum</i>	1	10	< 0.01	0.0	5.0	-	0	
<i>Ilex aquifolium</i>	0	7	< 0.01	0.0	1.3	-	0	
<i>Agrostis stolonifera</i>	19	34	< 0.05	3.1	4.4	< 0.05	9	n.s.
<i>Bromus hordeaceus</i>	4	14	< 0.05	1.0	2.6	n.s.	0	
<i>Dryopteris dilatata</i>	4	12	< 0.05	1.0	3.8	n.s.	3	n.s.
<i>Elytrigia repens</i>	5	13	< 0.05	3.5	2.8	n.s.	0	
<i>Anthriscus sylvestris</i>	2	9	< 0.05	2.0	1.4	n.s.	0	
<i>Carex riparia</i>	1	7	< 0.05	3.0	5.1	-	0	
<i>Glyceria declinata</i>	0	4	< 0.05	0.0	2.0	-	0	
<i>Picea abies</i>	0	4	< 0.05	0.0	1.5	-	0	
Increased in abundance only:								
<i>Cirsium arvense</i>	42	42	n.s.	1.5	2.6	< 0.001	20	< 0.001 (+)
<i>Dactylis glomerata</i>	38	37	n.s.	1.4	2.5	< 0.001	15	n.s.
<i>Centaurea nigra</i>	23	16	n.s.	2.0	3.5	< 0.01	11	< 0.01 (+)
<i>Carex flacca</i>	15	11	n.s.	2.2	4.1	< 0.01	8	< 0.05 (+)
<i>Cerastium fontanum</i>	32	26	n.s.	1.6	2.4	< 0.01	8	< 0.05 (+)
<i>Veronica chamaedrys</i>	14	16	n.s.	1.6	3.0	< 0.01	4	n.s.
<i>Brachypodium sylvaticum</i>	17	17	n.s.	2.6	4.1	< 0.05	4	n.s.
<i>Bromopsis erecta</i>	8	7	n.s.	2.8	5.6	< 0.05	5	n.s.
<i>Helianthemum nummularium</i>	7	3	n.s.	1.9	4.3	< 0.05	3	n.s.
<i>Holcus lanatus</i>	47	45	n.s.	2.8	3.7	< 0.05	24	n.s.
<i>Ranunculus repens</i>	34	37	n.s.	2.0	2.8	< 0.05	14	n.s.
<i>Carex hirta</i>	12	9	n.s.	1.8	3.7	< 0.05	0	
<i>Betula pubescens</i>	10	12	n.s.	2.0	3.7	n.s.	7	< 0.05 (+)
<i>Centaurea scabiosa</i>	11	7	n.s.	1.3	3.4	n.s.	5	< 0.05 (+)
<i>Crataegus monogyna</i>	30	43	n.s.	2.1	2.7	n.s.	19	< 0.05 (+)
<i>Sambucus nigra</i>	11	11	n.s.	1.4	1.9	n.s.	5	< 0.05 (+)

Table 5.5. The 63 common vascular plants displaying significant declines in range and/or abundance between 1949-2004. n_1 , number of plots in which a species was found in 1949-51; n_2 , number of plots in 2003-04; $p(\chi^2)$, significance of change in number of occupied plots (chi-square test); t , significance and direction of change in abundance (two-tailed t -tests); $p(t)$, significance and direction of change on continuously occupied sites (paired two-tailed t -tests).

Species name	n_1	n_2	$p(\chi^2)$	t	$p(t)$	Species name	n_1	n_2	$p(\chi^2)$	t	$p(t)$
Decreased in occupancy and/or abundance:						<i>Daucus carota</i>	16	7	< 0.05	n.s.	n.s.
<i>Chaerophyllum temulum</i>	19	4	< 0.001	-		<i>Epilobium montanum</i>	8	1	< 0.05	-	
<i>Fragaria vesca</i>	19	4	< 0.001	n.s.		<i>Equisetum palustre</i>	10	3	< 0.05	n.s.	
<i>Leontodon hispidus</i>	19	4	< 0.001	n.s.	n.s.	<i>Erodium cicutarium</i>	7	1	< 0.05	-	
<i>Luzula campestris</i>	10	0	< 0.001	-		<i>Euphorbia exigua</i>	4	0	< 0.05	-	
<i>Luzula multiflora</i>	8	0	< 0.001	-		<i>Galium palustre</i>	17	6	< 0.05	n.s.	
<i>Plantago lanceolata</i>	37	16	< 0.001	n.s.	n.s.	<i>Galium saxatile</i>	12	3	< 0.05	n.s.	
<i>Poa pratensis</i> s.l.	26	5	< 0.001	n.s.	n.s.	<i>Galium uliginosum</i>	6	0	< 0.05	-	
<i>Potentilla erecta</i>	11	0	< 0.001	-		<i>Galium verum</i>	17	6	< 0.05	n.s.	n.s.
<i>Potentilla sterilis</i>	14	1	< 0.001	-		<i>Gentianella amarella</i>	7	1	< 0.05	-	
<i>Anthoxanthum odoratum</i>	15	3	< 0.01	n.s.		<i>Lamium amplexicaule</i>	5	0	< 0.05	-	
<i>Anthyllis vulneraria</i>	7	0	< 0.01	-		<i>Lotus corniculatus</i>	23	12	< 0.05	n.s.	n.s.
<i>Caltha palustris</i>	7	0	< 0.01	-		<i>Orchis mascula</i>	4	0	< 0.05	-	
<i>Carex disticha</i>	7	0	< 0.01	-		<i>Potamogeton natans</i>	4	0	< 0.05	n.s.	
<i>Erophila verna</i>	7	0	< 0.01	-		<i>Potentilla anserina</i>	19	9	< 0.05	n.s.	n.s.
<i>Euphrasia nemorosa</i>	9	1	< 0.01	-		<i>Rorippa microphylla</i>	5	0	< 0.05	-	
<i>Pilosella officinarum</i>	19	5	< 0.01	n.s.	n.s.	<i>Rumex acetosa</i>	13	4	< 0.05	n.s.	
<i>Ranunculus acris</i>	16	4	< 0.01	n.s.		<i>Rumex acetosella</i>	16	6	< 0.05	n.s.	n.s.
<i>Ranunculus ficaria</i>	19	5	< 0.01	n.s.	n.s.	<i>Senecio aquaticus</i>	4	0	< 0.05	-	
<i>Sagina procumbens</i>	11	1	< 0.01	-		<i>Sinapis alba</i>	4	0	< 0.05	-	
<i>Senecio vulgaris</i>	14	3	< 0.01	n.s.		<i>Taraxacum officinale</i>	34	21	< 0.05	n.s.	n.s.
<i>Succisa pratensis</i>	13	3	< 0.01	n.s.		<i>Thymus pulegioides</i>	13	5	< 0.05	n.s.	n.s.
<i>Trifolium dubium</i>	16	4	< 0.01	n.s.		<i>Trisetum flavescens</i>	14	4	< 0.05	n.s.	
<i>Cynosurus cristatus</i>	13	4	< 0.05	< 0.05 (-)		<i>Veronica officinalis</i>	12	3	< 0.05	n.s.	
<i>Achillea millefolium</i>	23	12	< 0.05	n.s.	n.s.	<i>Viola reichenbachiana</i>	13	4	< 0.05	n.s.	
<i>Aira praecox</i>	7	1	< 0.05	-		Decreased in abundance only:					
<i>Bellis perennis</i>	19	7	< 0.05	n.s.		<i>Stellaria graminea</i>	10	7	n.s.	< 0.001 (-)	n.s.
<i>Calluna vulgaris</i>	8	1	< 0.05	-		<i>Agrostis capillaris</i>	24	23	n.s.	< 0.05 (-)	< 0.05 (-)
<i>Carex ovalis</i>	5	0	< 0.05	-		<i>Anemone nemorosa</i>	14	6	n.s.	< 0.05 (-)	< 0.05 (-)
<i>Catapodium rigidum</i>	5	0	< 0.05	n.s.		<i>Juncus conglomeratus</i>	10	5	n.s.	< 0.05 (-)	n.s.
<i>Centaureum erythraea</i>	8	1	< 0.05	-		<i>Primula vulgaris</i>	14	9	n.s.	< 0.05 (-)	
<i>Cirsium acaule</i>	16	6	< 0.05	n.s.	n.s.	<i>Quercus robur</i>	24	25	n.s.	n.s.	< 0.05 (-)
<i>Danthonia decumbens</i>	4	0	< 0.05	n.s.							

Discussion

Habitat change

The results from Bedfordshire clearly indicate a marked shift in the species composition of a range of lowland semi-natural habitats since the 1940s. Nationally arable weeds have suffered the most dramatic decline of any group in the British flora during the second half of the twentieth century (Robinson & Sutherland 2002). In this study the composition of most arable sites had completely altered due to cropping regimes and conversion to pasture (Table 5.3). In comparison, dramatic changes on wasteland plots were due to autogenic succession to grassland or scrub following abandonment (e.g. disused mineral workings, allotments, etc.). The post-war transformation of grassland to high-productivity swards has been well documented (Fuller 1987; Green 1990). Acid grasslands, in particular, have suffered a high extinction rate in lowland England (e.g. Preston 2000; Chapter 4) and declines in the abundance of characteristic species reported in this study (e.g. *Galium saxatile*, *Rumex acetosella*) closely mirror national trends (e.g. Preston et al. 2002a,b; Braithwaite et al. 2006).

The stability of woodland plots in this study was striking and supports the general view that lowland woods have suffered relatively few changes during the twentieth century (Rackham 1980; Preston 2000; Preston et al. 2002b; Kirby et al. 2005; Chapter 4). However, the decline of species associated with open woodland conditions (in this study *Chaerophyllum temulum*, *Fragaria vesca*, *Potentilla sterilis*, *Primula vulgaris*, *Viola reichenbachiana*) suggests that some woods may be reverting to a more “natural” state due to the decline of traditional management practices (Kirby et al. 2005). The decline of *Primula vulgaris* in eastern England has also been attributed to the combined effects of increased deer grazing, particularly by introduced Muntjac deer, and a changing climate (Rackham 1999). The relatively minor changes in some other habitats in Bedfordshire was surprising (e.g. rivers, lakes, swamps) and may reflect improvements in water quality in aquatic and wetland habitats during the second half of the twentieth century (Preston et al. 2003) and the fact that some nutrient-poor habitats (e.g. bogs, calcareous grassland, marshes, heaths) received greater protection from the 1940s onwards although as discussed below this did not always ensure that the condition of the site was maintained. The most dramatic losses in these habitats took place during the eighteenth and nineteenth centuries when large areas of unproductive land were first drained or ploughed-up for agriculture (Chapter 4).

Table 5.6. Results of the multiple binary logistic regression between species trends, colonisation and extinction rates and plant traits. Only significant traits were included in the model (see text). The regression coefficient (\pm SE) for the full model are presented with the level of significance (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s., not significant). The sign of each coefficient indicates whether the response variable was positively or negatively correlated with the respective explanatory variable. R^2 values are presented for individual traits and for the all 7 traits included in the model (model R^2). Mean values for all trait categories are given in Appendix 6.

	Species trend			Colonisation			Extinction					
	Regression coefficient	p	R^2	Regression coefficient	p	R^2	Regression coefficient	p	R^2			
Local range	0.070	(0.006)	***	54.4	0.050	(0.007)	***	41.0	-0.050	(0.007)	***	9.2
English range	0.001	(< 0.001)	***	40.7	0.002	(< 0.001)	***	42.3	0.0003	(< 0.001)	n.s.	2.0
Specialism Index	-0.050	(0.019)	***	44.1	-0.010	(0.022)	***	40.2	-0.043	(0.024)	n.s.	1.8
L	-0.108	(0.033)	***	2.2	-0.080	(0.040)	*	1.7	0.186	(0.047)	***	6.0
F	-0.061	(0.023)	**	0.2	-0.583	(0.028)	**	0.2	0.004	(0.030)	n.s.	0.01
N	0.164	(0.024)	***	8.2	0.270	(0.029)	***	13.1	-0.061	(0.032)	n.s.	2.2
Plant height	< 0.001	(< 0.001)	***	1.6	< 0.001	(< 0.001)	***	1.5	< -0.001	(< 0.001)	***	6.4
Model R^2 (%)	69.7			65.1			21.7					

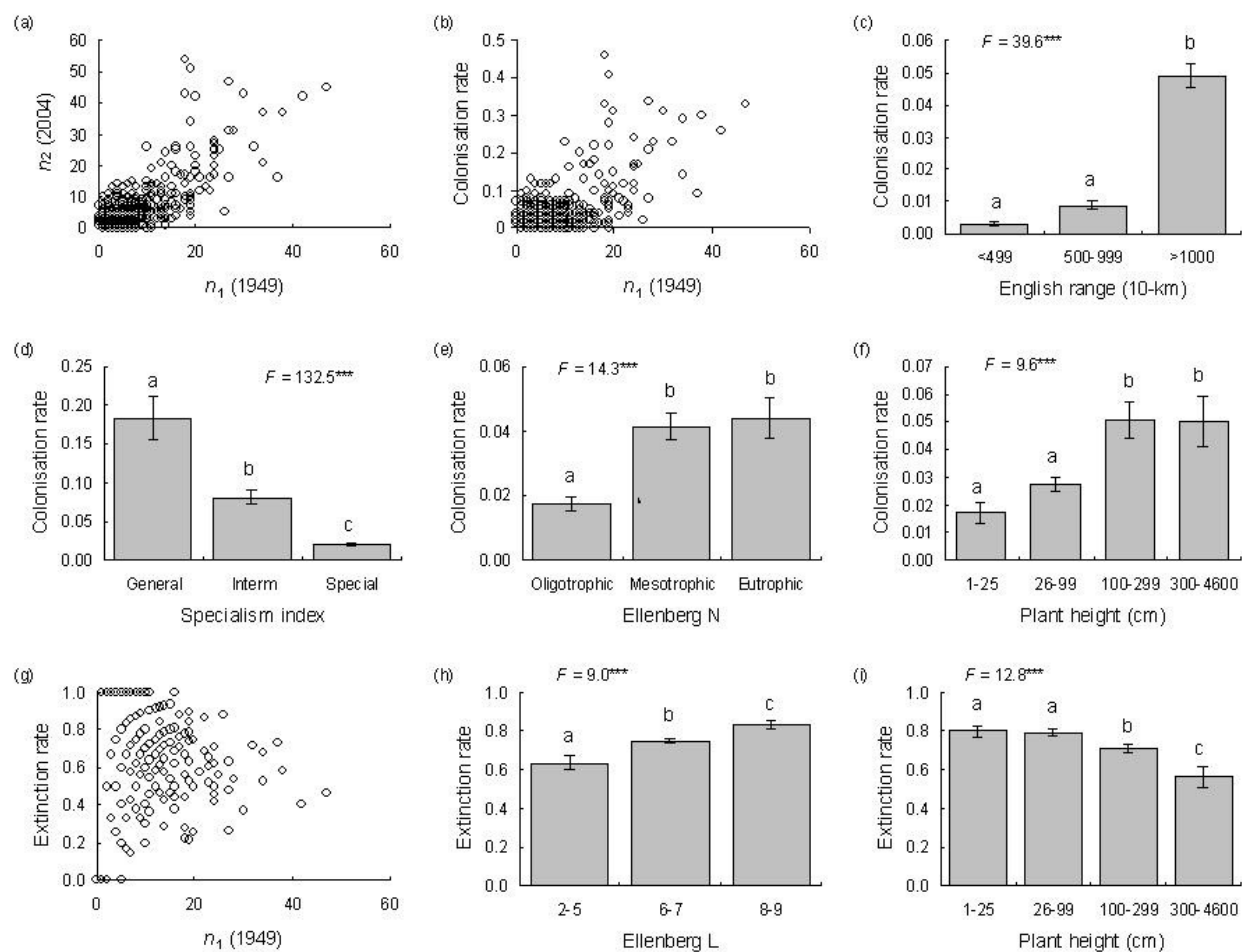


Figure 5.4. Relationship between (a) the number of plots occupied in 1949-51 and 2003-04; (b) the number of plots occupied in 1949-51 and colonisation rate; (c) colonisation rate and English range, (d) specialism index, (e) Ellenberg N and (f) plant height; (g) extinction rate and the number of plots occupied in 1949, (h) Ellenberg L and (i) plant height. Differences between means for trait categories in (c-f) and (h-i) were analysed using ANOVA with Tukey's multiple comparisons. *** $P < 0.001$. Means with different letters are significantly different from one another.

Plant trait responses to habitat modification

In Bedfordshire, species trends were clearly related to range size with widespread species having significantly higher colonisation rates but lower extinction rates than rarer species. This negative relationship between occupancy and extinction rate has been noted in a number of other studies (Fischer & Stöcklin 1997; Bennie et al. 2006) and indicates that, in fragmented habitats, the risk of extinction is greater for species with smaller populations and greater habitat specificity. Likewise, habitat specialists were less likely to colonise new plots following extinction, whilst widespread common species have a greater probability of colonising new plots from elsewhere in the landscape (Blomqvist et al. 2003; Bennie et al. 2006; Figs 5.3c & d).

Habitat specialists of unproductive soils showed the most consistent change with much lower colonisation rates than species of nutrient-rich habitats (Fig. 5.4e). In addition, specialists of more open habitats, such as grasslands, heaths and mires, had significantly higher extinction rates (Fig. 5.4h). Small plants also had significantly lower colonisation rates but higher extinction rates (Figs 5.4f & 4i). This correlation between low canopy height and a tendency to decline has been noted in other studies and suggests that small species are being out-competed by taller species adapted to more fertile conditions throughout intensively managed landscapes (Thompson 1994; McCollin et al. 2000; Preston 2000; Preston et al. 2002b; Smart et al. 2005; Tamis et al. 2005; Bennie et al. 2006; Chapter 4). These results add to the growing evidence that eutrophication has been one of the main drivers of floristic change during the second half of the twentieth century. In Britain, nutrient loading of terrestrial and aquatic ecosystems may well have reached a maximum during this period due to the accelerated inputs of N and other major nutrients (NEG-TAP 2001). In Bedfordshire, the primary sources were applications of inorganic fertilisers to arable fields and improved grasslands as well as polluted run-off from urban areas (Fig. 5.3d). Shifts in plants traits were also consistent with increases in substrate fertility observed in a number of lowland habitats caused by atmospheric N deposition (Stevens et al. 2005), fertiliser drift and runoff from adjacent agricultural habitats (Preston et al. 2003; Willi et al. 2005) or both (Bennie et al. 2006).

Smaller plants are clearly favoured by shorter vegetation where competition for light is less severe. Hence their decline is consistent with reduced grazing and management of grassland fragments in increasingly arable and urban landscapes. The results of the GB Countryside Survey, for example, showed that many linear grasslands (e.g. streamsides, road verges, etc.)

have become overgrown in recent decades due to reduced levels of cropping, cutting and grazing (Smart et al. 2003, 2005). Similarly, many broad-leaved woodlands and hedges have reverted to a more “natural” state following the cessation of traditional practices such as coppicing (Kirby et al. 2005). In Bedfordshire, the striking increase of trees and shrubs (e.g. *Fraxinus excelsior*, *Rubus fruticosus*), unpalatable perennials (e.g. *Cirsium arvense*, *Urtica dioica*) and competitive grasses (e.g. *Bromopsis erectus*, *Dactylis glomerata*, *Holcus lanatus*) indicate similar trends with a general shift towards taller, more competitive communities.

Soil acidification occurred in many habitats in Europe during the second half of the twentieth century resulting in shifts in the composition of weakly buffered ecosystems such as heathlands and acid grasslands (NEG-TAP 2001). In Bedfordshire, less disturbed and weakly buffered habitats (e.g. woodlands, heaths and mires) were between 0.4-0.7 of a pH unit more acid than in the 1940s, well buffered habitats showed little change (e.g. rivers, calcareous grasslands) and acid and neutral grasslands became more alkaline, presumably because of liming. Despite these changes, there were few clear effects of acidification on species trends, presumably because eutrophication and succession were more significant in modifying species composition.

Although dispersal is clearly an important process that can slow the decline of specialists in isolated habitat fragments (Fischer & Stöcklin 1997) I found only a poor relationship between regenerative attributes (e.g. clonality, seed bank, fertilisation, dispersal ability) and species trends. Thompson (1994) also showed that whether a species has increased or decreased in northwest Europe over the last 40-50 years appeared to be unrelated to dispersal in time or space. This is presumably because of the magnitude of recent land use changes. For most species the scale of dispersal is unlikely to be sufficient to counteract rapid demographic and environmental changes. Dispersal is therefore likely to have little influence on extinction probabilities within intensively managed lowland landscapes although more research is required to test its effectiveness in other regions.

Effectiveness of conservation

The results of this study highlights the extent to which designation of conservation sites in lowland Britain has failed as an instrument for maintaining habitat composition and extent in the post-war period. With the exception of a few well preserved habitats (i.e. calcareous grasslands, marshes and basic woods) designation had little effect on the extent of change

(Fig. 5.3b), especially where reserves were located in intensively farmed or urban landscapes. These sites have suffered greatly from truly extrinsic factors such as eutrophication and falling water levels, as well as more local changes in management such as the decline or cessation of traditional grazing and coppicing (Preston 2000; Nisbett & Shere 2006). The changes observed at Folly Wood (Figs 5.3e & f) provide a good example: since 1949 drainage of the surrounding agricultural land has dried-out this former mire allowing the establishment of birch woodland.

There are two probable reasons for this failure. First, one of the original aims in designating conservation sites in Britain (Sites of Special Scientific Interest, National Nature Reserves) was to select a series of 'natural laboratories' where natural changes in vegetation could be observed and analysed. On many sites this has often been at odds with a need to maintain a suite of rare (early succession) species present at the time of designation. Second, and perhaps most significantly, the legislation made no provision for funding positive management and hence designation *per se* was no guarantee that a site would be maintained in its original condition or that the species the site was originally designated for would survive. Consequently, succession, exacerbated by extrinsic factors, was a predictable fate for many sites given that the statutory instruments could neither alleviate these external factors, nor fund positive management within the site.

Conclusions

In this study more species displayed significant negative (66%) than positive trends (34%) indicating a decline in the diversity of semi-natural habitats in Bedfordshire between 1949 and 2004. These findings are similar to other studies (e.g. 63% and 37%, Smart et al. 2005; 62% and 38%, Bennie et al. 2006) and quantify the culmination of the impact of industrial agriculture and human settlement on the habitats of lowland Britain since 1945. The result has been a more homogenous lowland flora dominated by a small pool of tall, nutrient-demanding species at the expense of small, specialists of infertile soils (Smart et al. 2006). The defining feature of this period is possibly the interaction between exposure of less productive systems to unprecedented nutrient inputs in combination with the polarisation of land-use away from agriculturally marginal habitats. It is this interaction that could be uniquely important in driving species' extinction and homogenisation in intensively managed and densely populated temperate lowland landscapes. The failure of either greater regenerative capacity or

conservation designations to buffer species from extinction highlights the urgent need to control extrinsic factors affecting habitats such as eutrophication and reinstate appropriate management in order to protect against further losses in the future.



Plate 6

Trifolium ochroleucon, Brampton Meadow, Huntingdonshire.

Photo: K.J. Walker

Chapter 6

Change at the local scale: assessing the status of *Trifolium ochroleucon* Huds. (Fabaceae) in Huntingdonshire

Summary

Sulphur Clover, *Trifolium ochroleucon*, is a nationally scarce plant, which is locally abundant on calcareous clay soils in southeast England. In Huntingdonshire 35 populations have been recorded in a variety of grassland habitats. Since the 1960s over half (57%) have been lost to agricultural improvement of meadows and reduced management of linear strips of grassland (e.g. road verges, green lanes, woodland rides). Surviving colonies are confined to meadows and road verges where they are susceptible to eutrophication, physical disturbance and changes in management regime. The results highlight the importance of linear habitats such as roadside verges, as well as meadows, for ancient grassland species which have been lost from enclosed habitats in lowland England.

Introduction

Sulphur clover *Trifolium ochroleucon* Huds. (Fabaceae) is a nationally scarce perennial herb of ancient meadows and pastures, roadside verges, trackways, churchyards and wood-borders on chalky boulder-clays or, more rarely chalk (Bourne 1964; Coombe 1994; Ellis 2004; Adams 2007). It can also colonise rough grassland on railway embankments, disused airfields and newly created road verges where populations have presumably arisen from introduced seed. In Britain it has a Continental-type distribution being restricted as a native plant to southeast England. Like *Melampyrum cristatum*, with which it sometimes grows, it is relatively common in parts of Suffolk (v.cs 26 & 25) and North Essex (v.c. 19) (Jermyn 1974; Simpson 1982; Adams 2007). It is also locally abundant on chalky boulder clays in southeast Norfolk (v.c. 27; Ellis 2004), Hertfordshire (v.c. 20), Cambridgeshire (v.c. 29), Bedfordshire (v.c. 30) and Huntingdonshire (v.c. 31). It is very rare in Rutland (v.c. 55),

Northamptonshire (v.c. 32) and South Lincolnshire (v.c. 57). Elsewhere in Britain it occurs as a casual from imported seed.

Sulphur clover appears unable to withstand competition from coarse grasses in tall swards and therefore requires physical disturbance, cutting or grazing to persist in closed communities. It was probably more widespread in the early Post-glacial on chalky tills left *in situ* when the East Anglian ice sheets retreated (Adams 2007). As weathering leached the till surface its distribution would have contracted to areas where soils had high concentrations of chalk or where grazing reduced competition from other species. Over the last 1000 years it was probably most widespread in the grazed medieval landscapes of East Anglia but subsequently declined due to ploughing or improvement of meadows and pastures which started with enclosure in the eighteenth century, and in the twentieth century the realignment and widening of roads and ‘manicuring’ of roadside verges (Coombe 1994). As a consequence Preston et al. (2002a) give *Trifolium ochroleucon* a relatively high change index of -0.84 and Cheffings & Farrell (2005) list it as ‘Near Threatened’ in the current Red Data List.

This chapter describes the distribution and habitats of *Trifolium ochroleucon* in Huntingdonshire (v.c.31, now part of administrative Cambridgeshire) at the extreme northern edge of its European range, and provides an account of its decline since the start of systematic botanical recording began in the county in the 1960s.

Materials and methods

Study species

Trifolium ochroleucon is a pubescent, shortly rhizomatous or caespitose long-lived perennial (hemicryptophyte) clover with erect to ascending pubescent stems which can reach 53 cm in tall, unmanaged swards (Tabor 1996). Plants in spring mown grassland are much shorter (20-30cm) but produce more flowers (Tabor 1996). The shortly pubescent leaflets are similar to those of *T. pratense*, with which it often grows, but are more densely hairy above, elongate (oblong) and with green-veined stipules with a linear-lanceolate thread-like apex to 12 mm (Poland & Clement 2009). On most plants the majority of leaves are produced near to ground level and petiole elongation is much more restricted (up to 10 cm) than in *T. pratense* (C.D. Preston, pers comm.). These characters combined with a lack of clonal spread presumably account for its inability to compete within tall, closed swards. The inflorescences are 20-40

mm long, initially globose but becoming ellipsoid, and made up of numerous pale yellowish-white flowers that become brownish-orange when in fruit (Plate 6). The flowers are sessile and mature from the base of the inflorescence upwards and are subtended by a pair of nearly sessile leaves. The flowering period is very short, usually lasting only a few days between mid-June to early-July although plants can flower as early as May and as late as August depending on weather conditions. Little is known about its reproductive biology. Flowers are hermaphrodite and facultatively allogamous (source Bioflor database) and cross-pollinated by a range of insects. Self-compatibility appears untested. The fruit is an obovoid legume 20-25 mm; the seed is 1.0-1.8 mm, obovoid, weighing 1.87 g and dispersed within a persistent hairy calyx with long teeth. A single terminal velocity measurement of 2.42 m/s has been reported (LEDA traitsbase <http://www.leda-traitbase.org/LEDAportal/>). The dispersule is probably dispersed very locally and more distant movement by machinery or livestock is probably rare. Scarified seeds have 100% germination under a range of treatments from 11-21°C declining to 80% at 23/9°C (12/12 hours) and remain 98-100% viable in dessicated storage conditions for up to 15 years (Millenium Seed Bank Database <http://data.kew.org/>). Regeneration is presumably by seed as colonisation of 'new' habitats, such as railway cuttings, is common. In Essex successful establishment from the spreading of ripe seed heads and transplanted turves has also been reported (Adams 2007). There is no information on seed bank longevity but the ability of *T. ochroleucon* to regenerate following disturbance suggests that some seed must persist in the soil for long periods.

In Britain *T. ochroleucon* is confined almost exclusively to chalky boulder clay deposited during the penultimate (Wolstonian/Gipping) glaciation around 200,000 years ago and more rarely fine loams or clay-enriched soils derived from the Lower or Middle chalk. The soils are often well-structured and slowly permeable, although they become waterlogged in the winter and completely dryout in the summer. In Essex most populations are concentrated on the calcareous Hanslope Association soils, the Roding Apron and the Broxted-Debden ridge (Adams 2007). In Norfolk most populations occur on the Beccles 1 formation (Ellis 2004).

Most populations occur in open, species-rich mesotrophic grasslands that are mown or lightly grazed in the spring or late summer/autumn. Habitats include ancient meadows and pastures, roadside verges, trackways, churchyards, railway embankments and wood-borders. British populations are typically small although meadow and pasture populations can be extensive.

T. ochroleucon is a European Temperature species confined to the warmest and driest parts of southeast England where January and July temperatures are 3.4 and 16.3°C respectively and precipitation is below 600 mm (Hill et al. 2004). All British populations are lowland but it extends to 2000 m altitude in Europe. British populations belong to var. *ochroleucum* and occur at the absolute northern limit of the European range (Preston 2007) which extends throughout western and central Europe to Iran and the Caucasus in the east, and to northwest Africa in the south. European populations are more variable in indumentum, petal-colour and length of the calyx-teeth, especially the lowest. Plants in southern Europe with a pink corolla are var. *roseum* (Sell & Murrell 2009). *T. ochroleucon* is a diploid species ($2n = 16$) in the polyploid series in section *Stenostomum*.

Collation of records and field survey

Historical records for *T. ochroleucon* in Huntingdonshire (v.c. 31) were extracted from a variety of published and unpublished sources, including the card indexes of the BSBI vice-county recorder, plant records of the Huntingdonshire Fauna and Flora Society and Natural England Lowland Grassland Inventory. Additional records were compiled from discussions with botanists, unpublished surveys, floras and checklists (e.g. Gilbert 1965; Wells 2003). These provided localised records (to six figure grid references) for 35 site-populations (Table 6.1). With the exception of five sites with restricted access, all sites were visited in 2007 (late May to early July). At each location all suitable habitats were searched, the extent of the population recorded using a GPS and the number of patches counted within 100 × 100 m grid squares. At one site (Brampton Racecourse SSSI) the population was too large to count all patches; I therefore counted the number of patches in 20 random 10 × 10 m squares and then estimated the total population for the whole area.

