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Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins

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Summary

1. Declines in abundance and diversity of bumble bees (*Bombus* spp.) in Europe have been linked to agricultural intensification and the resulting loss of suitable foraging and nesting habitats. Environmental Stewardship (ES) is a new scheme in England offering the opportunity to restore habitats of value for these important pollinators to agricultural land. Scientific evaluation of the options prescribed within the scheme is essential to ensure that their objectives are met and that the benefits can be realized by the full bumble bee species assemblage.
2. We compared the efficacy of different ES options for field margins on arable land in enhancing the abundance and diversity of flowering resources and foraging bumble bees. Our study was conducted over 3 years using a multisite experiment.
3. Overall, uncropped margins sown with mixtures containing nectar and pollen-producing plants were more effective in providing bumble bee forage than margins sown with a grass mix, allowed to regenerate naturally or managed as conservation headlands.
4. A mixture of agricultural legumes established quickly and attracted on average the highest total abundance and diversity of bumble bees, including the rare long-tongued species *Bombus ruderatus* and *Bombus muscorum*. However, marked differences were observed between species and sexes in their responses to field margin management over time.
5. A diverse mixture of native wildflowers attracted more of the shorter-tongued *Bombus* spp. and provided greater continuity of forage resources, especially early in the season. Allowing *Cirsium* spp. to flower on such margins also increased their attractiveness to male bumble bees.
6. *Synthesis and applications*. Our results suggest that the legume-based ‘pollen and nectar flower mix’, as prescribed under Entry Level Stewardship in England, can quickly provide a highly attractive forage resource for bumble bees, but that issues of seasonal flowering phenology and longevity of the mixture need to be addressed. Establishment of ‘floristically enhanced margins’ under Higher Level Stewardship will be important to provide diverse perennial communities of forage plants and to support a greater range of *Bombus* spp. and other pollinators. The population-level responses of bumble bees to introduced seed mixtures and other agri-environment options require further study in order to maximize the benefits of such schemes in intensively farmed landscapes.

Key-words: agri-environment, arable farmland, *Bombus*, bumblebees, forage plants

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Introduction

The intensification of agriculture in western Europe over recent decades has led to declines in the populations of many wild plant and animal species formerly characteristic of farmland (Robinson & Sutherland 2002). In order to reverse these declines, it is mandatory for European Union (EU) member states to operate agri-environment schemes as part of the Common Agricultural Policy. The objectives of the schemes differ, depending on country and region, but all include measures whereby farmers are paid to manage their land for the benefit of particular habitats and species (Ovenden, Swash & Smallshire 1998). In England, Environmental Stewardship (ES) is a new agri-environment scheme that operates at two levels: the Entry Level (ELS) (Defra 2005a) is open to all farmers, while the Higher Level (HLS) (Defra 2005b) offers greater rewards to land managers for the delivery of a wider range of biodiversity benefits on targeted sites, such as those with existing high-priority environmental features.

Bumble bees (*Bombus* spp.) are considered important as pollinators because of their roles in enhancing the yields of entomophilous crops (Corbet, Williams & Osborne 1991; Free 1993), particularly fruit crops (Willmer, Bataw & Hughes 1994), and in maintaining populations of native plant species that have been fragmented within the agricultural landscape (Steffan-Dewenter & Tscharntke 1999). However, many bumble bee species have shown declines in abundance and contractions in range across Europe and North America since the mid-20th century (Williams 1982; Rasmont 1988; Buchmann & Nabhan 1996). In the UK, three species have been declared extinct and up to half the remaining 22 species are under threat (Edwards & Jenner 2005).

Their requirements for a season-long supply of pollen and nectar sources and undisturbed nesting, mating and hibernation sites make bumble bees susceptible to the effects of intensive farming. Changes in management practice, such as the conversion of species-rich hay meadows for silage production and the degradation of perennial vegetation in field margins and hedgerows, are likely to have had detrimental effects on all *Bombus* spp. (Osborne & Corbet 1994). Some species, including *Bombus sylvarum* and *Bombus ruderatus*, are thought to have been particularly affected by the loss of unimproved grassland in the UK (Fuller 1987) and are listed as priority species on the UK Biodiversity Action Plan (BAP) (Anonymous 1999). Suitable management of semi-natural areas where their populations persist is a conservation priority (Carvell 2002), but the potential to provide resources for these rarer species on farmland requires further investigation. While the more common species may benefit from mass flowering crops, such as oilseed rape *Brassica napus* ssp. *oleifera* (Westphal, Steffan-Dewenter & Tscharntke 2003), these temporary forage resources alone are unlikely to be sufficient to sustain their colonies throughout the season, or to support the full species assemblage in agricultural landscapes. Agri-environment schemes therefore offer an important opportunity to restore habitats of value to bumble bees in intensively farmed areas. It is, however, essential that management options within such schemes are both based on sound scientific evidence and subject to scientific evaluation to ensure that they are successful in attracting the desired species (Kleijn & Sutherland 2003; Knop *et al*. 2006).

One objective of the UK agri-environment schemes is to enhance the abundance and diversity of flowering plant species within arable systems through changes in management within or at the margins of fields. Field margins are a key feature of agricultural landscapes and there are well-documented agronomic and ecological reasons why they have become the focus of management options within the schemes (Marshall & Moonen 2002; Defra 2005a, 2005b). Margins act as buffers to protect hedgerows against pesticide and fertilizer drift, prevent the spread of pernicious weeds into crops, and provide important refuge habitats for wildlife (Marshall & Moonen 2002; Meek *et al*. 2002; Critchley *et al*. 2004). Initial assessments of these management options suggested that the potential benefits for bumble bees were mixed (Kells, Holland & Goulson 2001; Kleijn *et al*. 2001; Goulson *et al*. 2002), despite positive effects being recognized for other taxa. Conservation headlands, where pesticide and herbicide applications at the crop edge are reduced, are more likely to encourage annual plants than perennials and biennials, which are the preferred forage species for most bumble bees (Fussell & Corbet 1992; Dramstad & Fry 1995; Critchley *et al*. 2004). Uncropped margins left to regenerate naturally may provide suitable forage species on some sites but can encourage pernicious weeds such as *Cirsium* spp. and can take several years to develop suitable mid-successional communities (Corbet 1995; Carvell *et al*. 2004).

