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Declines in forage availability for bumblebees at a national scale

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ABSTRACT

We assessed national scale changes in the forage plants of bumblebees in Britain, as a means of providing quantitative evidence for the likely principal cause of declines in bumblebee species. We quantified the relative value of native and long-established plant species as forage (nectar and pollen) resources for bumblebees by collating visitation data from 14 field sites across Britain. Twentieth Century changes in range and frequency of these forage plants were assessed using data from the *New Atlas of the British and Irish Flora* (1930–1969 to 1987–1999) and the Countryside Surveys of Britain (1978–1998). Forage plants declined in both large-scale range and local-scale frequency between the two survey periods. These changes were of greater magnitude than changes in other native plant species, reflecting serious reductions in quality of foraging habitats for bees as well as a general decline in insect-pollinated plants. Seventy-six percent of forage plants declined in frequency within 1-km squares, including those (e.g. *Trifolium pratense*) of particular value for threatened bumblebee species. We consider how our findings relate to other recorded changes in the British flora, how they may help to explain declines in bumblebees and how they could contribute to a conservation strategy.

1. Introduction

Resource availability is often a critical factor in determining the distribution and abundance of species, and it is recognised that reductions in habitat quality as well as quantity are likely to cause population declines (Schultz and Dlugosch, 1999). Many social bumblebee (*Bombus* Latr.) species have undergone serious declines in recent decades across Europe and North America (Williams, 1982; Rasmont, 1988; Buchmann and Nabhan, 1996). Several factors have been suggested as possible contributors to these declines, including competition from the honeybee (*Apis mellifera*), changes in climate and the effects of predators and parasites (Williams, 1986). However, the principal factor is likely to have been the loss and degradation of habitats and critical food resources due to changes in land-use and agricultural practices (Goulson et al., 2005; Williams, 2005).

In Britain, as in other parts of Europe, the intensification of agricultural practices since the 1940s has resulted in the fragmentation, degradation and loss of semi-natural habitats (Robinson and Sutherland, 2002). For example, the area of unimproved lowland grassland in Britain is reported to have

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declined by over 90% between 1932 and 1984 (Fuller, 1987). Bumblebees forage for the colony as well as themselves, but only store several days' worth of reserves, so therefore require an almost continuous supply of food resources (nectar and pollen) within foraging distance from the nest throughout the period of colony activity (Prŷs-Jones and Corbet, 1991). Flower-rich, extensively managed vegetation is therefore considered an essential component of the agricultural landscape for bumblebees, providing foraging resources as well as nesting, mating and hibernation sites (Banaszak, 1992; Williams, 1986).

Analyses of change in the distributional ranges of British bumblebees have highlighted the likely extent of declines during the 20th Century. By the 1980s, only six of Britain's 19 *Bombus* species remained throughout their pre-1960 range (Williams, 1982). Three species are now considered to have become extinct, four (*Bombus distinguendus*, *B. humilis*, *B. ruderatus* and *B. sylvarum*) are currently on the UK Biodiversity Action Plan as priorities for conservation and others remain under threat (UK Biodiversity Group, 1998). This situation may threaten the pollination of many wild flowers and entomophilous crops (such as field bean, clover and various fruits) for which bumblebees are especially important (Corbet et al., 1991). They are therefore a key component of agricultural and semi-natural ecosystems that require urgent conservation.

The causes of rarity and decline among British bumblebees have recently been discussed by Goulson et al. (2005) and Williams (2005). They concluded that a combination of factors including a species' proximity to the edge of its European range and degree of food-plant or habitat specialization are likely to determine its sensitivity to environmental change, but noted that further studies on the rarer bumblebee species are still required. While these ecological factors continue to be debated, evidence of specific changes in abundance of essential habitat components, namely forage plants which provide nectar and pollen resources, has been largely anecdotal or derived at local scales. At the scale of individual sites, there is a link between the abundance and diversity of bumblebees and that of their preferred forage plant species (Bäckman and Tiainen, 2002; Carvell, 2002). More specifically, the abundance of the most rewarding forage plants at a site seems to be more important for many bee species than overall flowering plant diversity (Williams, 1989). Rasmont (1988) suggested that the loss of Fabaceae, historically sown as fodder crops, from grassland systems in France and Belgium was the major driver of declines in the longer-tongued bumblebees. However, quantitative evidence for declines or increases in forage plant abundance at national scales and over relevant time periods is so far lacking. It is important to understand the extent and direction of these changes in order to design appropriate measures to conserve bumblebee populations.