Habitats and management

A single 1 × 1 m quadrat was recorded at each extant site to characterise the associated species and National Vegetation Classification (NVC) communities assigned using the computer programme Tablefit (Hill 1996). In each quadrat the percentage cover of all species was recorded. Management was recorded for extant sites and the apparent reasons for loss on sites where *T. ochroleucon* was not refound.

Results

Number and size of populations

Fifty-nine records for *Trifolium ochroleucon* were traced for Huntingdonshire covering 40 1×1 km and 10 10×10 km squares (Fig. 6.1). Eight records could only be assigned to monads including seven for roadside populations around Easton in 1967 (TL1270, 1370, 1472, 1574, 1674, 1675, 1774) and a single unlocalised G.C. Druce record from Wennington Wood (TL2478). A further nine records were only attributable to hectads and included old records for Alconbury (TL17), Houghton (TL27), Colne, Somersham (both TL37), Upton (TL17) and Woodwalton Fen (TL28) for which there are no subsequent records. In total 42 records were attributable to 100×100 m squares representing 35 discrete site-populations (Table 6.1).

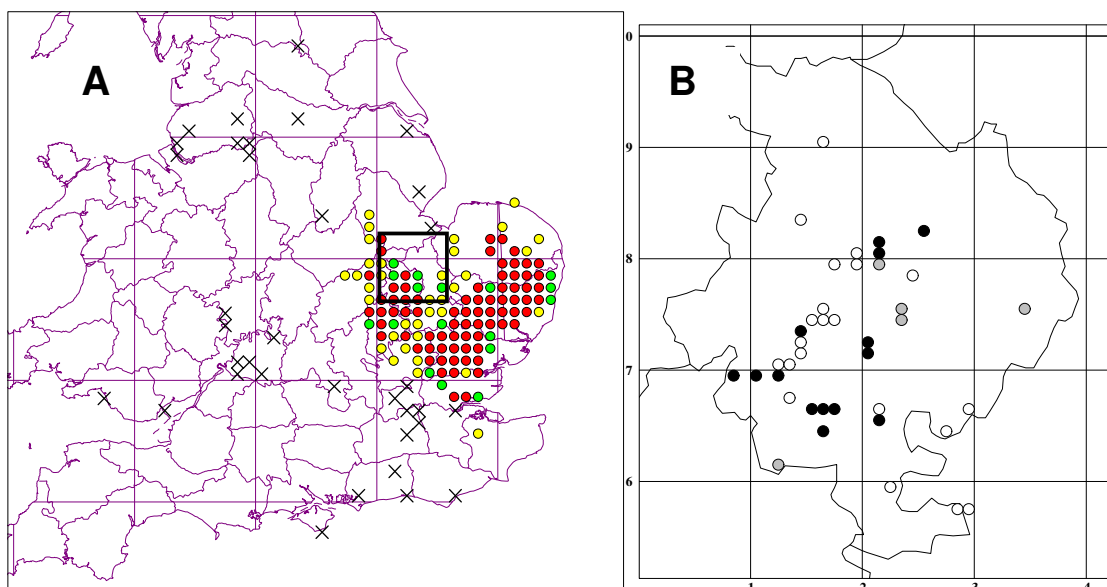


Figure 6.1. (A) The hectad distribution of *Trifolium ochroleucon* in southeast Britain showing post-1986 (red circles), 1970-1986 (green circles) and pre-1970 records (yellow circles). Introductions are represented by an x. (B) The 1×1 km distribution of *T. ochroleucon* in Huntingdonshire (v.c. 31). Solid circles, recorded since 2000; open circles, last recorded before 2000; grey circles are monads with populations not visited in the current survey due to restricted access. All squares in (b) are within grid square TL.

Trifolium ochroleucon was re-located on 13 of the 30 site-populations visited in 2007 (5 sites could not be re-visited due to restricted access). Nine of these populations, including six on protected roadside verges, together held 65 plants. A further three sites together held 236 plants (2 road verges and a small meadow) including a meadow bank on one site that had escaped improvement. By far the largest population, Brampton Racecourse SSSI, held an estimated 10,000 flowering patches scattered over 20 ha of ancient ridge and furrow grassland

within the precincts of Huntingdon Racecourse. Here there was an average of 13 plants (± 4) per 10×10 m. These findings are similar to population sizes in southeast Norfolk where 88% of populations surveyed in 2002 held less than 81 plants ($n = 46$) and 56% held less than 27 plants.

Table 6.1. Details of the 35 site-populations of *Trifolium ochroleucon* recorded in Huntingdonshire.

Site-population*	Grid ref.	Habitat	Last	2007	Management
<i>(a) Extant</i>					
Tilbrook, Bustard Hill RSV	TL085698	Roadside verge	-	31	Cut
Kimbolton Airfield	TL108696	Rough grass	-	2	No mgt
Stonely, Stocking Lane RSV	TL123695	Roadside verge	-	10	Cut
Woolley Hill RSV	TL149732	Roadside verge	-	13	Cut
East Perry, around lagoons	TL156667	Roadside verge	-	?	No mgt
Horse Close, Midloe Grange CWS	TL162648	Meadow	-	85	Grazed
Grafham Water, E of car park	TL163664	Roadside verge	-	7	Cut
Grafham Water RSV, near dam	TL171668	Roadside verge	-	120	Cut
Brampton Racecourse SSSI	TL203721	Meadow	-	10,000	Cut for hay
Woodwalton Hill RSV	TL210800	Roadside verge	-	6	Cut
Woodwalton Marsh CWS	TL212812	Meadow	-	10	Cut & raked
Great Paxton RSV	TL217653	Roadside verge	-	5	Cut
Upwood Meadows NNR	TL251827	Meadow	-	12	Grazed
<i>(b) Not present in 2007, probably extinct</i>					
Easton	TL125698	Rail embank	1968	0	Ploughed
Grafham Water, Littless Wood	TL133679	Rough grass	1974	0	Overgrown
Easton, opposite Sewell's Barn	TL135705	Meadow	1969	0	Ploughed
Grafham Water, W of carpark	TL136675	Rough grass	1972	0	Improved
Easton, NE of	TL143718	Meadow	1968	0	Improved
Sawtry, Lodge Farm	TL147836	Meadow	1971	0	Ploughed
Norman's Cross	TL161904	Roadside verge	1974	0	Destroyed
Coppingford Lane	TL170792	Green lane	1985	0	Unknown
Hotel Ride, Monks Wood NNR	TL196806	Woodland ride	1985	0	Overgrown
Saul's Lane, Monks Wood NNR	TL198794	Green lane	1963	0	Destroyed
Great Paxton, Bankside	TL213653	Meadow	1979	0	Unknown
Offord-Buckden Mills	TL216669	Riverbank	1979	0	Overgrown
Hardwicke, Weald Farm	TL226596	Green lane	1972	0	Overgrown
Papworth St. Agnes, N of	TL272649	Meadow	1974	0	Improved
Hardwicke Road, Hardwicke	TL283572	Meadow	1969	0	Improved
Great Gransden, Caxton	TL294571	Roadside verge	1985	0	Overgrown
Hilton, SE of	TL297661	Meadow	1980	0	Ploughed
<i>(c) Not visited</i>					
Abbotts Ripton, railway cutting	TL218797	Rail embank	1972	?	No access
Staughton Moor, old airfield	TL125616	Rough grass	1973	?	No access
Great Stukeley Lodge	TL234755	Rail embank	1981	?	No access
Sapley Railway cutting, E face	TL236743	Rail embank	1978	?	No access
Bluntisham, disused railway	TL345752	Rail embank	1969	?	No access

* Conservation designations are indicated after the site name: RSV – protected roadside verge; CWS – county wildlife site; NNR – National Nature Reserve; SSSI – Site of Special Scientific Interest.

Habitats

In Huntingdonshire, as elsewhere in southeast England, the majority of populations are confined to chalky boulder clay (till) deposited over Oxford Clays during the penultimate (Wolstonian/Gipping) glaciation around 200,000 years ago (Wells 2003). This glacial drift has a high content of chalk, flints, quartzite pebbles, limestone and ironstone fragments which have been weathered differentially to produce soils with a range of pH from strongly calcareous to mildly acidic. It is often well-structured and slowly permeable, although it becomes waterlogged in the winter but completely dryout in the summer. On these soils *Trifolium ochroleucon* occurs in species-rich meadow and roadside grassland (Table 6.2), with smaller numbers in linear strips of grassland (e.g. railway banks, green lanes) and rough, unmanaged grassland. In Huntingdonshire single populations have also been recorded from riverbanks and species-rich woodland rides, but no plants were found in either of these habitats in 2007.

Table 6.2. The habitats of *Trifolium ochroleucon* in Huntingdonshire.

Habitat	Total	Extant	Lost	% lost	Not visited
Meadow (grazed and/or cut)	11	4	7	64	0
Roadside verge (cut)	10	8	2	20	0
Railway embankment (inc. disused)	5	0	1	100	4
Rough grassland (unmanaged)	4	1	2	67	1
Green lane	3	0	3	100	0
Riverbank	1	0	1	100	0
Woodland ride	1	0	1	100	0
Total	35	13	17	57	5

Table 6.3. National Vegetation Classification communities in which *Trifolium ochroleucon* has been recorded on road verges and in meadows in Huntingdonshire.

NVC grassland type	Road verge	Meadow
MG1e <i>Arrhenatherum elatius</i> mesotrophic grassland	4	0
MG5b <i>Centaurea nigra</i> – <i>Cynosurus cristatus</i> grassland	0	1
MG6a <i>Cynosurus cristatus</i> – <i>Lolium perenne</i> grassland	0	1
CG4a/c <i>Brachypodium pinnatum</i> calcareous grassland	3	0
CG6b <i>Helictotrichon pubescens</i> calcareous grassland	0	2
U1f <i>Festuca ovina</i> - <i>Agrostis capillaris</i> - <i>Rumex acetosella</i> acid grassland	0	2
W24b <i>Rubus fruticosus</i> - <i>Holcus lanatus</i> underscrub	0	1

All the Huntingdonshire sites support relatively short, species-rich grassland conforming to a range of NVC grassland types (Rodwell 1992; Table 6.3): the vegetation on road verges is relatively uniform either supporting short, species-rich *Centaurea nigra* sub-community of

Arrhenatherum elatius mesotrophic grassland (MG1e) or, where the soils are more chalky *Helictotrichon* [*Avenula*] *pratensis*-*Thymus polytrichus* [*praecox*] and *Holcus lanatus* sub-communities of *Brachypodium pinnatum* calcareous grassland (CG4a/c). In contrast, meadow habitats are more diverse. These range from mesotrophic *Cynosurus cristatus* grassland (MG5-6), *Helictotrichon* [*Avenula*] *pubescens* calcareous grassland (CG6) and the *Hypochaeris radicata* sub-community of the *Festuca ovina*-*Agrostis capillaris*-*Rumex acetosella* acid grassland (U1f). The variation within meadow communities presumably reflects the differential leaching, disturbance and moisture regimes that occur over very small distances on the ridges, furrows and banks.

Table 6.4. Species associated with *Trifolium ochroleucon* (in >40% of 4m² quadrats) in roadside verges (n = 6) and meadows (n = 7) in Huntingdonshire. ‘% frequency’ is the overall frequency out of 13 quadrats recorded. A further 67 species were recorded in < 40% of quadrats (not shown). For comparison, the constancies of species in 52 quadrats containing *T. ochroleucon* in Norfolk (Ellis 2004) are also shown.

	Road verge	Meadow	% frequency	Norfolk
(a) Constant species in both roadside verges and meadows				
<i>Achillea millefolium</i>	V	V	85	IV
<i>Centaurea nigra</i>	V	IV	85	V
<i>Dactylis glomerata</i>	V	IV	85	V
<i>Festuca rubra</i>	V	IV	85	IV
(b) Constant species on roadside verges				
<i>Plantago lanceolata</i>	V	III	69	V
<i>Carex flacca</i>	V	III	62	II
<i>Potentilla reptans</i>	V	I	54	IV
<i>Arrhenatherum elatius</i>	IV	III	54	IV
<i>Lathyrus pratensis</i>	IV	III	54	IV
<i>Brachypodium pinnatum</i>	IV	II	46	II
<i>Heracleum sphondylium</i>	IV	II	46	III
<i>Medicago lupulina</i>	IV	II	46	III
(c) Constant species in meadows				
<i>Briza media</i>	I	V	54	I
<i>Cynosurus cristatus</i>	I	V	54	I
<i>Trisetum flavescens</i>	III	IV	62	V
<i>Galium verum</i>	II	IV	54	I
<i>Lolium perenne</i>	II	IV	54	V
<i>Holcus lanatus</i>	I	IV	46	IV
<i>Primula veris</i>	I	IV	46	I
<i>Sanguisorba minor</i>	I	IV	46	-
(d) Species relatively common in both habitats				
<i>Lotus corniculatus</i>	III	III	54	III
<i>Festuca pratensis</i>	III	III	46	II
<i>Trifolium pratense</i>	III	III	46	I
<i>Helictotrichon pubescens</i>	II	III	46	I
Average number of species	25.2 ±1.7	27.0 ±2.7	26.1 ±1.6	25

Agrostis stolonifera and *Phleum bertolonii* were recorded as constant in Norfolk populations only.

In all Huntingdonshire sites *Trifolium ochroleucon* is associated with *Achillea millefolium*, *Centaurea nigra*, *Dactylis glomerata* and *Festuca rubra* (Table 6.4). Characteristic associates on road verges also include *Arrhenatherum elatius*, *Brachypodium pinnatum*, *Carex flacca*, *Heracleum sphondylium*, *Lathyrus pratensis*, *Medicago lupulina*, *Plantago lanceolata* and *Potentilla reptans*, and in meadows *Briza media*, *Cynosurus cristatus*, *Galium verum*, *Holcus lanatus*, *Lolium perenne*, *Primula veris*, *Sanguisorba minor* and *Trisetum flavescens*. Overall roadside grassland were slightly less species-rich (25 ± 2 species m^{-2}) than meadow grassland (27 ± 3 species m^{-2}), but not significantly so (two-sample *t*-test, $T = 0.58$ $P = 0.574$, d.f. = 9) with no overall difference in sward height (13 ± 1 cm).

These results are very similar to those found by Ellis (2004) in Norfolk where the majority of stands of *T. ochroleucon* occur on roadsides in the *Centaurea nigra* subcommunity of *Arrhenatherum elatius* grassland (MG1e) although some stands showed stronger affinities to the *Lathyrus pratensis* subcommunity of *Cynosurus cristatus*-*Centaurea nigra* grassland (MG1a). Interestingly the average number of species per quadrat was the same as for roadside populations in this study (25 species). Of the 22 constant species listed for Norfolk and Huntingdonshire, half were common to both populations in both counties (Table 6.4).

Management

With the exception of three sites, all Huntingdonshire sites receive some form of protection and are managed to maintain species-rich grassland swards. Six populations occur on protected roadside verges that are mown twice a year, usually in late July after *Trifolium ochroleucon* has set seed and again in September-October. Two populations occur on County Wildlife Sites, one of which is cut and raked in the summer to prevent coarse grasses from becoming rank (Woodwalton Marsh). The other meadow (Horse Close) shows signs of past improvement, although *T. ochroleucon* is confined to low banks that have obviously escaped the worst of these activities. The site is now grazed intermittently throughout the year but under a regime that is favourable for meadow species (D. Felce, pers comm.). Two other meadows receive statutory protection: one is grazed by cattle in the summer and autumn months (Upwood Meadows NNR) and the other is cut for hay in July but not afterwards grazed (Brampton Racecourse SSSI). Both are in favourable condition and populations at both sites appear to be thriving. Two populations occur on sites which receive no management (Kimbolton Airfield, East Perry) although the grassland is kept relatively open by rabbits. Although not visited in 2007, populations on railway embankments receive no direct

management, though in the past the scrub would have been controlled by fires. These now only occur infrequently although some sections are kept open by rabbits.

Change in distribution since the 1960s

Of the 30 populations visited in 2007, *Trifolium ochroleucon* could not be relocated on 17 sites, representing a 57% decline over the last 40 years. This is an underestimate as at least seven further populations for which there were no detailed records have been lost from roadsides around Easton (B.N.K. Davis, pers comm.). The most common reason for these losses were sites becoming overgrown or partially shaded, presumably because of the decline in the cutting of linear strips of grassland over recent decades (riverbanks, woodland rides, green lanes, roadside verges) (Table 6.5). Eight meadows or areas of rough grassland had been converted to arable or improved. Some of the latter were clearly reverting to moderately species-rich grassland but lacked ancient grassland species such as *T. ochroleucon*. Two populations had been destroyed by road and track improvements and at two sites the habitat still appeared suitable but no plants could be found despite detailed searching.

Table 6.5. Reasons for the loss of *Trifolium ochroleucon* populations in Huntingdonshire.

Reason for loss	Number	%
Overgrown/shaded	5	29
Ploughed, now arable	4	24
Improved, now species-poor grassland	4	24
Destroyed by track improvements	2	12
Unknown, habitat still apparently suitable	2	12

As in Essex (Adams 2007) the greatest losses of *T. ochroleucon* have been from meadows and pastures (64% decline since the 1960 in Hunts) and to a lesser extent green lanes, riverbanks and woodland rides (Table 6.2). In contrast, populations on road verges have only declined by 20%. One can only presume that those on railway cuttings have suffered similar losses due to lack of management, although this requires further investigation.

The majority (77%) of surviving populations occur on designated sites, including six protected roadside verges, two county wildlife sites and two SSSIs/NNRs, where they receive some form of conservation management (Table 6.1). In contrast only two of the seventeen former sites (12%) have received any form of either voluntary or statutory conservation designation in the past.

Discussion

The decline of *Trifolium ochroleucon* in Huntingdonshire appears representative of many species associated with ancient grassland on low fertility soils in Eastern England. These include *Melampyrum cristatum* and *Orchis morio*, with which it often grows. Both have suffered similar declines in agricultural habitats, and are now confined to nature reserves or scattered fragments of unimproved habitat (Stroh 2007; Adams 2008; Davis 2009) (Table 6.6). Although meadows and pastures still support the largest populations of *T. ochroleucon* in Huntingdonshire, linear strips of grassland along roads, railway lines, woodland rides and green lanes, have become increasingly important as a refuge for *T. ochroleucon* in areas where agricultural changes have been most severe. Indeed in both Norfolk and Essex, where *T. ochroleucon* is much more common, it has virtually disappeared from meadows and pastures with most extant populations now confined to roadside verges, tracks and green lanes (80% in Norfolk) (Ellis 2004; Adams 2007).

Table 6.6. Species of ancient grasslands, woodland edges and road verges that have been shown to have declined in Huntingdonshire and adjacent counties.

Species	County	Number of sites	% loss	Source
<i>Orchis morio</i>	Hunts (v.c.31), Soke of Peterborough (v.c.32) and Cambridgeshire (v.c.29)	33	17 (49)	Stroh (2007)
<i>Melampyrum cristatum</i>	Huntingdonshire (v.c.31)	5	3 (40)	Davis (2009)
<i>Trifolium ochroleucon</i>	Huntingdonshire (v.c.31)	30 ¹	17 (43)	This study
<i>Trifolium ochroleucon</i>	Cambridgeshire (v.c.29)	55 ²	31 (44)	Bourne (1964)

¹ Only includes sites visited in 2007 and therefore may underestimate the true level of decline. ² Sites are 1 km grid squares and 'extant' if recorded since 1930.

The reasons for the decline in meadow populations are clearly shown in Figure 6.2. In Huntingdonshire the wholesale conversion of grassland to arable began after the Second World War and continued into the mid-1980s by which time the majority of species-rich grassland had disappeared. Today *T. ochroleucon* is therefore almost exclusively confined to protected roadside verges and meadows under sympathetic cutting or grazing management. However, roadside verge populations are extremely small and therefore susceptible to eutrophication from fertiliser drift and rain-wash, physical disturbance from road traffic and road workings and the installation of cabling and pipes as well as changes to frequency and severity of mowing regimes. In North Essex, where the species is probably most abundant, the frequent mowing and scuffing of road verges in the past served to reduce competition

from other plants unable to colonise the raw mineral soils although in recent years many populations have been destroyed by the dumping of surplus topsoil and decayed road metal (Adams 2007). Furthermore, the excessive flailing of dry verges has produced a monoculture of *Festuca arundinacea* whereas on moister verges, mulching with cuttings as a result of frequent mowing has tended to enrich the soil thereby encouraging the spread of tall nitrophiles such as thistles, docks, nettles and *Anthriscus sylvestris* (Adams 2007). In Essex the dumping of top-soil has produced similar results. In Norfolk excessive mowing also appears to be having detrimental affects on roadsides although the spread of tall/coarse vegetation and woody species from adjacent hedgerows due to lack of management and disturbance by traffic seem to be more widespread threats (Ellis 2004). In addition, many verges supporting *T. ochroleucon* are now very narrow due to road-widening and therefore populations are smaller and more susceptible to disturbance. Many populations are also more isolated thereby reducing the likelihood of re-colonisation or cross-pollination. Although not visited during the current survey populations on railway embankments may be suffering similar declines as the cessation of management on many embankments has led to scrub encroachment and spread of *Brachypodium pinnatum* in recent decades, presumably at the expense of low-growing species such as *T. ochroleucon*.

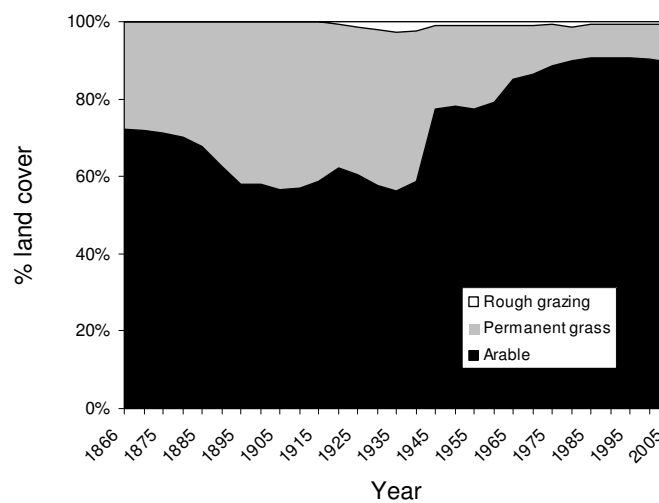


Figure 6.2. Changes in the proportion of land used for arable (including temporary grass), permanent grassland and rough grazing in Huntingdonshire and the Soke of Peterborough since 1860. Rough grazing was not recorded before 1895.

In general meadow populations are probably less threatened as those containing *T. ochroleucon* are likely to be managed as nature reserves. This is certainly the case for the four extant meadow populations in Huntingdonshire: here numbers of plants appear to be

increasing at one site (Brampton Meadow SSSI, Plate 6), where there are 1000s of plants, and there are apparently stable, albeit much smaller populations, on the other three.

On linear sites that are difficult to manage, ideal management would appear to be a regular cutting regime. Studies over a period of four years suggested that cutting twice a year, in April and again in September/October is the optimum regime: this resulted in improved flowering of *T. ochroleucon* when compared with a single cut in September/October (Tabor 1996). Such management obviously reduces the height of potential competitors, allows the plant to set seed and removes the bulk of the biomass in the autumn. Likewise in meadows *T. ochroleucon* seems to benefit from a traditional hay-cut regime with the grassland been “shut-up” for hay until July allowing sufficient time for plants to set seed. On such sites aftermath grazing in the autumn and winter months is presumably sufficient to reduce competition. Clearly pastures containing *T. ochroleucon* should be extensively grazed, especially during the summer flowering period.

Conclusions

The results of this study highlight the important role that meadows and pastures as well as linear habitats, such as roadside verges, now play as refuges, for *Trifolium ochroleucon*, as well as many other habitat specialists, within intensively managed landscapes. However, most Huntingdonshire populations are very small and are therefore highly susceptible to eutrophication, physical disturbance and changes in management regime. The survival of *T. ochroleucon* in enclosed habitats, such as meadows and pastures, will therefore be strongly dependent on the maintenance of appropriate cutting, and to a lesser extent grazing regimes. Prospects for these populations are good given that the majority of sites are under some form of conservation management. The future of roadside populations seems less secure as they are less well protected and are much more susceptible to physical disturbance from road building, pipe-laying, dumping and direct eutrophication from car pollutants. Adequate protection and appropriate management of the sites through voluntary schemes, such as ‘protected roadverges’, will therefore be vital the future conservation of *T. ochroleucon* in Huntingdonshire.



Plate 7

Pulsatilla vulgaris growing at Knocking Hoe, Bedfordshire, one of only five sites in Britain where it is still abundant. Photo: K.J. Walker.

Chapter 7

Reduced grazing and the decline of the threatened grassland herb *Pulsatilla vulgaris* Mill. (Ranunculaceae) in England

Summary

In England *Pulsatilla vulgaris* is a threatened perennial herb that declined dramatically during the 18th and 19th centuries due to ploughing of calcareous grassland. By the 1960s only 33 populations remained. I examined changes to these populations using documentary evidence and field survey. Trends were related to changes in grassland composition, structure and management. Responses to increased above-ground competition (caused by reduced grazing pressure) were simulated in a 10-year shading experiment. Since 1968 *P. vulgaris* disappeared from 16 sites and gradually declined on four others although overall numbers increased by 258% due to the re-introduction of winter sheep grazing on three sites. This produced a significantly shorter and more herb-rich sward, with a lower cover of *Bromopsis erectus* (c. 10%), than on sites where populations remained stable or declined (22% and 30% respectively). Experimental shading had a significant negative effect on plant survival and flowering performance. These results confirmed that reduced grazing has been the main cause of observed declines, especially on isolated nature reserves where livestock farming is no longer economically viable. This is one of the first studies to quantify this effect on a threatened plant and highlights the need to re-instate grazing, cutting or burning on isolated nature reserves that support populations of species dependent on short swards in otherwise intensively managed lowland landscapes.

Introduction

In England *Pulsatilla vulgaris* Mill. (“Pasque flower”, Ranunculaceae) is a threatened perennial herb of calcareous grassland confined mainly to south to southwest facing slopes, old quarries and ancient earthworks where insolation is high and above-ground competition is restricted (Wells & Barling 1971; Stewart, Pearman & Preston 1994; Bailey 1996; Rich 1997). Since its discovery near to Oxford in 1551 (Druce 1886) it has been recorded from c.120 sites in 71 10-km grid squares mainly on the chalk and oolitic limestones of southern England and scattered on magnesian limestone in northern England, extending as far north as

County Durham (Baker 1906; Fig. 7.1). Its present centre of distribution lies in central and eastern Europe (see map in Hensen, Oberprieler & Wesche 2005). Subspecies *vulgaris*, to which English populations belong, is the most widespread taxon extending from 61° N in Sweden to c. 45° N in the Bordeaux region of France and as far east as western Poland where it is replaced by subspecies *grandis* (Lindell 1998). A third taxon, subsp. *gotlandica*, is confined to limestone pavement on the Swedish island of Gotland (Jonsell 2001). During the early post-glacial *P. vulgaris* was probably widespread in steppe grassland throughout Europe but became restricted to fragmented sites with special edaphic and climatic conditions following the spread of deciduous woodland (Hensen et al. 2005). Forest cover is likely to have remained a barrier to more southerly migration, even following widespread deforestation in later periods, and this presumably accounts for its absence from the most southerly chalk in England (e.g. North and South Downs, Salisbury Plain) (Rose 1957).

In England historical records show that *Pulsatilla vulgaris* has been declining since at least 1750. Wells (1968) showed that 64% of the losses before 1900 coincided with Parliamentary Enclosure awards that allowed the ploughing of common lands, mainly between 1750 and 1850 (Jones 1969; Wells 1969). These losses were described most vividly by the Cambridgeshire botanist, Charles Babington (1860), who noted that “Until recently (within 60 years) most of the chalk district was open and covered with a beautiful coating of turf, profusely decorated with *Anemone Pulsatilla* [*Pulsatilla vulgaris*], *Astragalus Hypoglottis* [*Astragalus danicus*], and other interesting plants. It is now converted into arable land, and its peculiar plants mostly confined to small waste spots by road-sides, pits, and the very few banks which are too steep for the plough.” Similar declines were reported from elsewhere in lowland England (e.g. Druce 1886) and were driven by a rapidly increasing urban population and demand for home-grown corn.

During the 1960s a national survey of *Pulsatilla vulgaris* confirmed its survival on 29 sites (Wells & Barling 1971). Although many were on nature reserves most populations were very small or appeared to be declining. Observations from grazing exclosures (e.g. Carter 1967; Wells 1971) suggested increased above-ground competition, particularly with *Bromopsis erectus*, was the probable cause. The removal of plants by sightseers and gardeners was once considered to be a threat on some sites and more recently there has been concern, but no direct evidence, that atmospheric nitrogen deposition may be adversely affecting some populations (Rich et al. 1993; Crawley 2005).

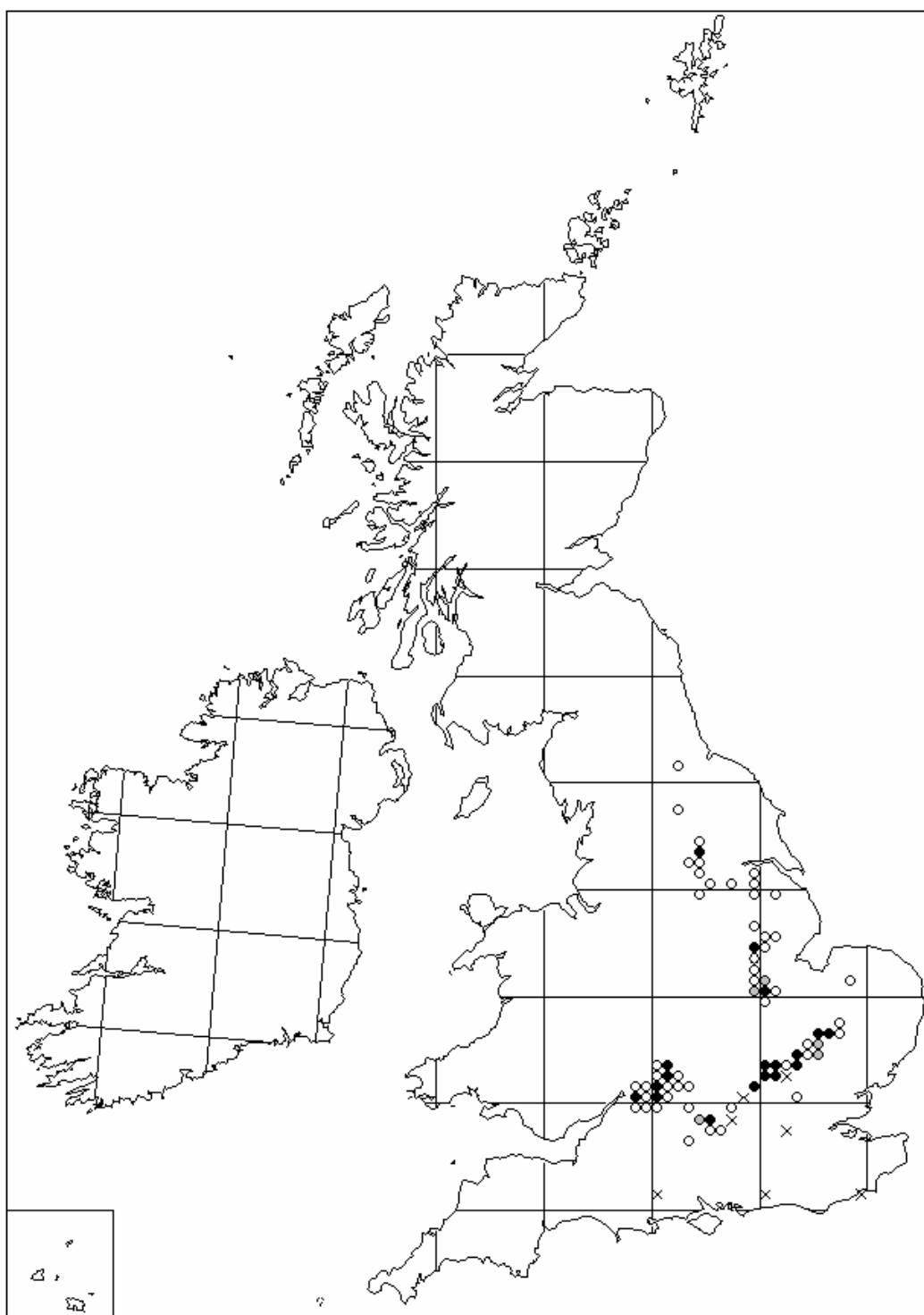


Figure 7.1. The distribution of *Pulsatilla vulgaris* in the British Isles in 10-km grid squares. Closed circles indicate where *P. vulgaris* has been recorded since 2000; shaded circles, last recorded between 1970 and 1999; open circles, last recorded before 1970. × denotes an intentional introduction.