Sowing a mixture of annual or perennial grassland species on arable field margins has been shown to overcome some of the above restrictions and significantly enhance the abundance and diversity of bumble bees and their forage plants (Carreck & Williams 2002; Meek *et al*. 2002; Carvell *et al*. 2004; Pywell *et al*. 2005, 2006). However, these studies have either been conducted at a single location or during a single year, where factors such as soil geology, the local *Bombus* spp. assemblage, climatic conditions and timing in relation to the establishment of field margin habitats may influence the outcome. Furthermore, many agri-environment scheme assessments have been compromised by a lack of standardized management practices or seed mixtures across study sites, caused by variation in farmer expertise and understanding of the desired plant communities (Kleijn *et al*. 2001). Options for field margins and arable land within the new ES scheme in England are accompanied by clear management guidelines involving standard agricultural techniques (Defra 2005a, 2005b). They may require greater intervention in the early stages to achieve successful establishment (Marshall & Nowakowski 1995), but the outcome is likely to better resemble the intended vegetation community and habitat quality for target species,

Table 1. Arable field margin treatments and management details with corresponding Environmental Stewardship agri-environment scheme options (the codes for which are shown in the respective ELS and HLS columns)

Experimental treatment	Abbreviation	Description	Management	Agri-environment scheme options 2004–05 ELS	2005 HLS
Crop	Crop	Conventional arable crop management (the control)	Managed as rest of the field in cereal crop rotation	NA	NA
Conservation headland	Cons head	Arable crop managed to encourage broad-leaved annuals on 6-m margin	Sown with cereal crop as rest of field; herbicide and insecticide application restricted*	EF9	NA
Natural regeneration	Nat regen	Uncropped 6-m margin cultivated to encourage rare annual plants	Cut early September every year; cuttings left; lightly cultivated in late September every year; no herbicide, pesticide or fertilizer*	EF11	HF20
Tussocky grass mixture	Grass	6-m margin sown with five tussock-forming grass species at 20 kg/ha	Sown in September 2001; cut in May and September 2002; uncut thereafter; no herbicide, pesticide or fertilizer*	EE3	NA
Wildflower mixture	Wildflower	6-m margin sown with 21 native wildflower species and four fine grass species at 37 kg ha^{-1}	Sown in September 2001; cut in May and early September 2002 then only in September 2003–04; cuttings removed; no herbicide, pesticide or fertilizer*	EE3	HE10
Pollen and nectar mixture	Pollen & nectar	6-m margin sown with four agricultural legume species and four fine grass species at 20 kg ha^{-1}	Sown in September 2001; cut in May and early September 2002 then only in September 2003–04; cuttings removed; no herbicide, pesticide or fertilizer*	EF4	HE10

*Under the prescriptions, selected herbicide application is permitted only to control pernicious weeds or invasive alien species (Defra 2005a, 2005b).

and thus achieve the objectives of the scheme. To our knowledge, there have so far been no comprehensive assessments of the effects of these new ES options with standardized management prescriptions on any taxon.

In this study we assessed the effects of ES options for arable land on bumble bees and their forage plants over 3 years using a multisite experiment. We tested the following hypotheses. H1: field margin management according to different ES options has significant effects on the abundance and diversity of flowering resources and foraging bumble bees. H2: the effects of margin management on bumble bees and their forage resources change over time, between years. H3: the effects of seed mixture composition on flowering resources and foraging bumble bees change during the season.

The results are discussed in terms of the efficacy of different ES options in attracting foraging bumble bees, and the potential role of agri-environment schemes in enhancing and sustaining bumble bee populations on arable farmland.

Methods

Study sites and experimental treatments

The experiment was conducted at six sites across central and eastern England: SU8389, SU5593, TL9614, TL4647, SP9761 and SE7766 (see Figure S1 in the supplementary material). All sites were predominantly arable farms, with soil types ranging from clay in the east to sandy or variable loams in central and northern locations. At each of the six sites, experimental plots were established in September 2001 along two cereal field margins (replicates) within the same field, in all cases but one on opposite sides, with an east and west aspect. Plots were contiguous, measuring 50 m long and 6 m wide. On each replicate margin, plots were managed according to one of six treatments, detailed in Table 1, five of which represented current and forthcoming agri-environment options and one of which represented conventional crop management as a control. Treatments were randomly assigned to plots at each site, with the exception of the crop and conservation headland, which were assigned at random to either end of each replicate to enable annual farming operations. Details of the seed mixtures used in the three sown treatments are given in Appendix S1 in the supplementary material.

Flowering resources

To gain a measure of forage availability and assess seasonal change in flowering resources within treatments, an estimate of the number of flowering units present within each plot was made. This was done for each bumble bee transect (see below), from May to late August, in the years 2002, 2003 and 2004. All flowering dicotyledon species were identified in the field (following Stace 1997) and the following scores were used to describe their abundance: 1, 1–25 flowers; 2, 26–200 flowers; 3, 201–1000 flowers; 4, 1001–5000 flowers; 5, more than 5000 flowers (super-abundant). One flower 'unit' was counted as a single flower or, in the case of multiflowered stems, as an umbel (e.g. *Daucus carota*), head (e.g. *Trifolium pratense*), spike (e.g. *Rhinanthus minor*) or capitulum (e.g. *Centaurea nigra*).

BUMBLE BEE MONITORING

Bumble bee activity was recorded from May to late August, with between six and 11 sampling visits to each site in 2002, and nine visits to each site in 2003 and 2004. Bumble bee nests are difficult to locate reliably by any standardized sampling method, and techniques to estimate the effects of field-scale management on populations were not developed at the start of the study (Knight *et al*. 2005). We therefore used standardized counts of foraging bumble bees visiting flowers within the field margin plots to measure the relative attractiveness of treatments and potential for forage provision. On each visit, foraging bumble bees were counted along 6-m wide transects, with the recorder walking down the centre line of each field margin plot (Banaszak 1980; Carvell *et al*. 2004). The direction in which margins were walked was varied between visits. The plant species on which each bumble bee was first seen foraging was noted. All *Bombus* spp. were recorded, but *Bombus terrestris* and *Bombus lucorum* were recorded collectively, as workers of these species cannot be distinguished reliably in the field. Any other individuals that could not be readily identified whilst foraging, such as *Bombus muscorum*, were captured and examined with a hand lens. The different castes (queen, worker, male) were recorded separately for *Bombus lapidarius* only, as sex separation of other species in the field can be unreliable. The cuckoo bumble bees (now subgenus *Psithyrus*, brood parasites of the social *Bombus* spp.) were counted together as a group for analysis. Bumble bee nomenclature follows Prys-Jones & Corbet (1991).