Attempts to quantify large-scale changes in biodiversity are often hindered by the quality and availability of data on species distributions (Thomas et al., 2004). However, repeated and systematic surveys in Britain over the past 30–50 years have generated two datasets which allow national changes in range and abundance of vascular plant species to be assessed. The *New Atlas of the British and Irish Flora* can be used to study change in number of occupied 10-km squares between 1930–1969 and 1987–1999 (Preston et al., 2002). This spans the likely period of most serious decline in bumblebee species (Williams, 1982). At a more detailed scale, the Countryside Surveys of Britain recorded the changing presence of all vascular plant species in fixed plots within 259 1-km squares between 1978 and 1998 (Haines-Young et al., 2000). These changes in species frequency have been used to infer changes in plant abundance between the two survey periods (Smart et al., 2005). The Countryside Surveys are likely to have covered the later phase of the period of bumblebee declines, but offer the most useful measure of national scale change in habitat quality.

In this paper we collate a number of datasets documenting bumblebee visitation to specified plant species in Britain, to produce a list of important nectar and pollen sources. We analyse changes in range and frequency of these forage plant species to quantify changes in resource availability for bumblebees at a national scale. We also consider whether the magnitude of such changes may help to explain 20th Century declines in British bumblebees. The forage species list is not exhaustive, and does not include entomophilous crops or garden flowers, but represents the collective findings of available surveys which meet particular criteria. Furthermore, the analysis is restricted to native species and long-established aliens (archaeophytes) (Preston et al., 2004), both because the value of recently introduced plant species (neophytes) as forage plants is less well known, and because numerical estimates of the spread of invasive plant species are influenced to a greater degree than natives by changes in recording practice.

2. Methods

2.1. *Collation of bumblebee forage plant data*

A number of datasets containing information on bumblebee forage plant visitation across Britain were collated. Data from both published and unpublished studies were used but, in order to ensure consistency, the following criteria were applied.

(a) All studies presented data as the number of bumblebee visits to a specified list of flowering plant species from one site (where more than one site was sampled during a study, datasets were considered separately). Studies conducted in gardens alone were excluded, as were those concentrating on crop species. Data were also restricted to flowering plant species classified as natives, probable natives or archaeophytes in Britain.
(b) Bumblebee visits were given to species level, but not necessarily separated by caste (we assume therefore that plants visited by queens, workers and males were represented in the collated data, even if not in all studies).
(c) Bumblebees were recorded using a standardised bee walk transect (Banaszak, 1980) or similar method.
(d) All studies were conducted within Britain, and over at least a two week time period up to and including the year 2000.

Datasets from a total of 14 study sites were found to match these criteria (Table 1), and were used to derive a list of visits

Table 1 – Sources of data on bumblebee forage plant visitation

Year of study	UK Site Location	Habitat types surveyed	Number of forage plants visited[a]	Number of social *Bombus* species	Reference
1999	Salisbury Plain Training Area, Wiltshire	Unimproved calcareous grassland	20	8	Carvell (2002)
2000	Castlemartin Range, Pembrokeshire, SW Wales	Unimproved mesotrophic grassland	9	10	Carvell (2000)
2000	Kenfig NNR, Glamorgan, S Wales	Mesotrophic and dune grassland	22	10	Carvell (2000)
1999	Shelfanger, Norfolk	Ancient hay meadow	13	6	Dicks et al. (2002)
1999	Hickling Broad NNR, Norfolk	Restored hay meadow	12	6	Dicks et al. (2002)
1998	South Uist, Western Isles, Scotland	Machair dune grasslands	11	5	Hughes (1998)
1998	Western Isles, Scotland	Machair dune grasslands	9	5	Macdonald, unpublished
1997	Strathpeffer, Highland Region, Scotland	Village edge and farmland	63	4	Macdonald (1998)
2000	Malton, North Yorkshire	Arable farmland, field margins	7	6	Pickett (2000)
1978	Wicken Fen, Cambridgeshire	Fen meadow	34	7	Prŷs-Jones (1982)
1990	Madingley Wood, Cambridgeshire	Woodland	24	6	Saville (1993)
1990	Croxton, West Cambridgeshire	Woodland and arable farmland	21	6	Saville (1993)
1982	Dungeness, Kent	Dune ridge grasslands	13	12	Williams (1989)
1983	Shoreham, Kent	Arable farmland and woodland edge	17	7	Williams (1989)

a A few species were excluded from the analysis if there was insufficient data from both plant surveys, or if they were considered recently established alien species (neophytes).

by individual bumblebee species to specific forage plants. The studies encompassed a wide range of semi-natural habitats (including a limited number within intensively farmed landscapes) and geographical locations across Britain.