In this chapter I assess changes to the 29 populations listed in Wells & Barling (1971) plus four more populations discovered soon after. *P. vulgaris* is an ideal species to study in this way because it is unlikely to have been over-looked or misidentified and there is a wealth of monitoring and survey information available. The aims of the study were three-fold: (1) to determine changes in the number and size of populations over the past 38 years; (2) to relate trends to changes in vegetation composition, structure and management; and (3) to assess the effects of above-ground competition on survival and flowering performance. The prospects for *P. vulgaris* are discussed in the context of the conservation and management of threatened species associated with short calcareous swards more generally.

Materials and methods

Study species

Pulsatilla vulgaris is an erect, long-lived perennial herb with flowering stems between 5 and 15 cm in height, and up to 40 cm when fruiting. It has a deep tap-root and a vertical, branched rhizome from which several leaf rosettes are produced each year. The basal leaves form a rosette and are long stalked, feathery, and bipinnatisect. They appear after anthesis and wither in the autumn. Flower buds develop during late summer and become dormant over the winter months when they are protected by a dense covering of silky-villose hairs and the remains of the previous year's leaves. Flowering occurs when temperatures exceed 15°C, usually in mid-April, and lasts for between 4 to 6 weeks. The 1 to 3 bell-shaped flowers have six petals, are protogynous and produce numerous bright yellow stamens and are pollinated by a variety of insects, especially bees (Apidae: *Apis*, *Bombus*). Dichogamy is incomplete allowing self-fertilisation although autogamous flowers tend to produce fewer seeds than those that have been crossed (Jonsson, Rosquist & Widén 1991; Lindell 1998; Hensen et al. 2005). However, experiments with the exclusion of pollinators have shown it to be mainly outbreeding due to the absence of spontaneous selfing (Hensen et al. 2005). Early flowering plants and those in small populations are often pollinator-limited and have lower seed-set (Widén & Lindell 1995). The fruit is an achene with a persistent feathery style (3-5 cm) and is probably dispersed over very short distances by wind. Although the internode between the stem leaves and the flower elongates after flowering, increasing the height at which the ripe seeds are exposed, the wind dispersal potential is still very low (Tackenberg et al. 2003). Despite the production of viable, highly germinable seeds, establishment of new individuals from seed

seems rare (observed at only one site in this study). Most regeneration is probably by fragmentation of the branched rootstock (Wells & Barling 1971).

In England *Pulsatilla vulgaris* is a xerophyte and largely calcicole, occurring on shallow (5-15 cm), drought-prone calcareous rendzinas (pH 7.1-7.9) and formerly on sandy, acid soils with no free calcium carbonate at one site in Eastern England (Wells & Barling 1971; Trist 1988). It occurs locally on similar acidic substrates in Sweden and Denmark. In England it is confined to short, herb-rich calcareous swards and with a low cover of *Bromopsis erectus* (Rodwell 1992) though it can persist for long periods in taller grassland in the absence of grazing, cutting or burning.

Study populations

Thirty-three native populations were included in this study (Appendix 8; see Appendix 9 for details of known introductions). For each site, changes in population size and management were compiled from various sources including Wells & Barling (1971), local floras, files in offices of conservation organisations, correspondence with local botanists and unpublished monitoring and survey reports (e.g. Crompton 1981; Welsh 1983; Everett 1988; Bailey 1996; Warden 2001; Tarpey 1999). All populations were visited between mid-April and mid-May over three years (2004-2006; hereafter referred to as the “2006 survey”) and population sizes estimated by counting the numbers of flowers in suitable habitat. For large colonies (> 10,000 crowns) population estimates were taken from census reports (e.g. Tarpey 1999). Details of changes in population sizes and site management are given in Appendix 10 and 11 respectively.

Vegetation composition and structure

At each extant site the associated vegetation was sampled from a series of 1 m × 1 m quadrats and compared to quadrat data collected in 1968 (see Wells & Barling 1971). In 2006 quadrats were located in approximately the same location as in 1968 using sketch maps and GPS and the % cover of all vascular plants, mosses and bare ground recorded. In 1968 abundance was recorded using the DOMIN scale. These values were converted to percentage cover using the Currall (1987) transformation. Vegetation data were assigned to British National Vegetation Classification (NVC) communities using the Tablefit computer programme (Hill 1996). In 1968 sward height was measured using a ruler (highest leaf intersect). In 2006 sward height was measured by taking the average of 10 drop-disc measurements around each quadrat. This

method was preferred because it provides a more accurate measure of vegetation structure on land managed for conservation purposes (Stewart et al. 2001).

Changes in species composition were analysed in relation to species richness and the Shannon diversity index (H') to take account of differences in abundance (Kent & Coker 1992). The evenness (J) of the vegetation was calculated by dividing H' by the base₁₀ logarithm of the total number of species in the sample. Sward structure variables included vegetation height (cm), % cover bare ground, broad-leaved herbs and graminoids (grasses, rushes, wood-rushes, sedges). The number of herbs and species indicative of high quality *Bromopsis* [*Bromus*] *erectus* (CG3) and *Bromopsis* [*Bromus*] *erectus*-*Brachypodium pinnatum* (CG5) grassland were calculated using the list of 'positive indicators' for British calcareous grasslands (Robertson & Jefferson 2000). These were originally selected to show if the ecological conditions are suitable for the survival of particular assemblages of grassland species, in the face of impacts such as eutrophication. Taken together their presence (or absence) therefore provides a direct measure of the condition of the site.

Changes in vegetation composition and structure variables, positive indicator species and common species (present in > 30% of quadrats) were analysed in relation to the overall trend between 1968 and 2006 (i.e. increasing, decreasing or stable) using a two-sampled *t*-test. Differences between populations in 2006 were analysed using Analysis of Variance (ANOVA) with Tukey's pairwise comparisons used to determine the significance of the differences between means. Arcsine transformation of percentage cover values was undertaken to achieve normality of residuals as required (Sokal & Rohlf 1981).

Above-ground competition

Following experiments with grazing exclosures in the 1960s Terry Wells put forward the hypothesis that declines in the numbers of *Pulsatilla vulgaris* on many sites was largely a due to increased above-ground competition following a decline or cessation of traditional grazing management. To test this Terry undertook a shading experiment at Monks Wood Experimental Station, Huntingdonshire, UK between 1970 and 1980. Plants raised from seed collected at Barnack Hills and Holes (Site 4) were planted in a chalk subsoil to a depth of 1 m and exposed to three levels of shading (dense, medium, light) simulated using black gauze screens erected over each plot. Each plot consisted of 12 regularly spaced plants 25 cm apart. Three replicates of each treatment and a control (no shade) were arranged in a randomised

latin square and the survival of transplants and flowering performance recorded in April and May of each year. The plots were fenced to exclude rabbits and weeded to remove competition from the surrounding vegetation.

To my knowledge this is the only experimental assessment of the effects of competition on *Pulsatilla vulgaris*. The results, though not analysed, were therefore clearly relevant and so I decided to include it within this study. My part included computerisation of the raw data and analyses of survival and flowering performance for each year separately using ANOVA with treatment and block as fixed factors and Tukey's pairwise comparisons used to determine the significance of the differences between means.

Results

Population details

All 33 populations studied occur in lowland regions of England (15-240 m altitude) with high mean January (3.5° C) and July temperatures (16.5° C) and low annual precipitation (700 mm) (Hill et al. 2002). Population sizes remained remarkably small over the course of the survey: in 1968 half the populations (57%) held less than 100 plants, nine supported 100-1000 (30%) and only four exceeded 1000 (13%). Similar proportions were found in 2006 (59%, 18% and 24% respectively) although three colonies had increased in size to over 10,000 crowns (Table 7.1). However, populations became significantly more geographically isolated between 1968 to 2006 with the average distance to the nearest population increasing from a mean of 8 ± 2 km to 22 ± 6 km (paired two-sample *t*-test, $t = -2.91$, $P < 0.01$). Populations were typically confined to moderately steep (mean $12 \pm 2^\circ$; range 0-30°) south to south-west facing slopes (mean $205 \pm 10^\circ$ N) supporting short (mean 7.5 ± 0.7 cm; range 1-21 cm) *Bromopsis erectus* (CG3) or more rarely *Bromopsis erectus-Brachypodium pinnatum* (CG5) and *Brachypodium pinnatum* (CG4) calcareous grassland (Rodwell 1992). The proportion of populations occurring in these three types increased from 62 to 67%, 9 to 14% and 3 to 14% respectively whereas the proportion of populations occurring in shorter calcareous grassland types declined (e.g. CG1, CG2 and CG7). The associated vegetation was typically very diverse (23 species m⁻²) and with a high cover of herbs (44 %) (Appendix 12).

Table 7.1. Changes in the status of *Pulsatilla vulgaris* in English counties, 1968-2006: (a) number of populations recorded, (b) trend in abundance, and (c) current population size.

County	(a) Number		(b) Population trend				(c) Population size			
	1968	2006	Increasing	Stable	Declining	Extinct	<100	100-1,000	1,000-10,000	>10,000
Bedfordshire	5	4	2	1	1	1	2	1	1	0
Berkshire	3	1	0	0	1	2	1	0	0	0
Buckinghamshire	3	1	0	0	1	2	1	0	0	0
Cambridgeshire	3	1	0	1	0	2	0	1	0	0
Gloucestershire - east	6	5	1	4	0	1	3	1	0	1
Gloucestershire - west	1	1	0	0	1	0	1	0	0	0
Hertfordshire	2	1	1	0	0	1	0	0	0	1
Leicestershire	1	0	0	0	0	1	0	0	0	0
Lincolnshire - north	1	0	0	0	0	1	0	0	0	0
Lincolnshire - south	3	1	0	1	0	2	1	0	0	0
Northamptonshire	4	1	1	0	0	3	0	0	0	1
Yorkshire – south west	1	1	0	1	0	0	1	0	0	0
Total	33	17	5	8	4	16	10	3	1	3

Characteristic associates (>80% of quadrats) included *Bromopsis erectus*, *Carex flacca*, *Cirsium acaule*, *Festuca ovina*, *Helianthemum nummularium* and *Sanguisorba minor* (Table 7.2). In addition, *Brachypodium pinnatum* was a common associate in limestone grassland and *Campanula rotundifolia*, *Helictotrichon pratense* and *Koeleria macrantha* in chalk downland (Appendix 12). Grazing had been more or less continuous (winter grazing or both winter and summer grazing) on eight sites and intermittent on thirteen others (Table 7.3). Seven sites had been ungrazed (except for rabbits) for over 40 years and four had either been agriculturally improved or destroyed. All but three of the 33 populations occurred on sites with some degree of official conservation designation (i.e. Site of Special Scientific Interest, National Nature Reserve).

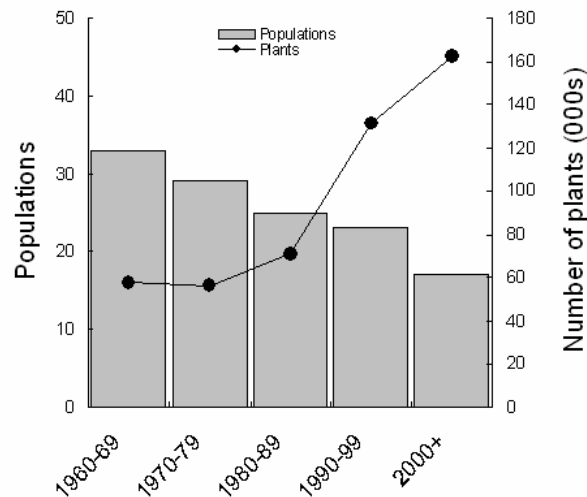


Figure 7.2. Changes in the number and size of populations of *Pulsatilla vulgaris* in England, 1960-2006.

Changes in the number and size of populations

Pulsatilla vulgaris was re-found on 17 of the 33 sites known in 1968 (Fig. 7.1). Of the 16 sites where it could not be re-located seven had no suitable habitat due to lack of management, four had been ploughed, two had been overgrazed, one had been destroyed by dumping rubble and at two sites the cause was unknown. Only 3 of the 16 'lost' sites had no official conservation designation (e.g. SSSI, NNR) as opposed to 1 of the 17 extant sites. On all four declining sites conditions were sub-optimal due to lack of grazing. Despite these losses the overall number of plants increased from an estimated 58,000 to 160,000 (258%) (Fig. 7.2).

Table 7.2. Changes in (i) composition and structure and (ii) cover of common species in grassland containing *Pulsatilla vulgaris* in relation to overall population trends, 1968-2006. *T* is the significance of the difference between 1968 and 2006 calculated using a paired two-sampled *t*-test. ANOVA *F* gives the significance of the differences between increasing, stable and declining populations in 2006 and means with the same letter are not significantly different from one another. Percentage cover data were arcsine transformed prior to analyses. Statistically significant results and constant species (present in > 80% of quadrats) are highlighted in bold (Appendix 12). * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

	Increasing			Stable			Declining			ANOVA <i>F</i>
	1968	2006	<i>T</i>	1968	2006	<i>T</i>	1968	2006	<i>T</i>	
(i) Grassland composition and structure										
Species richness	21.7	27.5 a	-3.4 **	22.5	22.6b	-0.0	21.1	22.0ab	-0.7	4.8 **
Diversity (<i>H'</i>)	1.0	1.1 a	-0.1	1.1	0.8b	1.9	1.1	0.8ab	1.8	6.1 **
Evenness (<i>J</i>)	0.8	0.7a	1.2	0.8	0.6b	2.4*	0.8	0.6b	2.0	4.5 *
Sward height (cm)	5.3	4.3a	0.8	9.2	9.5b	-0.1	8.1	13.9b	-2.3	9.7 ***
% cover bare ground	5.6	8.4	-1.5	4.6	11.7	-1.5	2.5	3.2	-0.5	0.7 NS
% cover broad-leaved herbs	38.8	60.2a	-4.7 ***	39.8	44.2a	-0.5	37.2	49.5b	-1.5	3.6 *
% cover graminoids	50.8	37.2a	3.2 **	51.9	54.6b	-0.4	50.1	50.7ab	-0.0	4.5 *
Number of herbs	13.2	18.7	-3.3 **	12.8	14.9	-0.9	13.3	16.7	-3.0 **	2.8 NS
Positive indicators	9.4	13.2a	-4.7 ***	9.5	9.8b	-0.3	9.0	11.2ab	-2.1	4.3 *
(ii) % cover of common species [†]										
<i>Asperula cynanchica</i> [¶]	0.2	<0.1	0.9	0.1	0.3	-0.8	0.3	0.5	-0.6	1.4 NS
<i>Brachypodium pinnatum</i> [¶]	2.7	5.4	-1.1	3.0	13.9	-1.2	2.8	6.3	-0.2	0.7 NS
<i>Briza media</i>	1.9	0.7	1.4	3.3	0.4	2.6*	1.0	0.3	1.6	4.5 *
<i>Bromopsis erectus</i> [¶]	26.6	10.2a	3.2 **	25.5	22.4ab	-0.1	35.3	30.0b	0.2	5.3 *
<i>Campanula rotundifolia</i>	1.7	0.3	2.5 *	1.3	<0.1	2.0	0.9	<0.1	1.6	1.6 NS
<i>Carex caryophylla</i>	1.3	0.7	0.7	0.5	0.7	-0.1	1.9	<0.1	5.4 ***	1.9 NS
<i>Carex flacca</i>	3.3	3.3	0.1	5.6	2.3	1.5	5.4	7.0	-0.6	1.9 NS
<i>Centaurea nigra</i>	1.5	0.3	1.6	0.3	1.0	-1.3	0.7	1.0	-0.5	1.1 NS
<i>Cirsium acaule</i> [¶]	3.2	6.4	-1.5	4.1	3.8	-0.1	5.4	1.5	2.0	1.2 NS
<i>Ctenidium molluscum</i>	4.3	0.9	2.3 *	2.9	0.3	1.7	12.1	0.0	-	0.5 NS
<i>Festuca ovina</i>	17.8	12.8a	0.1	17.1	7.2ab	1.7	7.5	2.5b	0.5	7.0 **
<i>Filipendula vulgaris</i> [¶]	1.1	3.6	-1.5	0.7	0.9	-0.4	0.7	5.0	-1.3	1.5 NS
<i>Helianthemum nummularium</i> [¶]	5.4	5.0	0.3	6.6	7.6	-0.4	4.8	7.7	-0.5	0.3 NS
<i>Helictotrichon pratense</i>	1.7	0.4	2.2 *	1.6	1.8	-0.2	0.8	0.5	0.3	1.1 NS

Table 7.2 continued.

	Increasing			Stable			Declining			ANOVA <i>F</i> 2006
	1968	2006	<i>T</i>	1968	2006	<i>T</i>	1968	2006	<i>T</i>	
<i>Hippocrepis comosa</i>	1.0	<0.1	2.5 *	<0.1	0.5	-1.0	1.3	1.3	-0.1	1.3 NS
<i>Leontodon hispidus</i> [¶]	1.5	4.9	-1.5	3.5	0.9	2.1 *	4.5	1.5	1.1	2.0 NS
<i>Koeleria macrantha</i>	1.4	0.4	2.1 *	2.0	0.1	2.2 *	0.4	<0.1	0.6	1.9 NS
<i>Linum catharticum</i> [¶]	<0.1	<0.1	1.7	<0.1	0.5	-	<0.1	<0.1	-1.2	<0.1 NS
<i>Lotus corniculatus</i> [¶]	1.4	3.0	-0.2	2.6	0.1	2.3 *	1.2	0.5	0.9	1.4 NS
<i>Plantago lanceolata</i>	0.7	0.3 a	1.1	0.7	0.1 b	1.4	1.3	1.0 b	-	7.6 **
<i>Plantago media</i> [¶]	0.4	0.2	0.6	1.7	0.3	0.9	0.4	0.5	-0.0	0.1 NS
<i>Pilosella officinarum</i> [¶]	3.5	2.1	0.6	2.5	3.0	0.2	1.6	<0.1	2.8 *	2.0 NS
<i>Pulsatilla vulgaris</i>	6.0	4.8 a	-0.3	4.7	1.4 b	2.0	2.0	3.5 ab	-0.3	5.6 *
<i>Sanguisorba minor</i> [¶]	5.9	12.4	-3.2 **	7.2	10.1	-0.2	7.4	14.3	-1.0	0.6 NS
<i>Scabiosa columbaria</i> [¶]	0.9	0.5	<0.1	1.6	0.2	1.0	0.6	0.5	0.2	0.5 NS
<i>Scleropodium purum</i>	5.7	0.0	-	0.6	<0.1	1.6	2.1	<0.1	2.1	2.2 NS
<i>Thymus pulegioides</i> [¶]	1.1	2.5	-0.8	0.2	0.5	-0.6	0.4	1.5	-1.3	0.9 NS
<i>Viola hirta</i>	<0.1	0.5	-1.7	0.1	0.3	-1.0	0.8	0.7	0.2	0.3 NS

[†] Species present in > 30% of quadrats (see Appendix 12); [¶] Positive indicators defined by Robertson & Jefferson (2000).

Changes in vegetation composition and structure

On sites where numbers of *Pulsatilla vulgaris* had increased the vegetation had become significantly more species-rich, in terms of the number and cover of herbs such as *Cirsium acaule*, *Filipendula vulgaris*, *Leontodon hispidus* and *Sanguisorba minor* (Table 7.2). The number of positive indicators also increased from 9.4 to 13.2 species m⁻² whereas there was a significant reduction in the cover of grasses, most notably *Bromopsis erectus*, which declined from c. 26% to 10%.

Few significant changes were observed on sites where populations remained stable although there was a slight but significant increase in vegetation dominance (*J*) and a decline in the abundance of small herbs, such as *Leontodon hispidus* and *Lotus corniculatus* ($P < 0.05$), and *Briza media* and *Koeleria macrantha* ($P < 0.05$). Similarly, there were few significant changes on sites where *P. vulgaris* declined. Although there was a significant increase in the number of herbs from 13 to 17 species m⁻² ($P < 0.01$), low-growing species of short, grazed turf (*Carex caryophyllea*, *Cirsium acaule*, *Pilosella officinarum*) all declined, presumably because of the increase in sward height (8-14 cm). Although this increase was not significant it should be noted that in 1968 the vegetation was significantly shorter on sites where populations subsequently increased (< 5.5 cm) than on those sites where populations remained stable or declined (> 8 cm). The cover of *Bromopsis erectus* was also significantly higher in 2006 on sites where *P. vulgaris* had declined (30%) than on those where it remained stable (22%) or increased (10%) ($F = 5.3$, $P < 0.05$).

Table 7.3. Management of *Pulsatilla vulgaris* populations in relation to trends in abundance, 1968-2006. 1-5 represent a decline in the intensity of grazing management.

Management since 1968	Increase	Stable	Decline	Extinct	Total
1. Winter + summer/autumn grazing	3	2	0	0	5
2. Winter grazing (since 1980)	2	1	0	0	3
3. Irregular grazing, mowing, burning	0	4	2	2	8
4. Over-grazed then under-grazed	0	0	2	3	5
5. Ungrazed for over 40 years	0	0	0	7	7
6. Improved/destroyed	0	0	0	4	4
7. Unknown	0	1	0	0	1

Population trends were clearly related to changes in vegetation composition and structure. On sites where *P. vulgaris* increased the vegetation was significantly shorter (Fig. 7.3a) and more species-rich (Fig. 7.3b) than on sites where populations remained stable or declined (Table

7.2). The cover of *P. vulgaris* and other low-growing species was also much higher (e.g. *Briza media*, *Cirsium acaule*, *Festuca ovina*, *Leontodon hispidus*, *Pilosella officinarum*). Conversely, the cover of robust grasses, sedges and herbs, most notably *Bromopsis erectus* (Fig. 7.3c) and to a lesser extent *Carex flacca* and *Plantago lanceolata*, were significantly higher on sites where *P. vulgaris* declined.

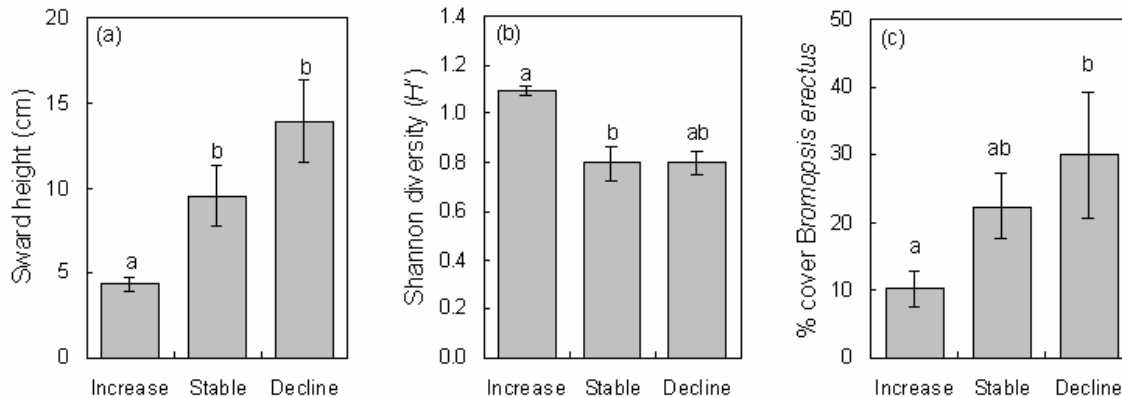


Figure 7.3. (a) Sward height (cm), (b) species diversity and (c) % cover of *Bromopsis erectus* (± 1 S.E.) on extant *Pulsatilla vulgaris* sites in England ($n = 14$) grouped in relation to population trends in the period 1968-2006. Means with the same letter are not significantly different from one another.

Effects of shading on survival and flowering performance

The effect of shading on the survival of *P. vulgaris* was significant ($P < 0.05$) after 7 years; the most shaded plots had the lowest survival rates declining from 31% to 0% between years 7 and 10 (Fig. 7.4a). Plants in moderate shade showed a similar pattern although more plants survived to the end of the experiment (53-11%) whereas controls and lightly shaded plots had the highest levels of survivorship declining from 92% and 94% to 70% and 44% respectively, although the differences were not significantly different from one another.

Flowering performance increased gradually over the course of the experiment reaching a peak in year 5 before declining to low levels by years 8 to 9 (Fig. 7.4b). Shading had a highly significant negative effect on flowering performance ($P < 0.001$; year 8 $P < 0.01$) in all except years one ($F = 1.4$; $P = 0.25$) and nine ($F = 0.4$; $P = 0.77$) when few shaded plants remained. The number of flowers was significantly higher on controls in all years, increasing from 9 to a maximum of 18.4 flowers per plant. Plants in lightly shaded plots followed a similar pattern although plants reached a lower maximum of 11.6 flowers in the same year before declining to less than 4 flowers per plant by year 10. Flowering was much lower in both medium and

densely shaded plots and never averaged more than 6.8 and 4.3 flowers respectively. Pairwise comparisons showed that from year two to seven, flowering performance was significantly lower in densely shaded than lightly shaded and control plots.

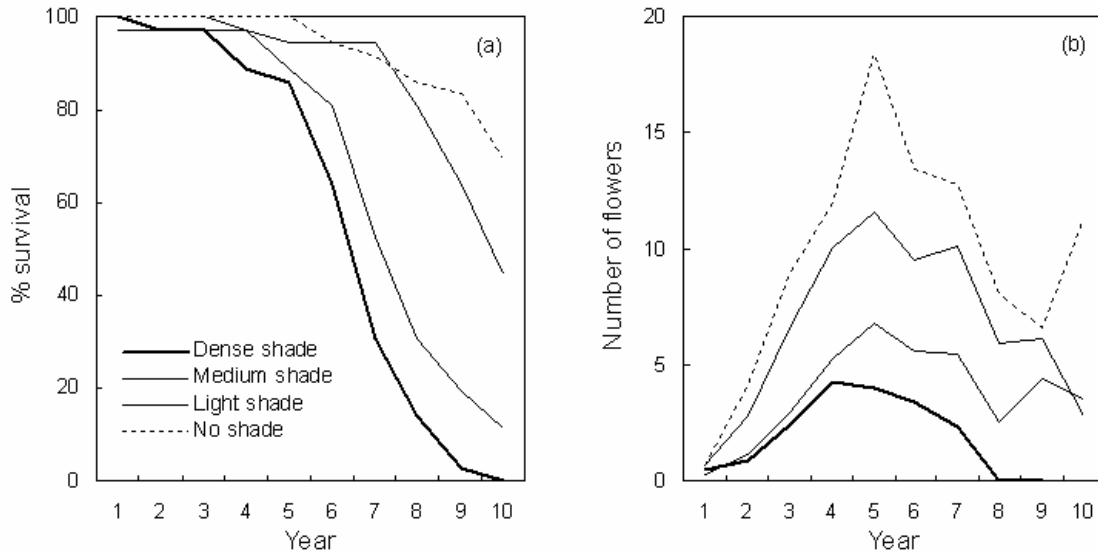


Figure 7.4. The effects of shading on the (a) survival and (b) flowering performance of *Pulsatilla vulgaris*. For survival, differences between treatments were significant in years 7 ($F = 12.0$; $P < 0.01$), 8 ($F = 19.2$; $P < 0.01$), 9 ($F = 10.5$; $P < 0.01$) and 10 ($F = 7.1$, $P < 0.05$). For flowering performance, differences between treatments were highly significant in years 2-7 and 9 ($P < 0.001$; year 8 $F = 4.1$; $P < 0.01$).

Discussion

Overall population changes

The historic decline of *Pulsatilla vulgaris* continued steadily after 1968 with a 50% reduction in the number of site-populations since then (Fig. 7.5). Its current distribution now represents just 27% and 14% of its former range at the 10-km and site-population scales respectively. A similar magnitude of decline has been reported for *P. vulgaris* in central Germany (Hensen et al. 2005) and for *P. patens* in Finland where 60% of populations have been lost since the 1930s (Uotila 1996). The similarity with the decline of *Orchis ustulata* in England (Foley 1992) is also striking, but not surprising given that the two species formerly grew together on a number of sites (and still do at one site in Bedfordshire). Of the 12 counties with surviving populations in 1968, two no longer support any plants and eight have single populations, five of which contain less than 100 plants (Table 7.1).

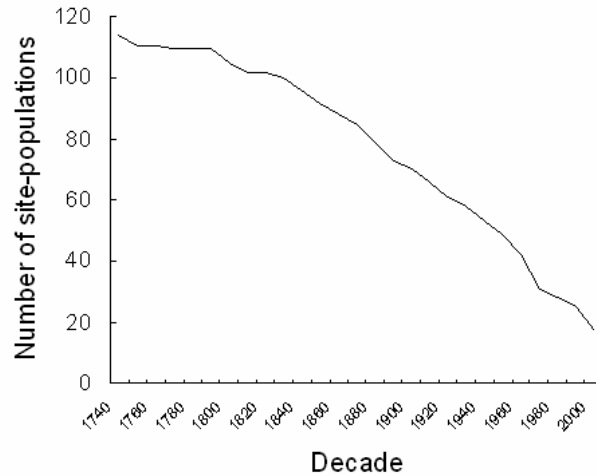


Figure 7.5. The decline of *Pulsatilla vulgaris* in England since 1750. The number of site-populations were derived from historical sources and were assumed to have been extant at the start of the recording period even where the first record for a site was much later.