Transects were carried out between 10:00 and 17:00, when weather conformed to criteria for the UK Butterfly Monitoring Scheme (temperature above 13 °C with at least 60% clear sky, or 17 °C in any sky conditions, with no count at all if raining) (Pollard & Yates 1993). The ambient temperature, percentage sunshine and wind speed were recorded at the end of each transect walk.

DATA ANALYSIS

Flowering plant abundance scores were expressed as the interval median value for each range, to give an estimate of the number of flowering units on each sampling visit, as follows: 1, 13 flowers; 2, 113 flowers; 3, 600·5 flowers; 4, 3000·5 flowers; 5, 15000 flowers. These data were summed into three variables according to whether (i) a plant had been sown as part of the experiment, (ii) was unsown and (iii) had been visited by foraging bumble bees.

The mean number of flowers and bumble bees, and the species richness of plants in flower or bumble bees recorded per sampling visit, per plot was calculated. This summarized data across the season in each year and between replicates at each site. The bee count data were log-transformed prior to analysis to normalize residual variation. Within-year differences between margin treatments in summary flower variables, in abundance of the eight most visited forage plants and in abundance of each bumble bee species, total bees and species richness were tested by analysis of variance (ANOVA), including site and treatment as factors (H1). Multiple pairwise comparisons were carried out on the means using Tukey's honest significant difference tests. Repeated-measures ANOVA was performed to test for average treatment effects across all years, and to assess whether these changed over time between years (H2).

Patterns of forage plant visitation by the different *Bombus* spp. were examined using principal components analysis (PCA) on the proportion of visits by each bee species to each plant species averaged over the 3 years, using Canoco software, version 4·5 (ter Braak & Šmilauer 1998). A separate PCA was carried out to examine the foraging visits of the different castes of *B. lapidarius*.

To test whether the effects of treatment changed during the season (H3), bumble bee and flower means were summarized further according to the early season (May–June) vs. mid-late season (July–August) sampling visits in each year. A preliminary nested ANOVA was performed on the log-transformed bumble bee means to examine the effects of site, treatment, year and season, and to test all the two-factor and three-factor interactions containing these terms (see Appendix S2 in the supplementary material). As bumble bees were most strongly influenced by margins sown with the wildflower or pollen and nectar seed mixtures, further analysis on seasonal effects examined just these two treatments. Repeated-measures ANOVA was used to assess whether the observed treatment effects of seed mixture composition on flowering resources and bumble bee abundance differed between the early and mid-late season time periods (H3).

All ANOVA and repeated-measures ANOVA analyses were undertaken using SAS 9·1 statistical software (SAS Institute Inc. 2004).

Results

EFFECTS OF ES OPTIONS ON FLOWER ABUNDANCE AND SPECIES RICHNESS

The field margin treatments established with relative consistency across all six sites, with the majority of sown species flowering on at least one sampling visit by the second, if not the first, year. Dicotyledon flower abundance and the number of species in flower (richness) varied between treatments and years as the vegetation communities developed over time (Table 2). All summary variables and key bee forage plants showed significant treatment by year interactions, with the exception of *Cirsium vulgare* and *Onobrychis viciifolia*. The pollen and nectar mixture produced the highest total flower abundance in the first year, nearly double that of the wildflower mixture, mainly because of the rapid establishment of *Trifolium hybridum*. This was replaced by *T. pratense* in 2003 and an increasing number of *Lotus corniculatus* flowers in 2004, with the overall abundance of bee forage flowers remaining constant between years in this treatment. The wildflower mixture produced few flowers, particularly of bee forage plants, in its first year, but numbers increased in 2003 and 2004 as the proportion of unsown species declined and the mixture established its perennial nature. Of the sown native species, *Leucanthemum vulgare* and *Achillea millefolium* achieved the highest mean flower scores at most sites, but only received 0·1% of foraging visits.

Flower abundance of unsown species was highest in the annually cultivated natural regeneration treatment, although only significantly so in 2002. The most prominent nectar source species in this treatment was *C. vulgare*. The presence of arable weed species was generally suppressed in the sown, compared with unsown and cropped, treatments. Flower abundance and richness in the conservation headland treatment were never significantly higher than in the crop or tussocky grass treatment (Table 2), highlighting the lack and inconsistency of pollen and nectar sources provided by this field margin option.

EFFECTS OF ES OPTIONS ON BUMBLE BEE ABUNDANCE AND SPECIES RICHNESS

During the 3 years of the experiment and across all six study sites, a total of 12 462 bumble bees, representing nine social bumble bee species and at least three cuckoo bee species (subgenus *Psithyrus*), was recorded. These included three species considered rare and declining in the UK: *B. muscorum* (at the site in Essex), *B. ruderatus* (in Cambridgeshire and Bedfordshire) and *Bombus ruderarius* (at all sites except in North Yorkshire and Bedfordshire), as well as the six ubiquitous species most commonly observed on farmland: *B. terrestris* and *B. lucorum* (recorded together), *Bombus pratorum*, *B. lapidarius*, *Bombus pascuorum* and *Bombus hortorum*, which were recorded at all sites.

Field margins sown with the legume-based pollen and nectar mixture attracted the highest total number and species richness of foraging bees in all years, with on average up to 269 times more bees recorded in this treatment than in the crop and conservation headlands (Table 3). Bumble bee abundance was also significantly higher on the pollen and nectar treatment than the natural regeneration and tussocky grass treatments in all years. The effects of site were not significant, but the overall treatment effects showed significant changes over time. In the natural regeneration treatment, total bumble bee abundance and richness decreased in the second and third years (2003 and 2004). In contrast, abundance and richness increased in the wildflower margins over time, showing no significant difference between this and the pollen and nectar treatment during the third year (Table 3). Overall, there was a positive correlation between the mean estimated number of flowers of bee forage plant species and mean total number of bumble bees per plot (Pearson's correlation coefficient 0·81, $P < 0{\cdot}001$; Fig. 1).