To measure the relative value of each plant species as a forage resource, a 'forage index' was calculated. A simple average across sites of number of bee visits to each plant species was not an appropriate measure of relative importance, as the forage plant species by sites table was unbalanced (i.e. many plant species were present at just a few sites and a more limited number present at most sites). Also, due to differences in habitat type and quality between study sites, overall visitation rates were higher in some datasets than others. To compensate for these effects, a general linear model (Ryan et al., 2000) of the form,

$$\log(y_{ij} + 1) = \mu + \alpha_i + \beta_j + \varepsilon_{ij}$$

was applied to the data, where y_{ij} is the number of visits to plant species i at a site j. μ is a constant and the coefficients α_i and β_j are effects for species and sites, respectively. The forage index was calculated as a least-squares mean for each plant species; in effect this provides a geometric mean number of visits to each plant species, allowing for missing values.

Because of difficulties in comparing visitation data from different study sites (Williams, 2005), forage indices were not calculated for individual *Bombus* species. Forage indices were calculated for all social *Bombus* species grouped, and also for two summary classes of longer- and shorter-tongued species. Long-tongued species included *B. hortorum*, *B. pascuorum*, *B. humilis*, *B. ruderarius*, *B. sylvarum*, *B. muscorum* and *B. distinguendus* and short to medium-tongued species included *B. terrestris*, *B. pratorum*, *B. lapidarius*, *B. lucorum* and *B. jonellus*, based on Williams (1989) and Prŷs-Jones and Corbet (1991). These are not absolute classifications of tongue length as this can vary between species and among castes of the same species.

2.2. *Quantifying range changes (1930–1969 to 1987–1999)*

Changes in the distributional range of bumblebee forage plants were quantified at the 10-km square scale using records collated for the periods 1930–1969 and 1987–1999 (Preston et al., 2002). In order to compensate for variations in recording intensity and geographical coverage, changes in range size were assessed using a 'change index' (Telfer et al., 2002). The full details of this change index are already described, but the method is briefly outlined here. The 2788 10-km grid squares which were surveyed in both recording periods were defined (excluding Ireland), and the proportion of these squares in which each species was recorded was calculated for each period and then logit-transformed. A weighted linear regression model was fitted to the relationship between these counts, and the standardised residual for each species taken to represent an index of its change in range size relative to the trend across all species (Telfer et al., 2002). Thus, while the change index does not represent species range increases or decreases in absolute terms, it allows an assessment of the performance of each species between the two periods in relation to the 'average' species. Plant nomenclature follows Stace (1997).

2.3. Quantifying frequency changes (1978–1998)

Changes in forage plant species frequency were based on data recorded at the 1-km square scale in 1978 and 1998 as part of the Countryside Survey (CS) (Haines-Young et al., 2000). A total of 259 1 × 1 km sample squares were selected at random from 32 land classes representing physiographically similar sampling domains across Britain. Within each square, a number of fixed plots were established. These plots covered both linear features, including hedgerows, stream sides and road verges (all 10 m^2) as well as fields and unenclosed land (all 200 m^2). Within each plot ($n = 1572$), the presence (frequency) of all vascular plant species was recorded once in 1978 and again in 1990 and 1998. Further information on the CS approach and recording methodology can be obtained from Haines-Young et al. (2000) and Smart et al. (2005).

Changes in plot frequency of individual plant species between 1978 and 1998 for which CS data were available were assessed by calculating the percentage change in number of occupied plots between the two survey periods (referred to as relative % change). All CS plots that contained a recorded presence for a species in 1978 and 1998 were used, with the minimum sample size for analysis set at six occurrences in either year.

2.4. Analysis

For the CS data on species plot frequency, recorder intensity and geographical coverage were the same for each survey, therefore magnitude of change could be assessed. For each species, the change in number of occupied plots between 1978 and 1998 as a proportion of the total number of plots sampled (1572) was analysed using the Z-test for two proportions.