Populations have also become significantly more isolated over the past 40 years with the average distance to the nearest population increasing from 8 km to 22 km. Most significantly eight populations are now separated from their nearest neighbour by more than 10 km and five by more than 35 km. The most isolated site, Ledsham in South Yorkshire, is 102 km from the closest extant site.

Despite these dramatic declines the total numbers of flowers in English populations more than doubled due to improvements in grazing regimes on three sites. Whether this represents a real increase is debatable for two reasons. First, *P. vulgaris* produces several shoots from a branched rhizome making it almost impossible to age or relate to the number of genets present ('type C perennials'; Grubb 1990). Second, genets are potentially very long-lived and so *P. vulgaris* may have persisted in a vegetative state for long periods under unfavourable conditions (e.g. herbivory, burning, above-ground competition). For example, it survived for up to 28 years in rank, ungrazed grassland on four sites included in this study (Barton, Pitstone and Smithcombe Hills, Southorpe Roughs) although plants became less abundant, became etiolated and flower production ceased (Wells 1968).

Causes of population declines

The main cause of population declines in lowland England has been increased competition with coarse grasses as a consequence of reduced livestock grazing (Robinson & Sutherland

2002). Of the 20 sites where *P. vulgaris* has either declined or gone extinct, 16 have been ungrazed for over 40 years or have only received intermittent grazing, mowing or burning (Table 7.3). These include earthworks and steep banks now completely isolated within arable landscapes, privately owned nature reserves where resources for management have been limited and grazing exclosures on formerly over-grazed sites.

Livestock farming has become less profitable in arable areas of lowland England since the 1950s making it difficult to sustain appropriate grazing management on unproductive sites (Nisbet & Shere 2006). On mixed farms the conversion of grassland to arable production has made owners less committed to grazing small areas, whereas their inaccessibility has deterred potential graziers because of increased transport and infrastructure costs. Even on livestock farms these problems have prevented the grazing of small fragments of semi-natural grasslands perceived to be unproductive and/or difficult to manage. Added to this has been an overall decline in rabbit grazing following the spread of myxomatosis in 1953 which is known to have caused dramatic successional changes, especially on sites with no history of livestock grazing (Sumpton & Flowerdew 1985).

The changes in grassland composition and structure observed in this study (Fig. 7.3a-c) were clearly related to these reductions in grazing pressure. These were first noticed in grazing exclosures (e.g. Wells 1968; Warden 2001) where they were attributed to the smothering effect of litter and increased competition from tall grasses. For example, Mitchley (1988) showed a positive correlation between interference ability and mean height of the rosette leaves in *Bromopsis erectus* grassland. This is because dominant species such as *B. erectus* often project their leaves into the upper canopy and overtop subordinate species, thereby reducing the amount of photosynthetically active radiation that reaches lower levels (Mitchley & Willems 1995). In addition, *B. erectus* is known to generate high 'shoot thrust', enabling it to attain early dominance in the vegetation by physically restricting the growth of surrounding species, especially low-growing hemicryptophytes such as *P. vulgaris* (Campbell, Grime & Mackey 1992). The results of the shading experiment confirm these findings with a significant decline in longevity, survivorship and flowering performance under increasing levels of shade (Fig. 7.4). Further evidence for this comes from a field experiment in Oxfordshire where *P. vulgaris* transplants had significantly greater survivorship and performance (number of leaves) where the surrounding 30 cm of vegetation had been removed (compared to none or 15 cm) (Warden 2001). These findings highlight the crucial

role that above-ground competition plays in restricting the amount of light reaching the base of the sward and thereby determining the relative abundance of low growing hemicryptophytes such as *P. vulgaris* in unproductive swards.

In comparison, other factors were relatively minor in causing losses. These included agricultural improvement (3 sites), disturbance by rabbits (one site; Trist 1988) and physical destruction by humans (one site). Despite concerns about the physical removal of plants there is no evidence to support this as the main cause of extinction at any English site, although the last known plants were removed from one site (Site 9, Broughton Far Wood) where under-grazing had caused a long-term population decline (Appendix 11).

Causes of population increases

Dramatic increases have been recorded on three sites following reinstatement of more appropriate grazing regimes (Fig. 7.2). Although all three had been heavily grazed by sheep and rabbits in the past, management had been neglected in the 1950s and 1960s. The reintroduction of winter or winter combined with summer/autumn grazing at relatively low intensities (5 sheep ha⁻¹), combined with an increase in rabbit numbers since the 1970s had produced a shorter, more diverse sward and a concomitant decline in the cover of *Bromopsis erectus* (Table 7.2). As discussed above the extent to which these represent an increase in genets is debatable. The lack of records of seedling establishment and relative inefficiency of seed dispersal suggest that colonisation of new areas is very limited (Wells & Barling 1971; Warden 2001). Indeed colonisation of new areas has only been observed twice since the 1960s: once on a steep SE-facing motorway embankment in Cambridgeshire c. 300 m from the nearest colony (Leslie 2004) and at Barnack Hills and Holes in Northamptonshire where plants were observed in an area of the reserve for which there are no historical records (C. Gardiner, pers. comm.). At both sites dispersal was probably adhesive either via mowing machinery (Cambridgeshire) or livestock (Barnack). Conversely, *P. vulgaris* has yet to colonise an area of grassland immediately adjacent to one of the largest populations (Knocking Hoe) that was briefly (and unsuccessfully) cultivated during the 1950s.

Genetic and conservation considerations

Habitat loss and more latterly under-grazing have resulted in a dramatic decline of *P. vulgaris* in England since 1750. The current range is characterised by a high level of fragmentation, since numbers and size of populations have declined considerably. As smaller populations are

more vulnerable to genetic drift and inbreeding depression, the risk of extinction due to genetic, demographic or environmental problems is much larger than in larger ones (Lande 1988; Schaffer 1987). In these circumstances a decrease in genetic diversity is expected (Soulé 1986) accompanied by a reduction in reproductive performance (e.g. Ouburg and van Treuren 1995; Oostermiejer et al. 1998; Vergeer et al. 2003). These findings have been confirmed for *P. vulgaris* in a study of eleven populations in central Germany, where it has undergone a similar decline to the one reported in this paper (Hensen et al. 2005). This study showed a significant positive relationship between genetic diversity and both population size and seed mass (per population). There was also a high level of within population variability which was attributed to life-history traits likely to preserve variability, namely allogamous pollination, a long life span and vegetative reproduction. Interestingly there was only weak, albeit significant differentiation between populations which was correlated to the geographical distance. To an extent this was expected and suggested genetic drift has been the major force driving differentiation between German populations as the former larger population became fragmented. However, the weakness of this relationship suggests that the loss of genetic variability through drift has been, to some extent, balanced by gene flow between closer populations. Since seed dispersal in *P. vulgaris* is limited it was concluded that the foraging radius of pollinators, currently thought to be in the order of several kilometres for honeybees (Steffan-Dewenter & Kuhn 2003) and bumblebees (Osborne et al. 2008), is critical in offsetting genetic drift as populations become smaller and more isolated. However, even if pollinators forage over several kilometres it seems very unlikely that they would travel from one *P. vulgaris* population to another given the small size and isolation of most British populations.

With the exception of some preliminary work by Bailey (1996) very little is known about the genetic variability in English populations of *P. vulgaris*. However, the results from Germany suggest that due to life-history characters *P. vulgaris* may have maintained higher levels of genetic variation than would be expected for a declining species, although small populations are likely to display lower levels of genetic variation than larger ones, even where gene exchange is occurring between sites in close proximity. As the distance between most English populations and their nearest neighbour population is well beyond the foraging radius of most pollinators (>10 km) we would expect to see a significant differentiation between isolated or outlying populations, both in terms of genetic variation and reproductive performance. Further work is needed to test this hypothesis.

Conclusions

As far as I am aware this is the first study to quantify the negative impact of reductions in grazing on populations of a threatened plant in Europe and strengthen concerns over the loss of low-growing species of infertile soils more generally. Although clearly related to changes in management an interaction with increasing atmospheric nitrogen deposition cannot be discounted, as eutrophication strongly favours competitive species and accelerates closing of the vegetation. Grazing to maintain an open sward (5-10 cm) will be vital to ensure the short-term survival of *P. vulgaris*, as well as a whole suite of other threatened species associated with short swards, on neglected sites. The resilience of *P. vulgaris* to defoliation, lack of grazing, burning and mowing suggests that there is much flexibility in how this can be achieved although winter sheep grazing (<5 sheep ha⁻¹ taking into account rabbit grazing) is probably ideal although additional summer grazing is unlikely to be detrimental (Rich 1997). On smaller sites where grazing is impractical, cutting in the spring is likely to be the most effective way of reducing the abundance of potential competitors such as *Bromopsis erectus* (Wells 1971). In the longer term the restoration of semi-natural habitats to link existing populations and promote gene-flow via pollinators, will be needed to maintain or even increase the genetic diversity of English populations.

Chapter 8

Conclusions

Using local floras to assess floristic and ecological change

The calculation of county extinction rates provides a simple, albeit crude measure of decline but the figures require careful interpretation because of the many factors that are likely to influence the results. Quantitative assessments of change have proved more difficult to undertake, mainly because of the lack of adequate baselines, but also because of changes in recording methods and intensity. In a few cases *relative* measures of change, derived from comparisons between recording periods, have proved very powerful because the method used (standardised residuals from a linear regression) takes into account differences in recording intensity between surveys. However, its reliance on the availability of quantitative (or semi-quantitative) information for the earlier period means this approach will not be possible for many British counties where data is either unavailable or of limited comparability. However, many similar studies are likely to be undertaken in the future as county flora surveys that repeat earlier grid-based surveys are completed.

Methods that provide *absolute* measures of change for a given locale, often a fixed plot (e.g. habitat study), are more spatially restricted but provide direct information on the habitat affected and environmental causes of change. Although habitat studies have only been recorded in a few counties, the results of the UK's Countryside Survey shows how useful this approach can be in highlighting trends for common species that are impossible to detect where recording is carried out at greater spatial scales.

What has been the scale of localised extinction over the past 350 years?

The results presented in this thesis reveal a period of heightened extinction at the local scale over the last 350 years with many of the worst affected counties losing between 10-20% of their native floras. In English counties the rate of extinction appears to have increased from

below 0.5 species per year in the nineteenth century to around 0.5 species a year since 1900 with counties in the south and east losing more species, on average (0.6 species a year) than those in the north and west (0.4 species per year). However, the rate of extinction appears to have increased since 1950 with many counties experiencing rates of nearly one species per year towards the latter part of the twentieth century.

Though broadly consistent across a range of landscapes, these results should be treated with caution for a number of reasons. Because area buffers against extinction the magnitude of localised extinction is negatively related to area. Thus the highest losses, as a proportion of the total species-pool, so far reported are around 20% in the smallest areas so far studied (e.g. cities, peri-urban landscapes, parishes). In comparison, counties appear to have lost around 10-15% whereas some of the largest regions so far studied have lost 5-8%. In Britain as a whole just under 1 % of our native flora has been lost since records began. In addition, the scale of extinction can be influenced by the history of botanical recording and the degree of certainty with which a species can be recorded as extinct.

Was extinction random across different habitats?

The results of the analyses of floristic changes in Chapters 4 and 5 support findings from numerous other European studies and show categorically that species associated with open semi-natural habitats with low fertility (e.g. lowland bogs, dwarf-shrub heath, acid and calcareous grassland) have suffered the highest rates of extinction over the last three centuries. The dramatic decline of arable species shown is also consistent with national declines of long-established weeds (archaeophytes) since the 1950s following the introduction of herbicides and improved methods of seed cleaning. In comparison, the stability of woodlands and marshes was striking and presumably reflects the contrasting history of modification. Both habitats are no longer used intensively for productive purposes (e.g. biomass harvesting, hunting, etc.) and, although there were localised losses due to agriculture, urban development and afforestation in the twentieth century, much of the habitat that was present over 100-200 years ago remains. These habitats were probably much more intensively used during the mediaeval period and it is possible that these activities eliminated extinction prone species before the start of botanical recording. Thus the resulting flora may have been relatively resistant to changes from 1800 onwards.

What environmental and land use drivers have caused species loss?

In this study the impacts of environmental or land use changes have been inferred from ecological requirements of the species that have declined as well as direct observations on fixed plots and populations of *Pulsatilla vulgaris* and *Trifolium ochroleucon*. In all cases the results clearly indicate the primary role of habitat destruction and fragmentation in causing localised extinctions in heavily populated and intensively managed lowland regions. As noted above, species associated with unproductive habitats have therefore suffered the greatest losses. The declines of the habitat specialists, *P. vulgaris* and *T. ochroleucon*, provide dramatic illustrations of the extent of these declines: over 50% of the populations of both species have been lost over the past 50 years and, in the case of *P. vulgaris*, 85% of populations have been lost over the past 350 years.

The extent to which eutrophication has contributed to these declines is more difficult to quantify as the effects are more subtle and pervasive. However, there is no doubt that short habitat specialists that are unable to persist within tall, closed swards will have declined where increased N deposition or eutrophication from terrestrial sources has caused a shift in the composition of a range of communities to taller, more competitive swards. The results for both *P. vulgaris* and *T. ochroleucon* also show that increased competition from coarse grasses, due to reduced grazing and cutting on areas that are difficult or uneconomic to manage, may now be a more pervasive threat for many species associated with short, unproductive swards. Contrary to widespread fears no evidence was found to suggest that introduced invasive species have caused or even accelerated the extinction of a species in semi-natural habitats in lowland landscapes.

What life-history attributes make a plant species more prone to localised extinction?

In this study the most important predictors of extinction risk were range size and traits associated with habitat specialisation and competitive ability. Declining species tended to be rare and often at the northern or southern edges of their range in lowland Britain. The most striking and consistent result was the decline of short species (less than 30 cm) associated with unproductive soils with extreme levels of moisture and/or pH. These losses presumably reflect the fact that taller, longer-lived species are better able to survive under more fertile conditions or where reduced disturbance leads to the development of taller swards. Under these conditions smaller species are likely to be selectively removed. The fact that species

associated with infertile soils with high or low moisture and pH are more extinction-prone presumably also reflects the fact that these sites were the most economically marginal and, therefore, were the last to be reclaimed by modern agriculture. Such habitats are also likely to be highly sensitive to external factors such as nutrient inputs, pollution and climate change, as well as site factors such as changes in management.

Although dispersal of seed and pollen is theoretically important in slowing the decline of specialists in isolated habitat fragments no relationship was found between any of the regenerative attributes (e.g. clonality, seed bank, fertilisation, dispersal ability) and species trends. However, these results do not necessarily mean that regenerative attributes have not had an effect. Traits such as dispersal, breeding system, clonality, etc. are notoriously difficult to classify into categories that reflect a species' ability colonise new sites. Conversely, the magnitude of recent land use changes may have been so great that for most species dispersal, however successful under stable conditions, has been insufficient to counteract the rapid demographic and environmental changes associated with habitat destruction and degradation.

Which species face the greatest risk of extinction in the future?

It is clear from the results of this study that in intensively managed areas species with the following ecological demands or life-history traits are far more at risk of extinction than species with different traits:

- Association with unproductive soils with high or low soil moisture and/or pH. The habitats that these soils support have suffered the greatest decline in area and quality and therefore species associated with them will have declined the most;
- Habitat specialists, especially species confined to a narrow range of ecological conditions which are unable to find 'new' habitat once a specialised habitat has been lost from the study region;
- Rarity, as low initial abundance is a key factor predisposing a species to extinction. In particular species currently at their southern range margin in lowland Britain are likely to become increasingly threatened towards 2050 as temperatures warm by an estimated 2° C;
- Low stature, as short species are unable to persist within taller, competitive swards that result from nutrient enrichment and lack of management.

Because many remaining species have high extinction probabilities and because extinction is often delayed (extinction debt *sensu* Tilman et al. 2002), a substantial proportion of local floras will continue to go extinct in the near future. Most of these losses are likely to take place on isolated patches of semi-natural habitat where the loss of important ecological interactions between populations, such as geneflow, has been effectively removed by fragmentation and conditions are often unfavourable due to the lack of management.

Effectiveness of conservation

One of the most unexpected results of this study was the extent to which conservation designation failed to protect species from localised extinction. Although conservation is intended to ‘buffer’ a species from extinction the findings of this study show clearly that presence on a conservation site alone was no guarantee of survival. For a variety of reasons, many conservation sites are now under-grazed leading to succession to taller communities and scrub. Succession, exacerbated by extrinsic factors, was therefore a predictable fate for many sites given that the statutory instruments could neither alleviate these external factors, nor fund positive management within the site.

The analyses of fixed plots in Bedfordshire revealed a similar picture: with the exception of calcareous grasslands, and to a lesser extent marshes, protection had little effect on the degree of change and in the case of some habitats (neutral grassland, acid woodlands and heath and mires) it actually made matters worse (i.e. the composition of protected sites changed more than on sites with no official designation). The findings for *Pulsatilla vulgaris* help to explain these findings, at least for species dependent on the maintenance of short swards. The results also highlight the urgent need not only to control extrinsic factors such as eutrophication but also to maintain, or where it has ceased, to reinstate appropriate management in order to prevent further losses in the future.

Limitations and future prospects

Clearly the methods used in this thesis leave many questions unanswered. Most important, by focussing on declining species I have only addressed half of the picture. Similar studies of successful species at local scales would compliment this study and help to further our understanding of the main ecological changes that have taken place over the last 350 years. Second, it is likely that some important traits have been omitted or more likely, that

quantifiable impacts were impossible to differentiate from other factors, using the statistical analyses and trait classifications presented in this thesis. My classification of dispersal, for example, could be revised in the light of more recent research (e.g. Ozinga et al. 2009), thus allowing a more sophisticated assessment of its contribution to overall species trends at the local scale. Third, the choice of study regions and species were self-selecting due to the high quality of the baseline survey data available to me. These were biased towards lowland, predominantly agricultural areas in the southern half of Britain and consequently the results should not be seen as representative of British flora as a whole. Further local studies are needed in different geographical areas, especially upland and coastal ecosystems which have yet to be analysed using this approach. Finally, experimental work played only a minor part in this thesis despite the fact that many of the findings from the trait analyses could be easily tested under more controlled experimental conditions. For example, experiments could help differentiate the relative importance of traits that appear to be autocorrelated with one another.

This study highlights the importance of the botanical recording at the local (county) scale that began with the wanderings of Tudor herbalists some 350 years ago. This tradition has produced one of the most detailed observational records anywhere in the world, and, despite the limitations described above, the findings presented in this thesis provide powerful examples of how they can be used to quantify floristic change and to help interpret the major environmental and ecological changes that have taken place.

Acknowledgements

I am greatly indebted to my supervisors, Chris Preston and Mark Hill at CEH and Brian Huntley at the University of Durham for their encouragement and support over the last ten years. Chris Preston in particular has been very generous with both time and ideas despite a heavy work load that included the publication of the *New Atlas of the British and Irish flora* in 2002. I would also like to give special thanks to Chris Boon who provided access to John Dony's original survey data and for spending many hours checking records for Bedfordshire (Chapters 4 & 5). The late Terry Wells encouraged me to complete the survey of *Pulsatilla vulgaris* (Chapter 7) and generously allowed me to use his original field survey information. Peter Rothery and Tim Sparks provided much needed statistical advice and Simon Smart contributed ideas and information on methodological aspects. Chris Preston, David Pearman, Tim Rich, Douglas McKean and Simon Smart made valuable comments on the text. I would also like to thank the many botanists consulted over the status of species in their vice-counties most notably Michael Braithwaite, Brian Davis, Lynne Farrell, Gill Gent, Mark Gurney, John Hammond, Trevor James, Seán Karley, Claire and Mark Kitchen, Alex Lockton, Roy Maycock, David Pearman, Sharon Pilkington, Peter Stroh, Trevor Tween, John Welham and Irene Weston. Staff in Natural England (formerly English Nature) kindly responded to many queries regarding specific sites including Clare Pinches, Graham Bellamy, Graham Stevens and Richard Jefferson. Bob Ellis, Christine Bailey, Jonathan Mitchley and Kathy Warden all allowed me to cite unpublished work and Duncan McCollin (and Elsevier Press) gave me permission to reproduce Figure 2.6. Carl Farmer provided the excellent photographs used in Chapter 5. Many herbaria were consulted and in particular I would like to thank Serena Marner for access to Druce's material in Oxford and David Simpson (Kew) for verifying the Northamptonshire specimen of *Eriophorum gracile*. My employers, CEH and, since 2007, BSBI, have been extremely generous in allowing me the time needed to complete this thesis, often to the detriment of other commitments.

Finally, and most importantly, I would like to thank my partner Clare for her love and support over the last decade and for the many memorable days we have spent in the field together.

List of papers & books published

Papers and books on related topics published by KJW during the course of the PhD. Those with an asterisk form the basis of chapters included in this thesis; where relevant a statement of my own contribution to this work is included in square brackets.

- Pearman D.A. & **Walker K.J.** 2004. An examination of J.W. Heslop Harrison's unconfirmed plant records from Rum. *Watsonia* 25, 45-63.
- Pearman D.A., Preston C.D., Rothero G. & **Walker K.J.** 2008. *The Flora of Rum: an Atlantic Island Reserve*. Henry Ling Ltd., Dorchester.
- Preston C.D. & **Walker K.J.** 2003. Creeping inflation in the length of county floras 1750-1960. *Watsonia* 24, 447-453.
- Smart S.M., Bunce R.G.H., Marrs R., LeDuc M., Firbank L.G., Maskell L.C., Scott W.A., Thompson K. & **Walker K.J.** 2005. Large-scale changes in the abundance of common higher plant species across Britain between 1978, 1990 and 1998 as a consequence of human activity: Tests of hypothesised changes in trait representation. *Biological Conservation* 124, 355-371.
- ***Walker K.J.** 2002 The ecology of a changing flora. *Transactions of the Suffolk Natural History Society* 38, 8-22.
- ***Walker K.J.** 2003. Using data from local floras to assess floristic change. *Watsonia* 24, 305-319.
- ***Walker K.J.** 2003. One species a year? An evaluation of plant extinctions in selected British vice counties since 1900. *Watsonia* 24, 359-374.
- Walker K.J.** 2003. *Eriophorum gracile* formerly present in Northamptonshire (v.c. 32). *BSBI News* 92, 16-18.
- ***Walker K.J.** 2007. The last thirty five years: recent changes in the flora of the British Isles. *Watsonia* 26, 291-302.
- ***Walker K.J.** & Pinches C.E. 2009. The status of *Trifolium ochroleucon* Huds. in Huntingdonshire (v.c. 31). *Nature in Cambridgeshire* 51, 3-11. [Fieldwork by KJW & CEP, analyses and writing by KJW]
- ***Walker K.J.** & Preston C.D. 2006. Ecological predictors of extinction risk in the flora of lowland England. *Biodiversity and Conservation* 15, 1913-1942. [Primarily work by KJW following discussion and planning with CDP]

- ***Walker K.J.**, Preston C.D. & Boon C. 2009. Fifty years of change in an area of intensive agriculture: plant trait responses to habitat modification and conservation, Bedfordshire, England. *Biodiversity and Conservation*. Available 'online first'. [Primarily work by KJW following discussion and planning with CDP and provision of information on John Dony's original survey by CB].
- ***Walker K.J.**, Pinches C.E. & Wells T.C.E. Submitted. Reduced grazing and the decline of the threatened grassland herb *Pulsatilla vulgaris* Mill. (Ranunculaceae) in England, UK. *Biological Conservation*. [Original survey work and shading experiment by TCEW, repeat survey by KJW & CEP, analyses and writing by KJW]

Appendix 1

Extinct native species in Northamptonshire (v.c. 32) with year of last record:

Ajuga chamaepitys, 1712; *Allium oleraceum*, 1873; *Anagallis minima*, 1956; *Aphanes australis*, 1950; *Arabis glabra*, 1960; *Arnoseris minima*, 1879; *Botrychium lunaria*, 1954; *Bromus interruptus*, 1907; *Bupleurum tenuissimum*, 1965; *Callitriche hamulata*, 1987; *Carduus tenuiflorus*, 1950; *Carex binervis*, 1979; *Carex dioica*, 1974; *Carex echinata*, 1950; *Carex laevigata*, 1905; *Carex muricata*, 1980; *Cerastium pumilum*, 1965; *Ceratophyllum submersum*, 1878; *Cirsium dissectum*, 1950; *Cladium mariscus*, 1950; *Clinopodium calamintha*, 1957; *Cochlearia officinalis*, 1950; *Colchicum autumnale*, 1980; *Cynoglossum germanicum*, 1883; *Drosera rotundifolia*, 1822; *Eleocharis multicaulis*, 1915; *Eleocharis quinqueflora*, 1971; *Eleocharis uniglumis*, 1956; *Eleogiton fluitans*, 1930; *Epipactis palustris*, 1956; *Erica tetralix*, 1980; *Eriophorum gracile*, 1878; *Eriophorum latifolium*, 1965; *Erophila majuscula*, 1905; *Euphrasia arctica*, 1935; *Euphrasia pseudokernerii*, 1969; *Festuca filiformis*, 1878; *Filago minima*, 1953; *Fritillaria meleagris*, 1822; *Galeopsis angustifolia*, 1969; *Galium parisiense*, 1926; *Galium pumilum*, 1914; *Galium tricornutum*, 1930; *Gentianella anglica*, 1965; *Gentianella campestris*, 1882; *Gymnocarpium dryopteris*, 1973; *Hypericum montanum*, 1980; *Hypochaeris glabra*, 1878; *Jasione montana*, 1965; *Juncus squarrosus*, 1880; *Juniperus communis*, 1712; *Linum perenne*, 1978; *Luronium natans*, 1986; *Lycopodium clavatum*, 1885; *Lythrum hyssopifolium*, 1912; *Lythrum portula*, 1880; *Marrubium vulgare*, 1975; *Mentha suaveolens*, 1930; *Misopates orontium*, 1951; *Moenchia erecta*, 1877; *Montia fontana*, 1965; *Myosurus minimus*, 1979; *Myriophyllum alterniflorum*, 1987; *Nardus stricta*, 1950; *Oenanthe crocata*, 1976; *Oenanthe lachenalii*, 1930; *Ophrys sphegodes*, 1852; *Orchis ustulata*, 1956; *Oreopteris limbosperma*, 1889; *Osmunda regalis*, 1822; *Parnassia palustris*, 1970; *Persicaria minor*, 1851; *Persicaria mitis*, 1965; *Pilularia globulifera*, 1746; *Platanthera bifolia*, 1960; *Polygonatum multiflorum*, 1907; *Potamogeton acutifolius*, 1910; *Potamogeton friesii*, 1948; *Potamogeton gramineus*, 1910; *Potamogeton obtusifolius*, 1984; *Potamogeton trichoides*, 1900; *Potentilla palustris*, 1950; *Rosa obtusifolia*, 1970; *Rosa rubiginosa*, 1987; *Rosa stylosa*, 1911; *Salvia pratensis*, 1884; *Silene gallica*, 1843; *Solidago virgaurea*, 1960; *Sparganium natans*, 1910; *Spiranthes spiralis*, 1847; *Stachys germanica*, 1870; *Stellaria neglecta*, 1972; *Teesdalia nudicaulis*, 1712; *Tephrosia integrifolia*, 1726; *Teucrium scordium*, 1884; *Thelypteris palustris*, 1930; *Thymus pulegioides*, 1975; *Torilis arvensis*, 1974; *Utricularia minor*, 1965; *Utricularia vulgaris*, 1989; *Valerianella carinata*, 1930; *Valerianella dentata*, 1975; *Valerianella rimosa*, 1882.

Appendix 2

Revisions to the Gent & Wilson (1995) list of localised extinct species in the vice-county of Northamptonshire (v.c. 32).

Species	Decision	Reason
<i>Anagallis minima</i>	Extinct	Not recorded since 1989
<i>Aphanes australis</i>	Extinct	Not recorded since 1989
<i>Arabis glabra</i>	Extinct	Not recorded since 1989
<i>Bromus interruptus</i>	Extinct	Not included in the Gent & Wilson list
<i>Callitriche hamulata</i>	Extinct	Not recorded since 1989
<i>Cardamine impatiens</i>	Exclude	British native, probably introduced to v.c.32
<i>Carex binervis</i>	Extinct	Not recorded since 1989
<i>Carex muricata</i>	Extinct	Not recorded since 1989
<i>Centaurea cyanus</i>	Exclude	Not native
<i>Cerastium pumilum</i>	Extinct	Not recorded since 1989
<i>Chamaemelum nobile</i>	Exclude	British native, probably introduced to v.c.32
<i>Chenopodium vulvaria</i>	Exclude	British native, probably introduced to v.c.32
<i>Cladium mariscus</i>	Extinct	Not included in the Gent & Wilson list
<i>Cochlearia officinalis</i>	Extinct	Not recorded since 1989
<i>Crepis foetida</i>	Exclude	Never confirmed, probably recorded in error
<i>Cystopteris fragilis</i>	Exclude	British native, probably introduced to v.c.32
<i>Daphne mezereum</i>	Exclude	British native, probably introduced to v.c.32
<i>Eleocharis uniglumis</i>	Extinct	Not included in the Gent & Wilson list
<i>Erica tetralix</i>	Extinct	Not recorded since 1989
<i>Erodium moschatum</i>	Exclude	British native, probably introduced to v.c.32
<i>Erophila majuscula</i>	Extinct	Critical segregate
<i>Eryngium campestre</i>	Exclude	British native, probably introduced to v.c.32
<i>Euphrasia arctica</i>	Extinct	Critical segregate
<i>Euphrasia pseudokernerii</i>	Extinct	Not recorded since 1989
<i>Filago gallica</i>	Exclude	Not native
<i>Galium parisiense</i>	Extinct	Not recorded since 1989
<i>Galium sternerii</i>	Exclude	Never confirmed, probably recorded in error
<i>Galium tricornerum</i>	Extinct	Not included in the Gent & Wilson list
<i>Gymnocarpium robertianum</i>	Exclude	British native, probably introduced to v.c.32
<i>Impatiens noli-tangere</i>	Exclude	British native, probably introduced to v.c.32
<i>Luronium natans</i>	Extinct	Not recorded since 1989
<i>Lythrum hyssopifolium</i>	Extinct	Not included in the Gent & Wilson list
<i>Myosurus minimus</i>	Extinct	Not recorded since 1989
<i>Myriophyllum alterniflorum</i>	Extinct	Not recorded since 1989
<i>Papaver hybridum</i>	Exclude	Rediscovered since 1970
<i>Pedicularis sylvatica</i>	Exclude	Rediscovered since 1971
<i>Plantago coronopus</i>	Exclude	British native, probably introduced to v.c.32
<i>Polygala vulgaris</i> subsp. <i>collina</i>	Exclude	Subspecies (species still extant)
<i>Potamogeton alpinus</i>	Exclude	Rediscovered since 1972
<i>Potamogeton obtusifolius</i>	Extinct	Not recorded since 1989
<i>Prunus cerasus</i>	Exclude	Not native
<i>Rosa obtusifolia</i>	Extinct	Not recorded since 1989
<i>Rosa rubiginosa</i>	Extinct	Not recorded since 1989
<i>Rosa stylosa</i>	Extinct	Not recorded since 1989
<i>Sagina subulata</i>	Exclude	Never confirmed, probably recorded in error

Appendix 2 continued.