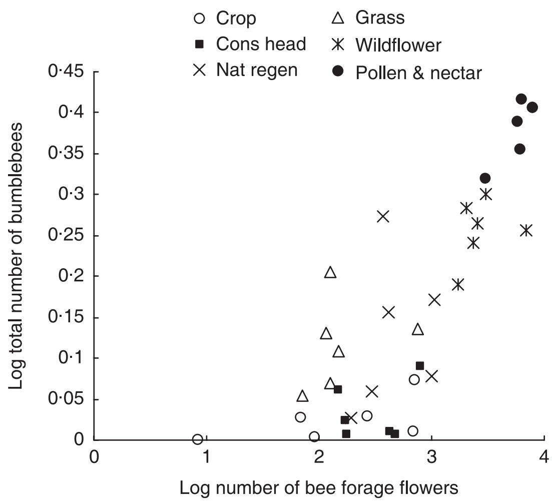

Fig. 1. The relationship between flower abundance of bee forage species and total bumble bee abundance on different ES field margin options. Values represent the log-transformed mean number of bees per plot at each site, averaged over 3 years. See Table 1 for treatment details.

At the species level, there were significant differences between margin treatments in abundance of the more common *Bombus* spp., although these were not always consistent between species and years (Table 3). *Bombus lapidarius* and *B. pascuorum*, the most commonly recorded species, were significantly more abundant in the pollen and nectar treatment than in all others. In the third year *B. lapidarius* was also recorded in higher numbers in the wildflower margins than in other treatments. *Bombus hortorum* preferred the pollen and nectar mixture, but in 2003 and 2004 differences between this and the wildflower treatment were not significant. *Bombus terrestris*, *B. lucorum* (recorded together) and *B. pratorum* were recorded in lower numbers, and their visits were more evenly distributed between the natural regeneration, tussocky grass, wildflower and pollen and nectar treatments. The cuckoo bumble bees showed mixed preferences in each year, but with a tendency to be more abundant where the flowering seed mixtures were sown.

The three declining UK *Bombus* spp. were generally recorded in low numbers (Table 3) and significant differences in abundance between treatments were not detected. At sites where they occurred, the majority of individuals were recorded in the pollen and nectar, followed by wildflower, treatment. For example, 98% of

Table 2. Flower abundance and species richness of plants in flower on different ES field margin options. Values represent treatment means per sampling visit, per plot, averaged across the six sites together with ANOVA test statistics. Individual species are those which received the highest percentage of foraging visits, presented in decreasing order from the left (AG, agricultural legume; NAT, native variety). 'Total bee forage species' includes all 40 plant species visited. NS, not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

	Field margin treatment	Tri prat AG	Tri hybr	Lot corn AG	Cir vulg	Tri prat NAT	Lotus corn NAT	Cen nigr	Ono vici	Total bee forage spp.	Sown spp.	Unsown spp.	Total all flowers	Richness all plants in flower
2002	Crop	0·0 b	0·0 b	0·0 b	0·2	0·0 b	0·0 b	0·0 b	0·0 b	7·7 b	0·3 c	28·9 b	29·2 d	1·2 d
	Cons head†	0·0 b	0·0 b	0·0 b	0·0	0·0 b	0·0 b	0·0 b	0·0 b	210·5 b	0·0 c	370·3 b	370·2 d	2·7 d
	Nat regen	0·2 b	0·2 b	0·3 b	39·6	0·2 b	0·7 b	0·0 b	0·0 b	919·6 b	13·9 c	3435·3 a	3449·2 bc	8·6 b
	Grass	0·4 b	2·5 b	0·5 b	10·0	0·3 b	0·7 b	0·0 b	0·0 b	342·1 b	10·6 c	1167·7 b	1178·3 cd	4·9 c
	Wildflower	0·0 b	8·8 b	0·0 b	4·8	281·0 a	140·6 a	8·3 a	1·2 b	750·8 b	2995·2 b	1108·7 b	4103·9 b	11·4 a
	Pollen & nectar	917·8 a	4143·5 a	1327·2 a	3·0	0·0 b	0·0 b	0·0 b	16·6 a	6528·4 a	6407·3 a	810·3 b	7217·6 a	6·1 c
2002 ANOVA	$F_{5,25}$	93·64	29·06	8·03	2·15	9·58	19·87	4·88	4·37	33·76	31·45	8·50	18·00	65·10
	Significance	***	***	***	NS	***	***	**	**	***	***	***	***	***
2003	Crop	0·0 b	0·0 b	0·2 b	0·5	0·0 b	0·0 b	0·4 b	0·0 b	328·6 b	3·2 b	757·5 ab	760·7 c	2·4 b
	Cons head	0·1 b	0·0 b	0·0 b	0·1	0·0 b	0·0 b	0·0 b	0·0 b	333·5 b	1·3 b	1291·8 ab	1293·1 c	3·6 b
	Nat regen	0·5 b	1·8 b	0·1 b	28·0	0·1 b	0·2 b	0·2 b	0·0 b	220·6 b	45·7 b	1951·2 a	1996·9 bc	7·4 a
	Grass	2·7 b	7·3 b	5·8 b	30·2	0·5 b	0·5 b	0·5 b	0·4 b	171·9 b	61·6 b	201·7 b	263·2 c	3·3 b
	Wildflower	0·1 b	42·3 b	1·0 b	47·2	2519·1 a	1527·9 a	46·1 a	2·4 b	4321·6 a	9901·8 a	99·8 b	10001·6 a	8·5 a
	Pollen & nectar	4091·8 a	1274·9 a	866·7 a	53·6	0·0 b	0·0 b	0·4 b	71·4 a	6375·0 a	6321·6 a	144·4 b	6466·0 ab	4·5 b
2003 ANOVA	$F_{5,25}$	12·53	7·49	7·52	1·12	10·69	6·13	8·49	2·98	15·17	17·77	4·63	13·44	17·95
	Significance	***	***	***	NS	***	***	***	*	***	***	**	***	***
2004	Crop	0·0 b	0·2 b	0·1 b	0·5 b	0·0 b	0·0 b	0·0 b	0·0 b	577·9 b	2·7 b	1191·6	1194·3 b	3·5 b
	Cons head	0·1 b	2·5 b	0·2 b	0·0 b	0·0 b	0·1 b	0·0 b	0·0 b	542·5 b	4·3 b	1281·4	1285·7 b	3·6 b
	Nat regen	1·9 b	3·2 b	0·4 b	30·9 a	0·2 b	0·0 b	0·5 b	0·0 b	523·8 b	22·4 b	1098·6	1121·1 b	6·2 b
	Grass	1·4 b	23·2 b	4·3 b	8·7 ab	0·7 b	7·8 b	1·3 b	0·0 b	153·7 b	112·2 b	136·7	248·9 b	3·6 b
	Wildflower	0·0 b	267·2 ab	0·0 b	10·4 ab	562·9 a	2954·4 a	75·0 a	4·2 b	4241·9 a	7446·3 a	90·6	7536·9 a	9·8 a
	Pollen & nectar	2183·4 a	1182·9 a	2214·9 a	11·6 ab	5·6 b	1·1 b	0·1 b	30·7 a	5708·4 a	5666·5 a	130·7	5797·1 a	5·4 b
2004 ANOVA	$F_{5,25}$	6·06	3·55	11·65	2·66	11·98	13·23	33·04	5·17	14·68	31·71	2·38	16·53	11·15
	Significance	***	**	***	*	***	***	***	**	***	***	NS	***	***
Repeated-measures	Treatment	18·87***	20·54***	15·91***	1·94^{NS}	12·52***	10·67***	24·40***	3·82*	33·51***	43·11***	8·82***	32·71***	67·47***
ANOVA $F_{10,50}$	Year	4·20*	10·46***	2·82^{NS}	3·17^{NS}	9·06**	10·65**	11·69***	2·32^{NS}	1·88^{NS}	4·57*	3·04^{NS}	1·47^{NS}	3·14^{NS}
	Year × treatment	4·19***	12·06***	2·82**	1·02^{NS}	9·08***	10·58***	10·91***	2·24^{NS}	3·09**	4·78***	3·45**	3·38**	2·81**