Differences between the mean range and frequency change in bumblebee forage plants and the mean change in range and frequency of all other non-forage plant species were analysed using two-sample T-tests. Analyses were repeated using randomisation tests that do not make assumptions about the distribution of the data (Manly, 1997), but these are not presented here as they did not change the results. Only species treated as natives, probable natives or archaeophytes (plants believed to have become established before 1500) by Preston et al. (2002, 2004) were included in the analyses. Species which had a British range size of less than 500 10-km squares (Preston et al., 2002), were removed from the list of non-forage plants to be comparable with the selected bee forage species that all occurred in more than 500 10-km squares. The grasses (Poaceae) were also excluded from the list of non-forage plants for this comparison. Relationships between the forage indices for all *Bombus* species, the long- or short-tongued species groups and forage plant species change were also assessed, using regression analyses, in order to determine whether the magnitude of recorded change was greater for more important forage plants.

3. Results

3.1. Bumblebee forage plants and the 'forage index'

A total of 145 plant species were identified as forage resources for bumblebees at the 14 study sites from which datasets were collated (Table 1). Of these species, 43% represented the Fabaceae (15%), Asteraceae (15%) and Lamiaceae (13%) and the majority were perennial or biennial. Plants with the highest overall forage index included *Ballota nigra*, *Centaurea nigra*, *Teucrium scorodonia* and *Lamium album*, though the latter two species were only visited by bees at one site. The long-tongued *Bombus* species group had high forage index values for *Ballota nigra*, *Trifolium pratense* and other Fabaceae whereas the shorter-tongued species showed a tendency to visit *Centaurea nigra*, *Rubus fruticosus* and other Asteraceae, with lower forage indices for the Fabaceae (Table 2). Data on changes in range and abundance of native and long-established forage plant species from the *New Atlas* and Countryside Survey were available for 97 and 68, respectively (see Appendix A; key species in Table 2). These lists included most species visited by bees at two or more sites and representatives from the majority of plant families in the full list.

3.2. Range changes in forage plants (1930–1969 to 1987–1999)

Of the 97 bumblebee forage plant species, 71% had a negative change index. Forage plants had significantly lower change indices than other, non-forage plant species ($n = 671$) ($t = -2.22$, d.f. = 155, $P < 0.05$; Fig. 1a). Bumblebee forage plants have thus declined in range size between 1930–1969 and 1987–1999 relative to other native or long-established species. Forage species with the largest negative change index included *Leucanthemum vulgare* (−1.14) and *Lamium purpureum* (−1.09), and the largest positive change index was for *Leontodon autumnalis* (+1.32). There was no significant relationship between the forage index of plants for all *Bombus* species grouped and their change index values (Table 2). The same was true when this analysis was repeated using the forage indices of long- and short-tongued species.

3.3. Frequency changes in forage plants (1978–1998)

Within Countryside Survey plots, 76% of bumblebee forage plant species declined and 24% increased in frequency between 1978 and 1998. Forage plants showed a significantly greater decline in CS plot frequency than other, non-forage plant species ($n = 257$) ($t = -3.07$, d.f. = 211, $P < 0.01$; Fig. 1b). Summing the total extent of decline in terms of number of plots from which a forage species was 'lost' (1012), this far exceeded the number of plots in which a species was 'gained' (105). In terms of magnitude of change for individual species, 26 of the 68 species tested showed significant changes in plot frequency ($P < 0.05$), but 24 of these were declines (Appendix A). Notable declines were recorded for*Centaurea nigra*, *Lathyrus pratensis*, *Leucanthemum vulgare*, *Lotus corniculatus*, *Rhinanthus minor* and *Trifolium pratense*. Forage species showing the greatest relative increase in plot frequency included *Ballota nigra* and *Odontites vernus*, though 1978 frequency was very low for these two species (Table 2). There was no significant relationship between the forage index of plants for all *Bombus* species grouped and their relative percentage change in plot frequency (Table 2). Analysing these data according to bee tongue-length, a positive relationship was found between the forage indices for long-tongued species and percentage

Table 2 – Forage index and change data for bumblebee forage plant species for which both New Atlas and Countryside Survey (CS) data were available, and which were visited by bumblebees at two or more study sites