Species	Decision	Reason
<i>Scleranthus perennis</i>	Exclude	Never confirmed, probably recorded in error
<i>Silene gallica</i>	Extinct	Not included in the Gent & Wilson list
<i>Spiranthes spiralis</i>	Extinct	Not recorded since 1989
<i>Stellaria neglecta</i>	Extinct	Not recorded since 1989
<i>Stratiotes aloides</i>	Exclude	Rediscovered since 1973
<i>Thymus pulegioides</i>	Extinct	Not recorded since 1989
<i>Torilis arvensis</i>	Extinct	Not recorded since 1989
<i>Trifolium scabrum</i>	Exclude	British native, probably introduced to v.c.32
<i>Ulex minor</i>	Exclude	Rediscovered since 1974
<i>Valerianella dentata</i>	Extinct	Not recorded since 1989

Appendix 3

Extinct British native species in Bedfordshire and Northamptonshire with the year in which the species was last recorded. Extant species are denoted by a dash; British native species introduced into the county but now extinct are given in parentheses. ? year of last record unknown.

	Beds	Northants		Beds	Northants		Beds	Northants
<i>Ajuga chamaepitys</i> ^{VU}	-	1712†	<i>Cicuta virosa</i> ^{NS}	1798†		<i>Fritillaria meleagris</i> ^{NS}	1967	1822†
<i>Alchemilla xanthochlora</i>	1969	-	<i>Cirsium dissectum</i>		1950	<i>Fumaria parviflora</i> ^{NSa}	1950	
<i>Allium oleraceum</i>	-	1873	<i>Cladium mariscus</i>		1950	<i>Galium pumilum</i> ^{NS}	1944†	1914†
<i>Anagallis minima</i>	1953	1956	<i>Clinopodium calamintha</i> ^{NS}		1957	<i>Galium tricornerutum</i> ^{CRa}	-	1830
<i>Antennaria dioica</i>	1926	-	<i>Cochlearia officinalis</i>		1950	<i>Genista anglica</i>	1875	-
<i>Aphanes australis</i>	-	1950	<i>Colchicum autumnale</i>	1798	1980	<i>Gentianella anglica</i> ^{NS}	1930	1965
<i>Apium inundatum</i>	1976	-	<i>Cynoglossum germanicum</i> ^{VU}	1944	1883	<i>Gentianella campestris</i>		1882
<i>Aquilegia vulgaris</i>	1930	-	<i>Dianthus armeria</i> ^{VU}	1976		<i>Geum rivale</i>	1976	-
<i>Arabis glabra</i> ^{VU}		1960	<i>Dianthus deltoides</i> ^{NS}	1798		<i>Gymnocarpium dryopteris</i>		1973†
<i>Arnoseris minima</i> ^{EXa}	1930	1879	<i>Drosera anglica</i>	1798†		<i>Hammarbya paludosa</i>	1798	
<i>Baldellia ranunculoides</i>	1976	-	<i>Drosera rotundifolia</i>	1942	1822	<i>Himantoglossum hircinum</i> ^{VU}	1953	
<i>Botrychium Lunaria</i>	1798†	1954	<i>Eleocharis acicularis</i>	1802†	-	<i>Hydrocharis morsus-ranae</i>	1856	-
<i>Bromus interruptus</i> ^{EW}		1907	<i>Eleocharis multicaulis</i>		1915	<i>Hypericum elodes</i>	1798†	
<i>Bupleurum tenuissimum</i> ^{NS}		1965	<i>Eleocharis quinqueflora</i>		1971	<i>Hypericum montanum</i>	1921	1980
<i>Buxus sempervirens</i> ^{NR}	?		<i>Eleocharis uniglumis</i>	1976	1956	<i>Hypochaeris glabra</i>	1953	1878†
<i>Callitriche hamulata</i>	-	1987	<i>Eleogiton fluitans</i>		1930	<i>Jasione montana</i>	-	1965
<i>Campanula patula</i> ^{NS}	1889		<i>Epipactis palustris</i>	1976	1956	<i>Juncus squarrosus</i>	-	1880
<i>Carduus tenuiflorus</i>		1950	<i>Equisetum hyemale</i>	1798		<i>Juniperus communis</i> ^{NR}	1889	1712†
<i>Carex binervis</i>	1969	1979	<i>Equisetum sylvaticum</i>	1798	-	<i>Linum perenne</i> ^{NS}		1978
<i>Carex dioica</i>	1805	1974	<i>Erica cinerea</i>	1976	-	<i>Luronium natans</i> ^{NS}		1986†
<i>Carex divisa</i> ^{NS}	1920†		<i>Erica tetralix</i>	1880	1980	<i>Lycopodiella inundata</i> ^{NS}	1953	
<i>Carex echinata</i>	-	1950	<i>Eriophorum gracile</i> ^{VU}		1878†	<i>Lycopodium clavatum</i>	1907	1885†
<i>Carex elata</i>	1911	-	<i>Eriophorum latifolium</i>		1965	<i>Lythrum hyssopifolium</i> ^{VUa}	1850	1912
<i>Carex hostiana</i>	1952†	-	<i>Erophila majuscula</i>		1905	<i>Maianthemum bifolium</i> ^{VU}	1835†	
<i>Carex laevigata</i>		1905†	<i>Euphrasia arctica</i>		1935	<i>Marrubium vulgare</i> ^{NS}		1975
<i>Carex muricata</i> ssp. <i>lamprocarpa</i>	-	1980	<i>Festuca filiformis</i>		1878†	<i>Medicago sativa</i> subsp. <i>falcata</i> ^{NS}	1953	-
<i>Cerastium pumilum</i> ^{NS}	-	1965	<i>Filago lutescens</i> ^{VU}	1930		<i>Melampyrum pratense</i>	1930	-
<i>Ceratophyllum submersum</i>	1887†	1878†	<i>Filago minima</i>	-	1953	<i>Mentha pulegium</i> ^{VU}	1907	-
<i>Chenopodium urbicum</i> ^{NRa}	1976		<i>Filago pyramidata</i> ^{ENa}	1890		<i>Mentha suaveolens</i>		1930
<i>Chrysosplenium alterniflorum</i>	1844†		<i>Frangula alnus</i>	1979	-	<i>Misopates orontium</i> ^a	-	1951

Appendix 3 continued.

	Beds	Northants		Beds	Northants		Beds	Northants
<i>Moenchia erecta</i>	1930	1877†	<i>Polygala serpyllifolia</i>	1976	-	<i>Sparganium natans</i>	-	1910†
<i>Montia fontana</i>	-	1965	<i>Polygonatum multiflorum</i>	-	1907	<i>Spiranthes spiralis</i>	-	1847
<i>Myosurus minimus</i>	-	1979	<i>Potamogeton acutifolius</i> ^{VU}	-	1910†	<i>Stachys germanica</i> ^{EN}	1805	1870†
<i>Myriophyllum alterniflorum</i>	1889†	1987	<i>Potamogeton alpinus</i>	1969	-	<i>Stellaria neglecta</i>	-	1972†
<i>Nardus stricta</i>	1955	1950	<i>Potamogeton friesii</i>	1976	1948	<i>Stellaria palustris</i>	1968	-
<i>Narthecium ossifragum</i>	1798	-	<i>Potamogeton gramineus</i>	-	1910†	<i>Teesdalia nudicaulis</i>	-	1712†
<i>Nymphoides peltata</i> ^{NS}	1910	-	<i>Potamogeton obtusifolius</i>	-	1984	<i>Tephrosia integrifolia</i> ^{NS}	-	1726
<i>Oenanthe crocata</i>	-	1976	<i>Potamogeton polygonifolius</i>	1886	-	<i>Teucrium scordium</i> ^{VU}	-	1884
<i>Oenanthe lachenalii</i>	-	1930	<i>Potamogeton trichoides</i>	1930†	1900	<i>Thalictrum minus</i>	1841	(1965)
<i>Oenanthe silaifolia</i> ^{NS}	1886	-	<i>Potentilla palustris</i>	1969	1950	<i>Thelypteris palustris</i> ^{NS}	1798†	1930
<i>Ophrys sphegodes</i> ^{NS}	1788†	1852	<i>Pulicaria vulgaris</i> ^{VU}	1864	-	<i>Torilis arvensis</i> ^{NSa}	-	1974
<i>Orchis ustulata</i> ^{NS}	-	1956	<i>Pyrola minor</i>	1878	-	<i>Tricophorum cespitosum</i>	1798†	-
<i>Oreopteris limbosperma</i>	1932	1889	<i>Ranunculus sardous</i>	1976	(1982)	<i>Utricularia minor</i>	1798†	1965
<i>Osmunda regalis</i>	-	1822†	<i>Rhynchospora alba</i>	1798†	-	<i>Utricularia vulgaris</i>	1889	1989
<i>Parnassia palustris</i>	1925	1970	<i>Sagina nodosa</i>	1926	-	<i>Vaccinium oxycoccus</i>	1798	-
<i>Pedicularis palustris</i>	1926	-	<i>Salix repens</i>	1911	-	<i>Valerianella dentata</i> ^a	-	1975
<i>Pedicularis sylvatica</i>	1969	-	<i>Salvia pratensis</i> ^{NS}	1880	1884†	<i>Valerianella rimosa</i> ^{CRa}	-	1882†
<i>Persicaria minor</i>	-	1851	<i>Schoenus nigricans</i>	1798†	-	<i>Verbascum pulverulentum</i> ^{NS}	1875†	-
<i>Persicaria mitis</i> ^{NS}	-	1965	<i>Silene gallica</i> ^{NSa}	-	1843†	<i>Vulpia unilateralis</i>	1957†	-
<i>Pilularia globulifera</i> ^{NS}	-	1746†	<i>Silene noctiflora</i> ^a	1981	-	Total number of extinctions	94	94
<i>Pinguicula vulgaris</i>	1921	-	<i>Sium latifolium</i> ^{NS}	1976	-	Number of single records	21	24
<i>Platanthera bifolia</i>	1976	1960	<i>Solidago virgaurea</i>	-	1960			

Notes: Plant status follows Cheffings (2004): EX, extinct; EW, extinct in the wild; CR, critically endangered; EN, endangered; VU, vulnerable; NR, nationally rare taxa not in an IUCN category; NS, nationally scarce taxa not in an IUCN category. ^a Archaeophytes or probable archaeophytes after Preston et al. (2004). † Presence in the county based on a single record.

Appendix 4

UK Broad Habitat types (after Preston et al. 2003b) in relation to the Braun-Blanquet phytosociological units (Ellenberg 1988).

Broad Habitat type		Braun-Blanquet associations
1	Broad-leaved, mixed and yew woodland	Broad-leaved woods, scrub and wood-edge
3/16	Boundary/linear features and inland rock	Stony sites and walls
4	Arable and horticulture	Secalietea
6	Neutral grassland	Molinio-Arrhenatheretea ^a , Agrostietea stoloniferae
7	Calcareous grassland	Festuco-Brometea
8	Acid grassland	Sedo-Scleranthetea
10	Dwarf shrub heath	Nardo-Callunetea, conifers and allied heaths
11	Fen, marsh and swamp	Phragmitetea, Montia-Cardaminetea
12	Bog	Scheuchzerio-Caricetea nigrae, Oxycocco-Sphagnetea
13/14	Freshwater (includes standing water, canals, rivers, streams)	Lemnetea, Utricularietea, Potamogetonetea, Littorelletea, Isoëto-Nanojuncetea, Bidentetea
17	Built-up and gardens	Chenopodietea, Artemisietea, Agropyretea, Plantaginetea,
18/19/21	Coastal (includes supralittoral rock/sediment, littoral sediment)	Saltwater and sea coast
-	None	Wide amplitude

^a The majority of improved grassland species are included within the Molinio-Arrhenatheretea by Ellenberg (1988).

Appendix 5

Details of John Dony's fixed plots ('habitat studies') in Bedfordshire ($n = 107$). '% similarity' is the similarity in composition calculated using Czekanowski's Index of Similarity.

Habitat study ¹	Broad habitat	OS grid ref.	Altitude (m)	Soil type ²	Soil pH		No. of species		% similarity	Cause of change for sites with similarity < 40%	
					1949	2004	1949	2004			
1	Sharnbrook Summit, W	Calc grass	SP96856242	101	C/L	7.4	7.2	47	43	50	
2	Sharnbrook Summit, E	Calc grass	SP96856237	101	C/L	7.5	5.8	45	18	37	Natural succession - scrub
3	West Wood, ride	Neut grass	SP98936247	94	BCOCL	7.4	7.6	60	21	7	Natural succession - wood
4	West Wood, wood	Basic wood	SP98926250	94	BCOCL	7.4	4.9	37	12	26	Natural succession - wood
5	Great Hayes Wood, ride	Acid wood	SP96556184	101	BCOCL	7.0	6.1	47	34	31	Natural succession - wood
6	Great Hayes Wood, wood	Basic wood	SP96546185	101	BCOCL	5.2	5.4	26	27	46	
7	Wymington	Arable	SP96406275	101	BCOCL	7.5	6.5	30	28	22	Abandonment/setaside
8	Judge's Spinney	Basic wood	TL0175413	69	BCOCL	7.3	7.6	35	18	49	
9	Felmersham	River	SP99055785	38	A/RG	7.4	7.2	7	17	47	
10	Felmersham	Swamp	SP99055785	38	A/RG	7.4	7.2	33	25	17	River/drainage works
11	Oakely Bottom	River	TL0085529	35	A/RG	7.3	7.1	12	8	19	River/drainage works
12	Oakely Bottom	River	TL0085529	35	A/RG	7.3	7.1	6	16	23	River/drainage works
13	Oakely Bottom	Swamp	TL0085529	35	A/RG	7.3	7.1	44	28	17	River/drainage works
14	Biddenham	River	TL0125496	29	A/RG	7.0	7.8	24	14	6	Road
15	Biddenham	Neut grass	TL0125496	29	A/RG	7.0	7.8	22	21	9	Road
16	Felmersham	Swamp	SP99005803	40	A/RG	7.5	7.5	20	24	24	River/drainage works
17	Felmersham	Neut grass	SP99005803	40	A/RG	7.5	7.5	29	13	24	Converted to pasture
18	Stevington (SSSI)	Marsh	SP98265471	38	A/RG	7.2	7.3	36	43	42	
19	Stevington (SSSI)	Swamp	SP98265471	38	A/RG	7.0	7.2	31	40	38	Unknown
20	Pavenham (SSSI)	Marsh	SP98235483	38	A/RG	7.2	7.2	37	39	58	
21	Felmersham Gravel Pits	Swamp	SP98795814	40	A/RG	7.4	6.6	10	11	8	Unknown
22	Felmersham Gravel Pits	Neut grass	SP98795814	40	A/RG	7.4	6.6	29	28	9	Unknown
23	Sharnbrook	Arable	SP98975821	40	A/RG	7.5	5.7	27	20	14	Intensive arable
24	Willington	Swamp	TL1186504	20	A/RG	7.2	6.8	76	17	20	River/drainage works
25	Eaton Socon	Swamp	TL1799604	14	A/RG	7.4	7.3	16	22	18	River/drainage works
26	Eaton Socon	Marsh	TL1799604	14	A/RG	7.4	7.3	46	10	8	Recreation
27	Biggleswade Common	Marsh	TL1941476	29	AOG	6.0	4.1	28	37	26	Unkown
28	Willington	Waste	TL1015496	24	A/RG	7.0	7.6	44	23	7	Converted to pasture

Appendix 5 continued.

Habitat study ¹	Broad habitat	OS grid ref.	Altitude (m)	Soil type ²	Soil pH		No. of species		% similarity	Cause of change for sites with similarity < 40%	
					1949	2004	1949	2004			
29	Willington	Arable	TL1005496	23	A/RG	7.0	5.9	24	20	6	Converted to pasture
30	Holcot Wood	Basic wood	SP95924022	87	BCOCL	7.2	7.2	37	28	61	
31	Marston Thrift (SSSI)	Marsh	SP97504180	56	BCOCL	5.2	7.6	48	57	52	
32	Marston Thrift	Basic wood	SP97464175	56	BCOCL	5.2	4.0	26	26	29	Natural succession - wood
33	Wootton Wood	Basic wood	SP99724501	61	BCOCL	7.6	6.4	17	35	38	Unknown
34	Brogborough Pit	Neut grass	SP96903887	61	C	7.6	7.4	54	25	19	Gravel extraction
35	Heath and Reach	Heath/mire	SP91962834	110	LG	5.8	4.2	19	22	12	Natural succession - wood
36	King's Wood (SSSI)	Heath/mire	SP92482986	122	LG	5.4	4.4	49	23	24	Natural succession - scrub
37	Cooper's Hill (SSSI)	Heath/mire	TL0275376	108	LG	5.8	7.0	14	31	10	Converted to pasture
38	Clophill	Waste	TL0824371	69	LG	6.4	7.6	60	40	14	Road
39	Simpson's Hill Plantation	Acid grass	TL0815371	69	LG	5.4	5.1	31	20	20	Gravel extraction
40	Rowney Warren	Heath/mire	TL1236404	64	LG	6.6	8.2	60	46	45	
41	Horsemoor Farm	Acid grass	SP93593325	122	LG	6.2	3.6	40	17	13	Afforestation
42	Jackdaw Hill	Acid grass	SP99663865	91	LG	4.8	8.0	27	33	40	?
43	King's Wood (SSSI)	Acid wood	SP92952950	145	BCOG	5.4	5.3	24	25	30	Natural succession – wood
44	King's Wood (SSSI)	Acid wood	SP92952950	145	BCOG	5.4	7.6	13	36	17	Natural succession – wood
45	Aspley Wood	Basic wood	SP93843435	114	LG	5.4	7.3	25	32	12	Gravel extraction
46	King's Wood (SSSI)	Basic wood	TL0451405	69	BCOG	7.2	6.8	40	37	51	
47	King's Wood (SSSI)	Basic wood	TL0465401	96	BCOG	6.0	7.2	28	39	35	Unknown
48	Wilstead Wood	Basic wood	TL0730426	58	BCOG	6.0	6.2	74	55	47	
49	Wilstead Wood	Basic wood	TL0725426	58	BCOG	6.4	4.7	45	54	39	Unknown
50	New Wavendon Heath	Heath/mire	SP93133383	120	AOG	5.6	5.2	25	18	43	
51	Mermaid's Pond	Heath/mire	SP93853474	114	LG	4.2	4.7	9	20	13	Gravel extraction
52	Horsemoor Farm	Marsh	SP93639325	114	AOG	6.0	6.5	42	27	48	
53	Flitwick Moor	Marsh	TL0443345	64	AOG	4.4	5.6	52	16	5	Converted to pasture
54	Flitwick Moor	Marsh	TL0445346	62	AOG	6.0	6.2	42	19	22	Natural succession – scrub
55	Flitwick Moor (SSSI)	Heath/mire	TL0443346	62	AOG	6.0	5.1	7	36	5	Natural succession – scrub
56	Folly Wood (SSSI)	Heath/mire	TL0479353	61	AOG	6.0	3.8	21	7	8	Natural succession – wood
57	Westoning Moor	Marsh	TL0220324	73	AOG	5.2	3.6	39	22	13	Natural succession – wood
58	Moors Plantation	Basic wood	TL0209329	73	AOG	6.4	5.0	40	28	40	Alien species

Appendix 5 continued.

Habitat study ¹	Broad habitat	OS grid ref.	Altitude (m)	Soil type ²	Soil pH		No. of species		% similarity	Cause of change for sites where similarity < 40%	
					1949	2004	1949	2004			
59	Cooper's Hill	Marsh	TL0256374	79	AOG	6.2	5.4	39	39	54	
60	Heath and Reach	Waste	SP92002820	99	LG	6.2	6.6	45	59	40	Abandonment/setaside
61	Amphill	Neut grass	TL0219374	79	C	7.2	8.2	30	15	5	Natural succession – scrub
62	Amphill	Neut grass	TL0216374	79	C	7.2	7.5	36	29	33	Natural succession – scrub
63	Galley Hill	Heath/mire	TL2189484	43	LG	4.8	4.9	18	18	55	
64	Bunker's Hill	Heath/mire	TL1920476	38	LG	4.6	3.7	28	7	47	
65	Hill, Sandy	Waste	TL1798489	62	LG	6.0	3.6	29	8	0	Afforestation
66	Sutton Fen	Heath/mire	TL2072475	29	AOG	4.4	3.8	18	8	46	
67	Sutton	Waste	TL2080488	37	LG	7.2	6.5	22	12	4	Gravel extraction
68	Potton Wood (SSSI)	Basic wood	TL2520500	78	BCOCL	6.2	5.7	39	26	59	
69	Potton Wood (SSSI)	Neut grass	TL2517501	78	BCOCL	6.2	6.8	19	72	15	Unknown
70	Blackgrove Wood	Basic wood	SP97892362	98	C	6.4	6.7	49	15	28	Afforestation
71	Daintry Wood	Acid wood	SP99763133	122	BCOG	5.5	5.0	41	35	30	Afforestation
72	Cow Common	Swamp	SP97962302	93	A/RG	7.8	7.6	23	29	6	River/drainage works
73	Cow Common	Calc grass	SP97982303	93	A/RG	7.8	7.4	54	15	11	Converted to arable
74	Well Head	Swamp	SP99882043	122	A/RG	7.6	7.0	24	23	38	Unknown
75	Well Head	Marsh	SP99882044	122	A/RG	7.6	7.3	28	29	38	Unkwown
76	Arlesey	Neut grass	TL1874353	30	C	7.6	7.8	49	40	30	Gravel extraction
77	Knocking Hoe (NNR)	Calc grass	TL1307309	99	C/L	7.6	7.8	45	46	66	
78	Barton Hills (NNR)	Calc grass	TL0889299	122	C/L	7.7	7.9	38	35	59	
79	Ravensborough Castle	Calc grass	TL0975296	137	C/L	7.7	7.5	47	39	13	Converted to arable
80	Totternhoe Knolls (SSSI)	Calc grass	SP97842220	152	C/L	7.6	8.0	39	58	52	
81	Dunstable Cutting	Calc grass	TL0040234	137	C/L	7.6	7.4	44	47	18	Natural succession – scrub
82	Dunstable Cutting	Calc grass	TL0040234	137	C/L	7.6	7.9	35	38	46	
83	Dunstable Downs (SSSI)	Calc grass	TL0059210	213	C/L	7.7	7.9	37	46	53	
84	Galley Hill	Calc grass	TL0920272	152	C/L	7.6	7.2	43	54	40	Lack of grazing
85	Galley Hill (SSSI)	Calc grass	TL0921270	183	CWF	6.0	7.8	42	44	29	Lack of grazing
86	Galley Hill	Calc grass	TL0922274	140	C/L	7.6	7.5	41	52	14	Afforestation
87	Barton	Calc grass	TL0970302	130	C/L	7.8	7.6	45	27	3	Converted to arable
88	Leete Wood	Neut grass	TL0886294	145	C/L	7.8	7.6	58	38	32	Natural succession - scrub

Appendix 5 continued.

Habitat study ¹	Broad habitat	OS grid ref.	Altitude (m)	Soil type ²	Soil pH		No. of species		% similarity	Cause of change for sites where similarity < 40%
					1949	2004	1949	2004		
89	Maulden Firs	TL0930273	152	C/L	7.6	7.5	21	14	42	
90	Barton	TL0965296	137	C/L	7.7	7.8	45	56	53	
91	Totternhoe	SP97902235	122	C/L	7.8	7.4	41	14	6	Converted to pasture
92	Galley Hill	SP09232692	175	C/L	7.4	8.0	24	25	11	Intensive arable
93	Chiltern Green Common	TL1338196	175	CWF	5.2	5.9	24	26	0	Converted to arable
94	Whipsnade Heath	TL0179178	191	CWF	7.4	7.5	50	9	4	Natural succession - scrub
95	Greencroft Barn	TL0230139	177	CWF	6.0	7.1	31	27	2	Converted to arable
96	Horsley/Swamp Wood	TL1316190	145	CWF	5.2	4.9	33	32	35	Afforestation
97	Horsley's Wood	TL1319191	145	CWF	5.2	3.8	16	13	45	
98	Folly Wood	TL0568200	177	CWF	6.7	3.8	40	16	31	Natural succession - wood
99	Deadmansey Wood, 1st	TL0330166	177	CWF	7.6	4.1	34	26	33	Afforestation
100	Deadmansey Wood, 2nd	TL0340167	177	CWF	5.4	4.6	38	35	24	Afforestation
101	Deadmansey Wood, 2nd	TL0342167	177	CWF	5.4	3.5	32	17	24	Afforestation
102	Greencroft Barn	TL0226136	177	CWF	5.8	3.8	37	22	41	
103	Greencroft Barn	TL0219136	177	CWF	7.0	6.4	36	15	12	Converted to pasture
104	George Wood	TL0731271	140	BCOCL	6.2	5.9	57	21	38	Natural succession - wood
105	Legrave	TL0607247	116	A/RG	6.3	7.1	29	17	7	River/drainage works
106	Legrave Common	TL0599245	116	A/RG	6.8	7.6	39	26	41	
107	Chiltern Green	TL1278186	146	C/L	7.2	7.7	24	29	26	Intensive arable

¹ Protected sites: SSSI = Site of Special Scientific Interest; NNR = National Nature Reserve. ² Codes for soil types are as follows: A/RG - alluvium/river gravel; AOG - alluvium over greensand; BCOCL - boulder clay over Great Oolite Limestone; BCOG - boulder clay over greensand; C - clay; C/L - chalk/limestone; CWF - clay with flints; LG - Lower Greensand.

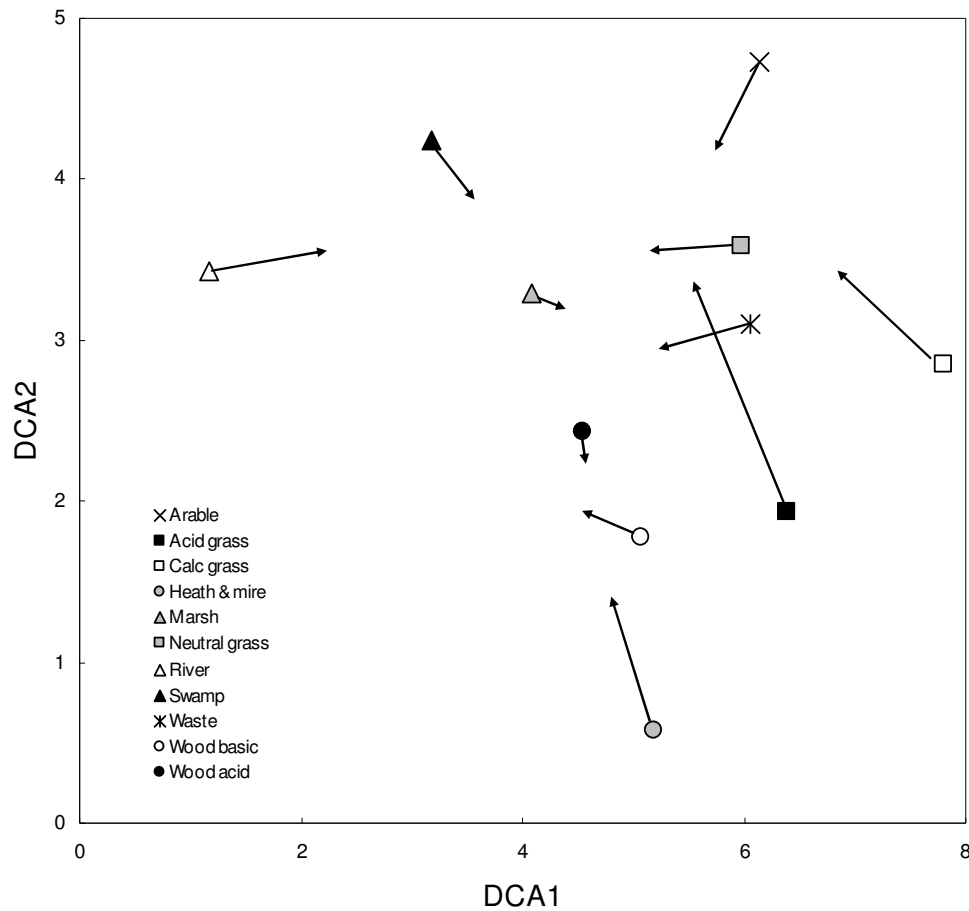
Appendix 6

Mean values (\pm SE) for colonisation and extinction rates in relation to plant trait categories.

Trait	Category	Colonisation rate			Extinction rate		
		<i>n</i>	mean	SE	<i>n</i>	mean	SE
Local range	Rare	399	0.01	0.001	343	0.81	0.017
	Intermediate	186	0.05	0.005	186	0.70	0.015
	Widespread	31	0.16	0.018	31	0.56	0.029
English range	Rare	61	<0.01	<0.001	55	0.82	0.044
	Intermediate	152	<0.01	0.001	140	0.82	0.025
	Widespread	361	0.05	0.004	337	0.72	0.014
Specialism Index	Cosmopolitan	16	0.18	0.029	16	0.62	0.042
	Intermediate	94	0.08	0.009	94	0.70	0.019
	Specialist	450	0.02	0.001	449	0.78	0.014
Ellenberg <i>L</i>	Shade	77	0.03	0.005	70	0.64	0.035
	Intermediate	376	0.04	0.003	340	0.75	0.015
	Light	156	0.02	0.003	145	0.83	0.022
Ellenberg <i>F</i>	Dry	425	0.04	0.003	383	0.75	0.014
	Moist	102	0.03	0.004	75	0.73	0.031
	Wet	82	0.01	0.002	77	0.83	0.032
Ellenberg <i>N</i>	Oligotrophic	238	0.02	0.002	229	0.78	0.018
	Mesotrophic	247	0.04	0.004	222	0.73	0.019
	Eutrophic	124	0.04	0.006	104	0.77	0.028
Ellenberg <i>R</i> _{diff}	Neutral	264	0.04	0.004	242	0.76	0.018
	Weak acid/alkaline	222	0.04	0.004	198	0.78	0.017
	Strong acid/alkal.	123	0.02	0.006	115	0.80	0.031
Plant height (cm)	1-25	89	0.02	0.004	85	0.80	0.027
	26-99	306	0.03	0.004	284	0.79	0.016
	100-299	142	0.05	0.002	126	0.71	0.025
	300-4600	50	0.05	0.004	41	0.56	0.052
Lateral spread	Little/none	350	0.03	0.003	314	0.78	0.015
	Limited	137	0.04	0.007	128	0.72	0.027
	Far-reaching	122	0.04	0.004	113	0.73	0.027
Longevity	Annual	145	0.03	0.004	129	0.85	0.021
	Biennial/perennial	471	0.03	0.003	431	0.73	0.014
Seed bank longevity	Transient	173	0.03	0.004	158	0.70	0.025
	Short-term persist	208	0.05	0.005	198	0.75	0.017
	Long-term persist	115	0.04	0.005	103	0.80	0.025
Dispersal ability	Wind	130	0.04	0.005	124	0.74	0.025
	Water	57	0.02	0.004	52	0.73	0.041
	Animal	102	0.05	0.008	95	0.71	0.030
	Unspecialised	129	0.04	0.006	120	0.74	0.023
Fertilisation	Asexual	38	0.07	0.015	36	0.72	0.040
	Self	205	0.03	0.003	190	0.78	0.020
	Cross	170	0.04	0.005	156	0.70	0.023

Appendix 7

Plots of first two Detrended Correspondence Analysis (DCA) axes showing the relative shifts in the species composition of John Dony's fixed plots (habitat studies) in Bedfordshire recorded in 1949 and 2004 (direction indicated by an arrow). The total number of plots revisited was 107. The initial 1949 composition of the plots were classified into 11 broad habitats using TWINSpan. The mean value for each broad habitat in 1949 is indicated by a centroid with a symbol and its relative position in 2006 by the end-point of the arrow. Overall there was a clear convergence between habitats with the majority of moving towards a more central position on the diagram. Eigenvalues for axis 1 and 2 were 0.70 and 0.54 respectively. Detrended Correspondence Analysis was carried out in CANOCO V.4.02 (Ter Braak & Šmilauer 1998) with default values for all parameters and detrending by segments.