†See Table 1 for definitions.

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Table 3. Bumble bee abundance and species richness on different ES field margin options. Values represent treatment means per sampling visit, per plot, averaged across the six sites together with ANOVA test statistics. Results for all species are presented for consistency, but where fewer than 10 individuals of a species were recorded in any year ANOVA was not performed. Rare species are shown in bold. NS, not significant; *$P < 0{\cdot}05$; **$P < 0{\cdot}01$; ***$P < 0{\cdot}001$

	Field margin treatment	*B. terrestris/ lucorum*	*B. lapidarius*	*B. pratorum*	*B. pascuorum*	*B. hortorum*	***B. ruderarius***	***B. muscorum***	***B. ruderatus***	Cuckoo bees	Total bees	Richness bees
2002	Sample size	233	1637	4	1120	110	6	15	9	41	3175	
	Crop	0·00 c	0·01 c	0·00	0·00 c	0·00 b	0·00	0·00	0·00	0·00 b	0·01 c	0·01 d
	Cons head†	0·02 c	0·04 c	0·00	0·00 c	0·00 b	0·00	0·00	0·00	0·00 b	0·06 c	0·02 d
	Nat regen	1·16 bc	2·16 b	0·04	0·22 c	0·00 b	0·00	0·00	0·00	0·02 ab	3·59 b	0·66 bc
	Grass	0·27 bc	0·55 bc	0·01	0·06 c	0·00 b	0·00	0·00	0·00	0·01 ab	0·91 bc	0·32 cd
	Wildflower	0·05 c	0·73 bc	0·00	1·64 b	0·32 b	0·00	0·00	0·00	0·01 b	2·75 b	0·94 b
	Pollen & nectar	1·09 ab	14·57 a	0·00	10·28 a	0·92 a	0·07	0·16	0·11	0·40 a	27·59 a	2·34 a
2002 ANOVA	$F_{5,25}$	4·67	25·70	1·62	120·05	11·48	1·00	1·00	1·00	3·20	32·21	56·81
	Significance	**	***	–	***	***	–	NS	–	*	***	***
2003	Sample size	110	2237	1	2573	724	8	19	65	119	5856	
	Crop	0·04	0·03 d	0·00	0·01 c	0·00 b	0·00	0·00	0·00	0·00	0·07 d	0·05 d
	Cons head	0·03	0·04 d	0·00	0·01 c	0·00 b	0·00	0·00	0·00	0·01	0·08 d	0·06 d
	Nat regen	0·17	1·16 cd	0·00	0·25 c	0·00 b	0·00	0·00	0·00	0·16	1·73 cd	0·56 cd
	Grass	0·19	1·26 c	0·00	0·35 c	0·06 b	0·00	0·00	0·00	0·28	2·13 c	0·75 c
	Wildflower	0·27	4·67 b	0·01	2·91 b	1·76 a	0·02	0·06	0·00	0·16	9·83 b	2·00 b
	Pollen & nectar	0·33	13·56 a	0·00	20·30 a	4·89 a	0·06	0·12	0·60	0·50	40·36 a	2·15 a
2003 ANOVA	$F_{5,25}$	2·89	51·73	1·00	27·58	17·35	0·85	1·00	1·00	2·17	55·82	49·08
	Significance	*	***	–	***	***	–	NS	NS	NS	***	***
2004	Sample size	144	1403	10	1494	197	1	4	27	151	3431	
	Crop	0·14	0·31 b	0·00 b	0·04 c	0·04 b	0·00	0·00	0·00	0·04 c	0·56 b	0·17 b
	Cons head	0·12	0·47 b	0·00 b	0·03 c	0·02 b	0·00	0·00	0·00	0·16 bc	0·80 b	0·21 b
	Nat regen	0·33	0·79 b	0·01 b	0·13 c	0·00 b	0·00	0·00	0·00	0·08 c	1·34 b	0·45 b
	Grass	0·17	0·42 b	0·00 b	0·15 c	0·10 b	0·00	0·01	0·01	0·11 bc	0·96 b	0·55 b
	Wildflower	0·34	3·99 a	0·07 a	1·95 b	0·56 ab	0·00	0·00	0·01	0·63 ab	7·56 a	1·81 a
	Pollen & nectar	0·23	7·01 a	0·01 b	11·54 a	1·10 a	0·01	0·03	0·23	0·38 bc	20·54 a	1·80 a
2004 ANOVA	$F_{5,25}$	0·64	19·63	4·23	19·32	4·43	1·00	1·00	1·16	3·59	24·10	19·88
	Significance	NS	***	**	***	**	–	–	NS	*	***	***
Repeated-measures ANOVA $F_{10,50}$	Treatment	3·85*	42·11***	–	43·29***	16·35***	–	1·00 NS	1·05 NS	4·16**	49·82***	52·86***
	Year	2·54^{NS}	4·75*	–	4·47*	15·97***	–	1·06 NS	0·95 NS	4·66*	5·77**	6·31**
	Year × treatment	2·96***	7·35***	–	1·28^{NS}	6·81***	–	1·00 NS	0·97 NS	1·91^{NS}	4·93***	7·34***

†See Table 1 for definitions.