Plant species	Forage index all *Bombus*	Forage index long-tongued	Forage index short-tongued	Number of study sites with bee visits	New Atlas Change index (1930–1969 to 1987–1999)	CS plot frequency 1978	CS plot frequency 1998	CS Relative % change 1978–1998	Z-test significance[a]
Ajuga reptans	2.17	2.08	0.89	2	−0.56	32	18	−43.75	*
Arctium agg.	1.48	1.35	0.14	2	0.05	16	15	−6.25	n.s.
Ballota nigra	3.85	3.56	0.89	2	−0.37	5	14	180.00	*
Bryonia dioica	1.03	0.74	0.40	3	−0.50	11	5	−54.55	n.s.
Centaurea nigra	3.82	2.66	3.32	7	−0.25	135	73	−45.93	***
Chamerion angustifolium	2.50	1.45	2.27	7	−0.01	65	46	−29.23	n.s.
Cirsium arvense	2.85	1.69	2.47	8	0.47	319	311	−2.51	n.s.
Cirsium palustre	3.36	2.79	2.19	3	0.15	131	117	−10.69	n.s.
Cirsium vulgare	2.82	2.24	1.90	8	0.80	228	163	−28.51	***
Convolvulus arvensis	2.65	0.85	2.76	3	−0.70	78	87	11.54	n.s.
Epilobium hirsutum	3.75	3.14	2.65	4	0.12	41	32	−21.95	n.s.
Filipendula ulmaria	1.55	−0.05	1.74	3	−0.10	110	84	−23.64	*
Glechoma hederacea	1.70	1.33	0.74	2	−0.56	65	57	−12.31	n.s.
Iris pseudacorus	1.36	1.05	0.40	2	0.16	12	13	8.33	n.s.
Lamiastrum galeobdolon	1.25	−0.20	1.53	2	1.07	6	5	−16.67	n.s.
Lathyrus pratensis	2.38	2.21	0.75	5	−0.17	101	56	−44.55	***
Leucanthemum vulgare	2.79	0.97	2.28	3	−1.14	20	7	−65.00	**
Lotus corniculatus	2.89	2.23	1.86	9	1.09	134	98	−26.87	**
Lychnis flos-cuculi	1.62	1.64	0.19	2	−0.79	13	11	−15.38	n.s.
Mentha aquatica	2.80	2.26	1.09	2	−0.11	38	23	−39.47	*
Odontites vernus	2.92	2.43	1.70	5	−0.46	6	16	166.67	*
Prunella vulgaris	2.00	1.80	0.57	7	0.60	178	145	−18.54	*
Ranunculus acris	0.78	0.76	0.01	2	0.30	205	191	−6.83	n.s.
Rhinanthus minor	2.85	2.39	1.67	7	−0.49	29	6	−79.31	***
Rubus fruticosus agg.	3.47	2.45	3.29	6	−0.29	279	275	−1.43	n.s.
Senecio jacobaea	2.29	0.70	2.34	5	0.11	109	115	5.50	n.s.
Stachys sylvatica	1.89	1.81	0.19	3	−0.49	50	51	2.00	n.s.
Trifolium dubium	1.19	0.76	0.50	2	−0.11	43	35	−18.60	n.s.
Trifolium pratense	3.31	3.26	0.91	8	−0.18	153	93	−39.22	***
Trifolium repens	2.36	1.64	1.79	10	1.31	576	507	−11.98	**
Vicia cracca	2.65	2.44	0.53	6	−0.37	30	35	16.67	n.s.

Species in bold type showed a significant decline in CS plot frequency.

[a] The Z-test assessed change in the number of occupied CS plots between 1978 and 1998 as a proportion of the total number of plots sampled: n.s. = not significant.

* $P < 0.05$.

** $P < 0.01$

*** $P < 0.001$.

change in plot frequency ($r^2 = 9.8$, $P < 0.01$), although this trend was influenced by high forage indices for the two plant species (*Ballota nigra* and *Odontites vernus*) which more than doubled in plot occupancy between the two surveys.

4. Discussion

This study was designed to broadly quantify 20th Century changes in availability of forage resources for bumblebees at a national scale using the best available data. Overall, a large proportion of forage plants declined in both large-scale range and local-scale frequency between the two survey periods of the *New Atlas* and Countryside Survey (CS). These changes were of greater magnitude than changes in other native and long-established plant species, reflecting serious reductions in the quality of foraging habitats for bees as well as a general decline in insect-pollinated plants.