Appendix 8

Details of the 33 English populations of *Pulsatilla vulgaris* included in this study. †, presumed extinct; Last yr., the year of the last record for extinct populations; Status, conservation status (SSSI, Site of Special Scientific Interest; NNR, National Nature Reserve; dSSSI, former SSSI, now de-notified).

No.	Site	Vice-county	Last yr.	10-km	Geology	Alt. (m)	Aspect	Status ¹	Management
1	†Aldbury Nowers	Hertfordshire	1969	SP91	chalk	170	225	SSSI	Ungrazed
2	Ancaster Valley	South Lincolnshire	-	SK94	limestone	80	130	SSSI	Grazed by c.30 sheep (winter)
3	Aston Upton	Berkshire	-	SU58	chalk	120	280	SSSI	Ungrazed but some mowing/burning
4	Barnack Hills and Holes	Northamptonshire	-	TF00	limestone	50	180	NNR	Grazed 1978+ (Sep-Feb) c.125 sheep wks ha ⁻¹
5	Barnsley Warren	East Gloucestershire	-	SP00	limestone	150	260	SSSI	Grazed (February-March, June+)
6	Barton Hills	Bedfordshire	-	TL03	chalk	110	180	NNR	Grazed (April-December)
7	Beaumonts Hay	East Gloucestershire	-	SP12	limestone	140	210	SSSI	Irregular grazing
8	Bourton Downs	East Gloucestershire	-	SP13	limestone	240	270	SSSI	Grazed (September-March)
9	†Broughton Far Wood	North Lincolnshire	1969	SE91	limestone	15	240	SSSI	Ungrazed
10	†Clipper Down	Buckinghamshire	1976	SP91	chalk	200	220	SSSI	Heavy grazing (spring-autumn)
11	Deacon Hill	Bedfordshire	-	TL12	chalk	170	220	SSSI	Ungrazed (one area heavily-grazed)
12	Devil's Dyke	Cambridgeshire	-	TL66	chalk	60	220	SSSI	Ungrazed (infrequently mown/burnt/grazed)
13	†Fleam Dyke	Cambridgeshire	1973	TL55	chalk	30	240	SSSI	Ungrazed
14	†Hildersham Furze Hills	Cambridgeshire	1990	TL54	sand	60	280	SSSI	Ungrazed following severe rabbit grazing
15	†Holywell Mound	South Lincolnshire	1990s	TF01	limestone	60	230	SSSI	Heavily grazed and improved
16	†Honington Camp	South Lincolnshire	1992	SK94	limestone	120	290	SSSI	Ungrazed (re-introduced recently)
17	Hornsleasow Roughs	East Gloucestershire	-	SP15	limestone	240	180	SSSI	Light grazing (exc. March-May)
18	Knocking Hoe	Bedfordshire	-	TL13	chalk	110	180	NNR	Grazed (sheep and rabbits)
19	†Pitstone Hill	Buckinghamshire	1996	SP91	chalk	200	240	SSSI	Ungrazed (exclosure therefore rabbits only)
20	Ravensburgh Castle	Bedfordshire	-	TL02	chalk	150	220	NNR	Heavily grazed up to 1980s then no grazing
21	Rodborough Common	West Gloucestershire	-	SO80	limestone	140	220	SSSI	Light mowing/grazing
22	†Shacklewell Hollow	Leicestershire	1992	SK90	limestone	60	170	SSSI	Site destroyed
23	†Smithcombe Hill	Bedfordshire	1981	TL02	chalk	140	160	SSSI	Ungrazed until recently
24	†Southorpe Paddock	Northamptonshire	1995	TF00	limestone	30	0	SSSI	Ungrazed until the 1990s

Appendix 8 continued.

No.	Site	Vice-county	Last yr.	10-km	Geology	Alt. (m)	Aspect	Status	Management
25	†Southorpe Roughts	Northamptonshire	1981	TF00	limestone	140	130	SSSI	Ungrazed until recently 2004
26	Steps Hill	Buckinghamshire	-	SP91	chalk	110	190	SSSI	Ungrazed until recently
27	†Sweetslade Farm	E Gloucestershire	1967	SP11	limestone	150	280	none	Ungrazed
28	Therfield Heath	Hertfordshire	-	TL33	chalk	110	190	SSSI	Rotational winter grazing 1986+ plus mowing
29	†Unhill Bottom	Berkshire	1978	SU58	chalk	120	220	dSSSI	Improved
30	Taylor's Hill, Hilcot	East Gloucestershire	-	SP01	limestone	220	220	none	Grazed
31	Ledsham	South-west Yorkshire	-	SE43	limestone	40	140	SSSI	Winter grazing
32	†Lockinge	Berkshire	1995	SU48	chalk	190	0	none	Ungrazed
33	†Sutton Heath	Northamptonshire	2001	TF00	limestone	20	130	SSSI	Improved, heavy grazing

Appendix 9

Known introductions of *Pulsatilla vulgaris* in England.

Site name	Vice-county	Year	10km	Details of introduction
Blagdon Gap, Martin Down	Wilts/Dorset	1983+	SU01	Known from this area since c.1983 where two small populations grow on either side of the vice-county boundary on ancient species-rich chalk banks (SU052184, SU048189). Accepted as native by some authorities but much more likely to have been planted given the distance to the nearest native populations (Edwards and Pearman 2004).
Aston Upthorpe (Site 3)	Berkshire	1999+	SU58	87 plants grown from Aston Upthorpe seed introduced in 1999.
Hartslock	Oxfordshire	1998+	SU67	Although there are no historic records for this site, 78 plants grown from seed collected at Barton Hills NNR were planted in 1998 to investigate translocation techniques (Warden 2001). 55 (70%) transplants were still alive in 2004 although flowering performance was low due to grazing off of inflorescences (88%) by small rodents (K Warden, pers comm., 2005).
Park Place Chequers	Berkshire Bucks	1998	SU78 SP80	Presumably planted (Crawley 2005). Discovered in 1998 (SP8405) but assumed to have been planted.
Ancaster Valley (Site 2)	South Lincs	1992+	SK94	68 plants raised from Ancaster seed introduced since 1992.
Copper Hill Quarry, Ancaster	South Lincs	1994-96	SK94	Formerly grew in this quarry but was lost after the site was re-quarried (J Gibbons in litt. to TCE Wells, 1966). In April 1994 68 plants, originating from Ancaster seed, were planted in the SSSI but many were scratched out by rabbits and pheasants within a few days of planting. Four plants survived for two years but subsequently died.
Sussex	Sussex	?	TQ02	No details; presumed planted.
Middlesex	Middlesex	?	TQ27	No details; presumed planted.
Kent	Kent	?	TQ91	No details; presumed planted.
Blows Down	Bedfordshire	1998	TL02	Discovered in 1998 on a chalk quarry face (TL040219) where it had been planted (C Boon, pers. comm.).
Hollybush Hill	Hertfordshire	1992	TL12	Discovered on a road verge (TL125263) in 1992 where it had been planted (T James, pers. comm.).
Stevenage	Hertfordshire	1995	TL22	Discovered on a suburban roadside verge in Stevenage (TL243262) where it had been planted (T James, pers. comm.).
Gog Magog Down	Cambs	1994+	TL45	In 1994 a few plants were planted in downland reverting from arable (TL487529). The seed came from the garden of a nearby cottage but was of unknown origin (L Evans, pers. comm., 2006).
Southorpe Paddock (Site 24)	Northants	1999	TF00	12 plants raised from Barnack seed introduced in 1999 (see Appendix 10).
Ledsham (Site 31)	NW Yorkshire	c.2000	SE43	A single plant raised from Barnack seed was introduced in 2000 (see Appendix 10).

Appendix 10

Changes in the numbers of *Pulsatilla vulgaris* on the 33 sites included in this study (site numbers given in parentheses). Totals are the maximum number of crowns recorded in any one year for each decade and were derived from a variety of sources (see main text for details).

Site-population	1960-69	1970-79	1980-89	1990-99	2000-06
(a) Increasing					
Barnack Hills and Holes (4)	2000	1300	14200	15000	20000
Barnsley Warren (5)	50000	50000	50000	50000	75000
Barton Hills (6)	1100	685	4000	5000	5000
Knocking Hoe (18)	300	50	460	300	1000
Therfield Heath (28)	1000	2897	?	60000	60000
(b) Stable					
Ancaster Valley (2) ¹	6	5	16	11	6
Beaumonts Hay (7)	<100	?	25	?	10
Bourton Downs (8)	500	?	500	?	471
Deacon Hill (11)	1	?	5	7	1
Devil's Dyke (12)	250	1500	1000	500	250
Hornsleasow Roughs (17)	200	?	?	100	100
Taylor's Hill (30)	?	42	110	15	?
Ledsham (31) ³	?	?	2	2	1
(c) Declining					
Aston Upthorpe (3) ²	300	101	35	10	26
Ravensburgh Castle (20)	39	0	300	5	4
Rodborough Common (21)	300	3	?	40	37
Steps Hill (26)	500	100	30	10	52
(d) Extinct					
Aldbury Nowers (1)	17	0	0	0	0
Broughton Far Wood (9)	9	0	0	0	0
Clipper Down (10)	15	1	?	?	0
Fleam Dyke (13)	25	2	0	0	0
Hildersham Furze Hills (14)	4	14	5	1	0
Holywell Mound (15)	200	?	1	?	0
Honington Camp (16)	53	?	10	1	0
Lockinge (32)	2	?	?	?	0
Pitstone Hill (19)	1	1	?	2	0
Shacklewell Hollow (22)	56	?	?	3	0
Smithcombe Hill (23)	30	?	1	0	0
Southorpe Paddock (24)	8	2	3	5	0
Southorpe Roughs (25)	5	6	10	Present	0
Sweetslade Farm (27)	7	?	?	0	0
Sutton Heath (33)	?	1	?	?	0
Unhill Bottom (29)	750	3	0	0	0

¹ Excludes 68 plants introduced since 1992. ² Excludes 87 plants introduced since 1999.

Appendix 11

Details of 33 *Pulsatilla vulgaris* populations included in Chapter 7.

Site 1. †Aldbury Nowers SSSI, Hertfordshire

During the 1960s a few plants were recorded in rank *Bromopsis erectus* grassland (CG3b) and scrub overlying chalk adjacent to an Iron Age camp. The site was ungrazed for many years and subsequently scrubbed over (recently cleared) except in a few places where small fragments of chalk grassland remain. *Pulsatilla* has not been seen since 1969 despite repeated searches (T. James, pers comm.).

Site 2. Ancaster Valley SSSI, South Lincolnshire

A small colony still occurs in lightly grazed limestone grassland (CG3) on an east-facing slope of a narrow limestone valley. The site was not grazed for many years leading to the development of rank *Brachypodium pinnatum* grassland and dense gorse scrub. The latter was removed in the late 1980s and has since been winter-grazed by c.30 sheep (J. Welhan, pers. comm.). Due to improvement in the condition of the grassland 68 plants (grown from Ancaster seed) were re-introduced on to the same slope (in 1992, 1993, 1998 and 2002) where they are now protected by wire cages during the flowering period. All plants have been monitored annually since the early 1990s; in 2005 6 native plants and 22 (32%) introduced plants were recorded.

Site 3. Aston Upthorpe SSSI, Berkshire

A tiny remnant of a once extensive population that stretched over a number of downs close to the Fair Mile (Druce 1886; Crawley 2005). This had been reduced to c.300 plants by the 1960s which survived on a NW-facing chalk slope although flowering was limited due to heavy grazing by rabbits. An enclosure was erected around the bulk of the population in 1961 with an inner enclosure to exclude rabbits (repaired 1976 and replaced in 1998). This resulted in a gradual decline in *P. vulgaris* due to increased competition from coarse grasses and the grazing off of inflorescences by wood mice (Carter 1967). The population continued to decline in the 1970s and 1980s despite occasional mowing/burning to control the growth of *Bromopsis erectus*. Mowing was re-introduced in 1996 and this led to an increase in flowering performance although by this time only 13 plants remained (Warden 2001). No plants have been recorded outside this enclosure since 1994 due to very heavy rabbit grazing. Eighty-seven plants grown from Aston Upthorpe seed were planted inside the new enclosure in October 1999 (Warden 2001); 55 (63%) were still present in 2004 (K. Warden, pers comm.).

Site 4. Barnack Hills and Holes NNR, Northamptonshire

Many thousands of plants (>15,000) occur over a large area of mediaeval limestone quarry workings where they are confined to shallow soils on S and SW-facing slopes. Grazing ceased in 1914 and by

the 1960s the grassland was very rank *Bromopsis erectus*-*Brachypodium pinnatum* grassland with a dense layer of leaf litter. Sheep grazing (September to late-December) was re-introduced in 1978 resulting in a dramatic increase in flowering. Monitoring in fixed plots showed an increase from 260 in 1978 to 4,727 crowns by 2005. The entire population is now estimated to exceed 20,000 crowns (C. Gardiner, pers. comm.). The management is now considered ideal (Rich 1997) and as a result *P. vulgaris* has spread to new areas of the reserve where it may have established from seed (C. Gardiner, pers comm.).

Site 5. Barnsley Warren SSSI, East Gloucestershire

The largest population in the UK with the majority of plants occurring at high density in exceptionally rich limestone turf on a steep (c.20°) SW-facing slope where soils are very shallow and there is much bare soil and limestone rubble. Small numbers of plants have also occurred sporadically on a W-facing slope nearby. Historically the site has been heavily grazed by sheep, cattle and horses and the vegetation burnt ('swaled') in February or March. This practice was abandoned in 1971; since then the site has been grazed by sheep, at high density, between February to March and then from June onwards. This management has resulted in an increase from around 50,000 to an estimated 75,000 crowns (D. Barling, pers. comm.).

Site 6. Barton Hills NNR, Bedfordshire

Several large populations occur towards the southern end of Barton Hills NNR in exceptionally rich chalk downland turf on steep, predominantly S- to SW-facing slopes and spurs where soils are very shallow and competition from coarse grasses is restricted (Wells 1968; Welsh 1983). A few plants also occur on ancient field systems at the north end of the reserve where grazing is more variable. Historically the site was heavily grazed by sheep but management was neglected from 1934 to 1954 resulting in the development of a dense sward of *Bromopsis erectus* (Wells 1968). This was burnt-off in 1954 and sheep grazing re-introduced for nine months of the year (2-3 ac⁻¹), although rabbit grazing declined dramatically due to myxomatosis. Since the mid-1980s the site has been grazed by rabbits all year (although populations have increased in recent years) and sheep (0.4 ha⁻¹) from May to December (inclusive) although this has been relaxed in recent years due to a rise in the rabbit population (Bailey 1996). This has resulted in an increase in the flowering population to over 5,000 crowns although flowering is suppressed in some years by heavy grazing (G. Bellamy, pers. comm.). The Barton population of *Pulsatilla* is well known and attracts many visitors during the flowering period. The tradition of picking flowers at Easter appears to have ceased although in 2006 around 70 plants were illegally removed presumably for horticulture (M. Gurney, pers. comm.).

Site 7. Beaumonts Hay, East Gloucestershire

This site forms part of the Brassey Reserve and Windrush Valley SSSI and supports a small population of *Pulsatilla* on a relatively steep SW-facing limestone slope. Grazing has been increased in recent years producing a much shorter, species-rich sward.

Site 8. Bourton Downs, East Gloucestershire

Around 500 plants are restricted to a small area of sheep-grazed, W-facing downland with extremely shallow soils. Historically the site has been heavily grazed by sheep, although since 1982 stock have been removed from March to late summer in order to allow *Pulsatilla* to flower and currently the population appears stable. This management is similar to Barnsley Wold but with more variable winter grazing (Rich 1997). In 1966 two patches of *Pulsatilla* were recorded in ungrazed *Brachypodium pinnatum* grassland about 1 km to the NW of the reserve (SP132321) but this area is now dense hazel scrub.

Site 9. †Broughton Far Wood SSSI (Clap-gate Pit), North Lincolnshire

In the 1960s 3-4 plants were recorded amongst ungrazed grassland and scrub in an abandoned limestone quarry. The plants were last recorded in 1969 when they were dug up (I. Weston, pers. comm.).

Site 10. †Clipper Down SSSI, Buckinghamshire

In the 1960s a few plants were recorded on a steep SSW-facing chalk slope which was being heavily grazed by sheep from November until April. The intensity of grazing was increased during the 1970s and 1980s (excluding November to March) leading to deterioration in the condition of the site (Everett 1988). The population was fenced (c.1986) for a number of years until grazing levels were reduced on the surrounding slope. The last reliable record was in 1976 although there are unconfirmed records of flowering in 1986 and more recently as vegetative plants (Greves 1997). No plants have been found in recent years despite repeated searches during the flowering period (L. Trowbridge, pers., comm.). This site currently falls within the Ivinghoe Hills SSSI complex and is managed favourably by a tenant farmer for the National Trust.

Site 11. Deacon Hill SSSI, Bedfordshire

Since 1960 small numbers of *Pulsatilla* have been recorded sporadically from several localities in the vicinity of Deacon Hill on steep, SW to NW-facing chalk downland slopes and spurs: (1) the NE slope of Barn Hole (TL119294); (2) narrow spur adjacent to Pegsdon Firs (TL121297); (3) combe NE of Pegsdon Firs (TL123296); and (4) the celtic field system below Deacon Hill itself (TL125298). Historically the northern half of the site (Deacon Hill) has been heavily grazed by sheep and rabbits. In contrast, grazing has been much lower in the southern half of the reserve leading to a decline as a

result of scrub encroachment and build-up of coarse grasses from the 1950s onwards. In recent years, scrub clearance and the reintroduction of grazing have led to an improvement in the quality of the grassland although no plants have been found in Barn Hole despite repeated searches.

Site 12. Devil's Dyke SSSI, Cambridgeshire

Historically *Pulsatilla* has been recorded sporadically along 7 km of a mediaeval chalk ditch and bank between Burwell and where the Cambridge-Newmarket railway crosses the dyke to the SE. The majority of plants are confined to the SW-facing banks particularly where the grassland has been kept open by rabbits, infrequent mowing or burning. A few plants also occur on the top of the dyke, where grass growth is reduced by trampling, and on the adjacent Newmarket Heath which is cut fortnightly, although no plants have been recorded from the heath since 1984. The dyke itself was not grazed for many decades leading to the development of a thick sward of *Bromopsis erectus*. Accidental burning of one section in the 1970s led to a dramatic increase in flowering numbers although numbers subsequently declined to pre-1970 levels. Since then localised mowing has led to localised increases on some sections (e.g. adjacent to Newmarket Heath) and in 2003 the introduction of winter-sheep grazing (and stock-fencing) led to increased flowering on the southern section. In the same year four plants appeared (with *Himantoglossum hircinum*) on the steep SE-facing bank of the A14 c. 300m to the N of the nearest plants on the Dyke itself (TL603632; Leslie 2004).

Site 13. †Fleam Dyke SSSI, Cambridgeshire

In the 1960s a small population was recorded on an ungrazed SW-facing bank of a mediaeval chalk ditch and bank immediately to the NW of a small tumulus. It was last seen in April 1973 when there were 2 plants in bud and several vegetative. A month later no plants could be found and there were two holes in the turf where it had been seen a month earlier (Lady Nora Barlow in litt. to S.M. Walters, 4.2.1974; Crompton 2009+).

Site 14. †Hildersham Furze Hills SSSI, Cambridgeshire

A small population formerly grew (with *Dianthus deltoides*) on the spine of the easterly (Sand) hill on a sandy soil (pH 5.2) derived from glacial sands and gravels (Wells and Barling 1971). During the 1950s there were never more than 3-4 clumps with 20-30 flowers (Trist 1988). Annual rabbit damage was intense, especially during droughts, although this declined following the advent of myxomatosis in 1954. Three plants survived on the spine of the hill into the mid-1980s despite the spread of rank grasses and blackthorn scrub (Trist 1988). By 1990 only one, non-flowering plant remained and it has not been recorded since despite improvements in the condition of the grassland and the removal of scrub (Crompton 2009+).

Site 15. Holywell Mound SSSI, South Lincolnshire†

In the 1960s around 200 plants were present in species-rich limestone turf on a SW-facing slope although few plants flowered due to heavy grazing and the occasional ‘picking’ of flowers by local school children (J. Gibbons in litt. to TCEW). In the 1960s the grassland was very short, herb-rich *Bromopsis erectus-Brachypodium pinnatum* grassland (CG5) with abundant *Thesium humifusum*. A few plants survived into the 1980s although the site was subsequently sprayed and partially improved. *Pulsatilla* has not been recorded for many years and the grassland is now a species-poor *Bromopsis erectus* grassland (CG3b) with few herbs.

Site 16. Honington Camp SSSI, South Lincolnshire†

In the 1960s a small colony occurred in rank *Bromopsis erectus* grassland (CG3d) on the W-facing outer embankment of an Iron Age hill fort surrounded by arable land. The site has been infrequently grazed leading to the development of a thick sward of *Brachypodium pinnatum* amongst scattered *Crataegus* scrub. No plants have been seen since 1992 despite repeated searches.

Site 17. Hornsleasow Roughs SSSI, East Gloucestershire

At this site *Pulsatilla* is scattered across a large area of former limestone quarries (“hills and holes”). This site has had periods of heavy (1960s) and light grazing (1970-80), mostly by sheep but with a few cattle. It is currently lightly grazed by sheep (<3 ha⁻¹) for most of the year (excluding March-May) and although this is not considered ideal management there are still around 100 plants scattered over a hectare of grassland but at low density. Since the relaxation in grazing the grassland changed from tightly grazed (c.2 cm) *Festuca ovina* turf (CG2d) to moderately rank (c.6 cm) but species-rich *Bromopsis erectus* grassland (CG3).

Site 18. Knocking Hoe NNR, Bedfordshire

Between 500-1000 plants grow on the SW-facing slope of a small chalk hill (‘the Hoe’; TL130139) in exceptionally rich calcareous turf with a number of other national rarities (*Hypochaeris maculata*, *Orchis ustulata*, *Seseli libanotis* and *Tephrosieris integrifolia*). A few plants also occur on a Celtic field system (within a grazing enclosure) just to the east (‘*Spiranthes* bank’; TL131308), and more sporadically within an abandoned enclosure on a steep S-facing slope to the W of Tingley Wood (TL132306). It was lost from other parts of the reserve that were ploughed for a short period in 1956 but it has not re-colonised this area. The site was sheep grazed throughout the nineteenth century although this declined after 1931 and since then it has had periods of heavy and light grazing by sheep, rabbits and cattle with occasional mowing and raking of cut material to maintain a tight sward. Few plants were recorded during the 1970s due to the decline in the rabbit population and the growth of coarse grasses (*Bromopsis erectus*). However, the population increased dramatically following the introduction of mowing and the recovery of the rabbit population in the 1980s although these caused

severe localised erosion in places (e.g. *Spiranthes* Bank) (Bailey 1996). The Hoe itself is currently heavily-grazed by rabbits with additional winter sheep grazing and management is now considered to be ideal with over 1000 flowers counted in 2005 (G. Stevens, pers. comm.). In contrast, numbers within the two less heavily grazed exclosures remain low due to greater competition with coarse grasses. The site receives few visitors but there are reports of over 1000 plants being dug-up in the past (Hope-Simpson 1948).

Site 19. †Pitstone Hill SSSI, Buckinghamshire

In the 1960s a few plants occurred on the steep S-facing slope of a mediaeval ditch in relatively short *Bromopsis erectus* grassland. It persisted in tightly-grazed grassland although plants were very difficult to locate in the mid-1980s due to heavy grazing pressure. An exclosure was erected around the site in 1986 and this has led to the build up of coarse grasses and scrub. The last record was at the top of the S-facing bank in 1996; it has not been recorded since despite repeated searches.

Site 20. Ravensburgh Castle SSSI, Bedfordshire

In the 1960s two sub-populations were recorded from adjacent chalk slopes of an Iron Age hill fort dating back to 400BC. The smaller of the two populations occurred immediately below the fort on a steep W-facing slope (TL098295); the larger colony extended eastwards from a S-facing spur overlooking the first site (TL097296). Over 300, mainly vegetative plants were recorded on this slope in 1981 and 30 below the hill fort (Welsh 1983). In 1964 the grassland was very rank but by 1980 the vegetation was very short with much bare chalk due to heavy grazing by sheep and rabbits. It has not been grazed since and is now dense *Bromopsis erectus* grassland with scattered hawthorn scrub. As a consequence, no plants have been seen on the W-facing slope for many years and only a few plants survive on the S-facing spur where the grassland is more exposed and the soils are very shallow.

Site 21. Rodborough Common SSSI, West Gloucestershire

In the 1960s *Pulsatilla* was recorded from two adjacent limestone slopes on Bear Hill (SO849027 and SO847029) and in rough grassland below the Iron Age hill fort on Rodborough Hill (SO848038). One of the colonies on Bear Hill still survives amongst rough *Brachypodium pinnatum* grassland (CG4) on a gentle S-facing slope. The other sites were lost due to scrub encroachment and lack of grazing (M.A.R. and C. Kitchen, pers comm.). Historically there has been light grazing by sheep and cattle and occasionally burnt ('swaling') in February or March by commoners but both practices have declined in recent decades. As a consequence the Bear Hill slope was mown in the 1990s and since 1999 winter grazing by cattle has been re-introduced by the National Trust leading to a reduction in the cover of *Brachypodium pinnatum* and a gradual increase in the numbers of *Pulsatilla*.

Site 22. †Shacklewell Hollow, Leicestershire

In the 1960s a small colony was recorded in species-rich limestone grassland (CG5a) on a shallow SW-facing slope. Three plants were re-discovered at this site in 1992 when the grassland was very rank due to the lack of grazing. However, the population was subsequently destroyed when the farmer dumped rubble over the area (D. Isaac, pers comm).

Site 23. †Smithcombe Hill SSSI, Bedfordshire

In the 1960s a small population occurred in rank *Bromopsis erectus* grassland (CG3a) surrounded by scattered *Viburnum lantana* scrub on a steep SSE-facing chalk slope. By the 1980s the scrub had become very dense and only a single vegetative rosette could be found (Welsh 1983). It has not been recorded since despite scrub clearance and the introduction of goat grazing.

Site 24. †Southorpe Paddock SSSI, Northamptonshire

In the 1960s a small colony was recorded in rough *Brachypodium pinnatum* grassland. The site has received variable amounts of grazing in the past and the last confirmed record was in 1995. In 1999 12 plants originating from Barnack seed were planted out but none survived for more than a year (C. Gardner, pers. comm.).

Site 25. †Southorpe Roughs SSSI, Northamptonshire

A few plants formerly occurred in rank *Bromopsis erectus-Brachypodium pinnatum* grassland in an area of old quarry workings. The site was not grazed for many years and by the 1980s plants were very difficult to locate amongst the rank grass and invading scrub. It was apparently last seen by Franklyn Perring in 1990 (L. Farrell in litt. to TCEW). It has not been seen since despite the recent reintroduction of sheep grazing (2004) and tree felling to reduce shade.

Site 26. Steps Hill SSSI, Buckinghamshire

In the 1960s over 100 plants were recorded in short, *Festuca ovina* turf on a steep SW-facing spur of chalk downland above Incombe Hole. The site was formerly very heavily grazed by sheep and cattle leading to localised poaching and the removal of most of the flowerheads during the spring (R. Maycok, pers. comm.). Grazing levels were subsequently reduced and this led to a gradual increase in *Bromopsis erectus* (CG3). Sheep now lightly graze the site from autumn to early spring (Greves 1997) and as a result vegetation remains fairly rank (>15 cm). In 2005 there approximately 50 plants were located in a limited area (20 × 15-m) surrounded by hawthorn scrub and many freely regenerating whitebeams.

Site 27. †Sweetslade Farm, East Gloucestershire

The majority of this population was ploughed-up in 1966. However, a small area of short limestone grassland (CG5a) was preserved to protect a few plants of *Pulsatilla* on WNW-facing slope. There are no subsequent records and the site is now completely covered by gorse scrub (M.A.R. and C. Kitchen, pers comm.).

Site 28. Therfield Heath, Hertfordshire

The second largest colony in the UK largely confined to very short, rabbit grazed turf on the steep S to SW-facing slopes of a narrow chalk spur known locally as Church Hill (TL332395). Small outliers also occur in rank *Bromopsis erectus* grassland (CG3a) on the adjacent Pen Hill (TL332397) and to the E of the tumuli marked on the OS map (TL332399). All these populations occur on common land within a golf course which was ungrazed for many years. Church Hill has a long history of heavy rabbit grazing and in the 1980s small areas were also mown in late February or early March using a tractor and 'Flymo'. Since 1986 rotational winter grazing has been carried out across much of the heath using temporary grazing compartments and, on Church Hill at least, this has led to an increase in the population. Numbers now exceed 60,000 with up to 12 rosettes m⁻² (Tarpey 1999). The area is used for recreation and trampling on the spine of Church Hill probably reduces the number of flowers each year. In addition, many flowers are picked in the spring and some plants have been dug-up for gardens. The population near the tumuli may have originated from seed spread by a local farmer (W.H. Darling) in 1953/54.

Site 29. †Unhill Bottom, Berkshire

This site was the remnant of an extensive population, possibly totalling over 55,000 plants, which spread over much of the adjacent chalk downland of Dean's Bottom (Crawley 2005). Much of this area was used for military training during the 1939-45 war and was subsequently ploughed-up. The population had declined to around 5000 plants by the late 1950s (Bowen 1968) and then to around 750 plants by 1967 when *Pulsatilla* was confined to a small area of ungrazed *Festuca rubra* grassland (CG6) on a NNW-facing slope. It apparently survived in this locality till at least 1978 but eventually disappeared when the grassland was improved and intensive sheep grazing introduced (Warden 2001).