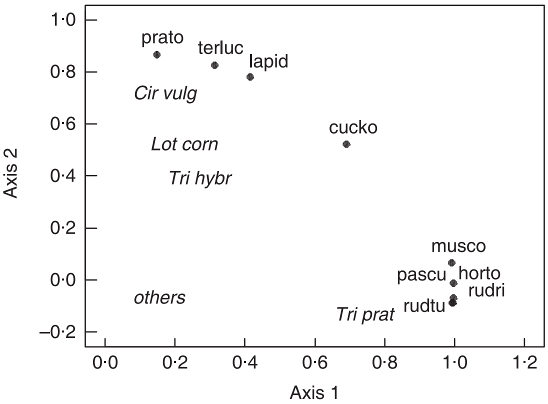

Fig. 2. PCA biplot based on the proportion of visits to different plant species by foraging bumble bees of each species. Abbreviations of bumble bee species (*Bombus* spp.) names: prato, *B. pratorum*; terluc, *B. terrestris*/*lucorum*; lapid, *B. lapidarius*; musco, *B. muscorum*; pascu, *B. pascuorum*; horto, *B. hortorum*; rudri, *B. ruderarius*; rudtu, *B. ruderatus*; cucko, cuckoo bumble bees. Abbreviations of plant species: *Cir vulg*, *Cirsium vulgare*; *Lot corn*, *Lotus corniculatus*; *Tri hybr*, *Trifolium hybridum*; *Tri prat*, *Trifolium pratense*; others, e.g. *Centaurea nigra*, *Rhinanthus minor*, *Papaver rhoeas*, *Brassica napus*, *Dipsacus fullonum*. Visits to native and agricultural varieties of *T. pratense* and *L. corniculatus* were combined for this analysis.

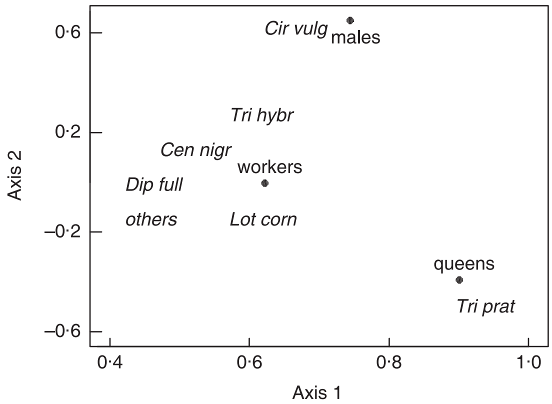

Fig. 3. PCA biplot based on the proportion of visits to different plant species by different castes of *Bombus lapidarius*. Abbreviations of plant species as in Fig. 2, also: *Cen nigr*, *Centaurea nigra*; *Dip full*, *Dipsacus fullonum*. Visits to native and agricultural varieties of *Trifolium pratense* and *Lotus corniculatus* were combined.

all records of *B. ruderatus* were from the pollen and nectar mixture.

BUMBLE BEE FORAGE PLANT VISITATION

Overall, 40 plant species were visited for pollen and/or nectar, including sown and unsown species. For all *Bombus* spp. and all years combined, 92% of visits were to just six species: *T. pratense* (agricultural and native varieties), *T. hybridum*, *L. corniculatus* (agricultural and native varieties) and *C. vulgare*. Patterns of forage plant visitation contrasted between species, as summarized by PCA. The first and second components accounted for 86% and 10% of variation, respectively (Fig. 2). The first axis separated the group of longer-tongued *Bombus*, including the rarer species, on the basis of their visits to *T. pratense*. The second axis separated the remaining four social *Bombus* spp. which are shorter-tongued and visited mainly *T. hybridum*, *L. corniculatus* and *C. vulgare*. The cuckoo bumble bees were placed centrally between these groups. A chi-square test, based on a contingency table with total visits to the top 10 forage species by the more commonly recorded bee species, confirmed these differences in flower choice between bee species ($P < 0{\cdot}001$).

PCA on the foraging visits of *B. lapidarius* revealed further contrasts between the different castes of this species (Fig. 3). The first component accounted for 63% of variation, separating queens on the basis of their visits to *T. pratense*. Of these, visits by early queens in May tended to be to the native variety in the wildflower mixture and those by the later, newly emerged queens to the agricultural variety in the pollen and nectar mixture. The second axis accounted for a further 21% of variation and separated workers on association with *L. corniculatus*, *C. nigra* and *T. hybridum* and males on the basis of their visits to *C. vulgare*. A chi-square test, based on a contingency table with total visits to the top 10 forage species by each caste, confirmed these differences in flower choice between queens, workers and males of *B. lapidarius* ($P < 0{\cdot}001$).

SEASONAL DIFFERENCES

Seasonal differences were detected in the effects of seed mixture composition (of the wildflower and pollen and nectar mixtures) on flower and bumble bee abundance. When the effects of season were added as an interaction term to the nested ANOVA on total bumble bee abundance, the three-factor interaction was not significant ($F_{2,10} = 1{\cdot}88$, $P = 0{\cdot}20$), suggesting that the strong treatment by season interaction ($F_{1,5} = 27{\cdot}45$, $P < 0{\cdot}01$) did not vary between years (see Appendix S2 in the supplementary material). Data were therefore averaged across the 3 years for the repeated-measures ANOVA on seasonal effects.

Flower abundance of all forage plants grouped together showed a significant treatment by season interaction ($F_{1,5} = 23{\cdot}1$, $P < 0{\cdot}01$), with on average more flowers in the wildflower mixture than in the pollen and nectar mixture during May–June, but with the pollen and nectar mixture providing more forage during July–August (Fig. 4a). This was reflected in the bumble bee response. Bee abundance was significantly greater in the wildflower than pollen and nectar mixture during May–June for *B. hortorum* ($F_{1,5} = 51{\cdot}6$, $P < 0{\cdot}01$) and *B. terrestris* ($F_{1,5} = 24{\cdot}9$, $P < 0{\cdot}01$) and all the common *Bombus* spp. were more abundant in the pollen and nectar than wildflower treatment during July–August ($F_{1,5} = 101{\cdot}8$, $P < 0{\cdot}001$ for total bees, with a significant treatment by season interaction $F_{1,5} = 27{\cdot}3$, $P < 0{\cdot}01$) (Fig. 4b). The plant species most influencing these trends were *T. pratense* and *L. corniculatus*, both showing significant effects of season on differences between treatments ($F_{1,5} = 18{\cdot}5$, $P < 0{\cdot}01$ and $F_{1,5} = 26{\cdot}6$, $P < 0{\cdot}01$, respectively). The native