The negative impacts of agricultural intensification on particular groups of animals and plants in Britain have been well recognised (Rich and Woodruff, 1996; Chamberlain et al., 2000; Robinson and Sutherland, 2002) and our results are consistent with these studies. The general trend for plants has been an increase in species characteristic of fertile habitats and decrease in species (often specialists) characteristic of less fertile, semi-natural habitats such as calcareous grassland (Preston et al., 2002). The former include some species which provide forage for bumblebees (e.g. *Cirsium arvense*), as well as the larval food plants (e.g. *Urtica dioica*) of certain butterfly species which have also increased since the 1970s (Smart et al., 2000). However, the majority of bumblebee

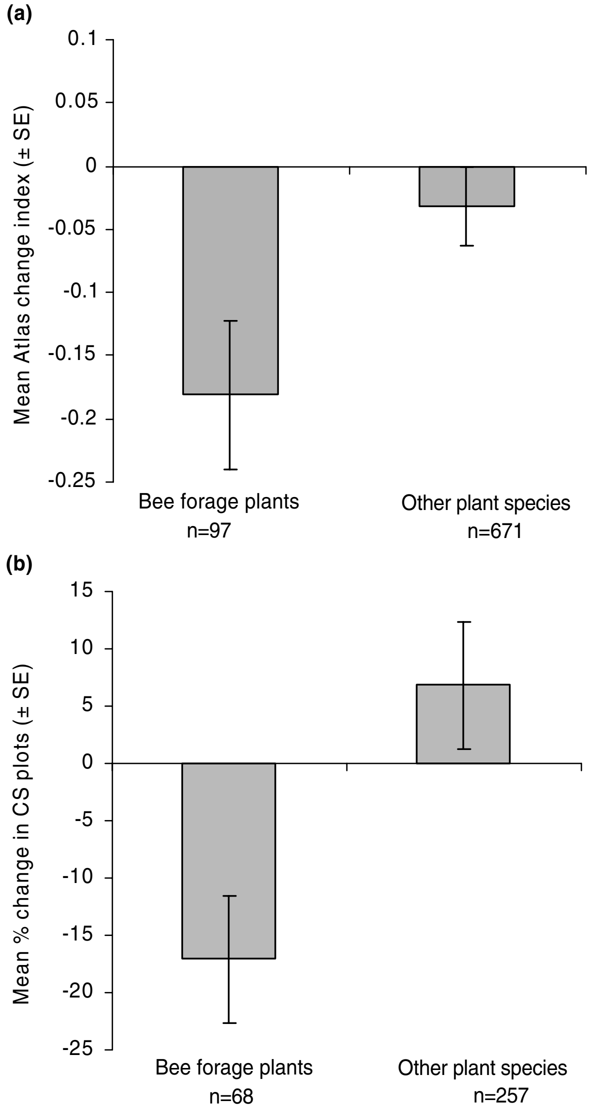

Fig. 1 – Changes in range size (a) and frequency (b) of bumblebee forage plants vs. all other native and long-established plant species in Britain. Range changes from 1930–1969 to 1987–1999 were measured by the Atlas change index for 10-km squares. Frequency changes from 1978 to 1998 were measured as relative % change in frequency of occupied Countryside Survey plots within 1-km squares.

forage plants are nectariferous perennials or biennials, often typical of established semi-natural vegetation receiving infrequent disturbance. It is therefore perhaps not surprising that as a group, they have declined relative to the ‘average’ native or archaeophyte species. These declines in range and abundance reflect the degradation of quality of foraging habitats for bumblebees in British landscapes which apparently persisted into the latter part of the 20th Century. Such changes can also be explained by recorded trends in specific management practices across England and Wales. Between 1962 and 1995 for example, large increases in silage production and autumn-sown cereals were accompanied by decreases in hay production, temporary clover leys and undersowing of legumes (Chamberlain et al., 2000).