Site 30. Taylor's Hill, East Gloucestershire

Although this population was originally discovered in 1847 it was not seen again until C.S. Downer found a few plants growing on a SW-facing limestone slope in 1971 (Holland, 1986). These had increased to 110 plants by 1982 whereas only 15 were located over a 200 m stretch of downland in 1996 (SP003157 to SP005156) (M.A.R. and C. Kitchen, pers comm.).

Site 31. Ledsham, South West Yorkshire

In 1984 a single plant was discovered in heavily grazed limestone grassland (CG4a) on a SE-facing limestone bank. For many years flower heads were grazed-off and so cages were placed around the plant to protect it from rabbits. In 1997 the plant was hand-pollinated with pollen collected (the same day) from Barnack Hills and Holes but the plant failed to set seed due to predation by slugs. As a result pollen from the Ledsham plant (male parent) was used to cross-pollinate five plants from Barnack (site 4) but without success (A. Headley, pers. comm.). A single Barnack plant was then translocated to within 4 metres of the Ledsham plant in order to encourage pollination but disappeared within a couple of years.

Site 32. †Lockinge, Berkshire

In 1962 two plants were discovered in rough grassland above Lockinge. It has apparently been seen again since 1987 (Crawley 2005) although no plants or suitable habitat could be found during a survey of the area in 2005 (SU427846).

Site 33. †Sutton Heath, Northamptonshire

A single flowering plant was discovered on a small ridge of limestone turf close adjacent to Sutton Bog in 1972 (Wells 2003) where it was seen again in 2003. The grassland shows signs of agricultural improvement and is heavily grazed. No plants have been found since despite repeated searches.

Appendix 12

(a) Associates of *Pulsatilla vulgaris* and (b) vegetation structure in 16 of the 17 extant populations (Site 30 not surveyed). Figures are frequency in quadrats ($n = 62$) with the mean % cover in parentheses. Species in <10% quadrats are listed after the table. For structure variables figures are means (\pm 1SE). Figures are presented for all 16 sites and for limestone and chalk sites only ($n = 7$ and 9 respectively). Mosses are denoted by an asterisk.

(a) Associates	All sites	Limestone only	Chalk only
<i>Pulsatilla vulgaris</i>	V (4.2)	V (3.6)	V (4.9)
<i>Bromopsis erectus</i>	V (24.2)	V (24.7)	V (23.7)
<i>Festuca ovina</i>	V (12.9)	IV (8.5)	V (17.6)
<i>Sanguisorba minor</i>	V (8.8)	V (8.7)	V (8.9)
<i>Helianthemum nummularium</i>	V (6.0)	V (7.2)	IV (4.7)
<i>Carex flacca</i>	V (4.2)	V (3.7)	V (4.7)
<i>Cirsium acaule</i>	V (4.2)	V (5.3)	V (3.1)
<i>Leontodon hispidus</i>	IV (2.8)	IV (2.8)	IV (2.9)
<i>Pilosella officinarum</i>	IV (2.5)	IV (3.2)	III (1.8)
<i>Briza media</i>	IV (1.5)	IV (1.9)	III (1.0)
<i>Helictotrichon pratense</i>	IV (1.3)	III (0.6)	V (2.0)
<i>Koeleria macrantha</i>	IV (1)	III (0.6)	V (1.4)
<i>Carex caryophyllea</i>	IV (0.9)	IV (0.9)	IV (0.9)
<i>Brachypodium pinnatum</i>	III (5.1)	V (7.4)	I (2.7)
<i>Ctenidium molluscum*</i>	III (3.6)	III (3.4)	III (3.7)
<i>Lotus corniculatus</i>	III (1.2)	III (1.6)	III (0.8)
<i>Campanula rotundifolia</i>	III (0.9)	II (0.9)	V (1.0)
<i>Scabiosa columbaria</i>	III (0.8)	III (1.1)	II (0.5)
<i>Plantago lanceolata</i>	III (0.7)	III (0.7)	III (0.6)
<i>Scleropodium purum*</i>	II (2.0)	III (3.5)	II (0.3)
<i>Filipendula vulgaris</i>	II (1.6)	I (0.5)	IV (2.9)
<i>Thymus polytrichus</i>	II (1.0)	III (1.8)	I (0.1)
<i>Thymus pulegioides</i>	II (1.0)	II (1.0)	III (1.0)
<i>Centaurea nigra</i>	II (0.8)	II (0.4)	III (1.3)
<i>Plantago media</i>	II (0.6)	II (0.9)	III (0.4)
<i>Polygala calcarea</i>	II (0.6)	II (0.9)	I (0.3)
<i>Hippocrepis comosa</i>	II (0.6)	I (0.5)	III (0.8)
<i>Campyliadelphus chrysophyllus*</i>	II (0.5)	II (0.2)	I (0.9)
<i>Campanula glomerata</i>	II (0.5)	I (0.2)	II (0.8)
<i>Viola hirta</i>	II (0.3)	III (0.3)	II (0.3)
<i>Homalothecium lutescens*</i>	II (0.3)	II (0.4)	I (0.1)
<i>Asperula cynanchica</i>	II (0.2)	II (0.2)	II (0.2)
<i>Ranunculus bulbosus</i>	II (0.2)	II (0.3)	II (0.2)
<i>Carlina vulgaris</i>	II (0.2)	II (0.3)	I (0.1)
<i>Pimpinella saxifraga</i>	II (0.2)	II (0.2)	I (0.2)
<i>Linum catharticum</i>	II (0.1)	III (<0.1)	II (0.1)
<i>Crataegus monogyna</i>	II (0.1)	II (0.1)	II (0.2)
<i>Galium verum</i>	II (0.1)	II (<0.1)	I (0.2)
<i>Anthyllis vulneraria</i>	I (0.6)	II (1.1)	
<i>Primula veris</i>	I (0.4)		II (0.9)
<i>Thesium humifusum</i>	I (0.2)	II (0.4)	I (<0.1)
<i>Fissidens dubius*</i>	I (0.2)	I (0.1)	I (0.3)
<i>Succisa pratensis</i>	I (0.2)	I (<0.1)	I (0.4)
<i>Tephrosieris integrifolia</i>	I (0.2)		II (0.5)
<i>Taraxacum officinale</i> agg.	I (0.1)	II (0.1)	I (<0.1)
<i>Prunella vulgaris</i>	I (0.1)	I (<0.1)	II (0.2)

Appendix 12 continued.

(b) Vegetation composition/structure	All sites	Limestone only	Chalk only
Vegetation height (cm)	7.5 (0.7)	7.0 (0.8)	7.9 (1.1)
Bare ground (%)	6.2 (1.2)	7.0 (1.7)	5.3 (1.6)
Number of species	23.0 (0.7)	23.1 (1.1)	22.8 (1.0)
Number grasses & sedges	6.2 (0.2)	6.4 (0.3)	6.0 (0.2)
% cover of grasses & sedges	49.1 (1.9)	46.0 (3.0)	52.0 (3.0)
Number herbs	14.6 (0.6)	14.0 (0.9)	15.2 (0.9)
% cover of herbs	44.1 (2.1)	46.0 (3.0)	42.0 (3.0)
Diversity	1.0 (0.0)	1.1 (0.1)	1.0 (0.0)
Evenness	0.7 (0.0)	0.8 (0.0)	0.7 (0.0)
% cover of <i>Bromopsis erectus</i>	24.2 (2.4)	24.7 (3.8)	23.7 (2.8)
Number of positive indicators	10.2 (0.4)	10.4 (0.5)	10.0 (0.5)
% cover of positive indicators	63.3 (2.5)	69.1 (3.8)	57.1 (3.0)
% fit to CG3 or CG5	60.5 (2.0)	54.7 (2.7)	66.8 (2.5)

Sites and number of quadrats recorded (1968, 2006): Ancaster Valley (2,1), Aston Upthorpe (1,1), Barnack Hills and Holes (4,3), Barnsley Warren (3,2), Barton Hills (2,4), Beaumonts Hay (2,1), Bourton Downs (3,2), Devil's Dyke (2,2), Hornsleasow Roughts (1,2), Knocking Hoe (3,1), Knocking Hoe - *Spiranthes* Bank (1,1), Ravensburgh Castle (2,1), Rodborough Common (4,1), Steps Hill (1,1), Therfield Heath – Pen Hill (2,1), Therfield Heath - Church hill (3,1). Species recorded in less than 10% of quadrats: *Aceras anthropophorum*, *Arrhenatherum elatius*, *Blackstonia perfoliata*, *Carex ericetorum*, *Centaurea scabiosa*, *Cerastium fontanum*, *C. pumilum*, *Cirsium arvense*, *C. vulgare*, *Cladonia* sp., *Cynosurus cristatus*, *Dicranum scoparium*, *Euphrasia nemorosa*, *Festuca rubra*, *Galium aparine*, *G. mollugo*, *Gentianella amarella*, *Gymnadenia conopsea*, *Helictotrichon pubescens*, *Heracleum sphondylium*, *Hieracium exotericum*, *Himantoglossum hircinum*, *Hylocomium splendens*, *Hypnum cupressiforme*, *Hypochaeris maculata*, *H. radicata*, *Leucanthemum vulgare*, *Luzula campestris*, *Medicago lupulina*, *Neckera complanata*, *Onobrychis viciifolia*, *Ononis repens*, *Ophrys apifera*, *Orchis mascula*, *O. morio*, *Pastinaca sativa*, *Phleum bertolonii*, *Picris hieracioides*, *Poa compressa*, *Polygala vulgaris*, *Polytrichum* sp., *Prunus spinosa*, *Quercus robur*, *Rhamnus cathartica*, *Rhinanthus minor*, *Rhytidadelphus squarrosus*, *R. triquetrus*, *Rosa canina*, *Seligeria* sp., *Senecio jacobaea*, *Serratula tinctoria*, *Seseli libanotis*, *Sonchus asper*, *Thuidium assimile*, *Trifolium pratense*, *T. repens*, *Trisetum flavescens*, *Veronica chamaedrys*, *Weissia* sp.

Bibliography

- Abbott C. 1798. *Flora Bedfordiensis*. W. Smith, Bedford.
- Adams K. 2007. Notes on Essex specialities 12: the status of sulphur clover *Trifolium ochroleucon* Hudson in Essex and eastern England. *Essex Naturalist (new series)* 24, 115-118.
- Adams K. 2008. Notes on Essex specialities 13: the status and distribution of Crested Cow-wheat *Melampyrum cristatum* L. in Britain, now largely confined to Essex. *Essex Naturalist (new series)* 25, 120-127.
- Allen D.E. 1963. Why and what? in Wanstall P.J., ed. *Local floras*, pp.14-20. Botanical Society of the British Isles, London.
- Babington C.C. 1860. *Flora of Cambridgeshire*. J. van Voorst, London.
- Bailey C. 1996. *An investigation into the factors influencing the distribution, relative abundance and genetic variation of Pulsatilla vulgaris at two sites in Bedfordshire*. Unpublished MSc thesis, Imperial College, Wye.
- Baker H.G. 1953. Race formation and reproductive method in flowering plants. *Evolution* 7, 114-143.
- Baker J.G. 1906. *North Yorkshire: Studies of its Botany, Geology, Climate and Physical Geography*. Longmans, London.
- Beckett G. & Bull A. 1999. *A Flora of Norfolk*. Privately published, Norwich.
- Beebee T.J.C. 2001. British wildlife and human numbers: the ultimate conservation issue? *British Wildlife* 13, 1-8.
- Bellamy D. 2000. Foreword, in Green I.P., Higgins R.J., Kitchen C. & Kitchen M.A.R., eds. 2000. *The flora of the Bristol Region*, p.v. Pisces Publications, Newbury.
- Bennie J., Hill M.O., Baxter R. & Huntley B. 2006. Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology* 94, 355-368.
- Best J. 1995. 'What time hath stole away', in Gent G. & Wilson R., eds. *The flora of Northamptonshire and the Soke of Peterborough*, pp.60-70. Robert Wilson Designs, Rothwell.
- Biesmeijer J.C., Roberts S.P.M., Reemer M., Ohlemüller R., Edwards M., Peeters T., Schaffers A.P., Potts S.G., Kleukers R., Thomas C.D., Settele J. & Kunin W.E. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313, 351-354.

- Bignal E.M. & MacCracken D.I. 1996. Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology* 33, 413-424.
- Blomqvist M.M., Vos P., Klinkhamer P.G.L. & ter Keurs W.J. 2003. Declining plant species of grassland ditch banks – a problem of colonisation or extinction? *Biological Conservation* 109, 391-406.
- Bobbink R., Hornung M. & Roelefs J.G.M. 1998. The effects of airborne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* 86, 717-738.
- Bond W.J. 1995. Assessing the risk of plant extinction in relation to pollinator and dispersal failure, in Lawton J.H. & May R.M., eds *Extinction Rates*, pp. 131-146. Oxford University Press, Oxford.
- Boon C.R. 1998. British and Irish floristic elements applied to the Bedfordshire flora. *Bedfordshire Naturalist* 52, 78-91.
- Bourne P.J. 1964. Sulphur clover (*Trifolium ochroleucon* Huds.) in Cambridgeshire. *Nature in Cambridgeshire* 7, 27-31.
- Bowen H.J.M. 1968. *The flora of Berkshire*. Holywell Press, Oxford.
- Bowen H.J.M. 1997. Observations on *Pulsatilla vulgaris*. *BSBI News* 76, 37.
- Bowen H.J.M. 2000. *The flora of Dorset*. Pisces Publications, Newbury.
- Braithwaite M.E., Ellis R.W. & Preston C.D. 2006. *Change in the British Flora 1987-2004*. Botanical Society of the British Isles, London.
- Briggs M. 1990. *Sussex Plant Atlas: selected supplement*. Booth Museum of Natural History, Brighton.
- Brown J.H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124, 255-279.
- Brunker J.P. 1951. *Flora of County Wicklow*. Dundalgan Press, Dundalk.
- Byfield A. & Pearman D.A. 1994. *Dorset's Disappearing Heathland Flora. Changes in the Distribution of Dorset's Rarer Heathland Species 1931 to 1993*. Plantlife and RSPB, London.
- Campbell B.D., Grime J.P. & Mackey J.M.L. 1992. Shoot thrust and its role in plant competition. *Journal of Ecology* 80, 633-641.
- Campbell M.S. 1945. *The Flora of Uig (Lewis)*. T. Buncle & Co., Arbroath.
- Carter H.H. 1967. Juniper Valley: some observations and problems. *Reading Naturalist* 19, 21-29.
- Cheffings C.M. 2004. New plant status lists for Great Britain. *BSBI News* 95, 36-43.

- Cheffings C.M. & Farrell L. 2005. The Vascular Plant Red Data List for Great Britain. *Species Status* 7, 1-116. Joint Nature Conservation Committee, Peterborough.
- Chocholoušková Z. & Pyšek P. 2003. Changes in composition and structure of urban flora over 120 years: a case study of the city of Plzeň. *Flora* 198, 366-376.
- Clapham A.R. 1969. *Flora of Derbyshire*. County Borough of Derby Museum & Art Gallery, Derby.
- Clapham A.R., Tutin T.G. & Moore D.M. 1987. *Flora of the British Isles*, third edition. Cambridge University Press, Cambridge.
- Colston A., Jackson M., Moore L. & Tero C. 1996. *Northamptonshire's Red Data Book: Species to Watch in the County*. English Nature and Northamptonshire Wildlife Trust, Northampton.
- Coombe D.E. 1994. *Trifolium ochroleucon*, in Stewart, A., Pearman, D.A. & Preston, C.D., eds *Scarce Plants in Britain*, p.415. Joint Nature Conservation Committee, Peterborough.
- Crawford R.M.M. 1997. Oceanicity and the ecological disadvantages of warm winters. *Botanical Journal of Scotland* 49, 205-221.
- Crawley M.J. 2005. *The flora of Berkshire*. Brambley Books, Harpenden.
- Crawley M.J., Harvey P.H. & Purvis A. 1996. Comparative ecology of the native and alien floras of the British Isles. *Philosophical Transactions of the Royal Society of London B* 351, 1251-1259.
- Crompton G. 1981. Surveying rare plants in the east of England, in Syngé H., ed. *Biological Aspects of Rare Plant Conservation*, pp.117-124. John Wiley and Sons, Chichester.
- Crompton G. 2009+. *Cambridgeshire Flora records since 1538*. Privately published website (<http://mnlg.com/gc/>).
- Crompton G. & Whitehouse H.L.K. 1983. *A checklist of the flora of Cambridgeshire*. Privately published, Cambridge.
- Currall J.E.P. 1987. A transformation of the Domin scale. *Vegetatio* 72, 81-97.
- Dandy J.E. 1969. *Watsonian Vice-counties of Great Britain*. The Ray Society, London.
- Davey F.H. 1909. *Flora of Cornwall*. F. Chegwidden, Penryn.
- Davis B.H. 2009. Crested cow-wheat (*Melampyrum cristatum*) in Huntingdonshire. *Report of the Huntingdonshire Fauna and Flora Society* 61, 17-20.
- DeCandido R. 2004. Recent changes in plant species diversity in urban Pelham Bay Park, 1947-1998. *Biological Conservation* 120, 129-136.

- Deering C. 1738. *Catalogus Stirpium, etc., or a catalogue of plants naturally growing and commonly cultivated in divers parts of England, more especially about Nottingham.* Nottingham.
- DERC 2003. Dorset's changing hedgebanks. A proposal to re-survey Professor Good's hedgebanks. Final project report to Defra (BD2107), Dorchester.
- Dony J.G. 1953. *Flora of Bedfordshire.* The Corporation of Luton Museum and Art Gallery, Luton.
- Dony J.G. 1967. *Flora of Hertfordshire.* Hitchin Urban District Council, Luton.
- Dony J.G. 1974. Changes in the flora of Hertfordshire. *Transactions of the Hertfordshire Natural History Society* 27, 255-264.
- Dony J.G. 1976. *Bedfordshire Plant Atlas.* Borough of Luton Museum and Art Gallery, Luton.
- Dony J.G. 1977. Change in the flora of Bedfordshire, England, from 1798 to 1976. *Biological Conservation* 11, 307-320.
- Druce G.C. 1880-1. Contributions to a Flora of Northamptonshire. *Journal of the Northampton Natural History Society* 1, pp.48, 92, 152, 179, 215, 271, 334.
- Druce G.C. 1882-3. Contributions to a Flora of Northamptonshire. *Journal of the Northampton Natural History Society* 2, pp.25, 50, 142, 227, 279, 315.
- Druce G.C. 1884-5. Contributions to a Flora of Northamptonshire. *Journal of the Northampton Natural History Society* 3, pp.26, 79, 104, 143, 179, 219, 276.
- Druce G.C. 1886. *The flora of Oxfordshire.* First edition. Parker and Co., Oxford and London.
- Druce G.C. 1886-7. Contributions to a Flora of Northamptonshire. *Journal of the Northampton Natural History Society* 4, pp.5, 37, 116, 173, 235, 324.
- Druce G.C. 1888-9. Contributions to a Flora of Northamptonshire. *Journal of the Northampton Natural History Society* 5, pp.29, 117, 149, 235, 249, 309.
- Druce G.C. 1890-1. Contributions to a Flora of Northamptonshire. *Journal of the Northampton Natural History Society* 6, pp.7, 56, 65, 100, 172, 249.
- Druce G.C. 1892-3. Contributions to a Flora of Northamptonshire. *Journal of the Northampton Natural History Society* 7, pp.64, 136, 161, 250, 292.
- Druce G.C. 1894-5. Contributions to a Flora of Northamptonshire. *Journal of the Northampton Natural History Society* 8, 5.
- Druce G.C. 1897. *The flora of Berkshire.* Clarendon Press, Oxford
- Druce G.C. 1898-9. Botany notes. *Journal of the Northampton Natural History Society* 10, pp.135, 208, 265.

- Druce G.C. 1900-1. Notes on the flora. *Journal of the Northampton Natural History Society* 11, 13.
- Druce G.C. 1904-5. Northampton plants. *Journal of the Northampton Natural History Society* 13, 290.
- Druce G.C. 1909-10. Additions to the Flora of Fenland. *Journal of the Northampton Natural History Society* 15, 221.
- Druce G.C. 1909-10. Botany of Fenland. *Journal of the Northampton Natural History Society* 15, 100.
- Druce G.C. 1909-10. Plant notes. *Journal of the Northampton Natural History Society* 15, 281-296.
- Druce G.C. 1910-11. Plant notes. *Journal of the Northampton Natural History Society* 16, 291-295.
- Druce G.C. 1922. Flora Zetlandica. *Report of Botanical Society and Exchange Club (supplement to part 3)* 6, 457-546.
- Druce G.C. 1926. *The flora of Buckinghamshire*. T. Buncle & Co., Arbroath.
- Druce G.C. 1930. *The flora of Northamptonshire*. T. Buncle & Co., Arbroath.
- Drayton B. & Primack R.B. 1996. Plant species lost in an isolated conservation area in metropolitan Boston from 1894 to 1993. *Conservation Biology* 10, 30-39.
- Duncan R.P. & Young, J.R. 2000. Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. *Ecology* 81, 3048-3061.
- Edwards B. & Pearman D.A. 2004. *Dorset Rare Plant Register*. Dorset Environmental Records Centre, Dorchester.
- Ellenberg H. 1988. *Vegetation Ecology of Central Europe*, fourth edition. Cambridge University Press, Cambridge.
- Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W. & Paulissen, D. 1991. Zeigerwerte von Pflanzen Mitteleuropa. *Scripta Geobotanica* 18, 1-248.
- Ellis R.W. 2004. A survey of *Trifolium ochroleucon* Hudson (Sulphur Clover) in Norfolk, 2002. *Transactions of the Norfolk and Norwich Naturalists' Society* 37, 68-85.
- English Nature 1994. *Grassland Inventory. Bedfordshire*. English Nature, Peterborough.
- English Nature 1995. *Grassland Inventory. Northamptonshire*. English Nature, Peterborough.
- Evans P.A., Evans I.M. & Rothero G.P. 2002. *Flora of Assynt*. Privately published.
- Everett S. 1988. *Rare Vascular Plant Survey of Southern England*. CSD Report Number 23, Nature Conservancy Council, Peterborough.

- Ferguson C., Briggs J. & Willby N. 1998. Floating water-plantain in Britain – under-recorded and overlooked? *British Wildlife* 9, 298-303.
- Fischer M. & Stöcklin J. 1997. Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-1985. *Conservation Biology* 11, 727-737.
- Fitter A.H. & Peat H.J. 1994. The Ecological Flora Database. *Journal of Ecology* 82, 415-425.
- Foley M.J.Y. 1992. The current distribution and abundance of *Orchis ustulata* L. (Orchidaceae) in the British Isles - an updated summary. *Watsonia* 19, 121-126.
- Frankland L. 2001. Gone – one wild flower a year. *BSBI News* 86, 44-45.
- French C.N., Murphy R.J. & Atkinson M.G.C. 1999. *Flora of Cornwall*. Wheal Seton Press, Camborne.
- Fuller R.J. & Gough S.J. 1999. Changes in sheep numbers in Britain: implications for bird populations. *Biological Conservation* 91, 73-89.
- Fuller R.M. 1987. The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930-84. *Biological Conservation* 40, 282-300.
- Galloway J.N. & Cowling E.B. 2002. Reactive nitrogen and the world: 200 years of change. *Ambio* 31, 64-71.
- Garbutt A. & Sparks T.H. 2002. Changes in the botanical diversity of a species rich ancient hedgerow between two surveys (1971-98). *Biological Conservation* 106, 273-278.
- Gent G. & Wilson R., eds 1995. *The Flora of Northamptonshire and the Soke of Peterborough*. Robert Wilson Designs, Rothwell.
- Gerarde J. 1597. *The Herbal or Generall Historie of Plantes*. London.
- Gibbons E.J. 1975. *The flora of Lincolnshire*. Lincolnshire Naturalists' Union, Lincoln.
- Gibbons E.J. & Weston I. 1985. *Supplement to the Flora of Lincolnshire*. Lincolnshire Naturalists' Union, Lincoln.
- Gilbert J.L. 1965. *Flora of Huntingdonshire: Wildflowers*. Peterborough Museum Society, Peterborough.
- Gilmour J.S.L. 1963. The changing pattern, in Wanstall P.J., ed. *Local floras*, pp.9-13. Botanical Society of the British Isles, London.
- Good R. 1948. *A geographical handbook of the Dorset flora*. Dorset Natural History and Archaeological Society, Dorchester.
- Graham G.G. 1988. *The flora and vegetation of County Durham*. Durham Flora Committee and the Durham County Conservation Trust, Durham.

- Graham G.G. & Primavesi A.L. 1993. *Roses of Great Britain and Ireland*. Botanical Society of the British Isles Handbook No. 7. BSBI, London.
- Green B.H. 1990. Agricultural intensification and the loss of habitat, species and amenity in British grasslands: a review of historical change and assessment of future prospects. *Grass and Forage Science* 45, 365-372.
- Green I.P., Higgins R.J., Kitchen C. & Kitchen M.A.R. 2000. *The flora of the Bristol Region*. Pisces Publications, Newbury.
- Greenwood E. F. 1999. Vascular plants: a game of chance? in Greenwood E.F., ed. *Ecology and landscape development: a history of the Mersey basin*, pp.195-211. Liverpool University Press and National Museums and Galleries on Merseyside, Liverpool.
- Greenwood E.F. 2003. Understanding change: a Lancashire perspective. *Watsonia* 24, 337-350.
- Greves S. 1997. *A Species Action Plan for Pasqueflower (Pulsatilla vulgaris) in Berkshire, Buckinghamshire and Oxfordshire*. English Nature, Thatcham.
- Grime J.P., Hodgson J.G. & Hunt R. 1988. *Comparative plant ecology: a functional approach to common British species*. First edition. Unwin Hyman, London..
- Grime J.P., Hodgson J.G. & Hunt R. 2007. *Comparative plant ecology: a functional approach to common British species*. Second edition. Castlepoint Press, Dalbeattie.
- Grose D. 1957. *The flora of Wiltshire*. The Natural History Section, Wiltshire Archaeological and Natural History Society, Devizes.
- Grubb P.J. 1990. Demographic studies on the perennials of chalk grassland, in Hillier S.H., Walton D.W.H. & Wells D.A., eds. *Calcareous Grasslands – Ecology and Management*, pp. 207-255. Proceedings of the Nature Conservancy Council and British Ecological Society Symposium, University of Sheffield, 14-16th September 1987. Bluntisham Books, Bluntisham.
- Gulliver R.L. 1990. The rare plants of the Howardian Hills, North Yorkshire, 1794-1988. *Watsonia* 18, 69-80.
- Hall P.C. 1980. *Sussex Plant Atlas*. Booth Museum of Natural History, Brighton.
- Halliday G. 1997. *A Flora of Cumbria*. Centre for North West Regional Studies, Lancaster.
- Hanski I. 1998. Metapopulation dynamics. *Nature* 396, 41-49.
- Harrison P.A., Berry P.M. & Dawson T.P., eds 2001. *Climate Change and Nature Conservation in Britain and Ireland: Modelling Natural Resource Responses to Climate Change (the MONARCH Project): Technical Report*. UKCIP, Oxford.

- Harrison S. & Bruna E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22, 225-232.
- Hensen I., Obeprieler C. & Wesche K. 2005. Genetic structure, population size, and seed production of *Pulsatilla vulgaris* Mill. (Ranunculaceae) in Central Germany. *Flora* 200, 3-14.
- Hill M.O. 1996. *Tablefit. Version 1.0. For the Identification of Vegetation Types*. Institute of Terrestrial Ecology, Huntingdon.
- Hill M.O. & Šmilauer P. 2005. *WinTWINs. TWINSPAN for Windows Version 2.3*. NERC Centre for Ecology and Hydrology, Monks Wood.
- Hill M.O., Mountford, J.O., Roy D.B. & Bunce R.G.H. 1999. *Ellenberg's Indicators Values for British Plants. ECOFACT Volume 2. Technical Annex*. Institute of Terrestrial Ecology, Monks Wood.
- Hill M.O., Roy D.B., Mountford, J.O. & Bunce R.G.H. 2000. Extending Ellenberg's indicator values to a new area: an algorithmic approach. *Journal of Applied Ecology* 37, 3-15.
- Hill M.O., Preston C.D. & Roy D.B. 2004. *PLANTATT. Attributes of British and Irish Plants: Status, Size, Life history, Geography and Habitats*. NERC Centre for Ecology and Hydrology, Monks Wood.
- Hodgson J.G. 1986a. Commonness and rarity in plants with special reference to the Sheffield flora. Part I: the identity, distribution and habitat characteristics of common and rare species. *Biological Conservation* 36, 199-252.
- Hodgson J.G. 1986b. Commonness and rarity in plants with special reference to the Sheffield flora. Part II: the relative importance of climate, soils and land use. *Biological Conservation* 36, 253-274.
- Holland S.C., Caddick H.M. & Dudley-Smith D.S. 1986. *Supplement to the Flora of Gloucestershire*. Grenfell Publications, Bristol.
- Hollingsworth P.M., Squirrell J., Hollingsworth M.L., Richards A.J. & Bateman R.M. 2006. Taxonomic complexity, conservation and recurrent origins of self-pollination in *Epipactis* (Orchidaceae), in Bailey J. & Ellis R.G., eds *Current taxonomic research on the British and European flora*, pp. 27-44. Botanical Society of the British Isles, London.
- Hope Simpson J. 1948. *Management Plan: Knocking Hoe, Appendix IV*. Nature Conservancy Council, Peterborough.
- Hosmer D.W. & Lemeshow S.L. 1989. *Applied Logistic Regression*. John Wiley & Sons, New York.