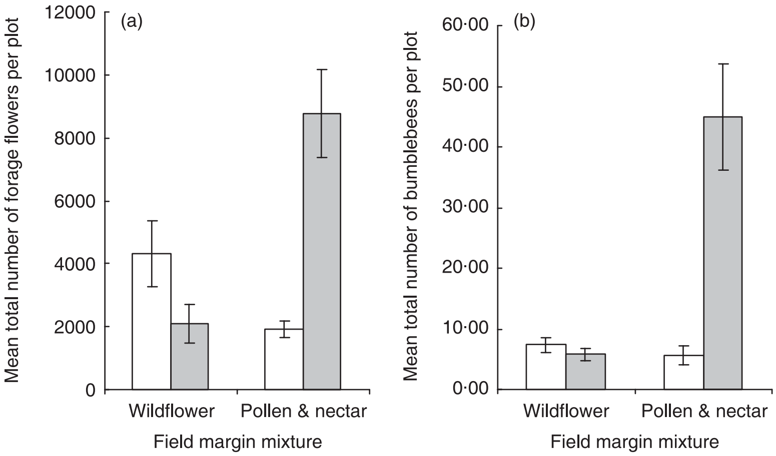

Fig. 4. Seasonal effects of seed mixture composition on abundance of (a) all flowers of bumble bee forage plants and (b) all bumble bee species. White bars, early (May–June) transects; grey bars, late season (July–August) transects.

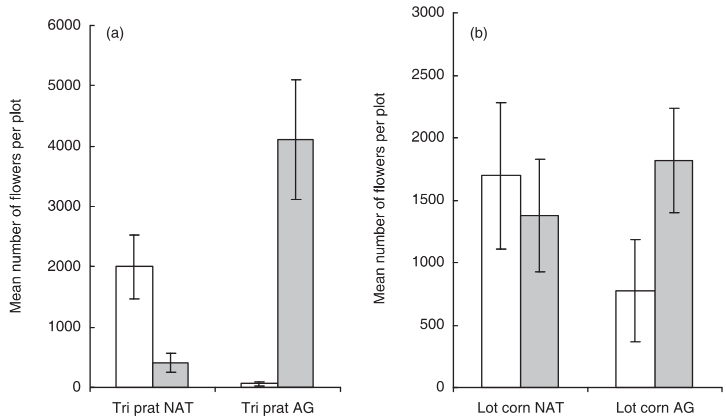

Fig. 5. Seasonal differences in flower abundance of native vs. agricultural varieties of (a) *Trifolium pratense* and (b) *Lotus corniculatus* in wildflower (NAT) and pollen and nectar (AG) mixtures. White bars, early (May–June) transects; grey bars, late season (July–August) transects.

varieties sown in the wildflower mixture began flowering in early May, producing more flowers than the agricultural varieties in the pollen and nectar mixture early in the season. This pattern was reversed during July–August, when the agricultural varieties reached peak flowering (Fig. 5).

Discussion

The management of arable field margins according to different options under ES had significant effects on bumble bees and their forage plants, confirming our first hypothesis. These effects were consistent across the six farms on which the experiment was conducted. Uncropped margins sown with a mixture containing four agricultural legume species attracted on average the highest abundance and diversity of bumble bees, including rare species. However, marked differences were observed between bumble bee species and between the sexes within species in their responses to margin management, which can be explained in part by differences in their foraging preferences. Our assessment of changes in flower abundance also revealed seasonal differences in forage provision, and significant changes in the composition of flowering plant species over 3 years depending on management option and seed mixture composition, confirming our second and third hypotheses.

IMPLICATIONS FOR ENVIRONMENTAL STEWARDSHIP OPTIONS

Removing arable field margins from the cropping system can potentially provide increased forage resources for bumble bees, as well as a greater diversity of habitats for other invertebrates (Feber, Smith & Macdonald 1996; Meek *et al*. 2002; Asteraki *et al*. 2004). While conservation headlands may encourage more annual plants than a conventionally managed crop (Critchley *et al*. 2004), our results showed that this did not translate into an overall increase in either flower abundance and richness of species in flower or the number and species of bumble bees recorded. Allowing natural regeneration on uncropped cultivated margins is a relatively simple management option that could achieve widespread uptake within the ELS and HLS schemes, creating opportunities for rare arable plants (W.R. Meek, unpublished data). However, bumble bee and forage plant abundance were only significantly higher with this option than on cropped margins during the first year after establishment, despite the occurrence of *C. vulgare*, which was attractive to the shorter-tongued species and, particularly, male *B. lapidarius*. It is possible that bees were less likely to visit this treatment when greater floral rewards were present in adjacent field margin plots. When tested in isolation, naturally regenerated margins can provide enhanced foraging habitat compared with conservation headlands (Kells, Holland & Goulson 2001). In general though, this management option is unlikely to provide a sufficient density or diversity of bumble bee forage resources unless injurious weeds such as *Cirsium* spp. are allowed to persist, which carries agronomic problems, or vegetation is left uncultivated and a perennial sward established over time (Carvell *et al*. 2004).

Sowing a mixture of perennial grass and wildflower or legume species has clear advantages in terms of further enhancing the quality of arable field margins for bumble bees. The positive response of different species to increased densities of their preferred forage plants has been well documented, both in semi-natural and agricultural landscapes (Dramstad & Fry 1995; Backman & Tiainen 2002; Carvell 2002). Our study suggests that it is the composition and seasonal flowering patterns of seed mixtures that are the most important factors influencing the abundance and diversity of bumble bees attracted to ES options for sown margins.

The 'pollen and nectar flower mixture', containing at least three legume species (at 20% of the mix) and non-aggressive grasses (at 80%), can be sown on arable field margins or set-aside land under both ELS and HLS schemes (Defra 2005a). This option may be of high conservation value for some of Britain's rarer bumble bees, as the legume component attracted three species not commonly recorded on farmland: the BAP species *B. ruderatus*, confirming preliminary observations by Pywell *et al*. (2005, 2006), and two species proposed for inclusion in the UK BAP, *B. muscorum* and *B. ruderarius* (S. Roberts, personal communication). However, this seed mixture had several shortcomings as a means of providing sustained forage throughout the season. The low abundance of flowers during May and June implied that it would not fully cater for bumble bee colonies in the early stages of their development. The use of alternative varieties of *Trifolium* spp., or changes in the cutting management of such margins, could be investigated in order to extend their flowering time. Also, despite establishing quickly and flowering well in the first 2 years, the results suggested a reduction in flower abundance of the two *Trifolium* spp. in the pollen and nectar mixture, along with a decrease in bee density in the third year. Resowing may therefore be necessary as the grass component of the mixture becomes dominant. Furthermore, the legume species tested in our study did not appear wholly suitable as forage plants for the shorter-tongued species (e.g. *B. terrestris* and *B. pratorum*) or, more specifically for males (e.g. *B. lapidarius*). An additional ELS option, the 'wild bird seed mixture' (EF2) offers the opportunity to sow appropriate forage plants, such as *Borago officinalis*, for these species, and could complement the pollen and nectar mixture if established on other parts of the farm (Defra 2005a; Carvell *et al*. 2006).