A decline in forage resources is likely to impact upon bumblebees by affecting both the fitness of individual colonies within each season and persistence of populations between years, depending on the scale at which it is considered. At the local scale, a reduction in nectar and pollen availability within the foraging range of the nest limits colony growth and, ultimately, the reproduction of sexuals (Goulson et al., 2002; Pelletier and McNeil, 2003). Our results from the CS dataset suggest that native forage species important during all stages of colony activity declined between 1978 and 1998. Significant decreases in plot frequency were found for spring forage plants such as *Ajuga reptans*, *Lamium purpureum* and *Salix cinerea* and mid- to late-season forage plants such as *Centaurea nigra*, *Lathyrus pratensis*, *Lotus corniculatus*, *Rhinanthus minor* and *Trifolium pratense*. The total extent of these declines in terms of the likely loss of forage was not compensated for by the increases shown by some species, although we discuss some of the caveats associated with these data below.

Given their relatively large foraging ranges (Darvill et al., 2004), bumblebees might be expected to be capable of adapting to these local-scale reductions in forage, if sufficient resources persisted elsewhere within their population range. However, our results at the larger scale, represented by change in number of occupied 10-km squares from the *New Atlas*, suggest that on the whole this may not have been possible. Since the 1940s, despite being geographically widespread species, bumblebee forage plants have been lost from a significant number of 10-km squares within their range (assuming, as seems likely, that the relative change in forage plants represents an absolute decline). As well as contributing to reduced colony densities at the local to regional scale, this may have restricted the dispersal distances of new queens from their natal colonies, either before or after hibernation, and thereby affected their capacity for population expansion. A much greater understanding of the dispersal abilities of bumblebees (Mikkola, 1978) is required to fully assess the potential of populations to track the changing distribution of forage resources at different spatial scales.

The general response to reduced forage resources suggested above is likely to vary considerably between species, as evidenced by the different patterns of response to 20th Century environmental change shown by bumblebee species in Britain and elsewhere (Goulson et al., 2005; Williams, 2005). This may be due to a combination of ecological, behavioural and morphological factors. For example, the effect of local decreases in forage abundance may be stronger for those species with shorter foraging ranges or more specific dietary preferences. Although we did not distinguish between pollen and nectar provision, the Fabaceae are thought to be especially important pollen sources for the longer-tongued species (Goulson et al., 2005), as reflected here by higher forage indices. The loss of Fabaceae within semi-natural vegetation may have particularly affected this group of bumblebees, some of which have been suggested to have relatively short foraging ranges (Knight et al., 2005). These inter-species differences, combined with the difficulties in measuring preference for particular forage plants (e.g. Williams, 2005), may explain why our forage index did not relate to the recorded changes in plant species. The studies from which visitation data were collated to produce the forage index represented a variety of semi-natural habitats at sites with and without the rarer *Bombus* species, with only heathlands (and to an extent farmland) being underrepresented. But we could not allow for the super-abundance of particular forage plants at certain sites, or for patterns of flower visitation which might have been revealed by studies conducted in the early 20th Century, prior to bumblebee declines. The forage index provides a useful measure of the relative value of plant species to long- vs. short-tongued species, and of certain groups of plants to all species, but it should not be interpreted as a definitive measure of floral preference by all bumblebees.

By focusing on native and long-established plant species associated with semi-natural habitats, our analysis did not consider the potentially positive effect that introduced plant species, including garden exotics and entomophilous crops, could have on bumblebee populations. For example, the increase in area of oil-seed rape in England and Wales since the 1970s (Chamberlain et al., 2000) has probably benefited shorter-tongued species such as *Bombus terrestris* (Westphal et al., 2003). Exotic species within gardens, such as *Pulmonaria officinalis* and *Nepeta* × *faassenii*, may also be important in some situations where native sources of forage are scarce or temporally unavailable (Macdonald, 1998). There is also evidence that urban areas support higher concentrations of nests of the short-tongued *B. terrestris* than arable or mixed farmland (Chapman et al., 2003; Knight et al., 2005) and that nests of this species grow more quickly in gardens than in mixed farmland (Goulson et al., 2002).

In drawing conclusions, we note the caveats associated with comparing the results of two large surveys conducted across different spatial and temporal scales (Preston et al., 2002; Wilson et al., 2004). The direction of change detected by each survey was not the same for every plant species, although the general pattern of forage declines was consistent. Declines in local or regional plant abundance could go undetected at the 10-km scale. Likewise the CS plot data may underestimate the degree of habitat degradation, as plant frequency has some shortcomings as a functional measure of the quality of floral resources available to bumblebees. For example, changes in the cutting management of permanent grassland might reduce the number of flowers and alter sward structure but would not necessarily be detected as changes in plant abundance or plot frequency. We have not considered changes in availability of bumblebee nesting sites here, as it is difficult to quantify the variety of characteristics associated with nest site preferences of the different species. However, many species rely on undisturbed grassy vegetation with a tussocky structure, often using the abandoned nests of small mammals (Kells and Goulson, 2003). The response of vole numbers to intensification and the loss of suitable grasslands (Gorman and Reynolds, 1993) is an indication that nesting sites for bumblebees may have declined alongside forage plants, and should be considered in the design of conservation measures.