- How W. 1650. *Phytologia Britannica*. London.
- Howitt G. 1839. *The Nottinghamshire flora*. Hamilton, Adams, & Co., London.
- Huntley B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for plant communities. *Annals of Botany* 67, 15-22.
- Jackson D.L. 2000. *Guidance on the Interpretation of the Biodiversity Broad Habitat Classification (terrestrial and freshwater): Definitions and the Relationship with other Habitat Classifications*. Joint Nature Conservation Committee report no. 307. JNCC, Peterborough.
- James T.J. 1992. Plants and plant communities at Ashwell, Hertfordshire, 1800-1991. *Transactions of the Hertfordshire Natural History Society* 31, 201-218.
- James T.J. 1997. The changing flora of Hertfordshire. *Transactions of the Hertfordshire Natural History Society* 33, 62-84.
- Jermyn S.T. 1974. *Flora of Essex*. Essex Naturalists' Trust Limited, Fingringhoe.
- Jones E.F. 1969. The decrease of *Pulsatilla vulgaris* in England. *Biological Conservation* 1, 327-328.
- Jonsell B., ed. 2001. *Flora Nordica. Volume 2. Chenopodiaceae to Fumariaceae*. The Bergius Foundation, Stockholm.
- Jonsson O., Rosquist G. & Widén B. 1991. Operation of dichogamy and herkogamy in five taxa of *Pulsatilla*. *Holarctic Ecology* 14, 260-271.
- Keech T.J. 1995. The climate, in Gent G. & Wilson R., eds *The Flora of Northamptonshire and the Soke of Peterborough*, pp.20-22. Robert Wilson Designs, Rothwell.
- Kent D.H. 1975. *The Historical Flora of Middlesex*. Ray Society, London.
- Kent M. & Coker P. 1992. *Vegetation Description and Analysis*. John Wiley and Sons, Chichester.
- Kéry M., Spillman J.H., Truong C. & Holderegger R. 2006. How biased are estimates of extinction probability in revisitation studies? *Journal of Ecology* 94, 980-986.
- Killick J., Perry R. & Woodell S. 1998. *The flora of Oxfordshire*. Pisces Publications, Newbury.
- King T. 1891. *The Clydesdale flora*, fifth edition. Hugh Hopkins, Glasgow.
- Kirby K.J., Smart S.M., Black H.I.J., Bunce R.G.H., Corney P.M. & Smithers R.J. 2005. *Long-term ecological change in British woodlands (1971-2001)*. English Nature Research Report Number 653, English Nature, Peterborough.
- Kunin W. 1992. Density and reproductive success in wild populations of *Diplotaxis eruroides* (Brassicaceae). *Oecologia* 55, 299-314.

- Lande R. 1988. Genetics and demography in biological conservation. *Science* 241, 1455-1460.
- Landolt E. 1977. *Ökologische Zieglerwerte zur Schweizer Flora*. Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich.
- Landolt E. 2001. *Flora der Stadt Zürich*. Birkhäuser, Basel.
- Lavergne S., Thuiller, W., Molina J. & Debussche M. 2005. Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115-year study in the Mediterranean region. *Journal of Biogeography* 32, 799-811.
- Lavin J.C. & Wilmore G.T.D., eds. 1994. *The West Yorkshire Plant Atlas*. City of Bradford Metropolitan Council, York.
- Lawton J.H. 1991. Are species useful? *Oikos* 62, 3-4.
- Leonard Y. 1999. *Scleranthus perennis* subsp. *prostratus* Sell (Caryophyllaceae), in Wigginton M.J., comp. & ed. *British Red Data Books 1 Vascular plants*, third edition, p.337. Joint Nature Committee Council, Peterborough.
- Leslie A.C. 1987. *Flora of Surrey supplement and checklist*. Privately published, Guildford.
- Leslie A.C. 2004. Vascular plant records. *Nature in Cambridgeshire* 46, 89.
- Lindell T. 1998. Breeding systems and crossing experiments in *Anemone patens* and in the *Anemone pulsatilla* Group (Ranunculaceae). *Nordic Journal of Botany* 18, 549-561.
- Lloyd L.C. & Rutter E.M. 1957. *Handlist of the Shropshire flora*. Caradoc & Severn Valley Field Club, Shrewsbury.
- Lockton A. & Whild S. 2005. *Rare plants of Shropshire*, third edition. Shropshire Flora Group, Shrewsbury.
- Lousley J.E. 1976. *Flora of Surrey*. David & Charles, Newton Abott.
- Lowe A.J. & Abbott R.J. 2003. A new British species, *Senecio eboracensis* (Asteraceae), another hybrid derivative of *S. vulgaris* L. and *S. squalidus* L. *Watsonia* 24, 375-388.
- Lusby P.J. & Slack A. 1994. *Galium sternerii* Ehrend., in Stewart A., Pearman D.A. & Preston C.D., comps & eds. *Scarce plants in Britain*, p.189. Joint Nature Conservation Committee, Peterborough.
- Mabey R. 1999. Preface, in Beckett, G. & Bull A. 1999. *A Flora of Norfolk*, pp.4-5. Privately published, Norwich.
- Margetts L.J. & David R.W. 1981. *Review of the Cornish flora 1980*. Institute of Cornish Studies, Redruth.

- Marks P.L., Wesley F.R. & Gardescu S. 2008. The vascular plant diversity of the Finger Lakes region of central New York State: changes in the 1800s and 1900s. *Journal of the Torrey Botanical Society* 135, 53-69.
- Marren P. 1999a. County floras. *British Wildlife* 10, 373-380.
- Marren P. 1999b. *Britain's Rare Plants*. T. and A.D. Poyser, London.
- Marren P. 2000. *Where have all the flowers gone? A study of local extinctions as recorded in the county floras*. Plantlife, London.
- Marren P. 2001. "What time hath stole away": local extinctions in our native flora. *British Wildlife* 12, 305-310.
- May, R.M., Lawton, J.H. & Stork, N.E. (1995) Assessing extinction rates, in Lawton J.H. & May R.M., eds *Extinction Rates*, pp.1-24. Oxford University Press, Oxford.
- McCollin D., Moore L. & Sparks T.H. 2000. The flora of a cultural landscape: environmental determinants of change revealed using archival sources. *Biological Conservation* 92, 249-263.
- McCosh D.J. 1988. Local Floras – a progress report. *Watsonia* 17, 81-89.
- McKinney M.L. & Lockwood J.L. 1999. Biotic homogenisation: a few winners replace many losers in the next mass extinction. *Trend in Ecology and Evolution* 14, 450-453.
- Micheals N. 1996. *Lowland Heathland in England. A Natural Areas approach*. English Nature Research Report No. 170, English Nature, Peterborough.
- Mitchley J. 1988. Control of relative abundance of perennials in chalk grassland in southern England. II. Vertical canopy structure. *Journal of Ecology* 76, 341-350.
- Mitchley J. & Willems J.H. 1995. Vertical canopy structure of Dutch chalk grasslands in relation to their management. *Vegetatio* 117, 17-27.
- Morton J. 1712. *The natural history of Northamptonshire*. Knaplock & Wilkin, London.
- Mountford J.O. 1994. Floristic changes in English grazing marshes: the impact of 150 years of drainage and land use change. *Watsonia* 30, 3-24.
- Nau B.S., Boon C.R. & Knowles J.P., eds 1987. *Bedfordshire Wildlife*. Castlemead Publications, Ware.
- NEGTA 2001. *Transboundary Air Pollution: Acidification, Eutrophication and Ground-level Ozone in the UK*. Centre for Ecology and Hydrology, Edinburgh.
- Newton A. 1971. *Flora of Cheshire*. Cheshire Community Council, Chester.
- Newton A. 1990. *Supplement to Flora of Cheshire*. Privately published, Leamington Spa.
- Nisbett A. & Shere P. 2006. *The Environmental Impacts of Changes in Livestock Farming in England*. Rural Development Service (Defra), Exeter.

- Notcutt W.L. 1843. A catalogue of plants observed in the neighbourhood of Daventry, Northamptonshire. *The Phytologist* 1, 500-508.
- Oostermeijer J.G.B., van Eijck M.W., van Leeuwen N.C. & den Nijs H.C.M. 1995. Analysis of the relationship between allozyme heterozygosity and fitness in the rare *Gentiana pneumonanthe* L. *Conservation Biology* 12, 1042-1053.
- Ordoyno T. 1807. *Flora Nottinghamiensis*. Newark.
- Osborne J.L., Martin A.P., Carreck N.L., Swain J.L., Knight M.E., Goulson D., Hale R.J. & Sanderson R.A. 2008. Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology* 77, 406-415.
- Ouberg N.J. & van Treuren R. 1995. Variation in fitness-related characters among small and large populations of *Salvia pratensis*. *Journal of Ecology* 83, 369-380.
- Ozinga W.A., Bekker R.M., Schaminée J.H.J. & van Groenendael J.M. 2004. Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology* 92, 767-777.
- Ozinga W.A., Römerman C., Bekker R.M., Prinzing A., Tamis W.L.M., Schaminée J.H.J., Henekens S.M., Thompson K., Poschlod P., Kleyer M., Bakker J.P. & van Groenendael J.M. 2009. Dispersal failure contributes to plant losses in Northwest Europe. *Ecology Letters* 12, 66-74.
- Page C.N. 1997. *The ferns of Great Britain and Ireland*, second edition. Cambridge University Press, Cambridge.
- Pearman D.A. 1997. Towards a new definition of rare and scarce plants. *Watsonia* 21, 225-245.
- Peñuelas J. & Filella I. 2001. Herbaria century record of increasing eutrophication in Spanish terrestrial ecosystems. *Global Change Biology* 7, 427-433.
- Perring F.H. 1963. Dividing the area, in Wanstall P.J., ed. *Local floras*, pp.28-36. Botanical Society of the British Isles, London.
- Perring F.H. 1970. The last seventy years, in Lousley J.E., ed. *The Flora of a Changing Britain*, pp.128-135. Botanical Society of the British Isles, London.
- Perring F.H. 1971. The vice-county guide. *Watsonia* 8, 435-447.
- Perring F.H. 1979. Foreword, in Trist P.J.O., ed. 1979. *An ecological flora of Breckland*, p.vii. EP Publishing Limited, Norwich.
- Perring F.H. 1995. Druce in Northamptonshire. *Watsonia* 20, 185-194.
- Perring F.H. & Walters S.M., comps & eds. 1962. *Atlas of the British flora*. Thomas Nelson & Sons, London.

- Perring F.H., Sell P.D., Walters S.M. & Whitehouse H.L.K. 1964. *A Flora of Cambridgeshire*. Cambridge University Press, Cambridge.
- Petch C.P. & Swann E.L. 1968. *Flora of Norfolk*. Jarrold & Sons, Norwich.
- Philp E.G. 1982. *Atlas of the Kent flora*. Kent Field Club, Maidstone.
- Poland J. & Clement E. 2009. *The Vegetative Key to the British Flora*. Botanical Society of the British Isles, London.
- Poschlod P. & Bonn S. 1998. Changing dispersal processes in the central European landscape since the last ice age – an explanation for the decrease of plant species richness in different habitats? *Acta Botanica Neerlandica* 47, 27-44.
- Preston C.D. 2000. Engulfed by suburbia or destroyed by the plough: the ecology of extinction in Middlesex and Cambridgeshire. *Watsonia* 23, 59-81.
- Preston C.D. 2003. Perceptions of change in English county floras, 1660-1960. *Watsonia* 24, 287-304.
- Preston C.D. 2007. Which vascular plants are found at the northern or southern edges of their European ranges in the British Isles? *Watsonia* 26, 253-269.
- Preston C.D. 2008. The aquatic plants of the River Cam and its riparian commons, Cambridge, 1660-1999. *Nature in Cambridgeshire* 50, 18-37.
- Preston C.D. & Yates S.E. 1995. Further localities for the Oxlip *Primula elatior* (L.) Hill in Cambridgeshire. *Nature in Cambridgeshire* 37, 35-41.
- Preston C.D. & Croft J.M. 1997. *Aquatic Plants in Britain and Ireland*. Harley Books, Colchester.
- Preston C.D. & Hill M.O. 1997. The geographical relationships of British and Irish plants. *Botanical Journal of the Linnean Society* 124, 1-120.
- Preston C.D. & Croft J.M. 1998. Britain's changing aquatic flora. *British Wildlife* 10, 18-28.
- Preston C.D. & Walker K.J. 2003. Creeping inflation in the length of county floras 1750-1960. *Watsonia* 24, 447-453.
- Preston C.D., Pearman D.A. & Dines T.D., comps & eds 2002a. *New Atlas of the British and Irish flora*. Oxford University Press, Oxford.
- Preston C.D., Telfer M.G., Arnold H.R., Carey P.D., Cooper J.M., Dines T.D., Hill M.O., Pearman D.A., Roy D.B. & Smart S.M. 2002b. *The Changing Flora of the UK*. DEFRA, London, UK.
- Preston C.D., Sheail J., Armitage P. & Davy-Bowker J. 2003a. The long-term impact of urbanisation on aquatic plants: Cambridge and the River Cam. *Science of the Total Environment* 314-316, 67-87.

- Preston C.D., Telfer M.G., Roy D.B., Carey P.D., Hill M.O., Meek W.R., Rothery P., Smart S.M., Smith G.M., Walker K.J. & Pearman D.A. 2003b. The Changing Distribution of the Flora of the United Kingdom: Technical Report. Centre for Ecology and Hydrology, Huntingdon, UK.
- Preston C.D., Pearman D.A. & Hall A.R. 2004. Archaeophytes in Britain. *Botanical Journal of the Linnean Society* 145, 257-294.
- Primavesi A.L. & Evans P.A., eds. 1988. *Flora of Leicestershire*. Leicestershire Museums, Art Galleries and Record Services, Leicester.
- Quinn R.M., Lawton, J.H., Eversham B.C. & Wood S.N. 1994. The biogeography of scarce vascular plants in Britain with respect to habitat preference, dispersal ability and reproductive biology. *Biological Conservation* 70, 149-157.
- Rackham O. 1980 *Ancient woodland: its history, vegetation and uses in England*. Edward Arnold, London.
- Rackham O. 1999. The woods 30 years on: where have all the Primroses gone? *Nature in Cambridgeshire* 41, 73-87.
- Ratcliffe D. 1984. Post-medieval and recent changes in British vegetation: the culmination of human influence. *New Phytologist* 98, 73-100.
- Ray J. 1660. *Catalogus Plantarum circa Cantabrigiam Nascentium*. Cambridge and London.
- Relhan R. 1785. *Flora Cantabrigiensis*. Cambridge.
- Rich T.C.G. 1997. *The management of semi-natural lowland grassland for selected rare and scarce vascular plants*. English Nature Research Report No. 216. English Nature, Peterborough
- Rich T.C.G. 1998. Squaring the circles – bias in distribution maps. *British Wildlife* 9, 213-219.
- Rich T.C.G. 2001. Flowering plants, in Hawksorth D.L., ed. *The Changing Wildlife of Great Britain and Ireland*, pp.23-49. Taylor & Francis, London & New York.
- Rich T.C.G. & Woodruff E.R. 1992. Recording bias in botanical surveys. *Watsonia* 19, 73-95.
- Rich T.C.G. & Smith P.A. 1996. Botanical recording, distribution maps and species frequency. *Watsonia* 21, 155-167.
- Rich T.C.G. & Woodruff E.R. 1996. Changes in the vascular plant floras of England and Scotland between 1930-1960 and 1987-1988: the BSBI Monitoring Scheme. *Biological Conservation* 75, 217-229.

- Rich T.C.G. & Lewis J. 1999. Use of herbarium material for mapping the distribution of *Erophila* (Brassicaceae) taxa sensu Filfilan & Elkington in Britain and Ireland. *Watsonia* 22, 397-403.
- Rich T.C.G. & Sydes C. 2000. Recording and the decline of two Nationally Scarce Plants *Ajuga pyramidalis* L. and *Melampyrum sylvaticum* L. *Watsonia* 23, 293-297.
- Rich T.C.G. & Lockton A. 2002. *Bromus interruptus* (Hack.) Druce (Poaceae) – an extinct English endemic. *Watsonia* 24, 69-80.
- Rich T.C.G. & Karran A.B. 2006. Floristic changes in the British Isles: comparison of techniques for assessing changes in frequency of plants with time. *Botanical Journal of the Linnean Society* 152, 279-301.
- Rich T.C.G., Cooper E.A., Rodwell J.S. & Malloch A.J.C. 1993. *Effects of Climate Change and Air Pollution on British Calcicolous Grasslands*. Final report to UK Department of the Environment.
- Rich T.C.G., Donovan P., Harmes P., Knapp A., et al. 1996. *Flora of Ashdown Forest*. Sussex Botanical Recording Society, East Grinstead.
- Rich T.C.G., Mardon D., Curtis I., Heyward S., Heyward V.G., McKean D., Hall T., Harris S., O'Rourke A., Cowan R.S. & Fay M. 2005. Is the enigma a variation? *Sagina boydii* F.B. White (Caryophyllaceae), Boyd's pearlwort. *Botanical Journal of the Linnean Society* 147, 203-211.
- Richards A.J. 1986. *Plant Breeding Systems*. Chapman and Hall, London.
- Riddlesdell, H.J., Hedley E.W & Price W.R., eds. 1948. *Flora of Gloucestershire*. Cotteswold Naturalists' Field Club, Cheltenham.
- Robertson H.J. & Jefferson R.G. 2000. *Monitoring the condition of lowland grassland SSSIs. I. English Nature's rapid assessment method*. English Nature Research Report No. 315. English Nature, Peterborough.
- Robertson J. 1982. Plant extinction in Bedfordshire. *Bedfordshire Naturalist* 36, 55-58.
- Robinson R.A. & Sutherland W.J. 2002. Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* 39, 157-176.
- Rodwell, J. 1992. *British Plant Communities. Volume 3. Grasslands and Montane Communities*. Cambridge University Press, Cambridge.
- Rose F. 1957. The importance of the study of disjunct distribution to progress in understanding the British flora, in Lousley J.E., ed. *Progress in the Study of the British Flora*, pp.61-78. Botanical Society of the British Isles, London.

- Roy D.B. & Sparks T. 2000. Phenology of British butterflies and climate change. *Global Change Biology* 6, 407-416.
- Salisbury E.J. 1924. Changes in the Hertfordshire flora: a consideration of the influence of man. *Transactions of the Hertfordshire Natural History Society* 18, 51-68.
- Salisbury E.J. 1967. Foreword, in Dony J.G. *Flora of Hertfordshire*. Hitchin Urban District Council, Luton.
- Sanderson N.A. 1998. *A Review of the Extent, Conservation Interest and Management of Lowland Acid Grassland in England: Volume II (County Descriptions)*. English Nature Research Report no. 259, English Nature, Peterborough.
- Schaffer M.L. 1988. Minimum viable populations: coping with uncertainty, in Soulé M.E., ed. *Viable Populations for Conservation*, pp.69-86. Cambridge University Press, Cambridge.
- Scott W. & Palmer R. 1987. *The flowering plants and ferns of the Shetland Islands*. Shetland Times, Lerwick.
- Sell P. & Murrell G. 2009. *Flora of Great Britain and Ireland. Volume 3, Mimosaceae – Lentibulariaceae*. Cambridge University Press, Cambridge.
- Shaffer H.B., Fisher R.N. & Davidson C. 1998. The role of natural history collection in documenting species decline. *Trends in Ecology and Evolution* 13, 27-30.
- Shaw P. 2005. Estimating local extinction rates over successive time-frames. *Biological Conservation* 121, 281-287.
- Sibthorp J. 1794. *Flora Oxoniensis*. Oxford.
- Simpson F.W. 1982. *Simpson's Flora of Suffolk*. Suffolk Naturalists' Society, Ipswich.
- Simpson N. D. 1960. *Bibliographical index of the British flora*. Brighton.
- Sinker C.A., Packham J.R., Trueman I.C., Oswald P.H. *et al.* 1985. *Ecological flora of the Shropshire region*. Shropshire Trust for Nature Conservation, Shrewsbury.
- Slater F.M. 1999. *Scleranthus perennis* subsp. *perennis* P. D. Sell (Caryophyllaceae), in Wigginton M.J., comp. & ed. *British Red Data Books I Vascular plants*. Third edition, p.336. Joint Nature Conservation Committee, Peterborough.
- Smart S.M., Clarke R.T., van de Poll E.J., Robertson E.J., Shield E.R., Bunce R.G.H. & Maskell L.C. 2003. National-scale vegetation change across Britain; an analysis of sample-based surveillance data from Countryside Surveys of 1990 and 1998. *Journal of Environmental Management* 67, 239-254.
- Smart S.M., Bunce R.G.H., Marrs R., Le Duc M., Firbank L.G., Maskell L.C., Scott W.A., Thompson K. & Walker K.J. 2005. Large-scale changes in the abundance of common

- higher plant species across Britain between 1978, 1990 and 1998 as a consequence of human activity: tests of hypothesised trait representation. *Biological Conservation* 124, 355-371.
- Smart S.M., Le Duc M., Marrs R.H., Maskell L.C., Thompson K. & Firbank L.G. 2006. Biotic homogenisation and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society, London B* 273, 2659-2665.
- Smith A.J.E. 2004. *The Moss Flora of Britain*. Second edition. Cambridge University Press, Cambridge.
- Sokal R.R. & Rohlf F.J. 1981. *Biometry*. Second edition. W.H. Freeman and Co., New York.
- Soulé M.E. 1986. *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Stace C.A. 1990. Foreword, in Crackles E. & Arnett R.R., eds *Flora of the East Riding of Yorkshire*. Hull University Press and Humberside County Council, Hull.
- Stace C.A. 1997. *New Flora of the British Isles*. Second edition. Cambridge University Press, Cambridge.
- Stace C.A. 2002. Knowing what we have: the ever-changing inventory. *Suffolk Natural History* 38, 23-36.
- Stamp L.D., ed. 1943a. *The Land of Britain. The Report of the Land Utilisation Survey of Britain. Part 58 - Northamptonshire and Part 59 - Soke of Peterborough*. Geographical Publications Ltd., London.
- Stamp L.D., ed. 1943b. *The Land of Britain. The Report of the Land Utilisation Survey of Britain. Part 55 - Bedfordshire*. Geographical Publications Ltd., London.
- Steffan-Dewenter I. & Kuhn A. 2003. Honeybee foraging in differentially structured landscapes. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270, 569-575.
- Stehlik I., Caspersen J.P., Wirth L. & Holderegger R. 2007. Floral free fall in the Swiss lowlands: environmental determinants of local plant extinction in a peri-urban landscape. *Journal of Ecology* 95, 734-744.
- Stevens C., Dise N.B., Mountford J.O. & Gowing D.J. 2005. Impact of nitrogen deposition on the species richness of grassland. *Science* 303, 1876-1879.
- Stewart A., Pearman D.A & Preston C.D., comps & eds 1994. *Scarce Plants in Britain*. Joint Nature Conservation Committee, Peterborough.

- Stewart K.E.J., Bourn N.A.D. & Thomas J.A. 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology* 38, 1148-1154.
- Stöcklin J. & Fischer M. 1999. Plants with longer-lived seeds have lower local extinction rates in grassland remnants 1950-1985. *Oecologia* 120, 539-543.
- Stroh, P. 2007. The current distribution of Green-winged Orchid *Orchis morio* L. in Huntingdonshire (vc31), the Soke of Peterborough (vc32) and old Cambridgeshire (vc29). *Nature in Cambridgeshire* 49, 3-11.
- Sumpton K.J. & Flowerdew J.R. 1985. The ecological effects of the decline in Rabbits (*Orctolagus cuniculus* L.) due to myxomatosis. *Mammal Review* 15, 151-186.
- Sutcliffe O.L. & Kay Q.N. 2000. Changes in the arable flora of southern England since the 1960s. *Biological Conservation* 93, 1-8.
- Sutherland D.S. 1995. Geology and soils, in Gent G. & Wilson R., eds *The Flora of Northamptonshire and the Soke of Peterborough*, pp.23-30. Robert Wilson Designs, Rothwell.
- Swan G.A. 1993. *Flora of Northumberland*. Natural History Society of Northumbria, Newcastle upon Tyne.
- Tabor R. 1996. Mowing for Sulphur Clover. *British Wildlife* 7, 174-175.
- Tackenberg O., Poschod P. & Bonn S. 2003. Assessment of wind dispersal potential in plant species. *Ecological Monographs* 73, 191-205.
- Tamis W.L.M., van't Zelfde M., van der Meijden R., Groen C.L.G. & Udo de Haes H.A. 2005. Ecological interpretation of changes in the Dutch flora in the 20th century. *Biological Conservation* 125, 211-224.
- Tarpey T. 1999. *Pasqueflower Count: Church Hill*. Unpublished survey report to the Conservators of Therfield Heaths and Greens.
- Telfer M.G., Preston C.D. & Rothery P. 2002. A general method for the calculation of relative change in range size from biological atlas data. *Biological Conservation* 107, 99-107.
- Ter Braak C.J.F. & Šmilauer P. 1998. *CANOCO. Reference Manual and User's Guide to CANOCO for Windows: Software for Canonical Community Ordination (version 4)*. Microcomputer Power, Ithaca, NY.
- Thomas A.S. 1960. Changes in vegetation since the advent of myxomatosis. *Journal of Ecology* 48, 287-306.

- Thomas I. 1995. Some Northamptonshire botanists, in Gent G. & Wilson R., eds *The Flora of Northamptonshire and the Soke of Peterborough*, pp.15-19. Robert Wilson Designs, Rothwell.
- Thompson K. 1994. Predicting the fate of temperate species in response to human disturbance and global change, in Boyle T.J.B. & Boyle C.E.B., eds. *Biodiversity, Temperate Ecosystems, and Global Change*, pp.61-76. Springer-Verlag, Berlin.
- Thompson K. & Hodgson J.G. 1996. More on the biogeography of scarce vascular plants. *Biological Conservation* 75, 299-302.
- Thompson K. & Jones A. 1999. Human population density and prediction of local plant extinction in Britain. *Conservation Biology* 13, 185-189.
- Thompson K., Hodgson J.G. & Rich T.C.G. 1995. Native and alien invasive plants: more of the same? *Ecography* 18, 390-402.
- Thompson K., Bakker J.P., Bekker R.M. & Hodgson J.G. 1998a. Ecological correlates of seed persistence in the north-west European flora. *Journal of Ecology* 86, 163-169.
- Thompson K., Hodgson J.G. & Gaston K.J. 1998b. Abundance-range size relationships in the herbaceous flora of Central England. *Journal of Ecology* 86, 439-448.
- Thompson K., Gaston K., & Band S.R. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. *Journal of Ecology* 87, 150-155.
- Tilman D., May R.M., Lehman C. & Nowak M.A. 2002. Habitat destruction and the extinction debt. *Nature* 372, 65-66.
- Trimen H. & Dyer W.T.T. 1869. *Flora of Middlesex*. Robert Hardwicke, London.
- Trist P.J.O. 1979. *An ecological flora of Breckland*. EP Publishing Limited, Norwich.
- Trist P.J.O. 1988. Hildersham Furze Hills. *Nature in Cambridgeshire* 30, 4-12.
- Uotila P. 1996. Decline of *Anemone patens* (Ranunculaceae) in Finland. *Symbolae Botanicae Upsalienses* 31, 205-210.
- Van Calster H., Vandenberghe R., Ruysen M., Verheyen K., Hermyand M. & Decocq G. 2008. Unexpectedly high 20th century floristic losses in a rural landscape in northern France. *Journal of Ecology* 96, 927-936.
- Van der Veken S., Verheyen K. & Hermy M. 2004. Plant species loss in an urban area (Turnhout, Belgium) from 1880 to 1999 and its environmental determinants. *Flora* 199, 516-523.
- Vergeer P., Rengelink R., Copal A. & Ouburg N.J. 2003. The interacting effects of genetic variation, habitat quality and population size on performance of *Succisa pratensis*. *Journal of Ecology* 91, 18-26.

- Vigurs E. & Thurston C.C. 1922. *A supplement to F. Hamilton Davey's Flora of Cornwall*. Royal Institution of Cornwall, Truro.
- Vines G. 2000. *Where have all the flowers gone? Loss and decline of species at the local level*. Plantlife, London.
- Vitousek P.M., Mooney H.A., Lubchenko J. & Melillo J.M. 1997a. Human domination of earth's ecosystems. *Science* 277, 494-499.
- Vitousek P.M., Aber J.D., Howarth R.W., Likens G.E., Matson P.A., Schindler D.W., Schlesinger W.H. & Tilman D.G. 1997b. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7, 737-750.
- Walker K.J. 2003. *Eriophorum gracile* formerly present in Northamptonshire (v.c. 32). *BSBI News* 92, 16-18.
- Walker K.J. 2007. The last thirty-five years: recent changes in the flora of the British Isles. *Watsonia* 26, 291-302.
- Walker K.J., Sparks T.H., & Swetnam R. 2000. The colonisation of tree and shrub species within a 38 year-old self-sown woodland: The Monks Wood Wilderness. *Aspects of Applied Biology* 58, 337-343.
- Warden K. 2001. *An investigation into techniques for the propagation and augmentation of a wild population of pasqueflower, Pulsatilla vulgaris, Miller, including observations on the reproductive biology of the species*. Unpublished MSc thesis, University of Reading
- Webb R.H. & Coleman W.H. 1849. *Flora Hertfordiensis*. W. Pamplin, London.
- Weiher E., van der Werf A., Thompson K., Roderick M., Granier E. & Eriksson O. 1999. Challenging Threophrastus: a common core list of plant traits. *Journal of Vegetation Science* 10, 609-620.
- Wells T.C.E. 1968. Land-use changes affecting *Pulsatilla vulgaris* in England. *Biological Conservation* 1, 37-43.
- Wells T.C.E. 1969. The decrease of *Pulsatilla vulgaris* in England – A reply to Dr. E.F. Jones. *Biological Conservation* 1, 328-329.
- Wells T.C.E. 1971. A comparison of the effects of sheep grazing and mechanical cutting on the structure and botanical composition of chalk grassland, in Duffey E. & Watt A.S., eds. *The Scientific Management of Animal and Plant Communities for Conservation*, pp.497-515. Blackwell Scientific Publications, Oxford.
- Wells T.C.E. 1989. The effects of changes in land use on the flora of Huntingdonshire and the Soke of Peterborough in the period 1949-89, in Wells T.C.E., Cole J.H. & Walker

- P.E.G., eds *40 Years of Change in the County*. Huntingdonshire Flora and Fauna Society, Huntingdon.
- Wells T.C.E. 2003. *A flora of Huntingdonshire and the Soke of Peterborough*. Privately published, Huntingdon.
- Wells T.C.E. & Barling D.M. 1971. Biological Flora of the British Isles no. 44. *Pulsatilla vulgaris* Mill. (*Anemone pulsatilla* L.). *Journal of Ecology* 59, 275-292.
- Welsh J. 1983. *Survey of Pulsatilla vulgaris populations in Bedfordshire*. Unpublished MS held by the author.
- Widén B. & Lindell T. 1995. Flowering and fruiting phenology in two perennial herbs, *Anemone pulsatilla* and *A. pratensis* (Ranunculaceae). *Symbolae Botanicae Upsaliensis* 31, 145-158.
- Wigginton M.J., comp. and ed. 1999. *British Red Data Books. Volume 1. Vascular Plants*. Third edition. Joint Nature Conservation Committee, Peterborough.
- Willi J.C., Mountford J.O. & Sparks T.H. 2005. The modification of ancient woodland ground flora at arable edges. *Biodiversity and Conservation* 14, 3215-3233.
- Williams M. 1970. The enclosure and reclamation of waste land in England and Wales in the eighteenth and nineteenth centuries. *Transactions of British Geographers* 51, 55-70.
- Williamson M.H. & Fitter A. 1996. The characters of successful invaders. *Biological Conservation* 78, 163-170.
- Woods R.G. 1993. *Flora of Radnorshire*. National Museum of Wales in association with the Bentham-Moxon Trust, Cardiff.
- Wynne G. 1993. *Flora of Flintshire*. Gee & Son, Denbigh.