Sowing a more diverse mixture of native wildflowers (at 20% of the mix) and non-aggressive grasses (at 80%) on arable margins or set-aside land is an option available under the HLS scheme (Defra 2005b). Our results suggest that, despite, on average, a lower density of bees and forage flowers, this option has the potential to cater across the whole season for a wider range of species than the pollen and nectar mixture as currently prescribed. This observation is supported by a study of bumble bees on field margins in Finland, where, although bee density was strongly related to margin width and flowering of the most visited forage species, *Trifolium medium*, species diversity did not follow this pattern and was only enhanced with the presence of plant species such as *Knautia arvensis* and *Galeopsis speciosa* (Backman & Tiainen 2002). As well as *T. pratense* and *L. corniculatus*, the mixture we tested contained species from the Asteraceae, such as *C. nigra*, which were attractive to both sexes of the shorter-tongued *Bombus* spp. These additional plant species are likely to enhance the value of field margins for other pollinators such as solitary bees and butterflies (Feber, Smith & Macdonald 1996; Westrich 1996). Agronomically, the wildflower mixture did not fully establish until its second year, but the resulting perennial vegetation is likely to persist over a 5–10-year time scale (Pywell *et al*. 2002). The native legume varieties sown here flowered significantly earlier than their agricultural equivalents, attracting the longest-tongued species *B. hortorum* as well as queens of *B. lapidarius*, for which other resources on farmland are often scarce in the early summer. By sowing both varieties in the same mixture, season-long forage could be provided. However, the implications for competition between species and conservation of genetic diversity within species require further consideration if native and agricultural cultivars are to be sown together (Walker *et al*. 2004).

The tendency for bumble bees to show species-specific preferences for certain flowers or plant families, as demonstrated in this study, has been well recognized (Heinrich 1976). Although we did not differentiate between pollen and nectar collection, evidence from other studies suggests that it may be the high value of legume (Fabaceae) pollen to the longer-tongued species, especially those founding colonies relatively late in the season, which accounts for their large number of visits to *T. pratense* and other Fabaceae (Brian 1951; Goulson & Darvill 2004; Carvell *et al*. 2006). This apparent specialization on plant species that have declined in the countryside, combined with proximity to their European range edges, may be the principal cause of rarity and decline in British bumble bees (Goulson *et al*. 2005; Williams 2005). Thus by restoring legume-rich habitats in arable areas, the assumption is that rare species can benefit within their range, as evidenced here. However, Williams (2005) highlights some of the problems associated with comparing forage plant preferences, as they depend on the abundance of each bee species and the availability of each forage plant at particular study sites. The consistent management of treatments across our six sites ensured that flower abundances of forage species were similar, although the *Bombus* spp. assemblages differed depending on region. In this case the PCA, which accounted for a high percentage of variation in visitation patterns, described the contrasts in forage use between species and explained the observed differences in their abundance between ES options.

Having gained evidence of the field-scale effects of different margin management options on bumble bees and their forage plants, the question remains regarding how these effects might translate to the landscape scale. Habitat heterogeneity has been reduced by intensification in agricultural landscapes at a range of spatial scales, with consequences for many taxa (Benton, Vickery & Wilson 2003; Tscharntke *et al*. 2005). Agri-environment schemes do not currently promote habitat heterogeneity as a stated aim. However, the potentially widespread establishment of options, such as the pollen and nectar mixture under ELS, interspersed with fewer but high-quality diverse wildflower mixtures under HLS, is likely to enhance significantly the heterogeneity and quality of the English lowland landscape for bumble bees. The relatively large foraging ranges of many species may enable them to exploit these new habitats, at least at the farm scale (Osborne *et al*. 1999; Steffan-Dewenter *et al*. 2002; Knight *et al*. 2005), although the dispersal abilities of bumble bees are still poorly understood. Furthermore, we did not assess the use of different ES options as nesting sites because of the difficulty of locating nests of all species and the limited total area under study. The tussocky grass mixture tested here is likely to provide suitable nesting habitat if left undisturbed (Kells & Goulson 2003) but interactions between the nesting and foraging components of introduced habitats require further investigation. It is also important that more direct measurements of colony density (Chapman, Wang & Bourke 2003; Knight *et al*. 2005) are employed to assess whether the abundance and species-richness benefits shown in this study translate to increased population density and persistence of bumble bee species in enhanced agricultural landscapes.

CONCLUSIONS

This study provides the first comprehensive assessment of the effects of different management options for arable land as prescribed under the new ES scheme in England on a high profile group of insects. As predicted, uncropped margins sown with mixtures containing nectar- and pollen-producing plants were more effective in providing bumble bee forage than margins sown with a grass mix, allowed to regenerate naturally or managed as conservation headlands. Our results demonstrate that, using evidence-based habitat creation, uptake of selected options within ELS in England could have a positive impact on bumble bees, including species of conservation concern. As with all such agri-environment initiatives, factors such as temporal variation in resource provision within the period of insect activity, and longer-term value as newly established vegetation communities change over time, must be considered in the design of management guidelines. Additional options within HLS are likely to be important in meeting these needs. ES therefore provides a mechanism for enhancing the currently impoverished *Bombus* assemblages of intensively managed landscapes in England, and potentially facilitating the pollination of certain crops and wildflowers, although these associations have yet to be tested directly (Ghazoul 2005). The population-level responses of bumble bees to introduced seed mixtures and other agri-environment options still require better understanding in order to maximize the benefits of such schemes in intensively farmed landscapes.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Appendix S1. Seed mixture details for the three sown treatments.

Appendix S2. Supplementary statistical analyses.

Figure S1. Map of England and Wales showing locations of the six study sites.