4.1. *Conclusions: towards effective conservation and further research*

This study has produced the first quantitative evidence for 20th Century declines in resource availability for bumblebees at a national scale in Britain, yet there is scope for much further work of this nature, such as that applied to British butterflies (Wilson et al., 2004). Analyses of changes in plant species range at a regional level suggest that certain forage species declined more seriously in East Anglia (representing much of Williams (1982) 'central impoverished region' of England) than in other UK regions (Preston et al., 2003). Yet populations of some rare *Bombus* species still persist in central and eastern England, albeit at apparently low densities (Carvell et al., 2006). The question of whether declines in bumblebee populations have depressed crop productivity or the reproductive potential of wild plants in Europe is still under debate (Ghazoul, 2005). However, bee diversity and proximity to natural habitats have been shown to enhance both crop productivity (Kremen et al., 2002) and seed set of isolated plants

Table 3 – Recommended forage plant species for wildlife seed mixtures and other restoration schemes in agricultural landscapes

Plant species	Rank performance[a]
Ajuga reptans	
Anthyllis vulneraria	11
Ballota nigra	
Centaurea nigra	5
Centaurea scabiosa	15
Cirsium vulgare	
Dipsacus fullonum	
Echium vulgare	
Glechoma hederacea	
Hypochaeris radicata	6
Knautia arvensis	14
Lamium album	
Lamium purpureum	
Lathyrus pratensis	8
Leucanthemum vulgare	1
Lotus corniculatus	3
Odontites vernus	
Prunella vulgaris	4
Rhinanthus minor	7
Rubus fruticosus agg.	
Salix cinerea	
Stachys officinalis	12
Stachys sylvatica	
Succisa pratensis	13
Symphytum officinale	
Thymus polytrichus	10
Trifolium pratense	2
Vicia cracca	9

a Species ranked in order of decreasing performance based on measures of relative success in establishment and persistence in grassland restoration experiments from Pywell et al. (2003), updated to include more recent studies (unpublished). Species with no ranking can be encouraged along hedgerows and woodland edges, particularly to provide spring forage. Note that other plant species not listed here may be equally valuable to bumblebees in certain regions.

(Steffan-Dewenter and Tscharntke, 1999), strengthening the conservation argument. Declines in a large number of insect-pollinated native plant species in Britain, as evidenced here, combined with declines in bumblebee species are undoubtedly a cause for concern. More detailed studies of recorded changes in bumblebee distribution and plant abundance and the functional links between plants and pollinators are required to address these questions.

An opportunity now exists to use knowledge from this and other studies to inform targeted habitat restoration, to reintroduce important forage plants to the farmed landscape through agri-environment schemes (Carvell et al., 2004; Pywell et al., 2005). A delay in this reintroduction of resources could further threaten populations of the rarer bumblebees which are mainly restricted to designated sites (Carvell, 2002). We recommend species such as *Trifolium pratense*, *Lotus corniculatus* and *Centaurea nigra* as components of wildlife seed mixtures. As well as the evidence that these are important forage plants to a range of *Bombus* species which have declined in the countryside, they have also been shown to perform well during restoration experiments (Pywell et al., 2003). Sympathetic management of vegetation along hedgerows and woodland edges should also encourage plants such as *Ajuga reptans* and *Lamium album* to provide spring forage. These recommendations are summarised in Table 3. Furthermore, it will be important to implement these practical measures which increase resources for bumblebees at scales and in regions which will influence national trends. This highlights the need for experimental and monitoring approaches focused up to the landscape scale, and on the population responses of rare as well as common *Bombus* species.

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Appendix A. Supplementary data

Supplementary data associated with this article (appendix with forage index and change data for the full list of forage plant species considered in the analyses) can be found, in the online version, at doi:10.1016/j.biocon.2006.05.008.

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